The Ecological Relations of the Vegetation on the Sand Dunes of Lake Michigan. Part I.-Geographical Relations of the Dune Floras.

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

PART I.—GEOGRAPHICAL RELATIONS OF THE DUNE FLORAS.

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY. XIII.

HENRY CHANDLER COWLES.

(WITH FIGURES 1–26)

I. Introduction.

THE province of ecology is to consider the mutual relations between plants and their environment. Such a study is to structural botany what dynamical geology is to structural geology. Just as modern geologists interpret the structure of the rocks by seeking to find how and under what conditions similar rocks are formed today, so ecologists seek to study those plant structures which are changing at the present time, and thus to throw light on the origin of plant structures themselves.

Again, ecology is comparable to physiography. The surface of the earth is composed of a myriad of topographic forms, not at all distinct, but passing into one another by a series of almost perfect gradations; the physiographer studies landscapes in their making, and writes on the origin and relationships of topographic forms. The ecologist employs the methods of physiography, regarding the flora of a pond or swamp or hillside not as a changeless landscape feature, but rather as a panorama, never twice alike. The ecologist, then, must study the order of succession of the plant societies in the development of a region, and he must endeavor to discover the laws which govern the panoramic changes. Ecology, therefore, is a study in dynamics. For its most ready application, plants should be found whose tissues and organs are actually changing at the present time in

response to varying conditions. Plant formations should be found which are rapidly passing into other types by reason of a changing environment.

These requirements are met *par excellence* in a region of sand dunes. Perhaps no topographic form is more unstable than a dune. Because of this instability plant societies, plant organs, and plant tissues are obliged to adapt themselves to a new mode of life within years rather than centuries, the penalty for lack of adaptation being certain death. The sand dunes furnish a favorable region for the pursuit of ecological investigations because of the comparative absence of the perplexing problems arising from previous vegetation. Any plant society is the joint product of present and past environmental conditions, and perhaps the latter are much more potent than most ecologists have thought. As will be shown in another place, even the sand dune floras are often highly modified by preexisting conditions, but on the whole the physical forces of the present shape the floras as we find them. The advancing dune buries the old plant societies of a region, and with their death there pass away the influences which contributed so largely to their making. In place of the rich soil which had been accumulating by centuries of plant and animal decay, and in place of the complex reciprocal relations between the plants, as worked out by a struggle of centuries, the advance of a dune makes all things new. By burying the past, the dune offers to plant life a world for conquest, subject almost entirely to existing physical conditions. The primary motive, then, which prompted this present study was the feeling that nowhere else could many of the living problems of ecology be solved more clearly; that nowhere else could ecological principles be subjected to a more rigid test.

This particular investigation was also prompted by the fact that the previous ecological studies of sand-dune floras have been carried on chiefly in European countries, and almost exclusively along marine coasts. There has been considerable difference of opinion as to the influence of salty soils and atmospheres upon the vegetation. It would seem that a comparison of dunes

along an inland fresh water lake with those along the sea should yield instructive results.

An ecological study of this character has a natural twofold division. In the first place the plant formations are to be investigated. The species characteristic of each formation must be discovered, together with the facts and laws of their distribution. The progressive changes that take place and the factors in the environment which cause these changes must be discussed. This phase of the subject is largely geographic, and will be the special feature of the present paper. In another paper it is the author's purpose to discuss the adaptations of the plants to their dune environment, paying especial attention to those species which show a large degree of plasticity, and which are found growing under widely divergent conditions. This second phase again has a natural twofold division, one part treating of gross adaptations such as are shown in plant organs and plant bodies, the other dealing with the anatomical structures of the plant tissues.

The material for the present paper has been gathered chiefly from the study of the dunes in northwestern Indiana in the vicinity of Chicago. These studies were carried on in the seasons of 1896, 1897, and 1898, frequent visits being made to various points at all seasons of the year. A portion of the summer seasons of 1897 and 1898 was spent in a more rapid reconnoissance along the entire eastern shore of Lake Michigan, including the group of islands toward the north end of the lake.

The work resulting in this paper has been carried on in connection with the Hull Botanical Laboratory of the University of Chicago, and the author gratefully acknowledges the kindly interest and cooperation shown by his associates among the faculty and students of the botanical department, especially Head Professor John M. Coulter, through whose influence the author was directed along lines of ecological research. The author further desires to express his great indebtedness to Dr. Eugen Warming, professor of botany at Copenhagen; his textbook on ecology and his treatises on the sand-dune floras of

Denmark have helped greatly to make clear the true content of ecology, and they have been a constant incentive to more careful and thorough work. Most of the photographs were taken especially for this paper by Mr. E. W. Martyn, a Chicago photographer. Some of the views were taken by Messrs. S. M. Coulter and H. F. Roberts, students in the Hull Botanical Laboratory. The map was prepared by Mr. S. M. Coulter.

II. General features of the coast of Lake Michigan.

Along the eastern shore of Lake Michigan there are hills of wind-blown sand almost continuously fringing the border of the lake. This line of sand hills also continues around the southern end of the lake and along the western shore as far as Chicago. These sand hills or sand dunes form striking topographic features in the landscape, and in this respect present a strong contrast to the level prairies or fields beyond.

Geologically speaking, the sand dunes belong to the most recent formations, as they are entirely post-glacial. In most cases the origin of the existing topographic forms is to be referred to the most recent phases of post-glacial history, and in many instances the topographic forms are either being made or unmade at the present time. As a rule the dunes are directly superposed upon the beach. On the northeastern shores of the lake, however, the dunes are commonly superposed upon bluffs of clay or gravel, sometimes 120 meters above the present beach.

In the lake region there is a decided prevalence of westerly winds, chiefly from the southwest or northwest. As a consequence, the dunes are found along the entire eastern and southern shores of the lake, whereas the dunes on the western shore, due to easterly winds are merely small hillocks of sand. Such small dunes have been seen at Waukegan, Ill., and on North Manitou and Beaver islands. The dunes toward the southern portion of the lake were created and fashioned, as a matter of necessity, almost entirely by the northwest winds. In order to secure any extensive formation of sand dunes, it is necessary for the wind to gather force by sweeping over the lake and to strike the coast

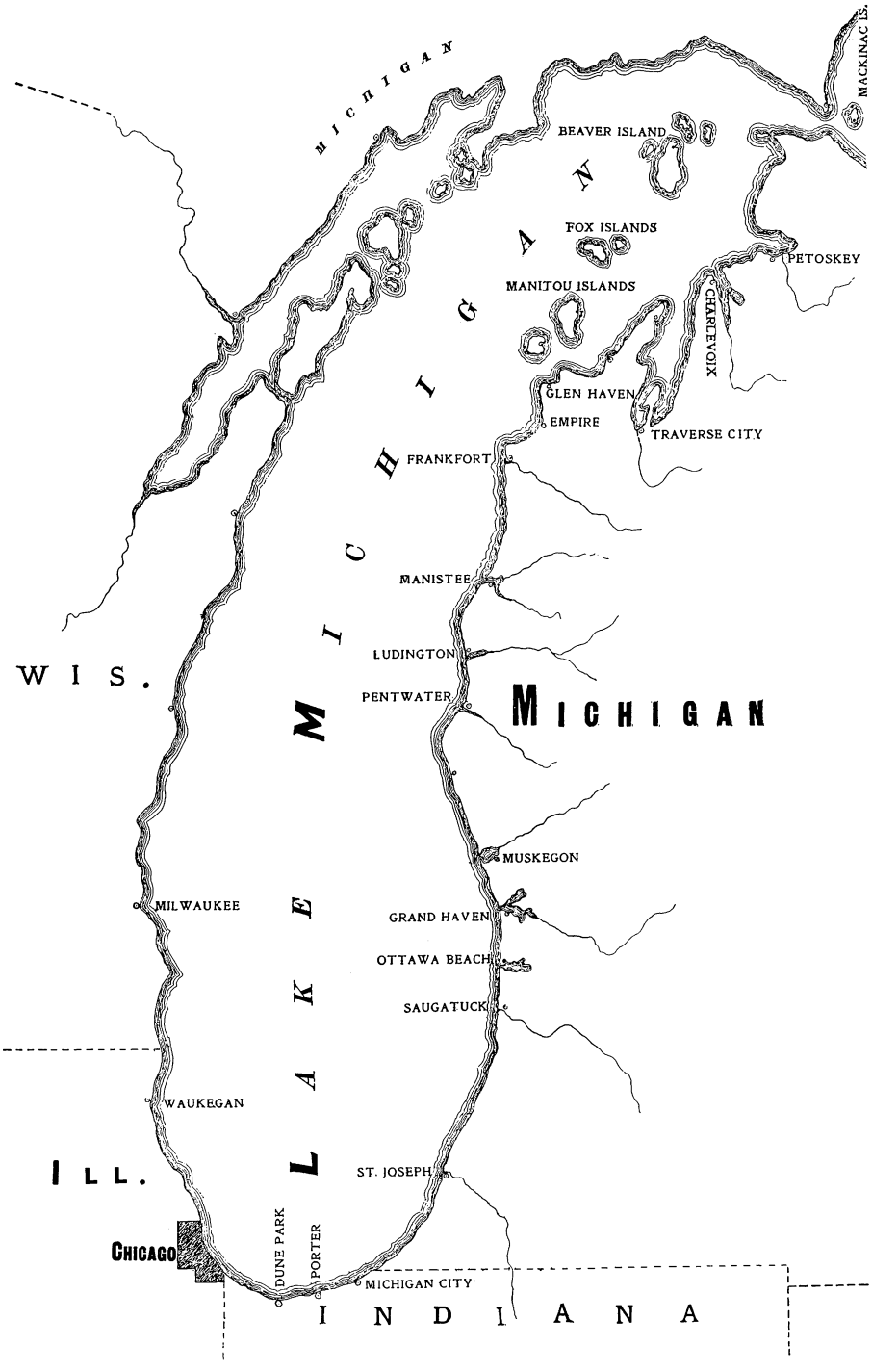

FIG. 1.—MAP OF THE SHORE OF LAKE MICHIGAN. SCALE, 1:2,850,000.

almost at right angles to the shore line. It will thus be seen that the most favorable theoretical locality for dunes in a region of northwest winds is on the southeast shore of a body of water in that region. As a matter of fact, the dune region increases in area and the dunes themselves increase in height and complexity as one passes from Chicago around the south end of Lake Michigan. The culmination of the dune formations actually occurs between Dune Park and Michigan City, and an examination of the accompanying map (*fig. 1*) will show that these localities have a shore line running nearly southwest to northeast. The contour of the dunes themselves also shows that they were shaped by northwest winds, as does the path formed by the sweeping of the wind.

The Dune Park region furnishes the most extensive area of present dune activity to be found along the southern coast of Lake Michigan, although the altitudes of individual dunes are much greater at many points in Michigan. Elsewhere the active dunes are usually confined to a very narrow belt fringing the shore, but at Dune Park the dunes are active from one to two kilometers inland, the front of the advancing dunes varying from 6 to 30 meters in height. The dune complex or area of dune activity at Dune Park covers perhaps 1000 hectares. The established dunes here as elsewhere cover a far greater area than do the active dunes, reaching inland three to eight kilometers. Between Chicago and Dune Park there is a most interesting series of parallel ridges, alternating with depressions, which often reach below the water level throughout the entire year. The origin of these ridges is scarcely within the province of this paper; their extreme regularity of contour, in addition to their persistent parallelism, seems hardly consonant with a dune origin. Because of the low altitude of these ridges and their protection from shore conditions, their flora is not typically xerophytic. Whatever the origin of these ridges, they represent a phase in the lake's history when its waters were much farther inland than at present. The active dunes at Dune Park are scarcely ever more than 30 meters in altitude, but there are

several established dunes which are more than 36 meters above the lake. The coast charts issued by the Corps of Engineers of the United States War Department figure a dune near Pòrter, Ind., which reaches an altitude of 57 meters above the lake. Of course, altitudes of individual dunes are subject to much change, although in the case of established dunes the figures need but slight revision. The highest series of dunes is along the Michigan shore between Michigan City and St. Joseph. A large number of dunes reach an altitude of more than 60 meters; several are over 90 meters high; and one is figured on the coast chart which has an altitude of 117 meters above the level of the lake. An inspection of the map will show that these dunes must have been shaped primarily by northwest winds.

The Michigan shore between St. Joseph and Frankfort, a distance of more than 250 kilometers, is fringed almost continuously with a narrow belt of dunes. Perhaps at no place within this region are there such extensive dunes in activity at the present time as at Dune Park, nor do the established dunes reach inland as a rule for more than a kilometer. At Dune Park there is a gradation in the altitude of the dunes as one goes inland, until the low sand ridges pass all but insensibly into the prairies beyond. Along the Michigan shore, however, there is a narrow fringe of dunes close to the lake, commonly much higher than at Dune Park, and the transition between these dunes and the normal inland country is rapidly passed and plainly marked.

A very striking feature along the Michigan shore is the tendency of rivers to form small lakes near their mouths. These lakes determine the presence of cities, since they furnish the best of harbors. An inspection of the map (*fig. 1*) shows the presence of such natural harbors at the mouths of rivers at Holland (Ottawa Beach), Grand Haven, Muskegon, Whitehall, Pentwater, Ludington, and Manistee. A large amount of the silt brought down by the rivers is deposited at the mouth, where the river currents are slackened by their opening out into the lake and by wave action. The waves pile up this sand along the beach and the winds pick it up and form extensive dunes at the

river's mouth. All along the Michigan coast the most extensive areas of active dunes are likely to be at the mouths of the rivers, so that dune formation is thus seen to be regulated by the supply of sand as well as by the relation of the coast line to the direction of the prevailing winds. Since the general direction of the Michigan coast line is north and south, and the prevailing winds southwest and northwest, dune formation tends to close up the mouths of the rivers on both sides. The result of this conflict between the river and air currents is seen in the formation of lakes whose entrance into Lake Michigan is constricted into a narrow passageway. The tendency of the wind to close these passageways is so great that navigation is often difficult, and the necessity for constant dredging and erection of windbreaks is obvious.

The dunes at the mouths of rivers furnish a rough measure for determining the relative influence of northwest and southwest winds in dune formation, since those on the south side are largely shaped by southwest winds and those on the north side by northwest winds, although each wind modifies the action of the other. At Saugatuck the southwest winds appear to dominate, since the dune south of the river is 78 meters high, while to the north the heights are inconspicuous. The course of the Kalamazoo river has been deflected to the northward at this point, although it is interesting to observe that the mouth is now being deflected to the southward, the river filling in on the northwest bank and eroding on the southeast. At Ottawa Beach the dunes are about equal on both sides, and less than 60 meters in height. At Grand Haven there is an immense active dune on the north side of the river, 66 meters high, and with an advancing lee slope 45 meters in height. This dune is deflecting the river to the southward, and attempts to stop its progress are not particularly successful. The dunes at Muskegon are largest on the south side of the river. At Pentwater, Ludington, and Manistee the dunes average about 45 meters in height. The fringe of dunes is interrupted at several points by clay bluffs, but this latter formation is far more extensive farther northward.

Active dune formation is conspicuous on projecting points of land as well as at the mouths of rivers; for example, active dunes are to be found on Little Point Sable, south of Pentwater, and Big Point Sable, north of Ludington. At many points along the coast the winds are breaking through the fringe of established dunes, so that the older dunes may be said to have started into activity again or to have become rejuvenated. In summation concerning the area between St. Joseph and Frankfort, it may be said that the influence of northwest and southwest winds in dune formation is nearly equal. Indeed, the two winds commonly work together to produce a composite result, so that the winds sweep and the dunes advance, as a rule, from west to east.

In northern Michigan, between Frankfort and Glen Haven, and also on North Manitou island, most of the dunes are perched high up on bluffs of clay or gravel. The bluffs are steep and approach the water's edge, varying in height from nothing up to more than 120 meters. Dunes are to be found upon the tops of the very highest of these bluffs in the district south of Glen Haven. These perched dunes are almost wholly established, and it seems as if their formation took place years ago when the lake was perhaps at a higher level. The most remarkable dune formation along the entire coast of Lake Michigan is to be found on Sleeping Bear point, just south of Glen Haven. The point stretches out into the lake, and is constantly growing to the northward and eastward by reason of the joint action of waves and winds. The point proper is geologically quite young, and, apart from the present beach and stationary beach dunes, is covered by an immense and active dune complex. At many points the wind has scooped out great hollows in the complex, exposing the gravel of a former beach. The advance of the dunes in this area is chiefly eastward, the exposed fossil beaches being chiefly toward the west. Two or three kilometers southward from the point, the region of low active dunes passes somewhat suddenly into an immense flat-topped hill, rising abruptly from the lake like a mesa or terrace. The height of the dunes on the point is seldom greater than 30 to 45 meters, while this peculiar

gravel terrace, or mesa, has an average height of 120 meters above the lake level, and an area of more than 2000 hectares, since it extends inland for about two kilometers, and along the coast for, perhaps, 15 kilometers. The Sleeping Bear itself, which gives its name to the point, and also to the bay, is a long established dune, with an altitude of 30 meters above the terrace on which it stands, or 150 meters above the lake. This dune stands alone, and is a landmark for miles in all directions. Farther to the south, dunes are perched upon these bluffs almost continuously, and there are reasons for supposing that the Sleeping Bear is but the last remnant of such a chain of dunes formerly superposed on the bluffs near Glen Haven. Toward the east and north, as well as toward the lake, the slopes of the mesa-like formation are quite abrupt, and beyond these slopes there is to be found an extensive dune complex, the grandest in variety and beauty to be found along Lake Michigan. It seems almost certain that the source of the sand for this dune complex was an ancient row of dunes at the top of the mesa toward the west This is made more probable by the fact that the Sleeping Bear, once firmly established, is now being torn up by the winds and carried northeastward. The dune complex is moving toward the east, the line of advance being parallel to the lake shore, as usual. This advancing dune is far and away the grandest along Lake Michigan, presenting an almost continuous front, measuring four kilometers from north to south, all in active progression. The average height above the country on which it is encroaching is about 60 meters, so that it presents a most imposing sight when viewed from the fields in front of its line of advance. The dune complex at Glen Haven is like that at Dune Park, but on a far grander scale; sometimes there are hollows within it more than 30 meters in depth scooped out by the wind, and reaching down to an ancient beach. Within the dune complex there are extensive old soil lines and many scarred trunks of trees, long buried by the dunes and now resurrected, though not to life.

At many other places along the northern shore of the lake there are high bluffs of clay, or gravel, whose summits are

crowned by established dunes. Only rarely are these dunes in action at the present time, and, where such action is observed, it is clearly due to the rejuvenation of dunes that had become established. The origin of these perched dunes is obscure and hardly within the province of this paper. The formation of dunes at the summit of a bluff is not unknown. A wind laden with sand may sweep up the slopes of a hill. As it reaches the summit its path is no longer narrowly restricted, and as it spreads out, its energy is dissipated and its load deposited. However, no such action was anywhere observed; on the contrary, at many points the wind is removing the dunes from just such locations. Consequently the author rather inclines to the belief that these perched dunes represent an earlier phase of dune formation, when lake or wind conditions were different from the present. Another possible mode of origin will be discussed in connection with the rejuvenated dunes.

The greatest altitude reached by the clay and gravel bluffs is at Empire, a few miles south of Glen Haven; at this point a height of 128 meters is attained. There is a high degree of oscillation in the altitudes even within a few meters. Where the clay bluffs are highest, the perched dunes are seldom as high as where the bluffs are lower. The greatest observed height of the perched dunes above the top of the clay was 60 meters. The greatest total observed height above the lake at Empire was 162 meters; at Frankfort 153 meters. South of Frankfort and north of Glen Haven the altitudes are much less. At Charlevoix and Petoskey there are no cliffs; the dunes are low and superposed directly upon the beach.

The islands in the north end of the lake are of great interest to the student of dunes, since they are exposed to winds from all directions; the position of the dunes thus indicates the direction of the dune-forming winds. In all cases the chief dune formation is on the west coast, and the most conspicuous active dunes are usually restricted to a narrow area at or near the southwest point of each island. Observation from the steamboat revealed the presence of such dunes on South Manitou, South

Fox, and High islands. The dunes on North Manitou and Beaver islands were visited. On North Manitou there are prominent areas of dune activity along the southwest coast, the dunes being superposed on bluffs of clay or gravel. There is a flat-topped terrace here, like that at Glen Haven, but in miniature, the height being only 15 meters and the area scarcely half a hectare; the dune perched on this bluff has been rejuvenated and carried inland a few meters, the greatest altitude being 45 meters above the lake. There are also small wandering dunes superposed directly upon the beach. On the west coast the bluffs are steeper and much higher, at times perhaps 60 meters above the lake; the summits are occasionally crowned by established dunes. On Beaver island the southwest coast was not visited, but there are rejuvenated dunes at various points along the west coast, sometimes 45 meters in height; these dunes are superposed upon the beach. The beach dunes here are exceedingly varied and extensive. As previously stated, there are low beach dunes along the east coast of Beaver island. On Mackinac island there are steep clay bluffs, but no dunes. Thus, the islands plainly show that westerly winds, and especially winds from the southwest, are the chief dune formers.

Surveying the lake region as a whole, the dunes are created and shaped almost entirely by westerly winds. In the southern portions of the lake, the northwest winds have the greater sweep and are the chief dune-formers. Northward the southwest winds are the chief factors in determining the location of dunes. In intermediate localities all westerly winds contribute about equally to dune formation, and there is progressive movement of active dunes to the eastward

III. The ecological factors.

The distribution of the plants in the various dune associations is governed by physical and biotic agencies which will be considered somewhat in detail in another place. At this point it seems advisable to give a general survey of these factors, especially in so far as they affect the distribution of plant societies in the region as a whole.

LIGHT AND HEAT.

Nearly all of the dune societies are characterized by a high degree of exposure to *light*. Particularly is this true of the beach and the active dunes. The intensity of direct illumination is greatly increased by reflection; the glare of the white sand is almost intolerable on a bright summer day. The *temperature* relation is even more marked in its influence upon plant life. Because of the absence of vegetation and the general exposure of sand dunes the temperature is higher in summer and lower in winter than in most localities. This great divergence between the temperature extremes is still further increased by the low specific heat of sand. On sandy slopes protected from cold winds the vegetation renews its activity very early in the spring, because of the strong sunlight and the ease with which the surface layers of sand are heated. Willow shoots half-buried in the sand frequently develop fully a week in advance of similar shoots a few centimeters above the surface. Similarly in the autumn the activity of plant life ceases early largely because of the rapid cooling of the superficial layers of sand, as well as because of direct exposure to the cold.

WIND.

The wind is one of the most potent of all factors in determining the character of the dune vegetation. The winds constantly gather force as they sweep across the lake, and when they reach the shore quantities of sand are frequently picked up and carried on. The force with which this sand is hurled against all obstacles in its path may be realized if one stoops down and faces it. The carving of the dead and living trees which are exposed to these natural sand-blasts is another evidence of their power. Fleshy fungi have been found growing on the windward side of logs and stumps completely petrified, as it were, by sand-blast action; sand grains are imbedded in the soft plant body and as it grows the imbedding is continued, so that finally the structure appears like a mass of sand cemented firmly together by the fungus. The bark of the common osier dogwood is red on the

leeward side, but white to the windward because the colored outer layers of the bark have been wholly worn away. On the windward side of basswood limbs the softer portions are carved away while the tougher fibers remain as a reticulated network. On the leeward side of these same limbs, the outer bark is intact and even covered more or less with lichens.

The indirect action of the wind produces effects that are considerably more far-reaching than any other factor, for it is the wind which is primarily responsible for sand dunes and hence for their floras. But more directly than this, the wind plays a prominent part in modifying the plant societies of the dunes. The wind is the chief destroyer of plant societies. Its methods of destruction are twofold. Single trees or entire groups of plants frequently have the soil blown away from under them, leaving the roots exposed high above the surface; as will be shown later this process is sometimes continued until entire forests are undermined, the débris being strewn about in great abundance. Again, swamps, forests, and even low hills may be buried by the onward advance of a dune impelled by the winds; in place of a diversified landscape there results from this an all but barren waste of sand.

SOIL.

The soil of the dunes is chiefly quartz sand, since quartz is so resistent to the processes of disintegration. The quartz particles are commonly so light colored that the sand as a whole appears whitish; closer examination reveals many grains that are not white, especially those that are colored by iron oxide. With the quartz there are conspicuous grains of black sand, largely hornblende and magnetite. These black grains often accumulate in streaks, persistent for considerable depths and apparently sifted by the wind; large quartz grains are mingled with these grains of magnetite and hornblende so that it would seem as if grains of higher specific gravity are sifted out together with those of greater absolute weight. The sand of the dunes is remarkably uniform in the size of the particles as compared with beach sand; this feature is due to the selective action

of the wind, since the latter agent is unable to pick up and carry for any distance the gravel or large sand particles of the beach.

As is well known, soil made up chiefly of quartz sand has certain marked peculiarities which strongly influence the vegetation. The particles are relatively very large; hence the soil is extremely porous and almost devoid of cohesion between the grains. These features are of especial importance in their effect upon the water and heat relations as shown elsewhere. As a rule, sandy soils are poor in nutrient food materials, nor do they rapidly develop a rich humus soil because of the rapid oxidation of the organic matter.

WATER.

A factor of great importance, here as everywhere, is the water relation. Nothing need be said of atmospheric moisture, since that is sufficient to develop a rich vegetation if properly conserved, as is shown by the luxuriance of neighboring floras. Because of the peculiar physical properties of quartz sand, precipitated water quickly percolates to the water level and becomes unavailable to plants with short roots. The water capacity of sand is also slight, nor is there such pronounced capillarity as is characteristic of many other soils. Again, the evaporation from a sandy surface is commonly quite rapid. All of these features combine to furnish a scanty supply of water to the tenants of sandy soil. The rapid cooling of sand on summer nights may, however, result in a considerable condensation of dew, and thus, in a small way, compensate for the other disadvantages.

The ecological factors thus far mentioned act together harmoniously and produce a striking composite effect upon the vegetation. A flora which is subjected to periods of drought is called a xerophytic flora and its component species have commonly worked out various xerophytic structural adaptations of one sort or another. Again, a flora which is subjected to extreme cold, especially when accompanied by severe winds, takes on various structural adaptations similar to those that are characteristic of alpine and arctic floras. The dune flora is a composite flora, showing both xerophytic and arctic structures. In those

situations which are most exposed to cold winds, one finds the best illustrations of the arctic type, while the desert or xerophilous type is shown in its purest expression on protected inland sandy hills. The discussion of the various arctic and desert structures and their relations to each other will be deferred to the second part of this paper.

OTHER FACTORS.

Certain other factors are of minor importance in determining the character of the dune flora. *Forest fires* occur occasionally, and, as will be shown later, they may considerably shorten the lifetime of a coniferous plant society.

Near cities the vegetation is unfavorably influenced by *smoke* and other products issuing from chimneys. In the neighborhood of the oil refineries at Whiting, Ind., the pine trees especially have been injured or destroyed. A careful study would probably show many plant species that have suffered a similar fate.

The *topography* is often a factor of considerable importance. Dune areas are conspicuous for their diversified topography. This factor determines to a great extent the water relation which has been previously considered, the hills and slopes being of course much drier than the depressions. The topography indirectly affects the soil, since it is mainly in the depressions that humus can rapidly accumulate. The direction of slope is a matter of importance, as will be shown in discussing the oak dunes; the greater exposure of the southern slopes to the sun results in a drier soil and a more xerophytic flora on that side.

Animals do not appear to exert any dominating influences on the dune floras. The dispersal of pollen and fruits by their agency is common here as elsewhere; so, too, the changes that animal activities produce in the soil. Near the cities the influence of man is seen, although such influences are slight unless the sand is removed bodily for railroad grading and other purposes.

The influence of *plants*, which so often becomes the dominant factor, is relatively inconspicuous on the dunes. The most

important function which dune plants perform for other plants is in the contribution of organic food materials to the soil. The oxidation or removal of decaying vegetation is so complete on the newer dunes that the accumulation of humus is not important. On the more established dunes the mold becomes deeper and deeper, and, after the lapse of centuries, the sandy soil beneath may become buried so deeply that a mesophytic flora is able to establish itself where once there lived the tenants of an active dune. The advance of a wandering dune often results in the burial of a large amount of organic matter; when this matter becomes unburied years afterward it may again furnish a soil for plants. Many fossil soil lines have thus been uncovered on the Sleeping Bear dunes at Glen Haven, Mich.

IV. The plant societies.

A plant society is defined as a group of plants living together in a common habitat and subjected to similar life conditions. The term is taken to be the English equivalent of Warming's *Plantesamfund*, translated into the German as *Pflanzenverein*. The term formation, as used by Drude and others, is more comprehensive, in so far as it is not synonymous. It may be well to consider the individual habitat groups in a given locality as plant societies, while all of these groups taken together comprise a formation of that type, thus giving to the word formation a value similar to its familiar geological application. For example, one might refer to particular sedge swamp societies near Chicago, or, on the other hand, to the sedge swamp formation as a whole; by this application formation becomes a term of generic value, plant society of specific value.

Plant societies may be still further subdivided into patches or zones; the former more or less irregular, the latter more or less radially symmetrical. Patches are to be found in any plant society, where one or another constituent becomes locally dominant; zones are conspicuously developed on the beach and in sphagnous swamps. The term patch or zone has a value like that of variety in taxonomy. Authors disagree, here as every-

where, upon the content and values of the terms employed; this disagreement is but an expression of the fact that there are few if any sharp lines in nature. The above, or any other terminology, is largely arbitrary and adopted only as a matter of convenience.

In the following pages an attempt is made to arrange the plant societies in the order of development, the author's belief being that this order more faithfully expresses genetic relationships than any other. In the historical development of a region the primitive plant societies pass rapidly or slowly into others; at first the changes are likely to be rapid, but as the plant assemblage more and more approaches the climax type of the region, the changes become more slow. In the dune region of Lake Michigan the normal primitive formation is the beach; then, in order, the stationary beach dunes, the active or wandering dunes, the arrested or transitional dunes, and the passive or established dunes. The established dunes pass through several stages, finally culminating in a deciduous mesophytic forest, the normal climax type in the lake region. Speaking broadly, the conditions for plant life become less and less severe through all these stages, until there is reached the most genial of all conditions in our climate, that which results in the production of a diversified deciduous forest. On the beach there are to be found the most extreme of all xerophytic adaptations in this latitude, and, as one passes through the above dune series in the order of genetic succession, these xerophytic structures become less and less pronounced, finally culminating in the typical mesophytic structures of a deciduous forest.

A. THE BEACH.

As the author hopes to show in a subsequent paper, the beach formations of Lake Michigan are of two distinct types. One may be called the xerophytic beach, the other the hydrophytic beach. The conditions that determine these two types are not altogether clear, though their distribution suggests some factors which will contribute to the solution of the problem. Dunes are invariably absent from an area occupied by

hydrophytic beaches, partly perhaps because hydrophytic beaches are seldom sandy, and partly because they are commonly found in protected locations. The hydrophytic beaches are found where the gradient of the lake bottom is very slight; as a consequence there is a wide zone of very shallow water in which typical swamp and shallow water plants flourish in great abundance. The bottom is very thickly strewn with gravel and shingle, closely resembling a reef in structure. On the other hand, a xerophytic beach is often sandy, is commonly associated with steep clay bluffs or dunes, and the gradient is much steeper, so that there is a comparatively narrow zone of shallow water. As a consequence, wave action is much more pronounced on the beach proper, as is shown by the great amount of driftwood stranded there. The scanty flora is in striking contrast to the diversified flora of the hydrophytic beach. The greater luxuriance of the flora on the hydrophytic beach is due, in part at least, to the greater freedom from the destructive action of the waves on account of the low gradient. The water supply is also conspicuously greater on the hydrophytic beach, again chiefly because of the low gradient. Inasmuch as dunes are associated only with the xerophytic beach, no further reference will be made to the other beach type.

The xerophytic beach is essentially a product of wave action and comprises the zone which is or has been worked over by the waves. Hence the beach may be defined as the zone between the water level and the topographic form produced by other agents; in the region under study the upper limit of the beach is commonly a fringe of sand dunes or a bluff of clay or gravel. The xerophytic beach in its typical expression is very naturally subdivided into three zones, which may be called the lower beach, middle beach, and upper beach. The lower beach is that zone which is situated between the water level and the line reached by the waves of common summer storms. The middle beach is the second zone, extending up to the line reached by the highest winter storms. The upper beach is essentially a former middle beach which is now beyond the

reach of the waves, and yet is unoccupied by dunes or other topographic forms.

1. *The lower beach.*

The lower beach has been defined as the zone of land washed by the waves of summer storms. It might almost be defined as that portion of the beach which is devoid of vegetation. Perhaps there is no flora in the temperate zone quite so sparse as that of the lower beach, unless we except bare rocks and alkaline deserts. A survey of the life conditions in this zone reveals at once the reason for the scanty vegetation. Land life is excluded because of the frequency and violence of storms; the waves tear away the sand in one spot only to deposit it in another. Even though a seed had the temerity to germinate, the young plant would soon be destroyed by the breakers. Nor is there great likelihood that seeds will find a lodgment in this unstable location. As will be seen later the seeds ripened by tenants of the middle beach are almost entirely scattered away from the lake instead of toward it. The action of both wind and wave tends to carry seeds away from the lower beach. Again, few seeds could endure the alternate extremes of cold and heat, wetting and drying so characteristic of this zone.

Water life is excluded because of the extreme xerophytic conditions which commonly prevail on the lower beach. While algæ may propagate themselves in the shallow pools or even in the wet sand during a prolonged season of wet weather, a cessation of activity if not death itself soon follows the advent of dry weather. During a period of rainy weather in the autumn of 1897 green patches were observed in wet sand a few meters from the mouth of a creek near Porter, Ind. Microscopic observation showed that the green coloration was due to the presence of millions of motile Chlamydomonas forms. These unicellular biciliate algæ were in process of active locomotion in the water held by capillarity between the grains of sand. In all probability these forms migrated to the beach from the waters of the creek during a period of wet weather. It is possible that they might pass into resting stages and live through a season of drought,

were it not for the wind which gathers much of its dune material from the lower beach.

Thus the lower beach is a barren zone between two zones of life. Below it there exist algæ and other hydrophytic forms which flourish in the fury of the breakers; above it there exists the flora of the middle beach, a flora adapted to the most intense xerophytic conditions. At no particular time, perhaps, are the conditions too severe for some type of life; vegetation is excluded because of the alternation of opposite extremes.

2. *The middle beach.*

The middle beach is situated between the upper limits of the summer and winter waves, comparatively dry in summer but washed by the high storms of winter. It may also be defined as the zone of succulent annuals. The upper limit of this beach is commonly marked by a line of driftwood and débris. The instability of the beach conditions is often shown by the presence of a number of such lines, marking wave limits for different seasons. A very heavy storm will carry the débris line far up on the upper beach, to all intents and purposes carrying the middle beach just so much farther inland, as the flora of the next season testifies. Another season may be without the visitation of heavy storms and the middle beach will encroach upon the territory of the lower beach. The limits of the middle beach are altered more permanently by changes in the lower beach. In many places the lower beach is growing outwards, reclaiming land from the lake, while at other points the lake encroaches upon the land. Speaking broadly, the middle beach advances or recedes *pari passu* with the advance or recession of the lower beach. To some extent the débris lines register these changes, as their notable departure from persistent parallelism may indicate; however, there is a considerable lack of parallelism in the débris lines of a single season, owing to variations in the direction of the wind and other factors.

The life conditions in this zone are exceedingly severe, and result in a flora of the most pronounced xerophytic characters. The fury of the winter storms as they wash over the middle

beach, tearing up here and depositing there, excludes almost entirely the possibility of survival through that period. In other words, biennials and perennials are practically excluded from maturing flowers and fruits, although their vegetative structures may flourish for a single season. In the summer the xerophilous conditions are extreme. Nowhere in the dune region are the winds more severe than here; the middle beach is close enough to the lake to feel all the force of its winds and yet far enough away for the wind to pick up sand from the lower beach and bring to bear upon the flora the intense severity of the sand-blast. No flora is more exposed to the extreme desiccating influences of the summer sun than that which grows upon the bare and open beach. Even though the roots can readily penetrate to the water level, the great exposure of the aerial organs to wind and sun results in the working out of that most perfect of all xerophytic organs, the succulent leaf. Just as succulent plants inhabit deserts where no other high grade plants can grow, so, too, they are able to withstand the severe conditions of the beach.

Along the entire eastern shore of the lake, the dominant plant of the middle beach is *Cakile Americana*. At many points this succulent crucifer is almost the only plant species found in this zone, and it is always the chief character species. Two other fleshy annuals are very common tenants of the middle beach: *Corispermum hyssopifolium* and one of the spurges, *Euphorbia polygonifolia*. It is a matter of interest to observe that two of these three character plants of the middle beach, Cakile and Euphorbia, are also characteristic inhabitants of the beach on the Atlantic coast. The significance of the presence of these and other marine forms along the shore of Lake Michigan will be discussed in another place. The above plants are rarely distributed uniformly over the middle beach. The favorite place for growth is along the lines of débris previously referred to; along these lines a greater number of seeds find lodgment than elsewhere, because the waves wash them up from lower levels and the protection of the driftwood prevents the winds from

carrying them on farther. Then, too, the driftwood may furnish some protection to the growing plants, especially protection from winds which might otherwise uproot them. Cakile and Euphorbia reach their culmination on the beach, and when found farther inland it is chiefly on the upper beach or on windward slopes of active dunes. Corispermum, on the other hand, appears to be rather more characteristic of the active dunes than of the beach. Cakile is much the hardiest of the three species, venturing farther out toward the lower beach than either of the other two Of the three, Cakile is the most succulent and perhaps thus best adapted to the extreme xerophilous conditions to which beach plants are subjected. Euphorbia, however, has a copious supply of latex and its prostrate habit would seem to offer some advantages for existence on the beach. Cakile and Corispermum are readily dispersed by the wind, the latter by means of its winged seeds, while the former is a sort of tumbleweed; broken Cakile plants are common sights all over the dunes in the autumn and winter. Corispermum and Euphorbia become less and less common toward the north; at Charlevoix and Petoskey, Cakile is almost the only plant growing on the middle beach, and even this latter species is less common than farther to the south. Thus it seems as though the life conditions on the middle beach are more severe northward than southward, as indeed might be expected.

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[*To be continued.*]