The Ecological Relations of the Vegetation on the Sand Dunes of Lake Michigan (Concluded)

Henry Chandler Cowles

Botanical Gazette, Vol. 27, No. 5 (May, 1899), 361-391.

Stable URL:
http://links.jstor.org/sici?sici=0006-8071%28189905%2927%3A5%3C361%3ATEROTV%3E2.0.CO%3B2-1

Botanical Gazette is currently published by The University of Chicago Press.

THE ECOLOGICAL RELATIONS OF THE VEGETATION ON THE SAND DUNES OF LAKE MICHIGAN.

HENRY CHANDLER COWLES.

[*Concluded from p. 308.*]

D. THE ESTABLISHED DUNES.

1. *The basswood-maple series.*

IT was shown in another place how the steep lee slopes of the slowly advancing dune-complex are first captured by social perennial herbs like Ammophila and Asclepias. Then shrubs like Cornus, Salix, and Prunus grow up and gradually drive out the herbs which grew there first, because they are ill-adapted to the shade. With these shrubs there often develop many young trees of the basswood, *Tilia Americana*. As these trees grow rapidly, it is not long before the thicket becomes a little forest, in which the dominant tree is the basswood. The basswood dune, more than any other type of established dune, is *sui generis*. It is to be found along the entire coast between Dune Park and Glen Haven.

The conditions that determine the development of the wonderfully characteristic flora are very obscure. The basswood dunes are always very steep and relatively near the lake. Unlike all other established dunes there is no approach to a vegetation carpet; the sandy soil is loose and bare and evidently more or less shifting. The movement of the sand is due directly to gravity and only indirectly to the wind. The only obvious condition which favors the rich development of plants is the almost complete protection from the wind.

The trees of the basswood dunes grow as thickly together as trees ever grow, and much more thickly than in any other dune forests. Everywhere the basswood is the dominant tree; no other tree begins to approach it in importance, although *Populus*

monilifera is often common. At the south end of the lake *Sassafras officinale* grows with the basswood in abundance. Trees that occur occasionally along the coast in this association are *Quercus coccinea tinctoria*, *Fraxinus Americana*, *Juglans cinerea*, *Ulmus fulva*, *Ostrya Virginica*, *Acer saccharinum*, *Betula papyrifera*, *Abies balsamea*, *Pinus Strobus*, *Tsuga Canadensis*, *Thuya occidentalis*.

One of the remarkable features of the basswood dunes is the luxuriant development of lianas. Scarcely anywhere away from the river bottom forests is there such a development of climbers in this region. *Celastrus scandens*, *Vitis cordifolia*, and *Rhus Toxicodendron* occur almost everywhere. *Ampelopsis quinquefolia* and *Smilax hispida* are not infrequent. The great liana development may be correlated, perhaps, with the dense growth of trees.

Shrubs are abundant about the margins of the miniature forests and in the more open places. Often these may be regarded as relicts of a former exclusive shrub vegetation. *Prunus Virginiana* and *Cornus stolonifera* are the most common tall shrubs, *Rosa Engelmanni* the most common low shrub. At the south end of the lake *Hamamelis Virginiana*, *Ptelea trifoliata*, *Rhus Canadensis*, and *Celtis occidentalis pumila* are common and very characteristic. The only herb that can be regarded as characteristic of this association is *Smilacina stellata*. *Elymus Canadensis* occurs in the open places. Many other herbs are occasionally present, but there is no necessity for mentioning them. The slopes of the crateriform depression in *fig. 22* have most of the typical plants of a basswood dune. The bare trees are chiefly basswoods, the others pines.

By all odds the most remarkable feature of the flora on the basswood dunes is its decided mesophytic flavor. The majority of the above-named species are usually pronounced mesophytes. Indeed, along the wooded bottoms of the Desplaines river far from dunes and dune influences, the following of the above plants may be found growing together: Tilia, Fraxinus, *Ulmus fulva*, Populus, Celastrus, Vitis, *Rhus Toxicodendron*, Ampelopsis, Smilax, Prunus, Cornus, Hamamelis, Ptelea, and Celtis. Thus half of the entire number recorded above are found in a single river

bottom forest. Of the fifteen most characteristic plants of the basswood dunes at the south end of the lake, eleven are found along the Desplaines bottoms; two of the remaining four, Sassafras and Smilacina, are common as mesophytes. Only two of the fifteen, *Rhus Canadensis*, and Rosa, are commonly xerophytic.

Apparently the life conditions on the basswood dunes are anything but similar to those of the river bottoms. The former appear to be xerophytic, the latter mesophytic and inclining to hydrophytic. The soil of the dunes is sand with scarcely any humus at all, and the slight water content is made less by the steepness of the slope. In the river bottom there is a deep alluvial soil rich with humus and with an abundance of water. Nor is the river bottom flora on the dunes the vanguard or the relict of a river bottom flora. At the south end of the lake, at least, the basswood dunes and river bottoms are separated from each other by many kilometers. The likeness of the floras suggests a likeness of conditions in the two apparently very dissimilar habitats. What this likeness is, if it exists at all, cannot easily be seen.

It is this river bottom flora on the dunes that furnishes the best examples of anatomical variation due to habitat conditions. Most remarkable gross variations are found in the leaves of nearly all the species. Celtis, a tall tree on the bottoms, is a thorny shrub on the dunes. The tissues, also, are highly modified so as to meet the requirements of the dune conditions. These great variations, not alone in a single species, but in a plant society transported, as it were, from the river bottoms to the dunes, will supply a large part of the material for the second or anatomical portion of this paper. It is also the author's intention to experiment with the river bottom and dune forms of the various species, and endeavor to determine whether or not these changes can take place within a single plant generation.

The development of an undergrowth of shrubs and herbs on the steep basswood dunes tends more and more to stop the sifting of the sand between the plants. The partial decay of the

FIG. 19.—Summit of a coniferous dune at Dune Park. The trees are white pines. The shrubs in front of them are junipers; those at the left, cedars. The grass in the foreground is Andropogon.

leaves which fall year after year gradually produces a humus. The conditions approach more and more those of the typical mesophytic forest, even though xerophytic dune societies may surround on every side. The growth of the humus permits the development of a low vegetation, consisting of lichens, mosses and forest herbs. The vegetation, shade, and humus conserve the water and cause a mesophytic soil in spite of the slope and sand. Seedlings of other trees, yet more indicative of the shady mesophytic forests than the basswood, make their appearance. The most prominent of these is the sugar maple, *Acer saccharinum*. Scarcely less important are the beech, *Fagus ferruginea*, and the hemlock, *Tsuga Canadensis*. These trees produce the densest shade and cause the extermination of the basswood and its associates. Each vegetation from the original Ammophila to the maple forest, therefore, gives a denser shade than the one preceding.

Accompanying the above-named trees are such typical mesophytic forest herbs as *Hepatica triloba*, *Trillium grandiflorum*, *Epiphegus Virginiana*, and *Arisaema triphyllum*. That the conditions not only in the soil but even in the air are less xerophytic than when the basswood was the dominant tree is shown by the great luxuriance of the vegetation. The trees are just as large as in inland forests and the xerophytic structures that were present in the basswoods and their associates are quite absent in the maples, beeches, and hemlocks. The air seems to be almost as mesophytic as in the inland forests. The maple and beech forests are not frequent on old dunes at the south end of the lake, but, for that matter, they are not so well-developed anywhere in this region as they are in Michigan. Mesophytic forests on old dunes were seen at Saugatuck, Grand Haven, Frankfort, and Charlevoix. At Frankfort there is a maple forest on the steep slope of an old dune which is as luxuriantly developed as in an inland location. At Charlevoix a hemlock was seen which had over 200 rings, showing the minimum length of time that the mesophytic flora could have existed on the dune. The mesophytic forest is the most permanent of plant societies

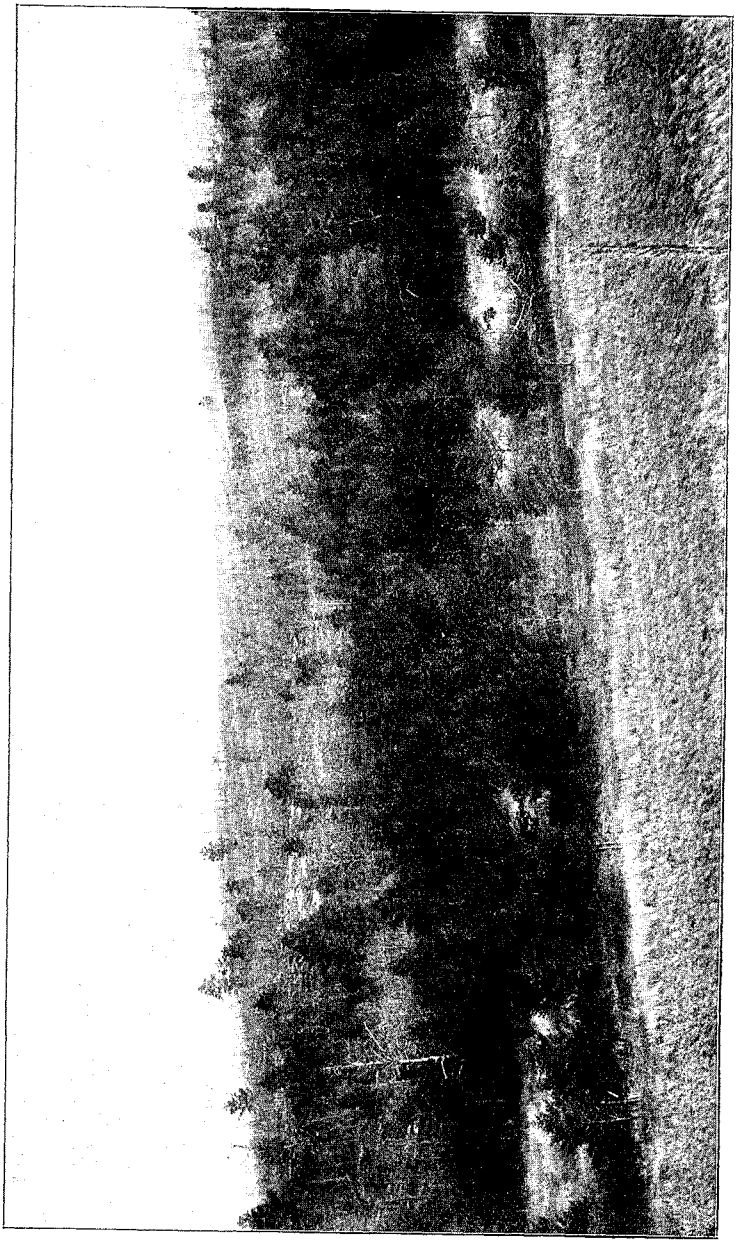

FIG. 20.—North slope of an oak dune at Dune Park, taken in winter, showing scattered pines among the oaks, and an abundance of pines at the lower levels.

in the lake region. It may be regarded as the culmination of the series which began with the lower beach.

2. *The evergreen series.*

a. The heath. — The life-history of a windward slope is vastly different from that which has just been described. If one views a region of established dunes from the lake side, he sees a landscape in which evergreens predominate, whereas a view from the land side often shows a decided dominance of deciduous trees. Not only the windward slopes but the summits have an evergreen flora. The key to these facts is exposure to desiccating factors, especially heat, cold, and winds. So far as the soil is concerned, there is but little difference between the conditions on the windward and leeward slopes. In both cases there is a vegetation carpet and a covering of humus. The more gentle slope favors the retention of moisture, though this factor is counterbalanced by the desiccating influence of the wind on the soil. At the south end of the lake the soil of the leeward slopes is drier than that of the windward slopes, because of the southern exposure and consequent drying influences of the sun. Even in this latter instance, the contrast between the floras of the two slopes is tremendous. It is the condition in the air, not the condition in the soil, which determines the difference here found. Both slopes have a mesophytic soil; the leeward slope also has a mesophytic air, but the windward slope has a xerophytic air.

The heath has several origins but one destiny. It may arise on the slow-growing embryonic dunes, in depressions on the upper beach, on the fossil beach, on gravel terraces, or in pastures. In all cases the dominant plant species come to be one or more of the following: *Arctostaphylos Uva-ursi*, *Juniperus communis*, *Juniperus Sabina procumbens*. The first two are common along the entire coast, the latter only northward. The term heath has been but little used in America, perhaps because we do not have the peculiar Calluna heaths of Europe. The term heath, as here used, may be defined as a xerophytic flora in

which there is a dominance of low evergreen shrubs. Warming and Graebner use the term heath much more comprehensively, speaking of moss and lichen heaths and coniferous heaths. Along Lake Michigan the heath formation becomes more and more prominent northward. A well-marked juniper or bearberry heath is rare at the south end of the lake, while extensive

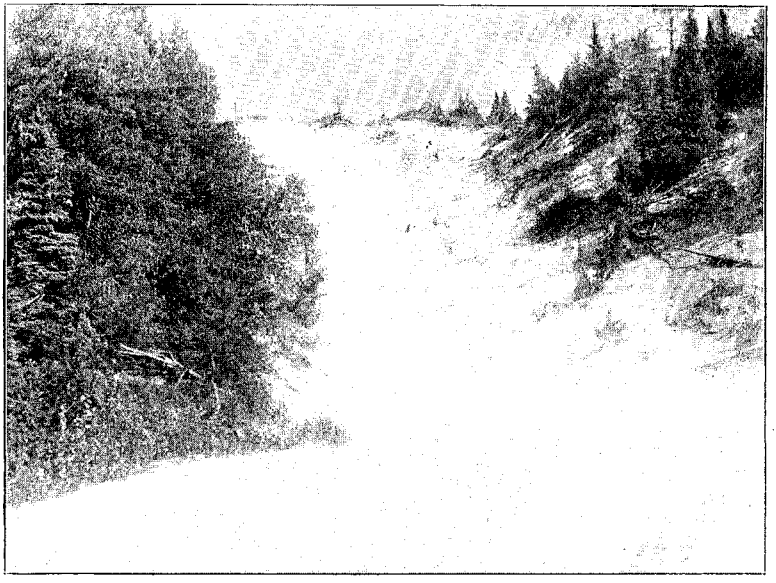

FIG. 21.—Rejuvenated dune on Beaver island. Wind-sweep at the center. Coniferous forests on each side that are not yet destroyed.

areas are covered by the heath on Beaver and North Maniton islands and on the neighboring mainland.

During the development of a heath, the vegetation partakes of the nature of the formation which preceded it, whether dune or beach or terrace. Before the true heath plants cover the soil, the open places are inhabited more or less abundantly by such plants as *Prunus pumila*, *Salix glaucophylla* and *adenophylla*, *Solidago humilis Gillmani* and *nemoralis*, *Aster laevis*, *Calamagrostis longifolia*, *Smilacina stellata*, *Lithospermum hirtum*, *Artemisia Canadensis*, *Rhus Toxicodendron*, *Rosa Engelmanni*. On fossil beaches

and terraces, embryonic heaths often have *Hudsonia tomentosa*, *Andropogon scoparius*, and *Campanula rotundifolia arctica* in addition to the above.

At the center of *fig. 6* there is shown a heath developing on a substratum of embryonic dunes; the bearberry has already covered a large portion of this area with a low heath carpet. *Fig. 24* shows the development of a heath on a fossil beach. In the foreground is a typical fossil beach flora, consisting of scattered grasses, sand cherries, etc. The small scattered tufts are Hudsonia. At the center is a low Ammophila dune, while back of this are patches of embryonic heath, composed of the bearberry and the procumbent juniper. Along the edge of the forest the heath forms a continuous carpet. *Fig. 25* shows a typical juniper heath when fully developed. At the left background the heath is younger and still made up of disconnected patches. *Fig. 26* shows the formation of a *Juniperus communis* heath in a pasture. Since this latter species is more or less erect, while the bearberry and procumbent juniper are creepers, the aspect of the heath shown in *fig. 26* is very different from those shown in *figs. 6* and *24*.

b. The coniferous forests.—Whatever the origin of the heath, it is rarely a climax type along the Lake Michigan shore. It almost uniformly develops into a coniferous forest sooner or later. The most conspicuous and extensive forests of this type are on the lakeward slopes, at the summit of these slopes, or at the summit of the taller inland dunes. These forests, like the heath, become more abundant and the growth more luxuriant as one passes northward along the lake shore.

The development of a forest from a heath is easy to understand and can be observed at almost all points. The heath vegetation is dense enough to prevent the tearing up of the soil by the wind, but not too dense for seedlings of various trees to get a start. The dense tangle of junipers and bearberries close to the soil is peculiarly well fitted to protect the trees while small and tender. In a very short time small and scattered trees become conspicuous on the heath. The transformation of a

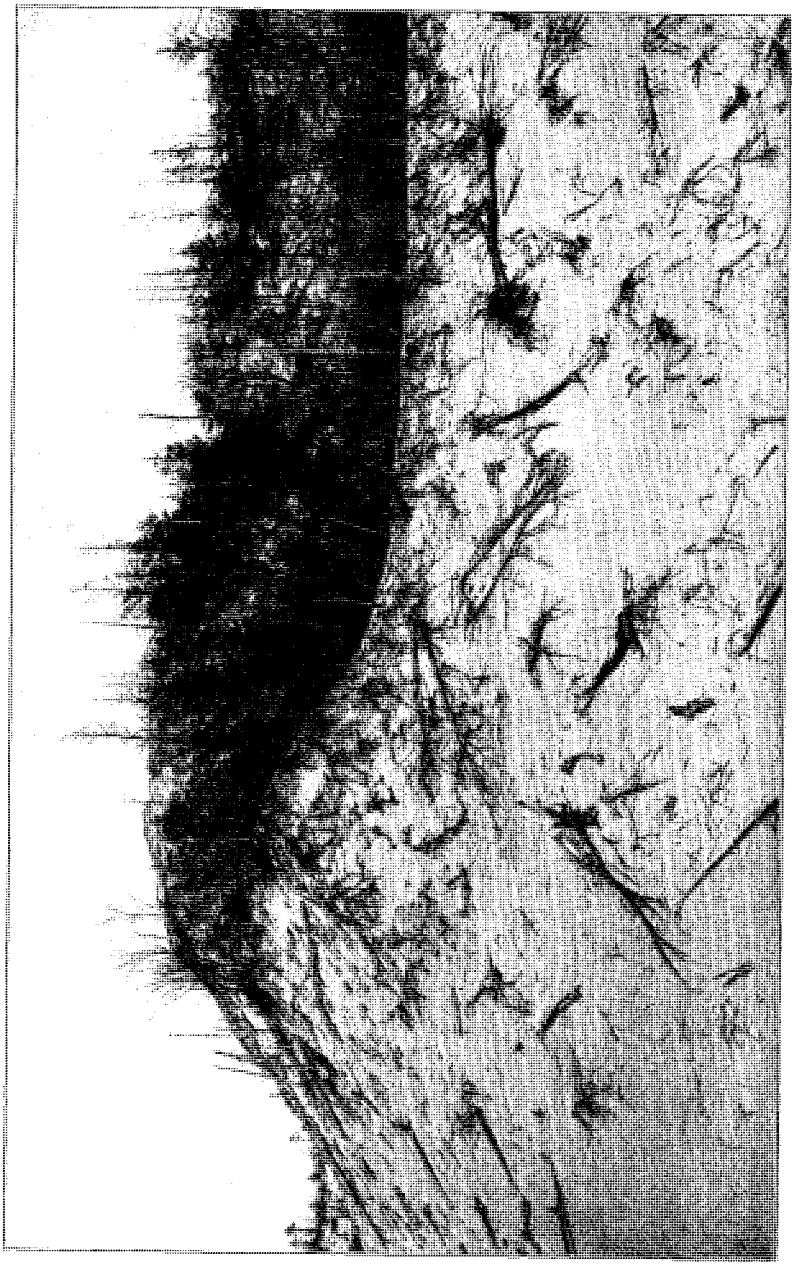

FIG. 22.—Crateriform depression at Dune Park, within which are basswoods and pines in a state of considerable luxuriance. The slope in the foreground is the side of a deep wind-sweep; the development of this wind-sweep brings about the destruction of the flora through the action of gravity.

heath into a forest is illustrated by *figs. 24* and *25*. In each case the heath is encroaching on a beach and is being followed up *pari passu* by the forest. The advance of the heath is secured mainly by vegetative propagation, that of the forest by germination of seeds. This fact, together with the need for protection to the seedlings, prevents the forest from overtaking the heath in the struggle for more territory. So far as observed, the heath always precedes the forest, when the latter is developed in an exposed situation.

In the region as a whole, the pines are by all odds the character trees of the coniferous forests, and especially the white pine, *Pinus Strobus*. This tree is found at all places along the coast. At the south end of the lake the scrub pine, *Pinus Banksiana*, is more abundant than the white pine, while at the north end the red pine, *Pinus resinosa*, is often as frequent as the white pine. The distribution of the pines is very surprising. The scrub pine is the most northern of the three pines mentioned, and its farthest known southern limit is about the south end of Lake Michigan. Peculiarly enough, it is far more abundant than all other conifers put together at the south end of the lake, while it is much less abundant to the north along the lake shore. It was not seen at all north of Glen Haven, though it is reported as common inland. The red and white pines have in general a more southern range than the scrub pine, and yet they are more abundant northward along the lake than is the latter. Furthermore, these pines become more abundant absolutely as one goes northward. The red pine was not seen south of Pentwater.

North of Grand Haven *Thuya occidentalis* becomes a frequent member of the coniferous forests; sometimes it becomes as dominant as the pines. The same may be said of *Abies balsamea*, though it was not seen south of Frankfort. *Juniperus Virginiana* is frequent, especially southward. With the evergreens are occasional deciduous trees, especially at protected forest margins; among these are *Betula papyrifera*, *Tilia Americana*, *Populus monilifera*, and *Ostrya Virginica*.

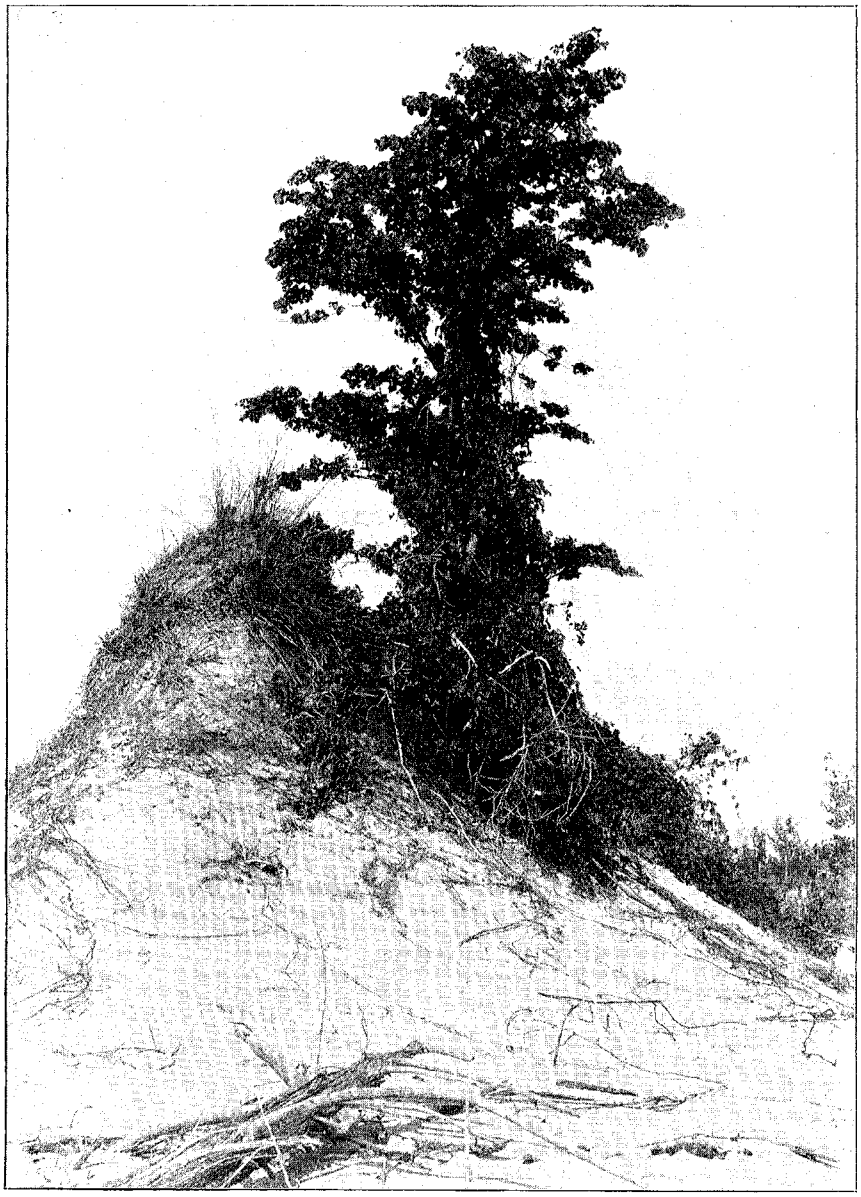

FIG. 23.—Rejuvenated dune at Dune Park. The basswood is the last remnant of a former forest. Clump of Calamagrostis at the left, showing the tenacity with which its roots hold the sand.

So long as the coniferous forests remain more or less open, the three dominant heath plants, *Arctostaphylos Uva-ursi*, *Juniperus communis*, and *J. Sabina procumbens*, retain their prominence. Of these Arctostaphylos is the most persistent, and may be regarded as the most characteristic plant of the forest undergrowth. There are occasional shrubs in the open places, such as *Shepherdia Canadensis*, *Diervilla trifida*, *Rosa Engelmanni*, *Prunus pumila*. Among the herbs in open places are *Calamagrostis longifolia*, *Aster laevis*, *Smilacina stellata*, *Arabis lyrata*, *Lithospermum hirtum*. Many mosses occur more or less shaded by the evergreens, especially Thuidium and other trailing varieties. *Fig. 19* shows a coniferous society at the summit of a dune. The trees are white pines; the shrubs in front of them, *Juniperus communis;* those at the left, *J. Virginiana*. The grass in the foreground is *Andropogon scoparius*. Coniferous forests on exposed slopes are shown in *figs. 6* and *21*.

The coniferous forests heretofore considered are chiefly on exposed slopes and summits. Sometimes there are coniferous forests farther inland developed on older and lower dunes. The protection here is greater and the air is less xerophytic. Extensive forests of this type were found between Frankfort and Empire and on Beaver island. The trees are chiefly pines or balsams just as before, but the evergreen undergrowth of junipers and bearberries is largely replaced by such plants as *Vaccinium Pennsylvanicum*, *V. Canadense*, *Epigaea repens*, *Gaultheria procumbens*, *Linnaea borealis*, *Melampyrum Americanum*, *Pteris aquilina*. In the more open and sterile places there is often a moss or lichen carpet, consisting largely of *Cladonia rangiferina* (or other Cladonia species) or *Polytrichum commune*. At the south end of the lake plant societies of this type become more like pine barrens. On the east coast of Beaver island there is a beautiful gradation series from the heath on the beach through a pine forest like that described in this paragraph into a pine forest in which there is almost no undergrowth at all. The scarcity of herbaceous or shrub vegetation is due to the dense shade and the carpet of pine needles. This last type is the summit of the

evergreen series, and is in all probability a climax type, at least in certain situations.

A very distinct type of coniferous forest is especially well developed at the south end of the lake. Since it is not developed in exposed situations, or even on old dunes, but in low depressions between dunes, it may be called a pine bottom. These societies are developed where the soil is almost hydrophytic. A common location for these miniature pine forests is about the gently sloping margin of an undrained swamp. *Figs. 9, 13, 14,* and *20* show them in such a situation. The line of demarcation between the sedge swamp and the pines is usually quite sharp. The surface of the soil where the pines grow may be less than a meter above the water level.

The character tree of the pine bottoms is always *Pinus Banksiana.* This species is, perhaps, less common than the white pine at the higher levels, but the white pine is rarely, if ever, present on the bottoms. No growth of trees anywhere in the dune region is so pure as the pine growth here. The most common shrubs in these locations are *Hypericum Kalmianum, Salix glaucophylla, Arctostaphylos Uva-ursi,* and *Juniperus communis. Linnaea borealis, Arabis lyrata, Fragaria Virginiana,* and species of Pyrola are frequent. The development of the pine bottom floras was seen at several points. One of the most interesting cases was in a region of oak dunes, where a railroad company had removed considerable sand and lowered the level several meters. Although surrounded on all sides by oaks and at some distance from a pine flora, the new flora at the lower level is developing into that of a pine bottom.

c. The rejuvenated dunes.—The instability of dune conditions is not confined to the dune-complex. The capture or establishment of a dune is liable to be stopped at any point and retrogression toward the active dune conditions instituted. Even a dune that has long been completely established may have its vegetation destroyed and pass again into a state of activity. This process may be called rejuvenation. Any dune may become rejuvenated if the physical conditions are favorable, but the

great majority of rejuvenated dunes are developed from established coniferous dunes; hence this type is discussed in connection with the evergreen series. The coniferous forests that develop on the windward slopes near the lake are peculiarly subject to destruction. The slightest change in the physical conditions is often sufficient to bring about the destruction of a

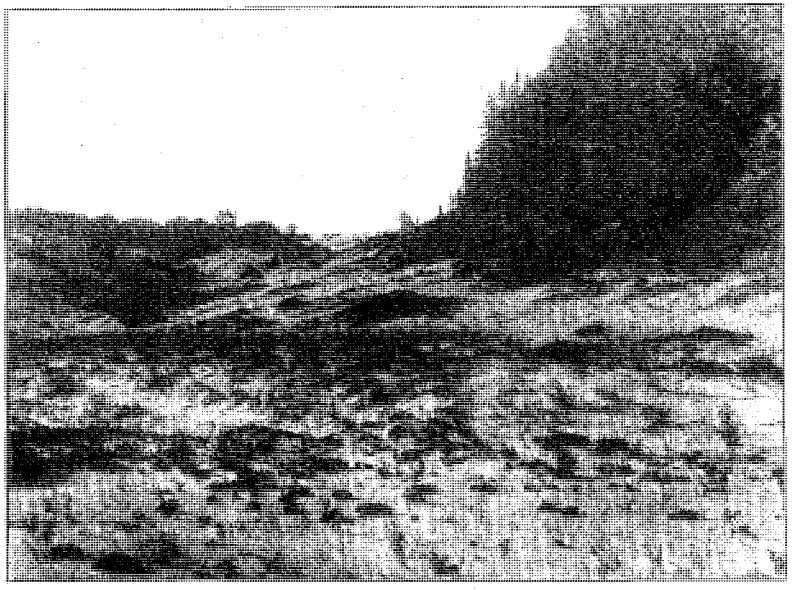

FIG. 24.—Beginnings of a heath on a fossil beach at North Manitou island. Grasses, sand cherries, and patches of Hudsonia in the foreground. Low Ammophila dune at the center. Patches of bearberry heath forming farther back. Advance of the coniferous forest out upon the heath.

coniferous society. The removal of a comparatively slight barrier may be enough to direct the entire wind energy against a pine forest.

The formation of a wind-sweep is, perhaps, the most common way for rejuvenation to begin. *Fig. 6* shows a windward slope tenanted by conifers that has become rejuvenated at three points. One of these wind-sweeps is seen at closer range in *fig. 21*. This latter sweep is forty-five meters in height, and the

angle of slope varies from twenty to thirty degrees. When once a sweep is formed the tendency to self-perpetuation becomes greater and greater, since the wind becomes more and more concentrated as the sweep grows deeper. The destruction of the forest vegetation is very soon accomplished at such a place. The desiccating influence of the wind becomes increased and

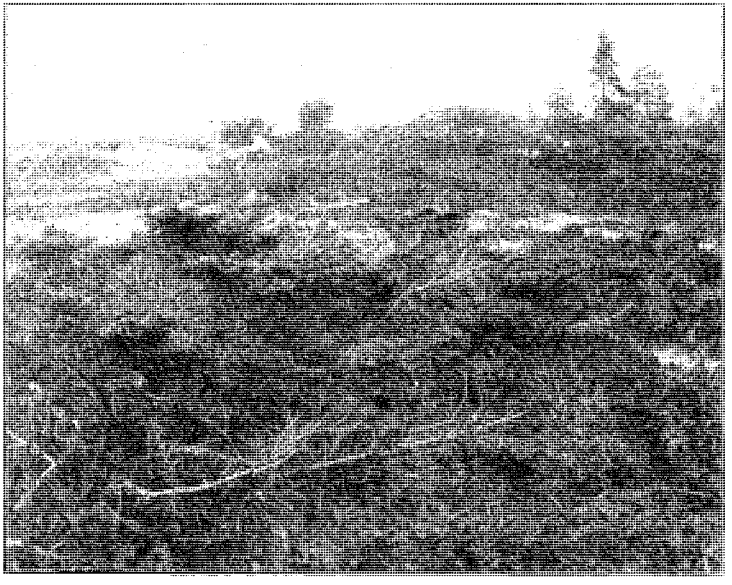

FIG. 25.—Juniper heath on North Manitou island. Young heath patches at the left background. Fully developed heath in the foreground. Advancing coniferous forest at the right background.

makes it difficult even for the xerophytic conifers to survive. At no place is the destructive action of the sand-blast seen so well as in these rejuvenated sweeps. The branches and even the trunks of the trees have the softer parts carved away, while the more resistant portions stand out in conspicuous relief. The leaves, especially of deciduous trees, are torn or withered or even altogether destroyed.

These destructive agencies are aided by another force that is altogether irresistible when the sweeps grow deeper, the force of

gravity. *Fig. 22* shows a plant society that is being destroyed mainly by gravity. The view is taken looking at the side of a deep gorge-like wind-sweep which the wind has cut. As the wind blows along, its energy increased by concentration, a large amount of sand is picked up along the base of the steep sides. The sand is as steep as it will lie, so that each removal causes a movement of the sand down the slope. The fallen trees shown in the photograph have been overturned and carried down the slope in just this way. That the direct action of the wind is also powerful enough to destroy without the assistance of gravity is proven by the dead but standing trees at the left, where the action of gravity happens to be much less.

Many plant species resist the process of dune rejuvenation to a surprisingly successful extent. *Fig. 23* shows the last remnant of a plant society that may have been somewhat extensive. The tree at the center is a basswood, a tree which could never develop in such an exposed situation. In all probability this mound is a fragment of a protected lee slope, on which the basswood grew and flourished for a time. The grass at the left is Calamagrostis; the tenacity with which it holds its ground has already been mentioned. Sometimes a group of cedars, *Juniperus Virginiana*, remain at the apex of a conical mound of sand, their associates having been swept away with the sand in which they grew. On the beach at Charlevoix there is a stranded clump of stunted trees of Thuya; they are probably the remnant of a society which has been otherwise destroyed.

As a wind-sweep is developed, and the evergreen vegetation destroyed, many plants that have been previously mentioned as characteristic of bare and exposed situations again make their appearance. The most prominent of these are *Artemisia Canadensis* (or *A. caudata*), *Elymus Canadensis*, *Solidago humilis Gillmani*, *Asclepias Cornuti*, *Œnothera biennis*, *Rosa Engelmanni*, *Calamagrostis longifolia*, *Prunus Virginiana*. In addition to these there come in, of course, the annuals and biennials mentioned in connection with the wind-sweeps on the dune-complex.

While rejuvenated dunes are to be found along the entire

coast, they reach their highest development northward, especially at the summit of the terraces and bluffs. Perched dunes, it would seem, are favorably located for destruction by the wind. At Frankfort and Empire the perched dunes are in the earlier stages of rejuvenation. At Glen Haven these dunes have been rejuvenated, the vegetation entirely destroyed, and the sand

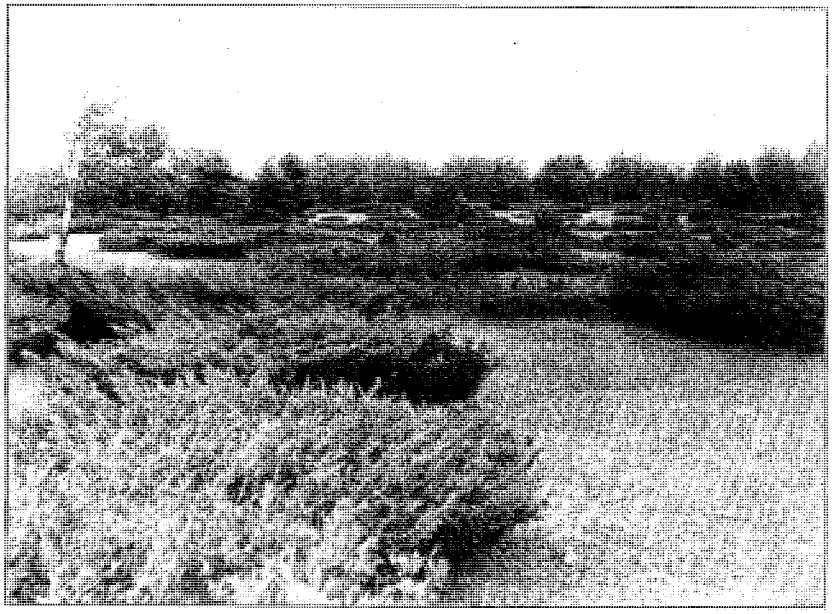

FIG. 26.—Development of a juniper heath in a pasture at Beaver island.

removed inland to form the gigantic moving dunes previously mentioned. The substratum on which the dunes rested remains as a bare gravel mesa, with only the Sleeping Bear left to tell the tale of its former occupation by coniferous dunes. It is barely possible that some of these so-called rejuvenated dunes have never been established, and that they have grown slowly to their present height *pari passu* with the vegetation. This is purely a theory without any facts whatever to support it. The evidence seems to point unmistakably to an establishment followed by

rejuvenation. Evergreen vegetation is very poorly adapted for any *pari passu* growth, such as is found on the embryonic dunes.

3. *The oak dunes.*

At the south end of the lake, and as far up the eastern shore as Manistee, there may be seen old dunes covered over with rather open and scrubby oak forests. These dunes have long been established and are entirely free from the destructive sand-laden winds which are so influential in determining the character of the other dune societies. As a rule the oak dunes are low and are separated from the lake by several series of dunes on which the vegetation is less stable.

The dominant tree on the oak dunes is the black oak, *Quercus coccinea tinctoria*.[5] This tree is far more abundant than all others combined. The only other tree that may be called characteristic in the Dune Park region is *Quercus alba*. On some oak dunes there are low trees or tall shrubs of *Sassafras officinale*, *Cornus florida*, *Amelanchier Canadensis*, and *Hamamelis Virginiana*. The characteristic shrubs are comparatively few except along the lower margins toward the swamp level, or on shaded northern slopes. The most abundant shrubs are *Vaccinium vacillans* and *V. Pennsylvanicum*, *Salix humilis*, *Viburnum acerifolium*, *Rosa blanda* and *R. humilis*, and *Rhus copallina*.

The herbaceous vegetation of the oak dunes is very diversified and interesting. The trees are always far enough apart to permit an extensive undergrowth of relatively light-loving plants. On the southern slopes, where there is considerable exposure to the sun, there is rarely a continuous vegetation carpet, but a more or less tufted vegetation with intervening patches of naked sand. A large number of herbs are characteristic of such places, for example: *Pteris aquilina*, *Koeleria cristata*, *Cyperus Schweinitzii*, *Carex Pennsylvanica*, *C. umbellata*, *C. Muhlenbergii*, *Tradescantia Virginica*, *Arabis lyrata*, *Lupinus perennis*, *Tephrosia Virginiana*, *Les-*

[5] The closely related *Quercus rubra* and *Q. coccinea* occur commonly in neighboring plant societies and may be present on the dunes, as may hybrids between any of the three forms here mentioned.

pedeza capitata, *Euphorbia corollata*, *Helianthemum Canadense*, *Viola pedata*, *Opuntia Rafinesquii*, *Œnothera rhombipetala*, *Monarda punctata*, *Aster linariifolius*, *Helianthus divaricatus*. In very open places there are various species of Geaster and Lycoperdon, *Festuca tenella*, *Polygonum tenue*, *Polygonella articulata*, *Talinum teretifolium*, *Mollugo verticillata*, *Draba Caroliniana*, *Linaria Canadensis*, *Krigia Virginica*.

On the shaded northern slopes *Pinus Banksiana* and *Pinus Strobus* often occur with the oaks (see *fig.* 20). The undergrowth is often a complete vegetation carpet, and consists of Vaccinium, Viburnum, and others of the above plants, together with many different forms. Among the plants here there may be mentioned various species of Cladonia and Peltigera, several mosses, *Aquilegia Canadensis*, *Epigaea repens*, *Phlox pilosa*.

In the background of *fig.* 9 there may be seen several oak dunes. The view was taken in the winter and shows a dominance of oaks, but the scrub pines are scattered here and there on northern slopes or in exposed situations. *Fig.* 11 shows the advance of an active dune on the north slope of an oak dune with a wealth of oaks and a few scattered pines. *Fig.* 20 is a view looking upon the north slope of an oak dune (taken in winter). The pines are abundant at the base and scattered on the slope. A view of the south slope would show no pines at all.

The conditions for the origin and development of an oak dune flora are obscure. At Grand Haven and Ludington the oak flora appears to follow the basswood flora. Remnants of the basswood flora are conspicuous in both places: Sassafras, Hamamelis, Vitis, Smilacina, *Rhus Toxicodendron*, Smilax, Celastrus. It may be that where the conditions are most favorable a maple forest develops after the basswood, but the oak forest elsewhere. At any rate the maple forests are more prevalent northward and the oak forests southward. While the oak forests at Grand Haven, Ludington, and Manistee are on steep, long-established lee slopes, the oak forests at the south end of the lake are often on rather low ridges, where the basswood may never have prevailed.

Quite probably the pine is the normal predecessor of the oak. The scattered pine trees shown in *figs. 9* and *20* may be the relicts of a more extensive pine flora that has been succeeded by the oaks. The oak cannot get a foothold until the dune has become well established and protected from the lake winds. If the pines are scattered, there is opportunity for the oak seedlings to develop successfully. Forest fires are more destructive to the pines than to the oaks; the former are more readily burned, and basal sprouts are less likely to appear afterward than in the case of the oaks. Near Dune Park there is a tract on which the pines have been burned and replaced by the oaks.

One of the most striking landscape features of the Dune Park region is the appearance of the pines at the lower levels (pine bottoms), and again on the highest summits. The oaks occupy an intermediate position as to altitude. The reason for this distribution seems to be that the pines have a much wider range of life conditions than the oaks. The oaks are excluded from the summits because of the extreme exposure to wind and cold; they are not xerophytic enough for such a habitat. They are excluded from the bottoms, because the conditions are too hydrophytic for them there. The pines are excluded from the intermediate positions not because of lack of adaptation, but because the oaks are better adapted for that position than are the pines. Where the oaks can live at all, they seem able to drive out the pines, while the pines occupy areas that are not adapted to the oaks.

The flora of the oak dunes, especially that found on sunny southern slopes, is a true xerophytic flora, but a xerophytic flora resembling that of the more southern type, where the adaptations are developed to protect against heat and the excessive transpiration which it causes. The flora on northern and windward slopes is predominantly evergreen, developing into a heath or a coniferous forest. This flora, too, is xerophytic, but of an arctic or alpine type, where the adaptations are developed to protect against the wind and cold and the dangers of excessive transpiration which they bring. The correctness of this view is

shown by studying the floras of the oak and pine dunes. The former has a flora related to those farther south, containing Opuntia, Euphorbia, and many other plants of southern range. The pine dunes, on the other hand, show the farthest southern limits of many northern plants—for example, the scrub pine itself. Linnaea, the bearberry, and many others have a northern range.

V. Conclusion.

No attempt will be made to summarize the results of this study, but a few of the more striking phenomena of the Lake Michigan dunes and their vegetation will be given. The dunes have been determined in the main by westerly winds. The great majority of the dunes are established, and many of them are perched high up on bluffs. The vegetation is xerophytic, belonging either to the arctic or desert type.

The xerophytic beaches are subdivided into three zones: the lower beach which is washed by summer waves and is essentially devoid of life; the middle beach which is washed by winter waves and is inhabited only by succulent annuals; the upper beach which is beyond present wave action and is inhabited also by biennials and perennials. There are also fossil beaches and gravel terraces with a flora resembling that of the upper beach, but less xerophytic.

Perennial plants are necessary for any extensive dune formation on the beach, since they alone furnish growing obstacles. Such plants must be pronounced xerophytes and be able to endure covering or uncovering. The most successful dune-formers are *Ammophila arundinacea*, *Agropyrum dasystachyum*, *Elymus Canadensis*, *Salix glaucophylla* and *S. adenophylla*, *Prunus pumila*, *Populus monilifera*. Ammophila and Agropyrum form low dunes that have a large area, because of their extensive rhizome propagation. The Elymus dunes do not increase in area since rhizome propagation is absent. The Salix dunes increase both in area and height, because of extensive horizontal and vertical growth. The Populus dunes are the highest and steepest, since the cottonwoods grow quite tall, but do not spread horizontally.

Small dunes are formed in more protected places by plants that are unable to exist on the beach, or where there is rapid dune formation. Among these secondary dune-formers are Andropogon, Arctostaphylos, Juniperus. Primary embryonic dunes may pass gradually into this second type, as this latter passes into the heath.

The stationary embryonic dunes on the beach begin to wander as soon as the conditions become too severe for the dune-forming plants. The first result of this change is seen in the reshaping of the dune to correspond with the contour of a purely wind-made form. The rapidity of this process is largely determined by the success or failure of the dune-formers as dune-holders. The best dune-holders are Calamagrostis, Ammophila, and Prunus.

There are all gradations between a simple moving dune and a moving landscape; the latter may be called a dune-complex. The complex is a restless maze, advancing as a whole in one direction, but with individual portions advancing in all directions. It shows all stages of dune development and is forever changing. The windward slopes are gentle and are furrowed by the wind, as it sweeps along; the lee slopes are much steeper. The only plant that flourishes everywhere on the complex is the succulent annual, *Corispermum hyssopifolium*, although *Populus monilifera* is frequent. The scanty flora is not due to the lack of water in the soil, but to the instability of the soil and to the xerophytic air.

The influence of an encroaching dune upon a preexisting flora varies with the rate of advance, the height of the dune above the country on which it encroaches, and the nature of the vegetation. The burial of forests is a common phenomenon. The dominant forest trees in the path of advancing dunes are *Pinus Banksiana*, *Quercus coccinea tinctoria*, and *Acer saccharinum*. All of these trees are destroyed long before they are completely buried. The dead trees may be uncovered later, as the dune passes on beyond.

In the Dune Park region there are a number of swamps upon

which dunes are advancing. While most of the vegetation is destroyed at once, *Salix glaucophylla*, *S. adenophylla*, and *Cornus stolonifera* are able to adapt themselves to the new conditions, by elongating their stems and sending out roots from the buried portions. Thus hydrophytic shrubs are better able to meet the dune's advance successfully than any other plants. The water relations of these plants, however, are not rapidly altered in the new conditions. It may be, too, that these shrubs have adapted themselves to an essentially xerophytic life through living in undrained swamps. Again it may be true that inhabitants of undrained swamps are better able to withstand a partial burial than are other plants.

Vegetation appears to be unable to capture a rapidly moving dune. While many plants can grow even on rapidly advancing slopes, they do not succeed in stopping the dune. The movement of a dune is checked chiefly by a decrease in the available wind energy, due to increasing distance from the lake or to barriers. A slowly advancing slope is soon captured by plants, because they have a power of vertical growth greater than the vertical component of advance. Vegetation commonly gets its first foothold at the base of lee slopes about the outer margin of the complex, because of soil moisture and protection from the wind. The plants tend to creep up the slopes by vegetative propagation. Antecedent and subsequent vegetation work together toward the common end. Where there is no antecedent vegetation, Ammophila and other herbs first appear, and then a dense shrub growth of Cornus, Salix, *Vitis cordifolia*, and *Prunus Virginiana*. Capture may also begin within the complex, especially in protected depressions, where *Salix longifolia* is often abundant.

Tilia Americana develops rapidly on the captured lee slopes, and the thicket is transformed into a forest. The trees grow densely, and there is little or no vegetation carpet. Associated with Tilia is a remarkable collection of river bottom plants, so that the flora as a whole has a decided mesophytic cast. These plants have developed xerophytic structures that are not present in the river bottoms. Acer and Fagus succeed Tilia and repre-

sent the normal climax type of the lake region, the deciduous forest.

On the established windward slopes the development is quite different from that described above. There is a dominance of evergreens instead of deciduous vegetation. The soil conditions are nearly alike on the two slopes, but the air is more xerophytic on the windward slopes. The evergreen flora starts as a heath formed of Arctostaphylos, *Juniperus communis*, and *J. Sabina procumbens*. The heath arises on fossil beaches, secondary embryonic dunes, or wherever the wind is relatively inactive and where the conditions are too xerophytic for the development of a deciduous flora. Before long the heath passes into a coniferous forest, in which *Pinus Banksiana*, *P. Strobus*, or *P. resinosa* dominate. Coniferous forests also occur on sterile barrens and in bottoms, where the conditions are also unfavorable for deciduous forests. A slight change in the physical conditions may bring about the rejuvenation of the coniferous dunes, because of their exposed situation. Rejuvenation commonly begins by the formation of a wind-sweep; the vegetation on either hand is forced to succumb to sand-blast action and gravity.

The evergreen floras are more and more common northward, while to the south there are developed forests in which *Quercus coccinea tinctoria* prevails. The oak forests are more common on inland dunes and on southern slopes. The oaks may follow the pines, when the areas occupied by pines become sufficiently protected from cold winds. The pines have a much wider range of life conditions than the oaks, since they appear at lower levels, higher levels, and on northern or windward slopes. The oaks flourish best on southern slopes. The flora of the oak dunes is xerophytic, but of the desert type, while that of the pine dunes is of the arctic xerophytic type. The pine dunes have a northern flora, the oak dunes a southern flora.

VI. Previous studies of sand dune floras.

A great deal of physiographic work has been done in sand dune areas in total disregard of the plant life, although the

results obtained from this study show that the vegetation profoundly modifies the topography. In like manner the flora has often been studied from a purely taxonomic standpoint, little attention being paid to the striking effects of the environment upon plant structures. More recently the ecological standpoint has been taken by a number of investigators, particularly to show the influence of the extreme environment upon plant organs and tissues. The second part of this paper will treat this phase of the subject in some detail. Very little previous work has been done on the geographic phase of the subject from the standpoint of historical development and the order of genetic succession of the various dune types. Still less has there been any adequate study of the modifying influence of vegetation upon topography. These latter phases of the subject have given color to the work which has resulted in this paper.

Warming's work on the sand dune vegetation of Denmark stands in the front rank. In his separate publications and in his text-book of ecology, the conditions on the Danish dunes are quite fully stated. The order of succession, speaking broadly, seems to be quite similar to that along Lake Michigan, but there appears to be less diversity of conditions, and the features appear to be developed on a smaller scale. The strand is succeeded by the wandering or white dunes, and these by the established or gray dunes. Beyond these are sandy fields. Just as along Lake Michigan, the dune floras may pass into the heath and these latter into coniferous forests.

There is a remarkable similarity in the flora of the Danish and Lake Michigan dunes. The same genera and often the same species occur in the two regions. *Cakile maritima* and *Lathyrus maritimus* grow on the strand. *Ammophila arundinacea* (=*Psamma arenaria*), *Elymus arenarius*, and *Agropyrum junceum* grow on the wandering dunes. Where the genera are not common or even nearly related, there are to be found in the two regions plants that have the same life habits. There is thus a striking similarity in the two regions in almost every respect, and that too in spite of the marine conditions in Denmark, as contrasted with

the inland fresh-water area in the United States. The life conditions appear to be essentially alike on all dunes, whether marine or not, and there are found not only identical life habits, but even identical plant species.

Warming reports Chlamydomonas on the strand in the same relations as along Lake Michigan. Among the sand-binding plants, Warming and Graebner give an important place to mosses. Along the Lake Michigan dunes, mosses do not appear to any great extent until establishment is nearly complete. On the Denmark coast, the Agropyrum dunes are lower than those formed by Ammophila, just as along Lake Michigan. The Danish dunes have also been studied by Raunkiaer, Paulsen, and Feilberg. Erikson has studied the similar dunes of southern Sweden, Giltay and Massart those of Holland and Belgium.

The dunes on the islands along the German coast have been carefully studied by Buchenau and to some extent by Knuth. Graebner, in his exhaustive work on the North German heath, discusses the origin of the heath on naked dune sand. He gives an important place to algæ and moss protonema, since they precede other vegetation, forming the first humus and causing the sand grains to cohere. It is doubtful if these lower plants are so important as sand-binders along Lake Michigan. Rothert and Klinge have studied the coast vegetation of Russia.

The French dunes have been very carefully studied by Flahault alone and also in association with Combres. Some work has also been done in France by Constantin and Masclef. Willkomm's work in Spain and Portugal, covering a period of nearly fifty years, is very complete and satisfactory. Daveau has worked out the conditions along the coast of Portugal. On these more southern dunes, the plant species resemble those along Lake Michigan less than do those in northern Europe, but the life habits are the same.

The dune flora of South Africa has been touched upon by Thode, that of Chile by Kurtz and Reiche, that of northern Siberia by Kjellman, that of New Zealand by Diels. The tropical dunes of Indo-Malaysia have been studied in detail by Schimper,

and are fully discussed in his work on the Indo-Malay strand flora and also in his recent Plant Geography. In the latter work there are several excellent discussions of sand dune vegetation, accompanied by photographs from a number of regions. The tropical dunes have totally different species, but even there the dominant dune-formers are grasses with the same life habits as Ammophila.

Dunes may be formed in deserts and inland regions apart from large bodies of water. Those in the Sahara and in the deserts to the northeastward have been more or less studied. Brackebusch has described dunes in Argentina.

In the United States dunes are common along the Atlantic coast, especially in Massachusetts, New Jersey, North Carolina, and Florida. On the Pacific coast they also occur extensively. None of these marine dunes have been exhaustively studied from the ecological standpoint. One of the best works that has ever appeared on strand floras is that by MacMillan on the shores at the Lake of the Woods. The dune formation is not extensive there, but is most admirably treated. As would be expected, there are many species common to Lake Michigan and the Lake of the Woods. The sand hills in the interior have been studied by Rydberg, Hitchcock, and Pound and Clements. Hill has studied the dune floras about Lake Michigan for many years, and although he has not written a great deal along ecological lines, he has had the ecological standpoint thoroughly in mind and the author has received from him a number of valuable suggestions.

THE UNIVERSITY OF CHICAGO.

BIBLIOGRAPHY.

BOERGESEN, F.: Beretning om et Par Exkursioner i Sydspanien. Bot. Tid. 21 : 139. 1897.

BOERGESEN, F., and PAULSEN, O.: Om Vegetationen paa de dansk vestindiske Öer. Copenhagen. 1898.

BORBÁS, V.: Die Vegetation der ungarischen Sandpuszten mit Rücksicht auf die Bindung des Sandes. Abstract in Bot. Cent. 19 : 92. 1884.

BRACKEBUSCH, L.: Ueber die Bodenverhältnisse des nordwestlichen Theiles der Argentinischen Republik mit Bezugnahme auf die Vegetation. Petermann's Mittheilungen **39** : 153. 1893.

BUCHENAU, F.: Vergleichung der nordfriesischen Inseln mit den ostfriesischen in floristischer Beziehung. Abhandl. Naturw. Ver. Bremen **9**. 1887.

——— Ueber die Vegetations-verhältnisse des "Helms" (Psamma arenaria Röm. et Schultes) und der verwandten Dünengräser. Abhandl. Naturw. Ver. Bremen **10** : 397. 1889.

——— Die Pflanzenwelt der ostfriesischen Inseln. Abhandl. Naturw. Ver. Bremen **11**. 1890.

——— Flora der ostfriesischen Inseln. Norden und Norderney. 1881, 1891. Also various articles on the floras of these islands.

——— Ueber die ostfriesischen Inseln und ihre Flora. Verhandl. des XI. deutschen Geographentages in Bremen. **1895–6** : 129. (Bot. Cent. **66** : 318.)

CLEGHORN, H.: On the sand-binding plants of the Madras beach. Jour. of Bot. **8** : 1858.

CONSTANTIN, J.: Observations sur la flore du Littoral. Jour. de Bot. **1** : 5. 1887.

DAVEAU, J.: La flore littorale du Portugal. Bull. Herb. Boiss. **4** : 209. 1896.

DIELS, L.: Vegetations-Biologie von Neuseeland. Eng. Bot. Jahrb. **22** : 202. 1897.

DRUDE, O.: Handbuch der Pflanzengeographie. Stuttgart. 1890.

——— Ueber die Principien in der Unterscheidung von Vegetationsformationen, erläutert an der centraleuropäischen Flora. Eng. Bot. Jahrb. **11** : 21. 1890.

——— Deutschlands Pflanzengeographie, I Teil. Stuttgart. 1896.

ERIKSON, JOHAN: Studier öfver sandfloran i östra Skåne. Bihang till Kongl. Svenska Vetenskaps-Akademiens Handlingar. **22**. 1896.

FEILBERG, P.: Om Gräskultur paa Klitsletterne ved Gammel Skagen. Söborg. 1890.

FLAHAULT, C. La distribution géographique des végétaux dans un coin du Languedoc. Montpellier. 1893.

FLAHAULT, C., et COMBRES, P.: Sur la flore de la Camargue et des alluvions du Rhône. Bull. Soc. Bot. France **41** : 37. 1894.

GIFFORD, J.: The control and fixation of shifting sands. The Engineering Magazine, January 1898. Also various articles in the Forester.

GILTAY, E.: Anatomische Eigenthümlichkeiten in Beziehung auf klimatische Umstände. Nederlandsch Kruidkundig Archief. II. 4 : 413. 1886. (Bot. Cent. 36 : 42.)

GRAEBNER, P.: Studien über die norddeutsche Heide. Eng. Bot. Jahrb. 20 : 500. 1895.

HILL, E. J.: The sand dunes of northern Indiana and their flora. Garden and Forest 9 : 353. September 1896.

HITCHCOCK, A. S.: Ecological Plant Geography of Kansas. Trans. Acad. Sci. St. Louis 8 : 55. 1898.

KJELLMAN, F. R.: Om växtligheten på Sibiriens nordkust. Ur Vega-Expeditionens vetensk. iakttagelser 1 : 233. 1882. (Bot. Cent. 13 : 305.)

KLINGE, J.: Die vegetativen und topographischen Verhältnisse der Nordküste der Kurischen Halbinsel. Sitzber. der Dorpater Naturforscher-Gesellschaft 1884 : 76. (Bot. Cent. 21 : 77.)

——— Die topographischen Verhältnisse der Westküste Kurlands. Sitzber. der Dorpater Naturforscher-Gesellschaft 1884 : 603. (Bot. Cent. 21 : 203.)

KNUTH, P.: Botanische Beobachtungen auf der Insel Sylt. Humboldt 1888 : 104.

——— Flora der Insel Helgoland. Kiel. 1896.

KRASSNOFF, A.: Geobotanical studies in the Kalmuck steppes. Trans. Imp. Russ. Geograph. Soc. 22 : 1. 1888. (Russian.) (Eng. Bot. Jahrb. 10 : Litteraturbericht 53.)

KURTZ, F.: Bericht über zwei Reisen zum Gebiet des oberen Rio Salado (Cordillera de Mendoza), ausgeführt in den Jahren 1891–1893. Verhandl. Bot. Ver. Prov. Brandenburg 35 : 95. 1893.

LAMB, F. H.: The sand dunes of the Pacific coast. The Forester 3 : 94. 1897.

LITWINOW, D. J.: Ob okskoi florje w Moskowskoi gubernii. Materialy k posnaniju fauny i flory Rossijskoi Imperii. Moscow. 1895. (Bot. Cent. 66 : 248.)

MACMILLAN, C.: Observations on the distribution of plants along shore at Lake of the Woods. Minnesota Botanical Studies 1 : 949. 1897.

MASCLEF, A.: Études sur la géographie botanique du Nord de la France. Jour. de Bot. 2 : 177. 1888.

MASSART, J.: La biologie de la végétation sur le littoral Belge. Mém. Soc. Roy. Bot. Belgique 32 : 1. 1893.

PAULSEN, O.: Om Vegetationen paa Anholt. Bot. Tid. 21 : 264. 1898.

POUND, R. and CLEMENTS, F. E.: The Phytogeography of Nebraska. I. General Survey. Lincoln. 1898.

RAUNKIAER, C.: Vesterhavets Öst- og Sydkysts Vegetation. Copenhagen. 1889.

REICHE, K.: Die Vegetations-Verhältnisse am Unterlaufe des Rio Maule (Chile). Eng. Bot. Jahrb. **21** : 1. 1896.

ROTHERT, W.: Ueber die Vegetation des Seestrandes im Sommer 1889. Korrespondenzblatt des Naturf.-Ver. zu Riga **32**. (Bot. Cent. **46** : 52.)

RYDBERG, P. A.: Flora of the Sand Hills of Nebraska. Contrib. U. S. Nat. Herb. **3** : 133. 1895.

SCHIMPER, A. F. W.: Die indo-malayische Strandflora. Jena. 1891.

——— Pflanzen-geographie auf physiologischer Grundlage. Jena. 1898.

THODE, J.: Die Küstenvegetation von Britisch-Kaffrarien und ihr Verhältniss zu den Nachbarfloren. Eng. Bot. Jahrb. **12** : 589. 1890.

WARMING, E.: De psammophile Formationer i Danmark. Vidensk. Meddel. fra den naturhist. Foren. **1891** : 153.

——— Exkursionen til Fano og Blaavand i Juli 1893. Bot. Tid. **19** : 52. 1894.

——— Plantesamfund. Copenhagen. 1895. German edition, translated by Knoblauch. 1896.

——— Exkursionen til Skagen i Juli 1896. Bot. Tid. **21** : 59. 1897.

WEBBER, H. J.: Notes on the strand flora of Florida. Abstract in Science, **8** : 658. 1898.

WILLKOMM, M.: Die Strand- und Steppengebiete der iberischen Halbinsel und deren Vegetation. Leipzig. 1852.

——— Statistik der Strand- und Steppenvegetation der iberischen Halbinsel. Eng. Bot. Jahrb. **19** : 279. 1895.

——— Grundzüge der Pflanzenverbreitung auf der iberischen Halbinsel. Leipzig. 1896.