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THE UNIVERSITY OF CHICAGO

AN ECOLOGICAL SURVEY OF THE PORCUPINE MOUNTAINS

A DISSERTATION

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-T A B L E O F C O N T E N T S-

	Page
INTRODUCTION - - - - -	1
EARLIER INVESTIGATIONS IN THE PORCUPINE MOUNTAINS - - - -	3
LOCATION AND PHYSIOGRAPHY - - - - -	5
CLIMATE OF THE REGION - - - - -	7
THE CLIMAX FORMATIONS - - - - -	11
I. THE HEMLOCK CLIMAX - - - - -	12
A. Aspect of the forest - - - - -	12
B. Composition and dynamics of the forest - - -	16
1. Consideration of individual species - -	17
2. Quadrat studies - - - - -	22
3. Initial physical factors and competition - - - - -	25
4. Equilibrium at any point - - - - -	28
C. Successions leading to the hemlock climax - -	29
1. Primary successions - - - - -	29
a. Physiographic influences - - - - -	29
b. The shore successions - - - - -	31
Types of shore - - - - -	34
2. Secondary successions in the hemlock climax - - - - -	36

8 mar 68

	Page
II. THE MAPLE CLIMAX - - - - -	38
A. General physiographic features - - - - -	39
B. Successional relations - - - - -	41
I. Xerarch successions on the first range -	41
(1) Summit of the range - - - - -	42
(a) Ecological factors - - - - -	42
(b) The plant associations - - -	45
(c) Quadrat studies - - - - -	47
(2) The escarpment and its asso- ciations - - - - -	50
(3) The talus slope - - - - -	53
(4) Forest below the talus - - - - -	58
II. Hydrarch successions in the valley of Carp River - - - - -	61
a. Carp River - - - - -	64
b. Carp Lake - - - - -	66
c. Flood plain - - - - -	69
SUMMARY - - - - -	71
REFERENCES - - - - -	77, 78, 79, 80

Map showing general position of the Porcupine Mountains in Ontonagon County, Michigan.

INTRODUCTION.

In his classic article on the climax forest of Isle Royale, Lake Superior, Cooper (5) refers to the transitional zone between the two great phytogeographic regions - the northeastern conifer forest and the eastern deciduous forest. Certain features of both regions, he says, are found in the southwestern portion of the island; but he did not carry out his first intention of tracing the relations between them. On the mainland of Michigan to the south, the maple forest is well developed, especially at certain inland points. Areas near the coast, however, may show many transitional features, such as occur in the Porcupine Mountains, which are about 125 km. south southwest of Isle Royale. These so-called mountains, which are really prominent hills or hilly ridges, represent the highest points of land reached in the Upper Peninsula. As Leverett (20) points out, they are "the most conspicuous features in this entire area, for they rise on their north slope very abruptly from the shore of Lake Superior to a height of 1400 feet above the lake".

The purpose of this ecological survey was to make a careful study of the climax formation of the region, including their relations to each other, and to correlate, if possible, the various plant associations occurring within them.

The Porcupine Mountains consist roughly of three ranges of hills, paralleling the coast (fig. 1), that nearest the shore being the most rugged. Back of these lies a table-land stretching south to the Gogebic Range.

It was not found possible to examine all of this territory; nor does it seem essential to an understanding of the vegetational development of the region. Practically all the detail studies were made in connection with the first range, and the valley of Carp River behind it. It must be admitted that this near-shore region received most attention because of its greater accessibility, yet aside from this it seemed of major importance for the following reasons: (1) on account of the pioneer conditions found on the first range, where the summit still remains unclaimed by vegetational development, (2) on account of the proximity of Lake Superior, permitting the observation of various stages of succession along the shore, (3) the proximity of a comparatively high altitude (for the region) to the wind-swept surface of Lake Superior, giving a definiteness to the larger problems of vegetation, (4) a forest covering which gives it unusual value for a study of the relation between two climax formations, (5) opportunity for observing practically primeval forest conditions.

Field work was carried out in the summer of 1922. Headquarters were first established at a point on Union

PART OF PORCUPINE MTS.

Map showing a portion of the Porcupine Mountains.

Bay (Sec. 16, T. 51 N. R 42 W.). This was found to be the most convenient location for the examination of the shore line and the hemlock forest of the north slope. Later, headquarters were located on the site of an old mining property near Carp Lake. All the work in connection with Carp River valley and the summit of the range was done from this point.

I wish to express my appreciation of the encouragement and co-operation of Dr. H. C. Cowles of the University of Chicago, under whose direction the work was undertaken. I also wish to thank Dr. Geo. D. Fuller of the same institution for suggestions in regard to the method of work. To the following gentlemen, I desire likewise to extend my thanks, Dr. A. J. Grout of New Brighton, N. Y., for the determination of about 45 species of moss, Dr. Bruce Fink of Miami University, Ohio, for the determination of about 60 species of lichens, and Dr. E. A. Bessey of the Michigan Agricultural College, for assistance in various ways. The nomenclature used in connection with the pteridophytes and spermatophytes is that of GRAY'S MANUAL, seventh edition.

EARLIER INVESTIGATIONS IN THE PORCUPINE MOUNTAINS.

The early interest attaching to an exploration of the mountains was based on the prospect of finding copper. Indications of this interest are shown in the abandoned shafts and workings in various parts of the region. In 1848

Fig. 1. - Carp Lake from top of first range, looking southwest: second and third ranges in the distance: escarpment of first range extending W. S. W. (extreme right); outlet of lake at far end.

the mountains were visited by W. D. Whitney (11) acting as botanist on a government expedition in charge of J. W. Foster. The following year, several places on the south shore of Lake Superior were visited - as far west - Whitney says, as the Ontonagon Valley and Carp River, both being in the vicinity of the Porcupines. In the second report on the region (12), which was published in 1851, Whitney gives a list of plants seen in the Upper Peninsula, including some from Isle Royale. This list, being very general, gives no clue as to what species were observed in the Porcupine Mountains. In JACKSON'S LAKE SUPERIOR(3), published in 1849, Bela Hubbard, a geologist, in discussing the origin and character of the soil in the Porcupines, points out that the sugar maple predominates throughout the elevated portions, while hemlock is the prevailing tree upon the lower lands.

During the next fifty years, apparently little was done in the way of botanical investigation in this region. In the summer of 1903, F. E. Wright (28), Assistant State Geologist, continued the work, earlier begun under the direction of Dr. L. L. Hubbard, of preparing data for an accurate geological report and map of the mountains. During a part of this time he was accompanied by Dr. A. G. Ruthven of the University of Michigan, who became interested in the biological aspects of the country. In 1904 and 1905, the

University Museum sent parties to northern Michigan to make biological studies in the Porcupine Mountains and in Isle Royale. One party, led by Dr. Ruthven, spent one month in the Porcupines and the remainder of the season on Isle Royale. The report of this expedition (1) came out in 1905. It covers both regions, listing 91 species of plants, and notes the ecological distribution of the more important species.

A list of over 600 plants found in the neighboring county of Gogebic should be mentioned. It was based on work done by Dr. E. A. Bessey and the writer (10) during portions of the summers of 1919 and 1920.

LOCATION AND PHYSIOGRAPHY.

The Porcupine Mountains are in Ontonagon County in the Northern Peninsula of Michigan, in lat. 47 N., long. 90 W. (see map). Their unique position, close to the south shore of Lake Superior, has already been pointed out. They reach a maximum altitude of 618 m. above sea level or 435 m. above the level of the lake. The top of the first range or ridge comes within 2 km. of the shore. Its north slope is rather gentle, but becomes increasingly steep as one approaches the summit, finally reaching a height of 275 m. above the lake in sec. 14, T. 51 N. R. 43 W. There is then a sudden descent of about 120 m. to the valley of Carp River, half of this descent being, in places, vertical rock face. At the base of the cliff there

Fig. 2. - Geological map of a portion of the Porcupine Mountains, showing their relation to the Keweenaw Series to the south. (After Irving).

is a talus slope extending in places several hundred meters down the side of the valley. This great cliff extends for a distance of about 10 km. across T. 51 N. R. 43 W. It is interesting to note Foster's impressions on first seeing this great outcropping of rock in 1848. He says "Suddenly the traveler finds himself on the brink of a precipice five hundred feet deep, at the base of which lies a small lake, so sheltered and hemmed in by the surrounding mountains that the wind rarely ripples its surface. Gloomy evergreens skirt its shores, whose long and pendant branches are so faithfully reflected on the surface that the eye can with difficulty determine where the water ends and the shore begins. From this lake flows the Carp River, and the beholder occasionally catches a glimpse of its waters as they wind through the narrow valley towards the great reservoir".

Geologically, the mountains form a crescent-shaped off-shoot or spur from the main range to the south (fig. 2). This latter extends from Keweenaw Point southwest to Wisconsin, including the well-known iron and copper ranges of the Keweenaw Series. The ranges of the Porcupines consist largely of eruptive rocks with interbedded sandstones and conglomerates, the strata tilted from 30° - 40° . They represent part of a pre-Cambrian upheaval, probably during early Proterozoic time. The present system of hills forms a comparatively small

Fig. 3. - Geological sections illustrating the struc-
ure of the Porcupine Mountains. (After Irving).

portion (fig. 3) of the original land mass, the rest having been removed by erosion during a very long period of time.

At the beginning of the glacial period, the general topography was probably much the same as at present. The mountains were laid bare at a relatively early date, making a cusp in the ice front, presumably between the Warren and Algonquin stages. According to Lane (19) the water was ponded on the north side of the mountains to a depth of 171 m. above the present surface of Lake Superior and on the south side at least 49 m. higher than this, the drainage being toward the Mississippi. Old beach lines on the north slopes show successive stages in the height of the lake, where the lake level was more or less stationary.

From what has been said, it is evident that the highest level lies back of the first range, though the latter is much the most rugged. The rough topography is, in general, conditioned by the geologic structure of the region. The main drainage lines are occupied by the Carp and Little Carp rivers, which flow roughly southwest. These parallel the general direction of the ridges, and finally turn northwest, emptying into Lake Superior. A portion of the drainage is also east and southeast into the valley of Iron River.

CLIMATE OF THE REGION.

The following data were obtained through the courtesy of the U. S. Weather Bureau at East Lansing; see also

report by Seeley (24). It is believed that tables I and II taken together give a fair index of the climatic conditions. Bergland, representing inland conditions, is about 27 km. south southeast of Carp Lake; it has an elevation of 215 m. above the surface of Lake Superior. Ontonagon is situated at the mouth of the Ontonagon River, 32 km. east of Bergland. The tables show that the mean temperature for the year is very nearly the same for both places.

-TABLE I-

MEAN TEMPERATURE AT BERGLAND FOR 11 YEARS

°C --	Jan.	Feb.	Mar.	Apr.	May	June	
	-12.9	-11.4	-4.1	4.1	10.5	16.3	
°C --	July	Aug.	Sept.	Oct.	Nov.	Dec.	Yr.
	18.6	16.9	12.7	6.8	-0.2	-7.7	4.1

-TABLE II-

MEAN TEMPERATURE AT ONTONAGON FOR 7 YEARS

°C --	Jan.	Feb.	Mar.	Apr.	May	June	
	-9.3	-10.8	-3.5	3.8	9.2	13.5	
°C --	July	Aug.	Sept.	Oct.	Nov.	Dec.	Yr.
	17.8	17.4	14.0	9.4	0.7	-5.8	4.2
	-	-	-	-	-	-	-

The differences in the average monthly temperatures of the two places indicate the probable moderating influence of the large body of water. The average maximum temperature for 5 years at Ontonagon was 34.6°C. and the average minimum -29.7°C. The mean monthly temperature at Bergland for 11 years was above 0°C. for 7 months of the year, beginning with April, and the mean monthly minimum above this for 6 months, beginning with May. Tables prepared by the U. S. Weather Bureau show that the average date of the last killing frost in spring is June 9, while that of the first killing frost in the fall is September 16, giving 89 days as the average length of the growing season. In this region the isotherms parallel the shore line, and the average temperature of points along the coast is several degrees warmer than inland points a few miles further back. During the hot summer months, however, the isotherms move back from the shore, so that the discrepancy between shore and inland conditions is not so great.

-TABLE III-

AVERAGE MONTHLY PRECIPITATION AT BERGLAND FOR 11 YEARS

	-- Jan.	Feb.	Mar.	Apr.	May	June	
cm	4.05	3.25	4.27	4.70	7.85	8.87	
	-- July	Aug.	Sept.	Oct.	Nov.	Dec.	Yr.
cm	9.05	8.82	8.72	7.30	5.20	5.45	77.55

-TABLE IV-

AVERAGE MONTHLY PRECIPITATION AT ONTONAGON FOR 6 YEARS

	Jan.	Feb.	Mar.	Apr.	May	June	
cm	5.95	4.65	3.89	2.61	5.72	5.25	
	July	Aug.	Sept.	Oct.	Nov.	Dec.	Yr.
cm	11.37	8.42	9.27	4.37	5.85	7.02	74.57

The above data, while not extending over as great a period of time as might be desirable, would seem to indicate that the average yearly rainfall for the region is about 76 cm. The figures show that the average precipitation along the coast during the months from November to February is 30% greater than the precipitation at Bergland 26 km. back from the coast. This may help to explain certain striking differences between the vegetation near the shore and that further inland. Slightly more than one-half the average rainfall occurs during the 5 months of the growing season (from May to September), apparently coming earlier in the season at inland points. The greatest average precipitation was in July.

The average number of cloudy days per month for 5

Fig. 4. - Exterior view of hemlock climax along a "forty" line where the timber has been cut: two sugar maples to the right, large hemlock in the background, salmon berry and three small hemlocks in the foreground; elevation about 100 m. above Lake Superior.

years at Ontonagon was 14, and partly cloudy 5, leaving an average of 137 clear days for the year. The prevailing direction of the wind at the same station is from the northwest, often veering around from the west.

The extent and ruggedness of the Porcupines allow for much local variation. The above climatic data are not meant to be more than general. Their character accords with the general mesophytic character of the vegetation in its larger aspects.

THE CLIMAX FORMATIONS.

There are two climax plant formations covering the ranges of the Porcupine Mountains. On the north slope of the first range occurs a typical hemlock forest. This gradually merges into a maple forest near the top of the slope. From this point maple forms the climax formation on the ranges to the south, though scattered patches of hemlock occur on the lower slopes. Any interpretation of the vegetation of the region must take into account the relation between these two formations, their relative position with respect to the larger physiographic features and the successions leading up to them. In this paper the hemlock climax will be considered first.

I. THE HEMLOCK CLIMAX

This is apparently the most mesophytic formation of the region. Its most typical development is on the lower half of the north slope of the first range. It is composed largely of three tree species: Tsuga canadensis (L.) Carr. (hemlock), Acer saccharum Marsh. (sugar maple) and Betula lutea Michx. f. (yellow birch). At the lower levels near the lake shore, the forest is almost entirely hemlock, while near the top of the ridge it merges into the less mesophytic maple forest.

Intensive studies were made at various points in the forest with a view to determining the relations between the three principal species. The life habits of each, from the seedling stage up, were studied as closely as time permitted. Interrelations of the species were also studied by means of quadrats and windfall areas.

A. Aspect of the Forest.

At first sight the forest appears to be almost a pure stand of hemlock. The boles are conspicuous below, but the upper portions of the trees, which are 25-30 m. or more tall, form a dense mass of interlaced foliage, with a ragged skyline. Here and there are occasional trees of yellow birch, with more open tops; also a few tall spindling maples, devoid of foliage, excepting near the summit, and

Fig. 5. - Shows distribution of yellow birch and maple, the conifers being removed; trees in the foreground are mostly maples; looking northeast toward Lake Superior; edge of forest to left; note abundant growth of salmon berry as a ground cover.

often indicating by the presence of dead twigs, the competition to which they are subjected.

In section 16, T. 51 N. R. 42 W., the hemlock had been removed from certain "forties", making it possible to obtain a view of the general composition of the forest from the outside. This is shown in fig. 4. The three species mentioned are practically the only ones in evidence from an exterior view of a section made in this part of the forest. Other large tree species, of less common occurrence, will be considered later.

In the area cut over, referred to above, only the conifers had been removed, leaving the two principal deciduous species standing, as shown in fig. 5. This gave an opportunity to estimate the relative distribution and character of the latter. An estimate was also made of the comparative number of species in the forest having a diameter not less than 1.5 dm. This was done by listing the individuals in a belt transect 220 m. long and 10 m. wide. It resulted in the following data so far as the principal species is concerned: hemlock, 80.5%; maple, 13.5%; yellow birch, 4.5%; basswood, 1.5%.

On entering the forest, one is impressed with the apparent age and maturity of the trees (fig. 6). The light is much reduced by the dense canopy above, formed principally

Fig. 6. - Interior view of mesophytic forest (sec. 16, T. 51 N. R. 42 W.): trees mostly hemlock; a large yellow birch in foreground at left; a portion of the crown of a maple at the right; looking north toward Lake Superior; note gentle slope.

by the fine spray of the hemlocks. An examination over a large area shows considerable diversity in regard to light conditions, the differences being due to more or less open areas caused by windfalls of varying ages. In reality the forest may be considered as a patchwork of these windfalls, which are ever appearing, maturing their growth and consequently producing a general shift in the position of the better lighted areas.

The forest floor is rather uneven and on the whole well drained, the general direction of the gullies being north (towards Lake Superior). A few of these gullies are occupied by small streams, even during the summer months, while others contain no running water, but are very moist, so that the moisture content of the soil is quite variable for different portions of the forest. This seems to be the controlling factor in causing certain departures from the ordinary composition of the forest (fig. 7).

There is comparatively little shrubby vegetation in the dense hemlock forest. Of the few shrubs found, probably Lonicera canadensis Marsh. (bush honeysuckle) is the most shade tolerant. The most important ecologically is Rubus parviflorus Nutt. (salmon berry), which is very quick to appear where an opening admits even a little more light to the forest floor. The bottoms of shallow draws

Fig. 7. - Shows a wetter, more open portion of the forest, in which the predominant large tree is arbor vitae: in the foreground, salmon berry, and seedlings of maple, balsam, and white spruce; other tree seedlings observed were yellow birch, basswood, and white ash.

are sometimes covered with it, even when partially shaded. Large numbers of woody sugar maple seedlings from 2-6 dm. tall often form a shrubby growth of considerable ecological importance. Other shrubs and shrubby trees found more or less frequently in or near the border of windfall areas are: Acer spicatum Lam. (mountain maple), Amelanchier canadensis (L.) Medic. (June berry), Salix rostrata Richards (Bebb's willow), Prunus virginiana L. (choke cherry), Cornus alternifolia L. f. (alternate-leaved dogwood), and Corylus rostrata Ait. (beaked hazelnut).

In general, the herbaceous vegetation forms a closer index to the moisture content of the surface soil than the woody vegetation. The most widely spread and shade-tolerant species of the hemlock forest is Aralia nudicaulis L. (wild sarsaparilla). Others of rather general distribution are: Galium triflorum Michx. (bedstraw), Aster macrophyllus L. (large-leaved aster), Clintonia borealis (Ait) Raf., Mitchella repens L. (partridge-berry), Oxalis Acetosella L. (wood sorrel), Trientalis americana (Pers.) Pursh. (star-flower), Lycopodium annotinum L. (stiff club moss) and Aspidium spinulosum (O. F. Müller) Sw. var. intermedium (Muhl.) D. C. Eaton. The following list is not so characteristic, but it includes some which are frequently found along water courses or low ground: Asplenium Filix-femina (L.) Bernh. (lady fern), Onoclea

Fig. 8. - Stand of sugar maple, approximately 75 m. north of the summit of the ridge in sec. 14. T. 51 N. R. 43 W.: the trees here are somewhat larger than is typical; note comparatively clear forest floor; maple seedlings in the foreground.

Struthiopteris (L.) Hoff. (ostrich fern), Phegopteris poly-
podioides Fee (beech fern), Circaea alpina L. (enchanter's
nightshade), Solidago latifolia L. (broad-leaved goldenrod),
Mitella nuda L. (bishop's cap), Streptopus roseus Michx.
(twisted-stalk), Cornus canadensis L. (dwarf cornel),
Chimaphila umbellata (L.) Nutt. (pipsissewa), Prenanthes alba
L. (rattlesnake-root), Aster paniculatus Lam., Ranunculus
recurvatus Poir. (rough cinquefoil).

Several species of moss and lichens lend color to
the general aspect of the forest. One of the most conspicuous
is Neckera pennata (L.) Hedw., forming green mats on the sides
of the trees and often extending several meters up. On rotting
logs in windfalls and along small creeks occur such moss species
as Brachythecium salebrosum (Hoffm.) Bryol., Plagiothecium
turfaceum Lindb., Hypnum Crista-Castrensis L., and the lichen
Sticta pulmonaria (L.) Schaer.

B. Composition and dynamics of the forest.

As before indicated, one of the major problems in
connection with the forest of the north slope, is to account
for its composition, especially as regards the relation be-
tween the hemlock and maple. As one ascends the slope the
maple contingent becomes greater and the hemlock less, so that
finally there appears to be at first sight an almost pure stand

of maple. (fig. 8).

The fact that the most conspicuous stand of almost pure hemlock forest is to be found on the north slope of the first range within about 1000 m. of the shore is probably to be accounted for by climatic conditions, rather than by differences in character of soil. The present composition of the hemlock climax has undoubtedly existed for centuries. In other words, the forest as a whole is in equilibrium as regards the relative numbers of the component tree species at a given altitude. A casual observation of the stages of succession in a windfall area, might lead one to think that maple should be the predominant tree (fig. 9). For this reason it seemed necessary to consider carefully such questions as the rate of growth, habit, shade tolerance, etc. of the more important species, and the relationship of their development, as shown by quadrat studies.

1. CONSIDERATION OF INDIVIDUAL SPECIES.

TSUGA CANADENSIS (hemlock).- This species continues to grow in diameter many years after its top has reached the crown of the forest, the result being that the stand consists of individuals with great diversity in their ages. Sapling stages are quite common, though their growth is often very slow. The tolerance of all stages for weak light explains

Fig. 9. - Seedlings of sugar maple in hemlock forest: those pictured are 1.5 - 3.0 dm. high, there being approximately 40 individuals per square meter.

the dominance of the species over maple, its nearest competitor in the forest. On account of this tolerance, suppression at some stage of its earlier growth is the rule rather than the exception.

The tree usually seeds at intervals of every 2 or 3 years, and in spite of reduced fertility, many more seedlings start than are able to mature, even though they are not noticeably abundant, as in the case of the maple. The production of seeds and seedlings is therefore not the critical factor in the regeneration of either species.

The species is extremely sensitive to sudden changes in the density of the forest, and seedlings respond quickly in rate of growth to slight increases in the amount of light admitted, but they are killed by too much light, and therefore the tree will not take a central position in an open windfall unless it is sheltered by faster growing species. On account of its shallow root system, it is very susceptible to surface fires.

ACER SACCHARUM (sugar maple). - This species, as it occurs in the hemlock climax, is tall and slim and free of limbs except near the top. The trees are apparently healthy, though all of them have undoubtedly suffered more or less suppression. As already noted, the seedlings occur in such numbers that a superficial observation might lead one to

Fig. 10. - View along an old wood road, which here acts as an artificial windfall: on each side of the road there is a dense growth of young maples, 2 - 6 m. high; salmon berry in the foreground.

conclude that the forest would, in a few generations, become a pure stand of maple. Closer observation soon shows that a very small percentage of these ever mature. According to Frothingham (13) the trees seed every 3-5 years under forest conditions; and even-aged groups of very close-standing seedlings are of common occurrence. They prefer maple leaf-mold and avoid areas covered with hemlock needles. The close and abundant growth of the seedlings results in such severe competition that the individuals are weakened and most of them succumb to suppression or disease. However, the seedlings are very tolerant of shade conditions, and a few here and there are able to persist, and take advantage of the increased light occasioned by a windfall. Indeed, the relative stand of maple and other hardwoods in the hemlock climax seems mainly to be conditioned by the number of windfall areas. In such areas, Rubus parviflorus often forms a ground cover, affording more or less protection to young seedlings which are exposed to strong sunlight.

BETULA LUTEA (yellow birch). - This tree, coming next to maple in its distribution, is an important element in the climax formation. In the forest it becomes slim and tall with a clean bole, having limbs only near the top. A specimen was observed along a woods road about 30 m. tall, with a broad crown, occupying half the height; this tree was

5.6 dm. in diameter and was fruiting heavily. It grows more rapidly than the maple and in its earlier stages requires much more light. Seedlings are comparatively rare in the hemlock forest; when found, they are apt to occur in well-lighted windfalls. Sometimes they are very numerous on a small area in full sunlight. They occur also on rotting logs with hemlock and other seedlings, and are apparently free from disease. The natural point of regeneration for the species is in windfall areas. Where an area has been slightly burned over, the seedlings are sometimes very numerous. At one point, where the forest had been cut away, the mature specimens of birch seemed more prone to rot than the maple, apparently suffering from a sudden influx of bright sunlight; in other words, maple seems to be a less critical tree in most of its stages, than the birch. The latter is a much less aggressive reproducer than the maple, in spite of the fact that it seeds more often. It may and often does become extensive in its habit (Frerthingham 13), producing large stands of even-aged trees, which shows that its seed production has a high enough "factor of safety" to be well within the limits required by nature. Besides reproduction by seeds, this species readily sprouts from the stump. It seems clear that its relative distribution in the hemlock climax is not based on the performance of its seeds, but on its less tolerance for shade con-

ditions than the maple and hemlock.

OTHER SPECIES OF TREES IN THE HEMLOCK FOREST. - Several other tree species occur, but they are of less importance ecologically than those mentioned. One of these of occasional occurrence is basswood (Tilia americana L.). It gets to be a large tree, with a clear bole nearly up to the forest crown. Seedlings were frequently found, having a distinctly prostrate habit, the leaves becoming very large in the shade. Thuja occidentalis L. (arbor vitae) occurs in low spots but is not a tree of general distribution. As a forest tree it often becomes very large. Its presence along the shore line will be discussed later. Pinus Strobus L. (white pine) is occasionally found as a very large tree, towering above the rest of the forest. My observations seemed to indicate that where one was found, several others were likely to occur in the same neighborhood. Abies balsamea (L.) Mill. (balsam) is not common. It is rarely found as a mature tree in the hemlock forest, though seedlings are often frequent in windfall openings, and occasionally colonies of young trees are found in like situations. Whether this species will mature in competition with others evidently depends on the size of the forest opening; in most cases it is suppressed by the more shade-tolerant trees. When it occurs as a mature tree in the forest, it is safe to infer that the opening was well lighted for a considerable length of time. Its behavior in this respect bears

out the findings of Cooper (5) on Isle Royale, where he showed that the birth-rate of this species is balanced by a high rate of mortality when in competition with certain other species.

Other tree species occasionally found in the hemlock climax are Picea canadensis (Mill.) BSP (white spruce), Quercus rubra L. (red oak), Fraxinus americana L. (white ash), and Ostrya virginiana (Mill.) K. Koch (hop hornbeam).

2. QUADRAT STUDIES.

This method was found useful in connection with the study of forest regeneration, and the distribution of the principal species. Where it became necessary to determine the average ages of the trees, this was done by means of tables prepared by Frothingham (13). The trees were too large to make felling practicable for this work. Besides the quadrat studies every other means that suggested itself was used for gaining a knowledge of the dynamics of the forest. The quadrats were 10 m. square.

QUADRAT 1 (fig. 11). - This quadrat shows the distribution of trees in the typical hemlock climax shown in fig. 6. It represents a condition of mature growth. Most of the trees here stand at an average distance of from 2 to 3 m. It is noticeable, however, that practically half of this quadrat is occupied by a giant hemlock 300 years old, whose

Tsuga canadensis *Tilia americana*
tc ta

Fig. 11. - Quadrat 1 (see fig. 6 for location): the numerals indicate the approximate ages of the trees: the quadrat is 10 m. square.

sphere of influence has undoubtedly extended much further than the younger trees. The forest floor here was free of large shrubs; of small woody plants, 50 specimens of Rubus parviflorus were counted, 14 of Lonicera canadensis and at least 300 seedlings of Acer saccharum. The most conspicuous herbaceous plant was Aralia nudicaulis. Other herbaceous plants noted were Phegopteris Dryopteris, Clintonia borealis, Galium triflorum, Mitchella repens, Mitella nuda, Cornus canadensis, and Lycopodium annotinum. In fact, both the woody and herbaceous vegetation were typical of a well-drained portion of the dense hemlock forest.

QUADRAT 2 (fig. 12). - This was taken in a windfall. It consists of comparatively young growth. The oldest standing specimens consist of a hemlock 130 years old, a white spruce 110, and a sugar maple 90 years old; and none of these had reached their full growth. The dominating influence of this hemlock is clearly shown in the diagram. Its dense spray is more effective in causing suppression than that of the maple or even of the white spruce. The best-lighted area of the quadrat is occupied by the younger growth, nearly one-third of which consists of balsam. The maple, 100 years old, shown near the top of the quadrat, was broken off several feet above the base by a secondary windfall, and in falling apparently leveled four other trees as shown,

Tsuga canadensis tc *Acer saccharum* as
Abies balsamea ab *Picea canadensis* pc
Betula lutea bl *Populus grandidentata* pg
 Fallen tree ●

Fig. 12. - Quadrat 2: taken in a windfall area in the hemlock climax.

consisting of two balsams, a yellow-birch, and a specimen of large-toothed aspen (Populus grandidentata). The last three species named are all faster-growing than hemlock or maple. Of the 14 trees which are standing, 5 are balsams, 5 hemlocks, 2 maples and 1 white spruce. The oldest balsam is 50 years, and it is certain the other balsams will be suppressed, probably before any one of them reaches 100. White spruce (Picea canadensis) is very rare in the hemlock forest, and it is likely that this single specimen will eventually disappear before the maturing hemlocks. This leaves the struggle between the 5 hemlocks and the 2 maples, and typifies the final stage in any windfall. It is very suggestive as to the light it sheds on the ultimate composition of the forest at this point.

Salmonberry and large seedlings of mountain maple and sugar maple formed a low woody growth that acted as a screen for the usual herbaceous vegetation. The quadrat contained several hundred sugar maple seedlings, the oldest being about 5 years. These latter were very much affected by anthracnose leaf spot and by an insect disease. Ninety hemlock seedlings were counted, mostly growing on rotting logs in the shadier part of the quadrat. Large-toothed aspen was represented by 15 seedlings; the largest individuals, though only 3 years old, were twice as tall as

the 5-year seedlings of sugar maple. Balsam seedlings were found in the sunnier parts of the quadrat, 25 individuals being counted. Several species of moss, already mentioned, were found on rotting logs in or near this quadrat. They are often of considerable ecological importance in the formation of seed beds.

In the quadrat studies above described, certain conclusions in regard to shade tolerance and its effect in the distribution of the species, seem inevitable. This will be considered in what follows.

3.- INITIAL PHYSICAL FACTORS AND COMPETITION.

It is evident that a great many factors enter in to the dynamics of the forest. A few of these have been pointed out as they affect the life history and occurrence of the dominant species of trees. In a consideration of the composition of the hemlock climax on the north slope, two questions arise. First, what causes the variation in composition from the base of the slope to the top of the ridge, a difference in elevation of approximately 300 m.? Second, what is the most effective factor governing the composition at any one point? Frothingham has pointed out that there are two sets of factors influencing the distribution and dominance of trees in the natural forest, namely, physical, including soil, humidity, light, etc. and physiological (biotic) including

aggressiveness in reproduction, tolerance of shade, rate of growth, form, size, longevity, and resistance to injury and disease. The first question seems to be answered by a consideration of the physical factors of moisture and light. Soil evidently has little to do with it; if all the hemlocks were removed from the north slope, maple could easily take possession, as is evident from its regeneration in windfalls, and its prominence in the ranges further south. Hemlock, rather than maple, is thus the critical tree on the north side of the first range. This species is known to prefer cool, moist slopes, where the drainage is fair. Good drainage, however, may be left out of consideration here, as it occurs on the ranges farther south where hemlock is not prominent. The greatest humidity lies low along the lake shore. Here dense fogs are frequent even in the earlier part of the growing season. The smaller ratio of humidity at the higher elevations allows a corresponding increase in the intensity of the light near the top of the ridge. As before noted, hemlock is known to be very sensitive in its response to light; it is also known to be more shade tolerant than maple. Thus it seems clear that the dominance of hemlock at lower elevations on the north slope, and its absence as a dense stand on higher elevations and on the ranges further south, is correlated with the physical factors of moisture

and light.

The answer to the second question involves the consideration of the relative physiological response of other species, especially maple and yellow birch, to the conditions imposed by the dominant hemlock. Hemlock and sugar maple, are the most conspicuous examples in the Lake Region of what Frothingham calls intensive reproducers, i.e., species which are more aggressive inside than outside the forest. The effective aggressiveness of each species is due to a combination of factors. Both species, when growing under forest conditions, are likely to have a suppressed period of growth for at least the first 50 years. Quadrat studies show a great variation in age of individuals, even among the adult trees forming the forest crown, mature trees varying from 100 to 300 years or more. One hemlock, measuring about 1 m. in diameter, was estimated at over 400 years. The greatest tolerance of maple, however, seems to be in the seedling stage, quadrat studies often showing hundreds of seedlings in the dense shade of the hemlocks. On the other hand, the seedlings of hemlock are rather critical in their light requirements, being killed by too much or too little shade. In general, they grow more abundantly in the more open part of the forest, but not necessarily in a windfall.

4. EQUILIBRIUM AT ANY POINT.

Though the different tree species vary widely as to their relative production of seeds and seedlings, it seems certain that all are productive enough to be well within the limits required by nature. It has been pointed out by various observers that the "factor of safety" in seed and seedling production is very large and that there is an enormous wastage in all cases. While this larger seed production may be important on denuded areas, it seems clear that it has little to do with the relative number of individuals of different species, where the dominant species are intensive, and where a balance has long been reached and maintained. This balance is changed little if any by excessive seed production of any species. It is conditioned by something more invariable than seed production. The true explanation seems to be the relative tolerance of the species for each other under the conditions imposed by the physical factors at that point. For example, the population of the yellow birch, which forms approximately 5% of the total tree population half way up the north slope, is a measure of its relative response to the conditions imposed by the hemlock and maple. Since the equilibrium of the forest represents the result of the effective response of each species, the balance may be shown diagrammatically as

Fig. 13.- Vector diagrams, illustrating approximate equilibrium (in number of individuals) at two points on the north slope of the first range: the upper figure illustrates the conditions halfway up the slope; the lower figure shows conditions of balance near the top; hemlock has been nearly replaced by maple; CD is represented largely by basswood and ironwood.

The first thing I noticed when I stepped
out of the car was the heat. It was a
welcome surprise, but I was not prepared for
it. The sun was shining brightly, and the
air was thick with humidity. I had heard
that the weather was bad, but I didn't
realize how bad it was. I was sweating
within minutes of getting out of the car.
I had to take a break and get some
water. I was not used to this kind of
weather. I had been told that it was
hot, but I didn't know it was this hot.
I was in for a real challenge.

in fig. 13. The vectors DA, AB, and BC, (upper figure), illustrate the effective response of the three principal species somewhere up the north slope. Evidently the magnitude of the vectors does not correspond to the number of individuals of each species; in other words, while population may indicate response, it is not a measure of it. The vector CD indicates the effective control of all other species. The lower figure illustrates the conditions of balance near the top of the ridge. If any one species were eliminated from the forest, it would soon come back in approximately the same proportion at any point.

C. Successions leading to the hemlock climax.

1. Primary successions.

The primary successions leading to the hemlock climax may be seen along the shore of Lake Superior, at the foot of the first range. The pioneer stages are present in most cases, but the transition is often rather abrupt. Lack of well marked zonation is probably due to the severe conditions along the shore.

a. Physiographic influences.

The development of the shore line is correlated with the post-glacial history of the Lake Superior region. On account of the gradual withdrawal of the lake,

Fig. 14. - Rocky shore a few miles west of Union Bay; shows sandstone beds dipping toward the north; the edges of the tilted strata off shore form a rocky terrace, breaking more or less the force of the waves; vegetation readily establishes itself in the joint and bedding planes, as shown; white coating on the rock surface is Parmelia lactea.

more and more of the north slope of the first range has been uncovered. This has probably been counterbalanced by erosion, and by the sinking of the coast in this region, which is believed to be taking place (1).

The rock shore is the predominant type. Where it is gravelly or sandy, a little investigation shows that the rock is not far underneath. The exposed rock is largely red sandstone, dipping everywhere at an angle, as shown in fig. 14. In places conglomerate is exposed and loose boulders along the shore are frequent. The width of the rock beach varies from 15 to 45 m. Sandy or gravelly beaches in more or less protected places may be narrower than this, so that the forest comes comparatively close to the water, as shown in fig. 15, which shows a narrow gravel beach.

There is such a variation in the slope and character of the rocky shore that it is difficult to divide it into any definite zones in accordance with the ecological factors influencing plant life. Its lower portion, being always subject to wave action, during both summer and winter, is devoid of plant life, except in sheltered corners of the rocks, which escape the direct pounding of the water. The lower limit of plant life is marked, roughly, by the maximum height of the waves in summer. The winter waves and

Fig. 15. - A narrow shingle beach, in which the forest comes unusually close to the water's edge, being protected from the winter storms by the ledge of rock off shore; note zone of white birch and arbor vitae lining the shore at this point, bordered by salmon berry and Cornus alternifolia; Equisetum arvense growing in the shingle.

ice usually reach much higher than this, and thus mark out the upper limits of a zone in which only the hardiest perennials are able to survive.

b. The shore successions.

Since the surface of the lake has been at the present level for a long period of time, the distribution of the pioneer associations at any point along the shore has reached a balance which will remain practically the same so long as the climatic, ecological and historical factors remain unchanged. In other words, it is probably incorrect to say that active invasion or retrogression is taking place at the present time, even admitting the slight changes in coast line, due to subsidence or erosion.

The pioneer associations along the shore are composed of crevice plants, of lichens and of mosses. On account of the fragmental nature of the rocks, crevice plants appear to be the most important pioneers; most of them are perennials. The seeds lodge in the moist cracks of joint and bedding planes, and germinate even where little or no soil is present. Gradually the seedling intercepts enough soil for the establishment of a firm root system, and then is able to persist for many years, and spread by means of offshoots. Two of the commonest and hardiest species in this connection are Juncus Dudleyi Wiegand and Deschampsia

Fig. 16. - Shows a wall of conglomerate paralleling the shore, and forming a protective barrier to the forest behind it: conifers and aspens growing under the xerophytic conditions at the top; the conifers include a small white pine (in the background), small specimens of white spruce, balsam, and arbor vitae, all growing in the crevices of the rock.

Fig. 17. - Shows Deschampsia caespitosa and Aster faxoni growing in a typical situation along the shore: note dip of the strata, and fragmental character of the rock.

caespitosa (L.) Beauv. (hairgrass). The former was found growing within 3 dm. of the water; the latter is undoubtedly the commonest grass growing in the crevices of the shore rocks.

Fig. 14 represents a typical situation for crevice vegetation. Such a habitat enables even woody plants to come in very early. In the foreground is shown a large specimen of ninebark (Physocarpus opulifolius) and in the background a small specimen of mountain ash (Pyrus sitchensis). The former has assumed more or less of the krummholz form of growth, especially on the lake or windward side; its habit of growth thus makes it more efficient as a conserver of soil and moisture.

The rate of succession along the outer shore is evidently not to be measured by the character of the plant life, the highest forms being found with the lowest. As before indicated, this rate is exceedingly slow, due to the severity of the situation. In spite of this, a large number of species are found. One group may be classed as typical crevice plants. Among these, besides those mentioned, are Campanula rotundifolia L. (bluebell), Aster Faxonii Porter, Senecio Balsamitae Muhl. (groundsel), Fragaria virginiana Duchesne (strawberry), Achillea Millefolium L. (yarrow), Equisetum arvense L. (horsetail).

Fig. 18. - Rock surface well above the wash of the waves: the crustose lichen is Parmelia lactea; the moss (dark patches) Grimmia apocarpa; Polypodium vulgare in crevices near the top of the boulder.

In the outer portion of the shore line, at least, shrubs often occupy the most exposed situations. The typical species are Physocarpus opulifolius (L.) Maxim. (ninebark), Rosa acicularis Lindl. var. Bourgeauiana Crepin (wild rose), Salix petiolaris Sm., and Cornus stolonifera Michx. f. (red-osier dogwood). The seedlings of Populus tremuloides often accompany the willows. Along the inner portion of the shore, tree seedlings are frequent, the commonest being those of Thuja occidentalis L. Here the usual successions occur, with lichens and mosses as pioneers. With a few exceptions, they are well above the wash of the winter waves. The wash of the higher water can often be very accurately traced on large isolated boulders of conglomerate. This material, on account of its differential weathering, supports a richer flora of lichens and mosses than the sandstone, and the transition from washed to unwashed surface often appears rather abrupt.

Several species of lichen and moss occur in the severest situations. The pioneer crustose lichen appears to be Rhizocarpon petraeum (Wulf.) Koerb. This form persists often under the lash of the winter waves. Other crustose forms common on the rocks further back are Placodium aurellum (Hoffm.) Tuck. and Lecanora cinerea (L.) Sommerf. A few species of moss, such as Ceratodon purpureus (L.) Brid., Leptobryum pyriforme (L.) Wils. and Funaria hygrometrica (L.) Sibth., occur in

Fig. 19. - Shows the roots of white pine running for several meters along the surface and finally acting as an agent of rock displacement: the roots on the far side of the tree are covered by a mat of Arctostaphylos Uva-ursi; small red pine and aspens bordering the shore in the background.

Fig. 20. - A broad type of shingle beach, devoid of vegetation on account of the wash of the winter waves.

exposed crevices. In some cases they undoubtedly have the way for higher plants. Further inshore various foliose and fruticose lichens and mat-forming mosses form a definite stage of the rock succession. Among these may be mentioned Grimmia apocarpa (L.) Hedw., Amblystegium varium (Hedw.) Lindb., Sticta amplissima (Scop.) Mass., Parmelia conspersa (Ehrh.) Ach., Stereocaulon paschale (L.) Hoffm. and various species of Cladonia.

Following the mosses and lichens one often finds the bearberry (Arctostaphylos Uva-ursi (L.) Spreng.) as a pioneer mat former. With the accumulation of more soil, shrubby species become more abundant. Besides those mentioned, the following occur:- Diervilla Lonicera Mill. (bush honeysuckle), Amelanchier canadensis (L.) Medic. (shad bush), Cornus alternifolia L. f. and Rubus parviflorus Nutt. (salmon berry).

In the development of this succession finally come the trees, their roots sometime spreading 3 - 10 m. before finding a suitable crevice for anchorage (fig. 19). Roots of this kind form an important barrier for holding back soil washed from above. The fallen trunks also assist in the same manner, as well as finally furnishing additional humus by their decay.

-Types of shore-

The character of the shore vegetation is largely in-

Fig. 21. - Types of shore line; see text.

fluenced by variations in physiography. This includes submerged ledges of rock, shore, cliffs, coves and the accumulation of shingle barriers. Submerged ledges, breaking the effect of the waves, and coves affording protected areas, are both factors in extending the forested area closer to the water's edge. The effect of these two influences may be seen in fig. 15.

It seemed possible to classify the shore into three general types, as shown in fig. 21. Fig. A shows a type in which the surface immediately back of the shore line is low. It often represents the mouth of a gully, and possibly of a drowned river (see Ruthven (23) p. 25). The area is swampy, usually being occupied by large specimens of Thuja occidentalis and Fraxinus nigra. It is sometimes separated from the immediate shore line by a narrow zone of shingle and driftwood. Back of the area, there is often an abrupt rise of from 6 to 10 m. to the typical hemlock forest.

In B, the hemlock forest extends practically up to the shore line, though there is always a fringe of other species on the immediate outskirts, the commonest being arbor vitae and white birch. Other species occurring are Abies balsamea, Acer saccharum and Acer spicatum. Stages intermediate between A and B occur.

C represents the conditions where the shore line

is bordered by a rocky cliff. In this case the area above is often forested to the very edge of the cliff. On account of the dip of the strata, such areas are so well drained that the vegetation becomes xerophytic in character. This was found to be true even where the soil was 3 dm. deep as was observed at one point. At this point the ridge had once been covered by a growth of pine, which had been blown down, and was being followed by a growth of white birch, aspen and balsam, the two former being on the lake side, being better able to adapt themselves to the unusually severe wind conditions.

2. Secondary successions in the hemlock climax.

In the latter part of the summer of 1919, an extensive fire swept over a portion of the north range, destroying several square miles of virgin hemlock forest. This fire extended as far east as the range line between townships 42 and 43. The conifers were killed outright, though many dead trunks were left standing (fig. 22). It was very evident that the deciduous trees, including the sugar maple and especially basswood, were more resistant to the effects of the fire than the conifers. This was especially noticeable in the zone between the burned and unburned areas, where the trees were singed. Fig. 22 shows how thoroughly the humus

Fig. 22. - A "burn" in the hemlock forest three years after the fire: note angular character of the sandstone fragments underlying the forest floor, the humus being completely destroyed; north slope of first range looking west.

was burned off, exposing what appears to be ordinary talus material, composed of angular, unwashed fragments of sandstone, mostly 1 - 3 dm. in diameter.

"Burn" associations had started over the entire area, being further advanced at some points than at others. The commonest herbaceous pioneers consisted of Erigeron canadensis L. (horseweed), Epilobium angustifolium L. (great willow-herb), Aster macrophyllus L., Aralia hispida Vent. (bristly sarsaparilla), and Polygonum Douglasii Greene. Amongst the shrubby species coming in next the following were noted:- Rubus parviflorus (salmon berry), Sambucus racemosa L. (red-berried elder), Diervilla Lonicera Mill. (bush honeysuckle), Rhus typhina L. (staghorn sumac), and Rubus idaeus L. var. aculeatissimus (C. A. Mey.) Regel & Tilling. These are followed by Prunus pennsylvanica L. f., (wild red cherry), Acer spicatum Lam. (mountain maple), seedling aspens and occasional seedlings of sugar maple (Acer saccharum). Hemlock seedlings undoubtedly come in at a later stage, finally displacing the maple. One of the most noticeable elements of this secondary succession is Rubus parviflorus. The plant spreads rapidly over large areas by stems just below the surface, these stems sometimes being several meters long. The foliage forms a "leaf mosaic" which reduces the light to such an extent that shade-tolerant species are able to make an early start, thus probably hastening the

Acer saccharum-as

Fig. 23. - Quadrat 3. This quadrat represents a stand of trees in a forest of almost pure maple; it was taken in sec. 14, about 100 m. from the summit of the ridge (see fig. 7).

climax stage.

II. THE MAPLE CLIMAX.

This is the formation associated with vegetational development at the top of the first range and over the ranges further south. Its mature form may be seen 100 m. south of the summit of the range (fig. 8). Here a 10 m. quadrat was laid out (fig. 23). It represents a stand of almost pure maple. The larger trees averaged about 4 m. apart, the forest canopy being rather dense for maple. The uniformity in the ages of several of the younger trees marked them out as the survivors of a single generation of seedlings. In fact, the presence of several dead saplings varying from 30 to 40 years suggested that these trees had already reached a critical period in their development. Thrifty specimens of *Tilia* and *Ostrya* were found just outside the limits of the quadrat. The soil at this point was a rich leaf mold of medium acidity. It was not deep, as indicated by the root systems of fallen trees, exposing the bare rock. Though the forest floor was comparatively open, immature shrubby vegetation was represented by specimens of Rubus parviflorus and Sambucus racemosa. The latter species gets to be very large and rampant in maple windfalls, dominating the ground cover. The following are typical herbaceous species:- Aspidium spinulosum

(O. F. Müller) Sw. var. intermedium (Muhl.) D. C. Eaton, Phegopteris Dryopteris (L.) Fée (oak fern), Adiantum pedatum L. (maiden hair), Botrychium virginianum (L.) Sw. (rattlesnake fern), Hystrix patula Moench. (bottle-brush grass), Milium effusum L. (millet grass), Solidago latifolia L. (broad-leaved goldenrod), Ribes Cynosbati L. (wild gooseberry), Smilacina racemosa (L.) Desf. (false spikenard), Actaea alba (L.) Mill. (white baneberry), Viola canadensis, L., Sanguinaria canadensis L. (bloodroot), Aralia nudicaulis L. (wild sarsaparilla), Polygonatum biflorum (Walt.) Ell. (true Solomon's seal), and Galium triflorum Michx. (bedstraw). The last-named species is one of the commonest of the smaller ground covers.

The maple climax, as above described, occupies a comparatively narrow zone on the north side of the first range. As will be shown later its development on the south side is as yet in the early stages, this development being closely related to the physiographic features of the range and the adjoining valley of Carp River.

A. General physiographic features.

That the top of the first range still holds out against the mesophytic forest is undoubtedly due to the peculiar topography of this range. As is evident from fig. 3, this topography is associated with the geological formation

Fig. 24. - Cliff and talus slope, first range: view from a point just east of Carp Lake, looking north; the cliff at this point is about 130 m. above the floor of Carp River Valley and 240 m. above Lake Superior; the face of the escarpment is approximately 65 m. high at this point; note fringe of forest between talus slope and river valley.

Fig. 25. - View of cliff in section 15, T. 51 N. R. 43 W., looking east: in the foreground are shown the last stages of the cliff, preceding the formation of a saddle; in places the soil has accumulated on the bare rock; note xerophytic character of the vegetation.

of Carp Lake, which was once much larger than at present. The dip of the strata toward the north has created a great cliff or escarpment, which is continually weathering away, producing a talus slope at its foot (fig. 24). This cliff extends west and west-southwest across T. 51 N. R. 43 W., a distance of about 10 km. It varies from point to point along the range as to elevation of summit, height of escarpment and width of talus slope. At one point opposite Carp Lake the talus descends into the lake; but at most points there is a fringe of forest between the foot of the talus and flood plain of the river, as shown in fig. 24. In sec. 14, there is a depression in the cliff where the escarpment has entirely disappeared leaving a saddle across the range. The same thing, though less marked, occurs about a mile west in sec. 15, and in varying degrees at other points along the range, making it possible at such places to descend into the valley without difficulty. Where a saddle is sufficiently low, as in sec. 14, the talus is almost entirely covered by soil washed from above, and the fringe of forest from below may extend clear across the depression. In sec. 15. (fig. 25) this process has not gone so far. There is still a rock face varying from 3 to 5 m. high. The relation between the various physiographic features as they appear at different points along the range is shown in fig. 26.

Fig. 26. - Typical cross-sections at various points through the summit of the first range.

A represents a stage of the cliff found opposite Carp Lake in sec. 22. Here the escarpment is high and the talus slope dips into the lake. At this point the trap and sandstone portions of the cliff can readily be distinguished. The trap is superimposed upon the sandstone, and has undergone a greater disintegration, forming a ledge as shown. B and C typify ordinary conditions where the escarpment is high and the talus slope from 200 - 300 m. wide, bordered by a more or less mesophytic forest at the foot. At D is shown a stage where the top has been rounded off to such an extent that xerophytic tree species, such as red and white pine, are able to gain a footing. The ~~former~~ is usually more abundant under the brow of the cliff, where it is more or less sheltered. The latter is found in the more exposed situations, being the first to creep over the top when the conditions become favorable. Stages B, C, and D may all be seen in section 14. E and F represent stages at a low point in the range, such as is shown in fig. 25, preceding the formation of a saddle. Here the talus slope is much reduced, the forest pushing well up toward the summit, even though the latter may still remain xerophytic.

B. Successional relations

I. Xerarch successions on the first range.

An ecological survey of the vegetation

Fig. 27. - Limit of forest growth on summit of ridge, looking east. The prevailing direction of the wind is from the southwest; this is more or less evident from the general direction of the branches in the small pines shown; clump of small red pines in background (to left); bearberry mat on rock in foreground.

involves an examination of the environmental factors and plant successions (1) at the summit (2) along the escarpment (3) on the talus slope (4) below the talus slope.

(1) Summit of the range.

(a) Ecological factors. In general, the forested area of the north slope may fall short of reaching the crest of the ridge, as shown in fig. 26, E, or may reach slightly over the summit, as at F. From this point to the brink of the precipitous cliff, which averages from 20 - 40 m., there is usually a large amount of bare rock surface. Where the soil has accumulated, it is of very slight depth. There seem to be two principal reasons for this condition, both being due to the presence of the escarpment; (1) the soil due to rock disintegration is washed over the south side of the crest nearly as fast as it is formed, (2) the escarpment itself forms an effectual barrier to the encroachment of the mesophytic forest below. This zone of bare or nearly bare rock surface therefore remains unprotected. Its exposed situation makes it especially susceptible to the dynamics of weathering, including the frost of winter, the heat of summer, full exposure to rain and to all winds from the south. A portion of the soil washed over the crest accumulates in a narrow strip along the top of the talus slope. The rest is gradually washed

Fig. 28. - A portion of the summit, looking east: Carp River in the valley below (at right); small red pines and stunted aspens to the left, back of which a transition zone occurs as shown in fig. 32, leading to the maple climax of the north slope; note pines growing from crevices in face of escarpment.

down through the talus, finally reaching the forested area at its foot. On the other hand, soil found on the north crest is soon checked in its descent by the forest. A certain amount of it collects in depressions and irregularities of the rock surface and along the edges of joint planes, affording a foothold for crevice plants and matted vegetation.

(b) The plant associations.

The pioneer stages at the summit consist of lichens and mosses on the bare rock surface, and on the ground. Among the commoner crustose lichens appear such forms as Lecanora cinerea, Rhizocarpon petraeum and Placodium aurellum. Following these come foliose species, Parmelia conspersa (Ehrh.) Ach. being the most conspicuous and covering a large proportion of the rock surface; Physcia obscura (Schaer.) Nyl., Lecanora garovaglii and Gyrophora hyperborea Ach. are less common. Where a slight amount of soil has accumulated on the rock surfaces, fruticose types appear, common species being Cladonia rangiferina (L.) Web., Cladonia sylvatica (L.) Hoffm., and Stereocaulon paschale (L.) Hoffm.

Associated with the lichens in the pioneer rock successions are moss species, such as Grimmia apocarpa, Polypodium piliferum Schreb. and Tortella tortuosa (L.) Limpr., the two latter being the commonest. One of the early mat

Fig. 29. - Close-up of rock surface, crest of ridge:
in the foreground, Juniperus communis var. depressa, Danthonia
spicata, Antennaria neodioica, Potentilla tridentata, Poly-
gonum Douglasii (lower right), and Parmelia conspersa, the
dominant lichen; Solidago randii var. monticola in the back-
ground.

formers is Selaginella rupestris (L.) Spring., often covering large areas on the rock surface. It is not uncommon to find superposed upon this mat the two common mosses already mentioned. The Selaginella mat becomes nearly 1 dm. thick in places, living plants growing on the dead mat of former generations. This paves the way for herbaceous plants, such as Danthonia spicata (L.) Beauv. (wild oat grass), Potentilla tridentata Ait. (three-toothed cinquefoil), and even for woody species, such as the bearberry (Arctostaphylos Uva-ursi (L.) Spreng.) and stunted specimens, (2 - 4 dm. high), of staghorn sumac (Rhus typhina L.). The roots of the latter creep over the rock surface for several decimeters until finally they may become anchored in a crevice. Arctostaphylos is especially well adapted to the severe conditions found on these rock surfaces. Often it occurs in large patches, thus aiding in the retention of more soil and the conservation of soil moisture. Large angular depressions in the rock surface may occasionally be found where enough moisture is retained to support even shrubby growth without being definitely anchored in a crevice. Such a case was illustrated by a low specimen (2 - 3 dm. high) of New Jersey tea (Ceanothus americanus L.) which had adapted itself completely to the shape of the depression, but could be pulled out bodily as a dense mat.

Much of the rock at the bare summit is more or less porous in texture; rock fragments are numerous but irregular. Joint and bedding planes are not as distinctly marked as on the face of the escarpment. Whenever a crevice occurs, however, soil readily collects, and a number of plants gain a footing. The summer flora is practically a xerophytic one; the occurrence of certain vernal species, however, indicates that during the spring there is a comparatively large amount of moisture on the ridge, due in part, probably, to the melting snow. Of the crevice plants, Danthonia spicata, already mentioned, is one of the most important, on account of its abundance and its densely tufted habit of growth. Other noteworthy crevice plants are Solidago randii Britton var. monticola Porter, Potentilla tridentata, Artemisia candata Michx., Woodsia ilvensis (L.) R. Br., Campanula rotundifolia L. (harebell), Viola arenaria DC. (sand violet), Aquilegia canadensis L. (wild columbine), Panicum depauperatum Muhl. and Panicum meridionale Ashe.

Where a small amount of dry soil has accumulated, the following occur: Antennaria neodioica Greene (everlasting), Lechea stricta Leggett (pinweed), Panicum xanthophysum Gray, Satureja vulgaris (L.) Fritsch. (basil), Aralia hispida Vent. (bristly sarsaparilla), Apocynum androesimifolium L. (spreading dog bane), Epigaea repens L. (trailing

arbutus), Hieracium scabrum Michx. (hawkweed), Epilobium angustifolium L., Aster macrophyllus L., Corydalis semper-virens (L.) Pers., Cerastium arvense L., Fragaria vesca L. var. americana Porter, and Carex adusta Boott.

It will be noted that the above are perrennial species. A few annuals occur, such as Silene antirrhina L., (sleepy catchfly), Erigeron canadensis L. (horse-weed), and Polygonum Douglasii Greene. These annuals lead a precarious existence, as their seeds must, in the main, be washed over the cliff each year. The distribution of the above herbaceous species varies considerably from one point of the ridge to another. Their presence results in the accumulation of humus, especially in depressions or in connection with dead mats of Selaginella.

Accompanying the herbaceous vegetation are a few species of low shrubs, the commonest being species of blueberry (Vaccinium pennsylvanicum Lam. var. angustifolium (Ait.) Gray and Vaccinium nigrum Britton). These often form large patches slightly back of the summit, where more soil has accumulated. Other species found along the summit are:- Juniperus communis L. var. montana Ait., Rosa acicularis Lindl., Salix humulis Marsh., Dier-villa Lonicera Mill., Shepherdia canadensis (L.) Nutt., and stunted specimens of Juneberry (Amelanchier cana-

Fig. 30. - Transition to mesophytic forest (maple climax), top of ridge, at a point in sec. 14, T. 51 N. R. 43 W.; see description of quadrats 4 and 5.

densis (L.) Medic.

A few dwarfed specimens of white pine (Pinus Strobus) are scattered along the summit, but the species is much more common over the crest of the ridge (fig. 24), where it receives more shelter and moisture. The gray pine (Pinus Banksiana Lamb.) was noticed at only one point.

The limit of forest growth is bordered by a very distinct transitional zone all along the summit. The general character of this is shown in fig. 28, but it varies a great deal in composition at different points of the ridge, approaching more mesophytic conditions at lower elevations. Gnarled and stunted specimens of red oak (Quercus rubra L.) are mingled with aspen (Populus tremuloides Michx.) and white birch (Betula alba L. var. papyrifera (Marsh.) Spach.), the latter sometimes appearing in almost pure stands.

(c) Quadrat studies.

A detailed study of the transitional zone was made at a point in sec. 14, just west of the saddle (see map). This is typical of most of the ridge. Beginning at the area of bare rock surface shown in fig. 29, situated approximately 25 m. back from the face of the cliff, a series of four quadrats was taken in succession, the last being in the mesophytic forest (fig. 30). These quadrats were 10 m. square, making the total width of the transitional

Fig. 31. - Quadrats 4 and 5; see
fig. 29 and text.

zone 40 m. at this point.

QUADRAT 4 (fig. 31) was taken to include a portion of the rock surface (fig. 29), as well as the marginal tree growth. Here the soil was thin and dry, the ground sloping gently toward the south. Several small red pines (Pinus resinosa) represented the typical tree growth. They stood comparatively close, with small dead ones intermingled. Amongst the red pines were a few small white pines and balsams. Aster macrophyllus L. formed a large proportion of the ground cover. Besides this were several other species already mentioned as typical of exposed portions of the ridge, such as Salix humulis, Vaccinium spp., Artemisia caudata, etc.

QUADRAT 5 typified the zone of scrubby red oaks (fig. 32), a characteristic belt very often following the conifers. The oak growth consisted mostly of sprouts (up to 3 m. high) coming from old root crowns in very shallow soil. This quadrat came just north of the crest, so that the surface sloped gently towards the north. The conditions, however, were still xerophytic, as indicated by the presence of such plants as Aralia hispida, Danthonia spicata, and large patches of Funaria hygrometrica. There were also a few scattered seedlings of aspen, white birch and sugar maple. There were some evidences of burning on this

Fig. 32. - Zone of transitional tree growth at quadrat 5: note red pines, small red oaks, and aspens; bare rock surface in places; the conspicuous grass is Danthonia spicata.

quadrat, so that conditions might not have been entirely typical. Funaria hygrometrica was found to be very common in burned areas over various parts of the region. In general the oak sprouts seem to be the ecological equivalent of young red pine. The ground cover was much the same as the preceding quadrat, with the exception of Polygonum dumetorum, a very common species along the edge of the mesophytic forest.

QUADRAT 6 represents a transitional stage from quadrat number 5, in which the oak constituent has reached a higher stage of development, the individuals attaining a height of from 7 - 10 m., with much less sprouting, though still indicating somewhat unfavorable conditions. The presence of red maple and numerous sugar maple in the northern half of the quadrat indicated the transition to the mesophytic maple forest.

QUADRAT 7. The striking feature of this quadrat was the dominance (in numbers) of sugar maple saplings 5 - 10 cm. in diameter. Intermingled with these were well developed specimens of red oak (up to 15 m. or more high), hop hornbeam (Ostrya virginiana) and yellow birch (Betula lutea).

Following quadrat 7, the maples gradually increase in size, often accompanied by basswood and a thick

growth of red-berried elder (Sambucus racemosa), the latter disappearing or becoming less frequent in the denser shade of the mesophytic forest further down the slope. Along the upper limit of the maple forest, it is not uncommon to see the flat, upturned root systems of trees, especially maples, which have adapted themselves to a layer of soil not over 1 dm. thick over the rock surface. This area is more or less subject to windfalls, apparently not because the velocity of the wind is greater here than nearer the summit, but because it forms a critical line between the low types of trees which spread their roots out through the shallow soil, with crevice connections in many cases, and the taller types which owe their increased size to a deeper, richer soil, but which offer a greater leverage to the force of the wind.

The above description of the transition from rocky summit to mesophytic forest applies in general to the higher portions of the range. Variations naturally occur, depending on the elevation, exposure, local topography and depth of soil.

(2) The escarpment and its associations.

The height of the rock face or escarpment varies at different points along the range, as shown in fig. 24. The upper portion may be vertical or nearly

Fig. 33. - Overhanging ledge of cliff shown in fig. 25. E: shows dip of the strata (sandstone); various plants gain a foothold in the moist crevices (see text p.51).

so. The lower portion curves around to meet the talus slope, which is very steep at the top; or there may be a series of lower escarpments with shorter talus slopes between as shown at the left (fig. 24). Owing to the dip of the strata, the face of the cliff is always very uneven, and the seams of the rock, on account of the direction of dip, often retain a sufficient degree of moisture to support the more xerophytic tree types. The unusual severity of the situation so far as vegetation is concerned, is due to the continual splitting off of rock fragments from the parent rock.

The cliff is often broken by ledges, due to different resistances of the various kind of rock to weathering; these may vary in width from a few decimeters to several meters, with corresponding accumulations of soil. On the vertical rock faces, a few species of lichens may be found, such as Lecidea lucida Ach., Gyrophora vellea (L.) Ach. and Amphiloma lanuginosum (Hoffm.) Nyl. The vertical face of sandstone represented in A, fig. 26, is marked by bands of the yellow lichen, Placodium elegans. Where ledges overhang, as shown in fig. 33, the conditions are more moist on account of the shade. Amphiloma lanuginosum and the leafy liverwort, Radula complanata, are usually abundant; also various foliose and fruticose lichens, such

Fig. 34. - Rock ledge on face of escarpment, looking east: in the foreground, two small white pines and small specimens of Prunus pennsylvanica, Rhus typhina, and Cornus circinata; also Arctostaphylos Uva-ursi, Artemisia caudata, and Danthonia spicata; in the background, a small red pine, and leaves of oak (Quercus rubra) showing below; Parmelia conspersa on rock surface above and below; Woodsia ilvensis and Campanula rotundifolia growing from rock crevices (in foreground).

such as Physcia obscura (Schaer.) Nyl., Parmelia caperata (L.) Ach., Ramalina calicaris (L.) Fr., and Gyrophora vellea (L.) Ach. In the crevices of such ledges occur two characteristic fern species, namely, Polypodium vulgare L. and Woodsia ilvensis (L.) R. Br.

The flora of the exposed ledges is very variable. On the smaller, newer ledges, a few lichen species, such as Lecidea lactea (Plot.) Schaer. and Parmelia conspersa (Ehrh.) Ach. may gain a footing. On larger ledges, the higher plants are usually well represented, from small herbaceous species to trees whose roots are anchored in some of the bigger crevices (fig. 34). Typical species are shown in the figure. Among others may be mentioned Potentilla tridentata, Panicum xanthophyllum, Ceanothus americanus, Rubus parviflorus, Amelanchier canadensis, Polystichum lonchitis, Thuja occidentalis, and Juniperus communis L. var. montana Ait.

When there is a marked difference in rate of weathering between the sandstone and trap, a broad ledge 10 - 15 m. across may be formed (fig. 26A). On account of the greater deposit of soil and consequent storage of moisture, the conditions here are much more stable. Such an area may develop a comparatively thick stand of pine, thriving under the protection of the cliff.

The destiny of the escarpment is the condition seen

Fig. 35. - View of first range, looking east, in sec. 14: Carp River and valley to the right; shows stage in reduction of escarpment and advance of forest up the slope.

where at present saddles cross the range. Cutting will continue at the top and face, and filling will continue at the bottom until the lines of cut and fill meet. Invasion of mesophytic types will principally be from below, the summit holding out longest against the final mesophytic forest. Fig. 35 shows a stage approaching such a condition.

(3) Talus slope.

In general the width of the talus slope depends on the height of the escarpment, especially where the latter is not broken by large ledges. When the face of the cliff is low, the band of talus is comparatively narrow, for here the rock fragments from above do not come in sufficient numbers to prevent invasion of the forest below. Where the cliff is high, many of the larger fragments may roll 200 or 300 m., effectively checking the growth of the forest beyond this point. The resulting area is desolate in appearance (fig. 36), very little vegetation gaining a foothold except near the top and bottom.

Where the cliff is principally sandstone, the rock fragments are smaller and more flattened than where trap predominates. In the former case soil apparently collects more quickly and vegetation makes a more rapid invasion.

Fig. 36. - Bottom of talus immediately west of saddle in sec. 14, looking east: angle of slope here is about 30° ; note line of forest as it creeps over the saddle across the low point of the range; the cliff at this point is very high and the talus field 200 m. or more in width; shows characteristic clumping habit of white birch when growing in talus.

As pointed out before, there are two points on the talus where soil first begins to accumulate, namely, the bottom of the slope along the margin of the forest and the very top - at the foot of the escarpment. Most of that at the top is due to fine material which is washed over from the summit and held in place. This finer soil, coupled with the shadier conditions directly under the cliff, gives rise to a narrow strip of vegetation composed of a complex of species, some pioneer and some more or less mesophytic in character. Among the more important of these are Pinus Strobus, Pinus resinosa, Quercus rubra, Prunus pennsylvanica, Populus tremuloides, Ceanothus americanus, Psedera quinquefolia, Rhus Toxicodendron, Cornus circinata, Rhus typhina, Celastrus scandens, Ostrya virginiana, Arctostaphylos Uva-ursi, and Symphoricarpos racemosus Michx. var. pauciflorus Robbins. This plant assemblage, especially as regards the more mesophytic species, is only temporary, for as the cliff recedes, the vegetation must recede with it. As the height of the cliff becomes less, the increased light and lessened degree of moisture make conditions intolerant for the more mesophytic species. Finally, with the disappearance of the escarpment, only xerophytic species are able to endure, such as occur on the more exposed portions of the smaller talus slopes. The border of the forest forms a tension

Fig. 37. - Lichens and mosses on the talus slope (see fig. 35); the conspicuous foliose lichen is Parmelia conspersa; the three Cladonias (lower right) are C. rangiferina, C. sylvatica and C. pyxidata; Hedwigia ciliata (extreme left).

line at the bottom of the talus. Conditions for growth here are more favorable, not only on account of soil accumulation, but on account of the partial shade. Again, the pioneer species consist of lichens, which become more abundant here than higher up on the more exposed portions of the slope. By far the most conspicuous is Parmelia conspersa, which covers the top of nearly every fragment of rock (fig. 37). The humus derived from this species paves the way for fruticose forms, such as Cladonia rangiferina (L.) Hoffm., Cladonia sylvatica (L.) Rabenh. and Cladonia pyxidata (L.) Hoffm. Following the lichens or sometimes closely associated with them are three species of moss, namely, Thuidium abietinum (L.) Br. & Sch., Hedwigia ciliata Ehrh. and Ceratodon purpureus (L.) Bride. The two fern species already mentioned, Polypodium vulgare and Woodsia ilvensis, follow the lichens and mosses. They are very common along the bottom of the talus slope, sending their roots down between the slabs. An early stage of the mesophytic forest may then follow directly as shown in fig. 36, where the talus is fringed by white birch. The conspicuous omission of the usual mat stage here is due to the ability of the white birch to invade the talus before almost any other woody form. Clumping specimens with several stems often occur on the bare talus, sending their

Fig. 38. - An advanced stage in the invasion of the talus slope: note small size of rock fragments (sandstone); pioneer tree species consist of Populus grandidentata, small oaks (Quercus rubra), and small white pines (Pinus strobus).

roots far down between the fragments. In such cases they form nuclei for other pioneer species. Populus tremuloides and Populus grandidentata are the pioneers along some parts of the forest front.

As the cliff wears down and the talus slope becomes proportionately narrower, invasion from both the bottom and top is accelerated (fig. 38). This is partially due to the fact that less new talus is put down, allowing the forces of weathering to establish a residual soil in which many species soon anchor themselves. One of the most efficient of these is Panicum linearifolium Scribn. Evidence seems to show that it starts almost entirely by seeds from above. The warm nature of the talus soil, coupled with its moist condition during the early part of the season, must produce favorable conditions for germination of the many seeds which undoubtedly find lodgment there. Probably a very small percentage of the seedlings are able to endure the very dry conditions which obtain during the summer. Other species of grass, such as Danthonia spicata, Oryzopsis juncea, and Oryzopsis asperifolia also come in early. Arctostaphylos Uva-ursi and Aster macrophyllus L. form mats over the bare fragments, the latter plant being more prominent as conditions become shadier. Its large leaves form a very effect-

ive mosaic 1 - 2 dm. above the surface, enabling more mesophytic species to start. Associated with these in varying proportions are the brake (Pteris aquilina L.), the salmonberry (Rubus parviflorus Nutt.) and the bush honeysuckle (Diervilla lonicera Mill.), the latter often being very common on the upper, dryer portions of the slope.

The pioneer tree growth consists of small scattered individuals. If white birch be the pioneer species, which seems not always to be the case, it is soon followed by the poplar species already mentioned and by scrubby specimens of red oak. Besides many seedlings of the above, several other woody species appear more or less during the early stages of invasion such as hop hornbeam (Ostrya virginiana (Mill.) A. Koch.), arrow-wood (Viburnum dentatum L.), choke-cherry (Prunus virginiana L.), buffalo-berry (Shepherdia canadensis (L.) Nutt.), Rubus procumbens Muhl., Rosa acicularis Lindl., and seedlings of basswood, white ash and sugar maple.

Early herbaceous species, as such, hardly form a definite stage in the succession in the sense of paving the way for woody growth. They may precede or accompany the latter, but are later controlled by reaction. Among the commoner species may be mentioned Erigeron canadensis L.

(horseweed), Silene antirrhina L. (sleepy catchfly), Satureja vulgaris (L.) Fritch. (basil), Aralia hispida Vent. (bristly sarsaparilla), Convolvulus spithameus L. (erect bindweed), Carex adusta Boott., Antennaria neodioica Greene (everlasting), Fragaria vesca L. var. americana Porter (wild strawberry), Epilobium angustifolium L. (fireweed), Adlumia fungosa (Ait.) Greene (climbing fumitory), Apocynum androesimifolium L. (spreading dogbane) and Campanula rotundifolia L. (harebell).

The sequence of the invading associations varies greatly at different points along the range. While Betula alba var. papyrifera is the dominant pioneer tree species at some points, at others it is Populus tremuloides or Populus grandidentata. The exact ecological relationship between these three species is an interesting problem, but it was not worked out. Eventually the invading forest merges with the permanent fringe of forest below the talus. The latter is often dominated by sugar maple and red oak, but here again considerable variation occurs, which will be considered later.

(4) Forest below talus slope.

This extends in general from the flood plain of the valley below to the bottom of the talus slope above, pushing up toward the summit or even reaching it at low points in the range. It may vary in width from a mere

Fig. 39. - View of escarpment, looking north; vertical rock face about 70 m. high at this point; below this 200 - 300 m. of talus material, being invaded by pines and aspens; below the talus slope is the front of the advancing forest, which slopes to the valley of Carp River below.

fringe of trees as at A, fig. 26, to several hundred meters at F. While the trees species are mainly deciduous, especially above, conifers often occur near the bottom. These include white and red pine, balsam, arbor vitae, white spruce and hemlock. In fact, the last named species sometimes forms groves of large trees, similar to the climax forest of the north slope.

A transect of the forested area was made at a point just east of the saddle in sec. 14. Near the top, the talus slope was being rapidly invaded by small oaks and aspens, as shown in fig. 38, Populus grandidentata being the dominant species, intermingled with scattering white birch and maple saplings. A little further down, the open spaces became fewer, the trees taller (up to 15 m.), gradually forming a canopy above, giving perceptibly shadier conditions. The soil contained more humus, derived largely from the leaves of the aspens. Here patches of Aster macrophyllus and Aralia nudicaulis formed a large proportion of the ground cover. Occasional small specimens of white ash, balsam, hop hornbeam, and basswood were noted as invaders at this stage. The unfavorable conditions for anchorage produce remarkable clumping of the stems in certain species, especially in the sapling stage of the hop hornbeam, sugar maple and red oak. Nine stems were counted in one specimen of

Fig. 80. - Lower edge of forest, bordering flood plain: the large tree in foreground is black ash; in the background, Betula alba var. papyrifera, Populus tremuloides, Acer rubrum, Cornus stolonifera, Salix rostrata and Salix petiolaris.

hop hornbeam. Basswood overcomes the difficulty by excessive sprouting. Approximately half way down the slope, a bench occurred, 15 - 20 m. wide, and nearly level. A striking feature here was the appearance of rather large conifers, including specimens of white pine (up to 5 dm. dia.) balsam, white spruce, and arbor vitae. Poplar as the dominant species was replaced by red oak and white birch. More mesophytic conditions were indicated by the presence of such species as Smilacina racemosa (L.) Desf. (false spikenard), Galium triflorum Michx. (sweet-scented bedstraw), Hepatica triloba Chaix (liver-leaf), Maianthemum canadense Desf. (false lily-of-the-valley), Streptopus roseus Michx. (twisted-stalk) and Mitchella repens L. (partridge-berry). Gradually the oaks were replaced by the sugar maple, which became the dominant species to the edge of the flood plain, with white pine still frequent as a subdominant. At the edge of the forest bordering the flood plain, the increased light and moisture conditions produce a marked change in the ground cover, with a great diversity of species coming in. Seedlings of aspen (Populus tremuloides) and hazel (Corylus rostrata) seem to be responses to the increased light. The frequent occurrence of wild black cherry (Prunus serotina) along the margin of the forest is undoubtedly a response to the same conditions. Groves of aspen

Fig. 41. - Gullying on south side of first range, about halfway down the slope: white birch and aspen in the background; in the foreground, small specimens of sugar maple and yellow birch; shows clumping specimens of hop hornbeam (upper right); ground cover mainly composed of Aralia nudicaulis.

saplings mixed with white birch are not uncommon (fig. 40). The appearance of many other woody species is due more to the increased moisture along the margin of the flood plain. Among these may be mentioned Fraxinus nigra Marsh. (black ash), Salix discolor Muhl. (glaucous willow), Viburnum Opulus L. (cranberry-tree), Alnus incana (L.) Moench. (speckled alder), Acer rubrum L. (red maple), Spiraea salicifolia L. (meadow-sweet) and Cornus stolonifera Michx. (red-osier dogwood).

The complex of forest and flood plain species is very variable in its composition. This may be explained partly by the very unstable conditions in the valley and partly by changes in the edaphic conditions produced by gullying down the side of the range, with the consequent deposition of new soil near the bottom of the slope. A noteworthy instance of the latter occurs opposite the saddle in sec. 14 (fig. 41). Gullying in this case is due to the increased drainage over the saddle, resulting mainly from the melting snow in the spring. In the summer, its upper portion at least may be dry.

II. Hydrarch successions in the valley of Carp River.

As before indicated, the mesophytic forest below the talus slope is bordered by Carp River or its flood plain. This flood plain is comparatively broad in the

Fig. 42. - "Cedar swamp", north edge of Carp River valley: the large trees near the center are arbor vitae (Thuja occidentalis); the shrubs in the background are Alnus incana, and Cornus stolonifera.

vicinity of the lake, due to the flat nature of the valley. At this point the river is a sluggish, meandering stream 20 - 40 m. wide, doing very little vertical cutting, but shifting its course from time to time. Carp Lake is merely a broadened part of the river. According to Wright (28) the valley resulted not from the erosive action of a former river but to the pounding action of the waves on the shores of a vanished lake which covered the area. The present floor of the valley is subject to periodical flooding, in which a certain amount of sediment and debris from higher levels is laid down. There is thus a lack of stabilization in the edaphic conditions which prevents the encroachment of the mesophytic forest. The line of demarcation between forest and flood plain is usually very abrupt, as shown in fig. 40. Flooding has the effect of producing irregularities and telescoping in the hydrarch successions paralleling the river, so that these successions are evidently not playing a prominent part in the formation of the forest. There are a few points along the range, however, where transitional bog forests may be found. One occurs between secs. 13 and 18, T. 51 N. (fig. 42). This is near the mouth of a drainage system coming directly from the ridge. This forest is quite limited in extent. Its interest lies in the suggestion it gives as to the character of the bog

forest which will eventually precede the mesophytic forest as the latter claims the entire valley. The typical tree species are arbor vitae, white spruce, balsam, tamarack and black ash. The forest floor is rough and often covered with a mass of shrubs, fallen logs and herbaceous growth. The soil is typical muck, having a fine texture. In July the water table was approximately 3 dm. below the surface. Characteristic herbaceous plants are Aralia nudicaulis, Aster macrophyllus, Galium asprellum Michx., Aspidium cristatum (L.) Sw., Clintonia borealis (Ait.) Raf., Circaea alpina L., Carex leptalea Wahlenb., and Habenaria hyperborea (L.) Rydb.

The hydrarch successions of the river and flood plain contain many of the elements of typical peat bog areas such as described by Davis (10a) for the Upper Peninsula. On the other hand, there is a lack of definiteness in the sequence of the associations; and the sphagnum element, with its accompanying vegetation, is not at all common. The latter condition is due to the influx of fresh water during at least a portion of the year. A year of unusually high flood may destroy the continuity of vegetational development along certain lines. This is well attested near the intake of Carp Lake by the dead and dying trunks of small black ash trees. Periods of excessive flooding

Fig. 43. - Carp River from the summit of the first range, looking E. S. E.: the river flows west, emptying into Carp Lake; flood plain in the distance covered by an alder swamp.

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may approximately be measured by the oldest of these. After such periods of high water, pioneer species again come in, initiating a new course of succession. A patchwork results, which is especially evident in the shrubby vegetation. This patchwork is further modified by the varying ability of the different species to withstand the presence of excessive water about their roots. The shorter-lived herbaceous forms often show more definite zonation, especially along such restricted areas as mud flats or sandy beaches bordering the river or lake. They are able to adapt themselves more readily to changing conditions.

In order to illustrate the tendency of the hydrarch successions in the valley, the associations found in the river, lake and flood plain, will be briefly described.

a. Carp River (fig. 43).

Where this stream flows through the flood plain it is comparatively shallow with a muddy bottom. The slow-moving current makes the ecological conditions very similar to those found along the margins of many of the smaller lakes in the Upper Peninsula. Among the immersed aquatics may be mentioned, Potamogeton pusillus L., Potamogeton heterophyllus Schreb., Potamogeton zosterifolius Schumacher, Potamogeton amplifolius Tuckerm.,

Fig. 44. - Carp River near north edge of flood plain: the shrub lining the bank at this point is principally Alnus incana; the aquatics are Sparganium eurycarpum and Nymphaea advena; top of first range just visible in the background (upper right).

Potamogeton natans L., Myriophyllum Farwellii Morong.,
Ranunculus aquatilis L. var. capillaceus DC., Hippuris
vulgaris L.

The commonest large aquatic is Nymphaea advena Ait. (yellow pond lily); it sometimes forms patches extending half way across the stream. Castalia tuberosa (Paine) Greene (white pond lily) is much less common, though it occasionally occurs in large patches; the same may be said of the water-shield (Brasenia Schreberi Gmel.). In many places the stream is fringed with overhanging shrubs as shown in fig. 44. Mud banks often occur at the bends, supporting various aquatic or amphibious species, such as Potentilla palustris (L.) Scop. (marsh cinque-foil), Sparganium angustifolium Engelm. (bur-reed), Eleocharis acicularis (L.) R. & S., Carex filiformis Good. (bog sedge) and Carex stricta Lam. The last two species form clumps at various points along the bank, thus enabling other species to obtain a footing.

The shrubby growth along the banks consists principally of the following:- Alnus incana (L.) Moench. (hoary alder), Ilex verticillata (L.) A. Gray (winter-berry), Cornus stolonifera Michx. (red-osier dogwood), Chamaedaphne calyculata (L.) Moench. (leather-leaf), Spiraea salicifolia Roi (meadow-sweet), Salix petiolaris

J. E. Smith, Salix pedicellaris Pursh (bog willow) and Salix lucida Muhl. (shining willow). Two fern species, namely Osmunda regalis L. and Aspidium Thelypteris (L.) Sw., often occur at the margin of the water, more or less shaded by the shrubs. Chara calyculata, though not the commonest shrub lining the river bank, is probably the most important in the formation of floating mats, these often starting from sedge hummocks. One effect of the mats is to cut off quieter bodies of water where various aquatic and amphibious species are more successful in establishing themselves.

One thing seems clear in connection with the successions along the margin of the river, namely their instability. Even when Carp Lake as such, is gone, the river will still continue, though not in its present bed, as the bottom of the valley will have been raised through sedimentation.

b. Carp Lake (fig. 1).

The lake lies parallel to the main ridges, covering the floor of the valley for a distance of about 2 km. Its broadest portion is near the east end, where it has a width of approximately 0.5 km. Excepting at this end, the mesophytic forest extends nearly to the water's edge. At the east end a broad delta has been

Fig. 45. - Delta, east end of Carp Lake, looking east:
in the foreground, Scirpus occidentalis, Equisetum fluviatile,
and Nymphaea advena; narrow channel of the river shown in the
background; first range in the distance, showing saddle in
section 14.

formed, where Carp River enters the lake (fig. 45). The submerged part of the delta extends well out into the lake, being several hundred meters broad at its widest portion (fig. 46). Here the water is shallow, varying from 3 - 10 dm. in depth. The west end of the lake is also shallow, and choked with aquatic growth and debris, especially near the outlet. In general the beaches are very narrow. Most of those on the north side are of the shingle type. In places they are entirely lacking, the shore line being directly bordered by a fringe of shrubs similar to those along the bank of the river. Sandy beaches occur on the south side and near the west end on the north side. They are broader than the gravel beaches and show more clearly the zonal development of vegetation. The edaphic conditions are naturally more stable around the margin of the lake than along the river. Especially is this true on the south side where deposition is occurring more rapidly than on the north.

The free-floating aquatic vegetation of the lake, being very similar to that of the river, need not be mentioned. The best evidences of plant succession are seen on the flat sandy beaches and on muddy flats near the delta. At the delta there is a zone of rushes extending from 50 - 100 m. out into the lake. Its outer part consists

Fig. 46. - East end of lake, looking south toward second range: the zone of rushes (Scirpus occidentalis) marks the shallow water over the submerged portion of the delta; the group of balsams along the opposite shore indicates the presence of a small stream flowing into the lake.

of the bulrush (Scirpus occidentalis (Wats.) Chase; then comes a zone of Equisetum fluviatile L. (pipes) covering a large area. The inner portion of the zone consists of a mixture of Glyceria borealis (Nash) Batchelder (northern manna grass), Leersia oryzoides (L.) Sw. (rice cutgrass), and along the muddy shore Eleocharis palustris (L.) R. & S., Acorus Calamus L. (sweet flag), Dulichium arundinaceum (L.) Britton, Polygonum amphibium L. (water smartweed), Glyceria canadensis (Michx.) Trin. (rattlesnake grass), Scirpus atrovirens Muhl., Eleocharis obtusa (Willd.) Schultes (blunt spike-rush) and Sagittaria latifolia L. forma Gracilis (Pursh) Robinson, apparently the common form in northern Michigan. The immediate shore is fringed with clumps of Salix lucida, interspersed with open areas covered with Calamagrostis canadensis (Michx.) Beauv. (bluejoint). Logs lying almost concealed tell the story of flooding at this point; this is also shown by standing specimens of Alnus incana and Salix petiolaris, dead above, but making vigorous new growths at the base.

In the shallow water bordering the sandy beaches, the rushes are often accompanied by areas of pipewort (Eriocaulon articulatum (Huds.) Morong. This may produce unusually long stems when growing with Scirpus occidentalis. Among the commoner species occurring on the

sandy beaches are the following:- Juncus brevicaudatus (Englem.) Pernald, Hypericum ellipticum Hook. (pale St. John's wort), Cladium mariscoides Torr. (twig-rush), Ranunculus Flammula L. (smaller spearwort), Mimulus ringens L. (monkey flower), Sium cicutaefolium Schrank (water parsnip), Agrostis hyemalis (Walt.) BSP. (hair grass), Carex erinita Lam., Carex rostrata Stokes, and Carex Oederi Retz. Both the sandy and gravelly beaches are very often backed by a shrubby association composed of Chamaedaphne calyculata, Ilex verticillata, and Alnus incana. With these often occur Spiraea salicifolia and Praxinus nigra, fringing the mesophytic forest.

It is evident from the above description that the transition from lake to mesophytic forest is rather abrupt; this is especially true on the north side of the lake, where the angle of slope is greatest. The few associations noted along the narrow beaches consist of plants which are able to endure submergence for brief periods. The shrubby growth backing the beaches, though only a little above the mean level of the lake, is high enough to escape mostly the destructive influences of high water.

c. Flood plain.

On account of the varying influence to which the flood-plain is subjected, the successions are not

in general, well marked. In the broader portions of the valley, as in sec. 24, T. 51 N. R. 43 W., there is a dense growth of Alnus incana, intermingled with occasional individuals of tamarack. In the northwest corner of the above section there is a small "tamarack swamp", forming a typical stage in the filling up of a peat bog. The ecological stages of such a bog have been well described by Transeau (25), Cooper (5), and others and will not be treated here. In sections 23 and 14, immediately east of the lake, the floodplain is covered by a grassy marsh (fig. 40), with a shrubby zone lining the river, as already described. The flora of this area is very composite in character. Portions of it are dominated by a dense growth of blue joint (Calamagrostis canadensis). The list of species observed here includes the following:- Asclepias incarnata L., Verbena hastata L., Aster puniceus L., Eupatorium purpureum L., Scirpus Cyperinus (L.) Kunth., Osmunda regalis L., Onoclea sensibilis L., Solidago serotina Ait., Anemone canadensis L., Chelone glabra L., Aspidium Thelypteris (L.) Sw., Pteris aquilina L., Glyceria canadensis (Michx.) Trin., Lysimachia terrestris (L.) BSP., Iris versicolor L., Cicuta bulbifera L., Scutellaria lateriflora L., Thalictrum dasycarpum Fisch. & Lall., Galium asprellum Michx., Geum strictum Ait., Impatiens biflora Walt., Rumex verticillatus L., Hypericum virginicum L.,

Campanula uliginosa Rydb., Phalaris arundinacea L., Clematis virginiana L., Leersia oryzoides (L.) Sw., Humulus Lupulus L., Ranunculus pennsylvanicus L. f., Galium Claytoni Michx., Radicula palustris (L.) Moench., Carex filiformis L., and Carex tribuloides Wahl.

The grassy marsh described above undoubtedly occupies the position of a former delta. It thus represents a stage in the gradual filling up of the valley with sediment and organic remains.

SUMMARY

The ranges of the Porcupine Mountains are entirely surrounded by a low plain, so that the mountains were islands for some time after the final retreat of the ice sheet. As the water subsided, the higher ranges to the south were first uncovered. Pioneer invasion probably took place where the wash of the waves was not too severe, following stages analagous to those found in the present shore line. At the present time, these southern ranges or hills, including Government Peak, the highest point, are clothed with a mesophytic forest to the very top (fig. 1). This mesophytic forest was possibly preceded by a xerophytic coniferous forest dominated by pine species, as

suggested by Ruthven (1,p. 27). In this case the pines began their invasion near the water's edge, following the heath mat stage. They made their last stand at the top of the mountains, being followed up and replaced by a mesophytic forest, the successions being correlated with the greater accumulation of soil near the base of the slope.

The top of the first range is unique in still holding out against the mesophytic forest. This is undoubtedly due to the peculiar topography of this range. As is evident from fig. 3, this topography is associated with the presence of Carp Lake, which once covered a much greater area than at present. The dip of the strata toward the north, coupled with the subsidence of Carp Lake, has created a great cliff or escarpment, which is continually wearing away, producing a talus slope at its foot.

The development of vegetation over the region has led to two climax formations, namely the hemlock climax and the maple climax.

The presence of the hemlock climax on the north slope of the first range seems to be conditioned by the physical factors of temperature, moisture and light. Greater humidity and more uniformity in temperature near the shore is due to the presence of a large body of water. The

average temperature of points along the coast is several degrees warmer than inland points a few miles back, and the average precipitation during the winter months is 30% more than at Bergland, 26 km. back from the shore. Reduced light intensity at the lower, more humid elevations on the north slope is probably more favorable to hemlock as compared with maple.

The maple climax occurs on the higher portions of the first range (excepting the summit) and on the ranges further south. As compared with hemlock, maple seems to be more tolerant of extremes of temperature and light.

The principal succession leading to the hemlock climax is along the shore. The pioneers in the more exposed situations are crevice plants. In the severer situations these can initiate only very short or incomplete lines of succession. Where conditions are less severe, which may be only a few meters further inshore, the pioneers consist of lichens, mosses and crevice plants, which lead to more definite lines of advance; but the irregularities of the shore line produce such varied conditions that there is often a lack of any gradual transition from lower to higher ecological forms. At practically all points along the shore, the climax forest has pushed down to the limit of its possible extension under present conditions; and this has

resulted in a telescoping of the ordinary transitional stages.

Lines of succession leading to the maple climax may be seen at the summit of the first range and in the valley of Carp River. In the first case the climax is reached through xerarch series, beginning with crustose lichens and xerophytic mosses on the exposed rock surface of the summit. One of the principal pioneers is Selaginella rupestris, which often forms a layer of humus 1 - 2 dm. thick. This together with various low-growing species, including crevice plants such as Danthonia spicata and Panicum depauperatum, paves the way for the heath mat, which is composed largely of two species of Vaccinium (see text). A zone of scrubby conifers and oaks then leads gradually to the maple climax on the north side of the summit.

On the south side the presence of the cliff forms a direct barrier to invasion from below, except where the escarpment has been worn down so as to produce a saddle across the range. Below the escarpment there is a talus slope of varying width, fringed by a mesophytic forest extending below to the flood plain of Carp River. In general this mesophytic forest is young and heterogeneous in character, but it is approaching the maple climax. Its upper border is irregular, but forms a more or less sinuous

curve representing a line of invasion on the talus. Since the width of the talus depends on the height of the escarpment, the line of invasion extends high at low points in the range.

Successional continuity on the talus is more or less broken, at least in the earlier stages. Lichens and certain moss species are undoubtedly important, but Betula alba var. papyrifera is one of the noteworthy pioneers adapting itself to unusually severe conditions. This is followed sooner or later by aspens, after which there is a gradual transition toward the mesophytic climax.

As the cliff wears down the summit of the range will eventually be claimed by the mesophytic forest. At present the xerarch series forms a connecting link between the maple climax in the valley and on the north side of the summit.

The lower edge of the mesophytic forest below the talus forms an abrupt border to the flood plain of Carp River. This is due to periodical flooding, which produces irregularities and telescoping throughout the hydrarch series on the comparatively flat floor of the valley. Any marked building up of the mesophytic climax from this source must therefore await a change in physiographic conditions along the river valley. This will

Fig. 47. - Diagram showing lines of vegetational development leading to the maple climax on the first range.

come with the gradual filling up of the valley through sedimentation, thus changing the conditions under which flooding now occurs. The present successions along the valley of Carp River and Carp Lake are of comparatively little moment; however they indicate the character of a portion of the hydrarch series which will eventually lead to a mesophytic climax covering the entire floor of the valley.

The principal zones of vegetation in connection with the development of the maple climax on the first range are shown in the diagram (fig. 47). The letters a, b, c, d, indicate the lines of succession. The line a begins with lichens, mosses, and crevice plants at the bare summit, and culminates in the maple forest on the north slope; b originates largely from seeds washing over the summit; c represents a line of invasion on the talus slope from the forest below; d is a broken line representing the discontinuous nature of the hydrarch succession from the valley of Carp River. Part of this succession leads to the mesophytic forest on the second range.

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