THE RELATION BETWEEN EVAPORATION AND PLANT
SUCCESSION IN A GIVEN AREA

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As a result of an investigation into the relative amounts of evaporation from the chamaephytic or ground layer of certain genetically connected, adjoining plant associations at Havana, Illinois, during the summer of 1910, Gleason and Gates (1) concluded: "that successions between associations are not caused by any conditions of evaporation."

In conclusion to a much more extensive series of investigations, bearing on the same subject, Fuller (2) concludes: "the decreased rate of evaporation . . . is the direct cause of successions between different associations." Weaver (3) concludes: "A study of the differences of the rates of evaporation in the various plant formations and associations shows that these differences are sufficient to be important factors in causing succession, at least through the earlier stages, where light values are usually high."

Each investigation dealt with neighboring associations in a limited area, thereby accentuating the action of local factors and minimizing the obscuring interference of climatic factors. An inspection of the pertinent data obtained in each of these investigations shows that they are similar; yet diametrically opposite conclusions are drawn.

To obtain new data on the relationship between evaporation and plant succession, three series of experiments were carried on during the summers of 1915 and 1916, at the University of Michigan Biological Station at Douglas Lake, Michigan. During 1915, twenty-six standardized Livingston atmometers were employed for a period of 40 days, inclusive of the time of maximum evaporation during the year. In 1916, sixteen newly standardized instruments were employed during varying periods inclusive of the severest summer evaporation in years. Each instrument was set up in close proximity to certain plants. The

1 Contribution from the University of Michigan Biological Station at Douglas Lake, Michigan, No. 41.

2 Owing to the press of duties attendant upon the establishment of the University of Michigan Botanical Garden, Dr. H. A. Gleason was unable to collaborate, as planned.
experimentation and the calculation of the results to a standard basis followed the normal methods used for such work.

The object of this experimentation was the determination of the relationship between evaporation and plant succession in a local area. Douglas Lake region presents an admirable opportunity for such experimentation. A detailed discussion of the vegetation of the area will be found in Gates (4). A brief résumé of the pertinent facts is as follows: Aside from a few small associations, local along streams and around lakes, the vegetation of the region falls readily into three divisions, each characterizing a soil type. Bog associations, particularly the Chamaedaphne, Larix, Picea and Thuja associations, occupy the low wet soil. The sandy uplands were dominated by the pine association—now, following lumbering and fire, largely replaced by the aspen association. Clayey soil on the uplands is occupied by the hardwood or beech-maple association, except where it has been destroyed by lumbering or fire.

Experiments were carried on separately with the vegetation of each soil type. The Thuja association, chosen for the bog experimentation, is typically composed of a large number of trees of *Thuja occidentalis*, growing close together. The ground vegetation in a dense patch of Thuja is virtually nil. In open places, as along roads and trails, ericads and ericad-like plants are conspicuous. A few of the most abundant species are *Ledum groenlandicum*, *Streptopus amplexifolius*, *Moneses uniflora*, *Pirola asarifolia incarnata*, *Mitella nuda*, *Rubus trifulorus*, *Cornus canadensis*, *Carex spp.*, *Habenaria obiusata*, *Chamaedaphne calyculata* and *Vaccinium oxyccoccus*.

The pine type—once represented by *Pinus strobus* and *Pinus resinosa*, now by scattering seedlings, small trees, and a few old trees of the same species mixed in with the aspen association—was investigated during 1915. At least 96 percent of the trees in the aspen association belong to the following four species: *Populus tremuloides*, *Populus grandidentata*, *Betula alba papyrifera*, and *Prunus pensylvanica*. Among the higher shrubs are *Salix rostrata*, *Rhus glabra*, and *Viburnum acerifolium*; among the lower shrubs, *Diervilla lonicera* (which is frequently exceedingly abundant), *Vaccinium pennsylvanica*, *Gaultheria procumbens*, *Rubus idaeus aculeatissimus*, and *Rubus alleghieniensis* are quite common. The fern, *Pteris aquilina*, is frequently more abundant than any of the shrubs. With the shrubs are seedlings and small trees of *Quercus rubra*, *Acer rubrum*, *Acer sac-
charum, Fagus grandifolia, Tilia americana, Pinus resinosa, and Pinus strobus. Among the herbaceous species are several grasses (Panicum xanthophyllum, Danthonia spicata, Poa pratensis, Agrostis hiemalis,

<table>
<thead>
<tr>
<th>No.</th>
<th>Location, Hardwood Series</th>
<th>Cc. in 40-Day Period</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Cutover in 1914-15</td>
<td>590</td>
</tr>
<tr>
<td>2</td>
<td>Cutover in 1914-15</td>
<td>364</td>
</tr>
<tr>
<td>3</td>
<td>Open place in old cut</td>
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<td>4</td>
<td>Cutover in 1913-14</td>
<td>428</td>
</tr>
<tr>
<td>5</td>
<td>Cutover in 1912-14</td>
<td>416</td>
</tr>
<tr>
<td>6</td>
<td>New margin of woods</td>
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</tr>
<tr>
<td>7</td>
<td>Within margin 90 meters</td>
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</tr>
<tr>
<td>8</td>
<td>Pine Point hardwoods</td>
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</tr>
<tr>
<td>9</td>
<td>Opening in dense woods</td>
<td>187</td>
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<tr>
<td>10</td>
<td>Within dense Aspen thicket</td>
<td>120</td>
</tr>
<tr>
<td>11</td>
<td>Dense hardwoods</td>
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</tr>
<tr>
<td>12</td>
<td>Very dense hardwoods</td>
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<tr>
<td>13</td>
<td>Burntover hardwoods near Bryant’s</td>
<td>473</td>
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<tr>
<td>14</td>
<td>Bare ground near laboratory</td>
<td>524</td>
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<tr>
<td>15</td>
<td>Burntover pine land near Bryant’s</td>
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<td>16</td>
<td>Pine in Aspen Series</td>
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<td>Exposed place in upper flat</td>
<td>347</td>
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<td>18</td>
<td>Exposed place on hill</td>
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<tr>
<td>19</td>
<td>Exposed place in lower flat</td>
<td>315</td>
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<td>20</td>
<td>Exposed place on hill</td>
<td>310</td>
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<tr>
<td>21</td>
<td>Aspens in lower flat</td>
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<td>Crest of slope in Aspens</td>
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<tr>
<td>23</td>
<td>Aspens in upper flat</td>
<td>198</td>
</tr>
<tr>
<td>24</td>
<td>Aspens in middle flat</td>
<td>197</td>
</tr>
<tr>
<td>25</td>
<td>Aspens in middle flat</td>
<td>195</td>
</tr>
<tr>
<td>26</td>
<td>Foot of slope in Aspens</td>
<td>178</td>
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</tbody>
</table>

Fig. 1. Diagram showing the total evaporation and the rate per day for 40 days (July 10 to August 19, 1915) from different stations in hardwood and pine land in the vicinity of Douglas Lake, Michigan.

Agrostis alba, and Oryzopsis asperifolia), a very few sedges, and other plants, such as, Convolvulus spithamaeus, Aster laevis, Hieracium scabrum, Hieracium venosum, Solidago canadensis, Melampyrum lineare, Fragaria virginiana, Smilacina stellata, besides such common weeds as, Erigeron canadensis, Rumex acetosella, Lepidium virginicum, Epilobium
angustifolium, and Erigeron ramosus. Overtopping all other vegetation are a few scattered giant trees of Pinus strobus and Pinus resinosa.

The principal trees in the hardwood or beech-maple association are Fagus grandifolia, Acer saccharum, Tsuga canadensis, Betula lutea, and Tilia americana. Shrubs occur largely in openings, Acer pennsylvanicum being most abundant. A large number of herbaceous species grow near the ground. Among the more frequent of these are Aralia nudicaulis, Maianthemum canadense, Trillium grandiflorum, Tridentis americana, Aster macrophyllus, Streptopus longipes, Streptopus roseus, Medeola virginiana, Clintonia borealis, and Actaea alba.

Clearings made in different years, now covered with mixtures of vegetation, furnish series from bare ground up to the hardwood association. Another series leads from bare ground, through aspens, to

Fig. 2. Diagram showing the daily rate of evaporation in cc. and the precipitation in cm. for the intervals between readings from certain stations in the hardwood series, 1915.
the pine association; while a third series leads from open water to the *Thuja* association. In wet soil, seedlings of *Thuja* are present under many conditions. On sandy land, healthy seedlings of *Pinus strobus* and *Pinus resinosa* occur under a large number of conditions. Similarly on the better soil are seedlings of *Acer saccharum* and *Fagus grandifolia*. On other portions of the lumbered land such seedlings have become small trees, with every prospect of reproducing the original forest. For the purposes of the present investigation, young seedlings, 15 to 25 cm. in height were chosen, as these are in a most critical stage.

In 1915 three atmometers were run at the level of *Acer saccharum* seedlings in the dense hardwood forest under three conditions: atmometer No. 11 under ordinary shade (Fig. 6), No. 12 under very heavy shade, and No. 9 in an opening caused by the removal of a large tree. Atmometers No. 6 and No. 7 were run in a large patch of vigorous 1 to 3 year old seedlings near the edge of the forest. The edge was the result of the preceding winter's clean-cut lumbering—therefore exposed to light and wind (Fig. 5). Atmometer No. 6 was placed at the very edge, while No. 7 was run about 90 meters in the forest. Atmometers No. 1 and No. 2 were run alongside of *Acer*
seedlings, growing unprotected in the open sun in an area cleared during the preceding winter (1914–15). In this same area three atmometers were started in 1916. The second year had allowed the brambles to encroach upon the fireweeds—clothing the ground with a dense covering of vegetation. The maple seedlings were likewise one year older and their vigor was positive proof that they were amply and easily meeting conditions. The introduction of cattle into the area in the middle of the summer necessitated the withdrawal of the atmometers. The healthy condition of the seedlings in the fall, however, was evidence that these seedlings could withstand even such an extremely dry summer as that of 1916.

In 1915, atmometers No. 4 and No. 5 (Fig. 7) were run near maple seedlings in an area cleared in the winter of 1913–14. Weeds and brambles were also present. Atmometer No. 3 was run by maple seedlings in an open place in a thicket-tree growth—long since cut and lightly burnt—into which brambles have entered thickly. Atmometer No. 8, the last of this series, was run on Pine Point in a mixture of hard-wood and cedar in which all the large Thujas had been cut out.
A similar series of experiments was run in connection with the establishment of pine plants in the aspen association. Pine seeds are furnished by large trees bordering the lake and scattered sparingly in the main body of the pine land. The ground conditions are various. Open sandy soil may be quite plantless where fire damage has been very severe. The ground is sometimes covered with a dense carpet of moss or sod, which makes seeding ineffective.

Eleven atmometers were set out on a line running back from the lake near the Biological Station under conditions as follows: No. 20 in an open growth of aspen, the ground covered with Pteris; No. 18 near the preceding in a growth of Pteris under the open sky; No. 26 at the foot of a slope in a dense aspen thicket, in which the ground was entirely obscured by the luxuriant growth of Pteris; No. 21 about 20 meters from the preceding at the crest of a slope where the ground flora was predominantly formed by Gaultheria procumbens under a fairly open aspen thicket (Fig. 8). Atmometers No. 24 and No. 25 were run in a dense aspen thicket, where Pteris was also luxuriant. This thicket was separated from the uplands by a steep partially cleared slope about 10 meters high. Atmometers No. 17 and No. 19 were run on this slope. On the uplands there were fewer pine seedlings, both because of the distance from seed trees and the greater
fire damage. Three atmometers were run in close proximity to small pine seedlings, two of which, No. 22 and No. 23, were under a fairly dense aspen stand, while No. 16 was exposed to the sky.

Fig. 6. Floor of a hardwood or beech-maple forest showing atmometer No. 11 in a dense mass of *Acer saccharum* seedlings. Seedlings of *Acer pennsylvanicum* are also present. July 22, 1915.

Until the winter of 1911–12, south of Bryant’s hotel, there was a patch of hardwood. East of it was pineland, now vegetated with a very open growth of aspen. A north and south ravine sharply separated these two areas of different vegetation. As the area to the east is in line with the prevailing westerly winds, it has had abundant opportunity to become thoroughly seeded with *Acer saccharum* and other hardwood plants. The hardwood was cut in the winter of 1911–12 and fireswept in May, 1915. To determine whether there was any particular characteristic of evaporation which possibly could have influenced the fact that *Acer* seedlings were not present in the pineland, although present on the hardwood land, two atmometers were run—No. 13 in the burnt-over hardwood land and No. 15 about 200 meters distant in the pine land.

The evaporation conditions attendant upon the establishment of *Thuja* seedlings in boggy soil were investigated with 16 atmometers in 1916. Seed trees of *Thuja* are smaller, less abundant, and more local-
ized in their distribution than pine or maple, which explains why Thuja was not found in some of the smaller bogs. Atmometers No. 39 and No. 40 were run in a small Chamaedaphne bog in which Larix and *Picea mariana* were conspicuous invaders. This bog has been thoroughly fireswept and no Thuja is present. Atmometers No. 41 and No. 42 were started by Thuja seedlings on the beach and at the edge of the beach thicket respectively, but after the first week had to be
discontinued. In a small slashed bog along a little stream east of Douglas Lake, atmometers No. 37 and No. 38 were run in moderately open conditions near healthy Thuja seedlings. At East Point there are several bogs in different stages of development. Atmometer No. 27 was run near a Thuja seedling at the edge of the fringing dune, exposed to winds from the lake, No. 28 near Thuja seedlings at the inner edge of the bog, No. 29 in the densest part of the bog in which a Thuja seedling could be found growing, while No. 30 was run, in August, in the deepest and darkest spot which could be found. Thuja seeds but no Thuja seedlings were present. Atmometer No. 36 was run in a small bog in the aspens south of the Biological Station. Larix, Thuja and Picea were present, but fire had seriously damaged the vegetation.

**Fig. 7.** A view in a hardwood area cut over in 1913-14, showing atmometer No. 5. The conspicuous weed is *Erigeron canadensis*. July 22, 1915.
Reese's bog, the largest bog in the vicinity of the Biological Station, is a well-developed Thuja bog. Atmometer No. 34 was run near a Thuja seedling in the marginal foss at the foot of a hill, where the soil was very wet. Although exposed to the sun, the opportunity for free circulation was poor. Atmometer No. 35 was near a Thuja seedling in a dense thicket of 10-20-foot saplings in very wet soil—likewise hemmed in from the wind. Atmometers No. 32 and No. 33 were in Thuja on slightly higher ground where the soil was dry at the surface and the circulation good—No. 32 in a slight opening in which a layered sprout was healthily growing and No. 33 in a very dense thicket of small trees under which was no green ground vegetation (Fig. 9). Ungerminated composite and Thuja seeds were found in the layer of dead Thuja leaves. Atmometer No. 31 was run by a Thuja seedling in a good-sized clearing where the seedlings were exposed to full sunlight.

Atmometer No. 14 represents the evaporation conditions of the bare ground near the lake in the immediate vicinity of the laboratory, in 1915.

In each experiment, unless otherwise noted, the atmometer was
run in immediate proximity to a young healthy seedling of maple, pine, or white cedar and represents the conditions successfully met by those seedlings. Where virgin hardwood forest is cleared during a winter, the vegetation in the following spring consists of such forest species as can withstand the new conditions. This includes the seedlings of *Acer saccharum*. Weeds appear later in the season, but not in great abundance during the first year. During this time maple seedlings have little or no protection from the full sun, yet large numbers of them survive. Is a downward change in evaporation a necessary prerequisite to succession or is the evaporation changed as a result of succession? If the former is the case, since *Acer saccharum* seedlings are normal to the floor of the climax vegetation where the rate of evaporation is very low, it might be logical to suppose that maple seedlings will not be found except where the rate of evaporation is much less than that over bare ground. If the latter is the case, maple seedlings will be found growing wherever the soil is suitable, regardless of the rate of evaporation of the habitat and regardless of any change that their development may subsequently have upon the habitat.

![Fig. 9. View in a Thuja bog, showing atmometer No. 33 in the center of the background where the shade is so dense that no green ground vegetation is present. August 12, 1916.](image-url)
The results and their interpretation follow: Taking up the hardwood series first, the following results were obtained. In the area cut over during the winter of 1914–15, where sufficient time had not yet elapsed for weeds to invade and change the evaporating conditions of the ground layer, the rate of evaporation was 590 and 561 cc. for 40 days in the middle of the summer of 1915. This rate was 3.37 times as great as that from the floor of the normally dense hardwood forest in this region. In the area cut during the winter of 1913–14, where weeds and brambles had entered in quantity, the evaporation rates were 416 and 425 cc. from two stations. A relative slowing up of the rate of evaporation even during the season was plainly evident in atmometer No. 4, as the development of weeds during the course of the season came to protect the instrument and the Acer seedling to a greater and greater degree. In fact this protection from weeds was sufficient to cause a lower rate of evaporation than was obtained from atmometer No. 3 run in an open weedless spot in an area where hardwoods had made considerable progress in revegetating a former cut. There, the rate was 453 cc. during the same length of time. At the edge of the woods, where atmometer No. 6 was stationed in a luxuriant growth of Acer saccharum seedlings, a rate of 378 cc. was obtained for the period of experimentation. Ninety meters in from the margin, the rate had decreased to 240 cc. Within the woods the rate was 175 cc. in a spot of average density, 147 cc. in a very dense situation, and 187 cc. in a small opening in the dense forest. These results show a wide range of conditions from bare ground without shade—the severest conditions maple seedlings could be called upon to withstand—to the mature forest with its dense shade. Seedlings in the open received sunlight. Under more advanced conditions in the vicinity it was seen that such seedlings were developing into trees, while the vast majority of the multitudes of seedlings in the dense forest did not persist for more than a year or two, unless they were in openings.

This is a clear case in favor of the contention that the seedlings of the dominant species of certain associations become established irrespective of the evaporating conditions—in fact, with the additional advantages accruing from an increased amount of sunlight, seedlings of mesophytic species thrive better under more xerophytic conditions than that which the mature forest furnishes.

In the presence of sunlight, Thuja seedlings readily develop in either sandy or boggy soil, having a sufficient supply of water, under the
entire range of evaporation conditions present in the region. Thuja seedlings commence development on the open beach, but are destroyed by ice action. On the low fringing dune, where the evaporation was 618 cc. from atmometer No. 27, Thuja seedlings were more frequent.

At Bryant's bog, where conditions were intermediate between the sand dune and a normal cedar bog, atmometers No. 39 and No. 40 gave 590 and 555 cc. respectively for the season of 1916. As previously noted, this bog has been repeatedly devastated by fire and there are no Thuja seed trees in the immediate vicinity. The absence of Thuja, therefore, can not be attributed to the conditions of evaporation.

In certain of the East Point bogs, conditions pre-eminently suitable for the development of Thuja prevail. Although Thuja seedlings are found under a wide range of evaporation conditions, there are places in the bog where it is too dark for them to grow. Darkness is here attended by low evaporation. With an increase in light, evaporation is increased. Since a certain amount of light is necessary for the development of the Thuja seedling, low evaporation is not in itself a sufficient reason for the absence of Thuja seedlings. Darkness results from the dense canopy formed by the trees, but even in the darkest places Thuja seeds may be found. The evaporation from such a spot where no Thuja seedlings were present was 155 cc. for the season of 1916. In a small opening nearby, where Thuja seedlings were actively growing, the evaporation was 225 cc. The increased rate of evaporation in itself could hardly be held responsible for the presence of seedlings in one case and not in the other. The development of seedlings in openings tends to restore a dense canopy and thus to lower the evaporation from the chamaephytic layer. When a clearing of considerable size is made, the evaporation is increased to a much greater extent, as in the case of atmometer No. 3, in Reese's clearing with an evaporation of 587 cc. Many Thuja seedlings were present.

Reese's bog occupies a low rolling site at the head of Burt Lake. A road and several trails improve its circulation. A comparison of atmometers No. 33 and No. 35 brings out the effect of circulation. Atmometer No. 33 on the ground beneath a canopy of Thuja so dense as to prevent ground vegetation, gave 435 cc., a higher rate than 345 cc. from No. 35 in the crown of a small Thuja seedling in an opening nearby. In the latter case, the development of edge conditions in the
foliage of the trees around the opening greatly checked the circulation. Likewise atmometer No. 34 by a small Thuja seedling in the marginal foss at the foot of a high ridge, where air drainage was poor, gave 391 cc., a lower result than the 435 cc. from No. 33, which was further in the bog, but free from the influence of ground vegetation owing to the dense canopy of Thuja saplings.

Atmometer No. 36, run in a small relic bog in the aspens north of Reese's bog gave 335 cc. and atmometers No. 37 and No. 38, run in a slashed bog to the east of Douglas Lake, gave 344 and 307 cc. respectively. In each case Thuja seedlings were developing at a rapid rate. Based upon one week's record, the evaporation near a Thuja seedling on the beach for the season of 1916 would have been 562 cc. and 487 cc. at the edge of the beach thicket.

In the pine series, investigated during 1915, the evaporation varied from 347 cc. in an open spot in an aspen grove, through 310 and 321 cc. on an exposed hillside, 197, 198, 196, and 187 cc. in the ordinary aspen association to 178 cc. at the foot of a slope in the densest part of the aspens. In each case the results express the conditions withstood by one to three-year-old pine seedlings of which there were large numbers throughout the aspens. Pine seedlings easily withstand as wide a range of conditions as the region presents. In no case therefore could it be said that evaporation conditions were the determining factor in their ecesis. The presence of all ages and sizes of pine trees is excellent evidence of how well the pine is developing and in consequence the succession is progressing. Aspen seedlings are abundant in the open sandy ground. As they develop, the increasing shade and the checking of the wind are instrumental in causing a decrease of evaporation from the chamaephytic layer, for example, atmometers No. 18 and No. 24, with rates of 315 and 196 cc. respectively.

The two atmometers run during 1915 in connection with the area south of Bryant's, the one in pine land and the other in hardwood land—each of which was very openly vegetated—gave the following results: The evaporation from the immediate vicinity of a pine seedling in pine land was 513 cc. Atmometer No. 13, run in hardwood land devastated by fire, one and one half months previous, gave a rate of 473 cc. for the same period. The fact that the evaporation rate was 473 cc. in the hardwood land, where maple seedlings were present, and 513 cc. in the pine land, where pine seedlings were present, whereas maple seedlings developed successfully under the highest rate (590 cc.)
obtained in the region, means that the evaporation from the chamaephytic layer is not the fundamental factor in the ecesis of such seedlings.

The fact that the rate of evaporation from the chamaephytic layer is decreased in the development of mesophytism has been demonstrated by many investigators: Transeau (5) at Cold Spring Harbor, Gleason and Gates (1) in Central Illinois, Fuller (2) near Chicago, Weaver (3) in southeastern Washington and adjacent Idaho, and the present investigation in northern Michigan all strongly bring out the same conclusion. If there is a causal relationship between evaporation from the chamaephytic layer and succession, which I believe no one disputes, either the decreased evaporation causes plant succession or plant succession causes a decrease in evaporation. Dr. Gleason and I (1) made the latter interpretation. Fuller (2) says: "the decreased rate of evaporation caused by the heavier vegetation is the direct cause of succession between different associations." The data of the present investigation indicate that evaporation is changed in the course of succession and not preceding it.

In the succession towards mesophytism a conspicuous feature is the fact that the seedlings of the dominant species of a genetically higher association commence their development under the conditions furnished by the existing association. Instead of a change of evaporation preceding the development of a different vegetation, that which is controlling and changing the rate of evaporation from the chamaephytic layer is the invading dominant species which have successfully withstood the conditions imposed upon them by the existing association. It is quite obvious that they can not change nor control conditions before they are present.

An increase in density of an association, itself, likewise causes a decrease in the rate of evaporation from the chamaephytic layer. Except a change of dominant species obtain, however, succession has not taken place. Variations in evaporation from typical stations of a given association in a given area are not likely to be as great as the difference obtained between two genetically related associations. If one should add to Fuller's statement, previously quoted, to have it read: "The evaporation thus controlled and changed is one of the principal factors in permitting the development of a different lower story vegetation," its validity could be readily appreciated for those secondary species whose physiological limitations precluded their development in the lower genetic association. The fundamental
thing in succession is the replacement of the dominant species of the existing association by those of the invading association. Changes in the flora of the ground layer are secondary events.

With these facts in mind, one can not dodge the issue that, in a given local area, invasion takes place under the existing conditions. With the development of the invading species the evaporation conditions of the ground layer are changed, which is usually accompanied by a change in the ground flora. In other words, a change of evaporation conditions of the ground layer is the result and not a fundamental cause of succession.

SUMMARY

1. Experimentation was carried on in the vicinity of Douglas Lake, Michigan, during the summers of 1915 and 1916, with 42 standard Livingston atomometers. The usual methods of experimentation and calculation of data were employed.

2. As the investigation was carried on in a small area, the influence of edaphic factors was not obscured by the action of broad climatic factors.

3. Invasion, which is the initial stage of succession, must take place under the conditions already existing.

4. The change of conditions coincident with mesophytic succession brings about a decrease in the rate of evaporation in the ground or chamaephytic layer.

5. In a given area, the differences in the amount of evaporation under which seedlings develop are largely due to the surrounding vegetation, which by its size and density controls the evaporation beneath it.

6. The complete range of evaporation conditions present in this region, namely, from bare ground to the mature forest, is completely within the physiological limits of the seedlings of *Acer saccharum*, *Pinus strobus*, *Pinus resinosa*, and *Thuja occidentalis*. Given suitable soil conditions, maple seedlings will develop under evaporation conditions at least 337 percent more xerophytic than the normal hardwood forest, or 400 percent more xerophytic than the very dense forest.

7. Within their soil requirements and in the presence of light, the establishment of the pine, beech-maple and *Thuja* bog associations—three of the most important tree associations in northeastern North America—is independent of any particular conditions of evaporation. Consequently a decrease in evaporation is not a prere-
quisite to succession. A change in dominant species in an area is fundamental to succession.

8. The change in the rate of evaporation from the chamaephytic layer is produced by the development in density of the invading vegetation. Being coincident with and not antecedent to it, the change in evaporation is a result and not a cause of succession.

9. While it is necessary for certain species to develop under existing conditions to bring about succession, other species, of narrower physiological limitations, can not develop until conditions are brought within their range. Such species are secondary species, unable to cause succession.

10. Even though evaporation conditions are within suitable limits, succession will not take place unless the disseminules of the dominant species of a higher genetic association arrive and develop.

11. The average evaporation from the chamaephytic layer of the average aspen association for 40 days during the summer of 1915, at Douglas Lake, Michigan, was 4.9 cc. per day; for the normal density of the beech-maple forest, 4.4 cc. per day; while the highest average rate for the season obtained from open ground was 14.7 cc. per day. For a single week the highest rate was 21.6 cc. per day.

For 47 days during the summer of 1916, the average evaporation from the chamaephytic layer of a densely developed Thuja bog was 4.8 cc. per day. A rate of 26.6 cc. per day was recorded from an atrometer in open ground at the crest of the low bluff a short distance from the laboratory.

List of Plants Mentioned, with Authorities


*Acer pensylvanicum* L.
*Acer rubrum* L.
*Acer saccharum* Marsh.
*Actaea alba* (L.) Mill.
*Agrostis alba* L.
*Agrostis hiemalis* (Walt.) B.S.P.
*Aralia nudicaulis* L.
*Aster laevis* L.
*Aster macrophyllum* L.
*Betula alba* papyrifera (Marsh.) Spach.
 (*B. papyrifera* Marsh.).

*Betula lutea* Michx. f.
*Chamaedaphne calyculata* (L.) Moench.
*Clintonia borealis* (Ait.) Raf.
*Convolvulus thamnus* L.
*Cornus canadensis* L. (*Chamaepericlymenum canadense* Asch. & Graebn.).
*Danthonia spicata* (L.) Beauv.
*Epilobium angustifolium* L. (*Chamaenerion angustifolium* Scop.).
I. INTRODUCTION

The relation of the rusts to their hosts has long occupied the attention of many workers, not only because of their economic importance, but more especially by reason of the extremely interesting biological problems which they offer. Not only have the rusts afforded a wide field for the study of the questions of immunity, susceptibility, physiological varieties, heteroecism, etc., but they, together with a few other groups such as the Peronosporales and Erysibaceae, make up part of the group of fungi which de Bary has called obligate parasites. This group of fungi is characterized by the requirement of a living host as the source of food supply. Saprophytes, on the other hand, obtain their food from dead organic material. Between the two classes are the intergrading facultative parasites and facultative saprophytes, determined by the degree a fungus is independent or dependent upon a living host. The saprophytic and facultative parasitic fungi have long been studied with attention to their food relations, but most of the work upon the obligate parasites has been confined to other lines, since the parasitic condition itself puts great difficulties in the way of an investigation of the nutrition of the fungus.

One must not overlook the fact that there are two conditions in obligate parasitism. In the first, we have the problems concerned with immunity and susceptibility, a condition which is common to all parasites whether obligative or facultative as well as to the facultative saprophytes. The other condition is that which goes to produce the

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