The University of Chicago
FOUNDED BY JOHN D. ROCKEFELLER

THE CLIMAX FOREST OF ISLE ROYALE LAKE SUPERIOR, AND ITS DEVELOPMENT

A DISSERTATION

SUBMITTED TO THE FACULTY OF THE OGDEN GRADUATE SCHOOL OF SCIENCE IN CANDIDACY FOR THE DEGREE OF DOCTOR OF PHILOSOPHY

(DEPARTMENT OF BOTANY)

BY
WILLIAM S. COOPER

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THE CLIMAX FOREST OF ISLE ROYALE, LAKE SUPERIOR, AND ITS DEVELOPMENT. I

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 165

WILLIAM S. COOPER

(WITH MAP AND FOURTEEN FIGURES)

Introduction

Eastern North America north of Florida and Mexico is divided into two great phytogeographic regions, the eastern deciduous forest and the northeastern conifer forest. In each of these a number of lines of succession may be traced, all those of a region leading to a certain forest type as the final or climax stage. This final type in its large features is determined by climate, and is much the same throughout the region which it dominates. In the eastern deciduous forest the climax type is made up of *Acer saccharum* Marsh (sugar maple) and *Fagus grandifolia* Ehrh. (beech), with the addition of various other species in some portions of the country. The nature of the climax forest of the northeastern conifer region has not hitherto been determined.

Isle Royale lies just within the limits of the northeastern conifer region, barely within, for one of the farthest outposts of the deciduous forest is located on its southwestern end, where there is a considerable area dominated by the sugar maple, in mixture with more northern trees. Except for the maple and a few of its companion species, the flora of Isle Royale belongs strictly to the northeastern conifer region.

The purpose of the present work was to determine the climax forest of Isle Royale, its composition and character, and to trace the various lines of succession leading to it. It is thus a successional study of a small component portion of the northeastern conifer forest.

At the beginning of the investigation Isle Royale was selected as a field of study because it shows transitional features between the two great forest regions, my original purpose being to devote particular attention to the relations between the conifers and the maple. Circumstances made it impossible to give adequate study to the region dominated by the latter, therefore the work developed into an investigation of the balsam-birch-spruce forest (the northeastern climax) and its attendant successions. For a study of the northeastern conifer forest a more centrally located area might have been preferable; for instance, at some point midway between Lake Superior and James Bay. It will be shown, however, that Isle Royale affords a very fair sample of the forest growth of the northeastern region. It also possesses certain very important advantages which would be lacking in a more centrally located area. Because of its insular position the forest has been less liable to destruction by fire, and the many bays and channels separating various portions of the main island and the outlying islets have served as effective barriers against its spread. Though they have occurred many times during the island's history, it is certain that fires have been far less frequent and destructive here than upon the mainland. The forest may thus be studied in a condition that is as near to being undisturbed as will be found anywhere. Comparative freedom from the destructive agency of man is a second advantage. Again, the island has had a simple physiographic history during the present vegetative cycle, and thus the relation of vegetation to physiography may be the more readily made out. Further, the proximity of the lake shores permits the observation of the earliest stages in the establishment of vegetation upon the rock surfaces, these stages being frequently absent or poorly developed in an inland locality. Finally, the fact that the field of study is an island gives definiteness to the area covered by the investigation.

Headquarters were established at the Park Place Hotel on Rock Harbor (sec. 4, T. 66 N., R. 33 W.), and field investigations were carried on upon the island during the summers of 1909 and 1910. Most of the detailed work was done in the vicinity of Park Place, but the coast was visited from Hawk Island to Blake Point on the northwest, and from Blake Point to the head of Siskowit Bay on the southeast. Excursions into the interior were made from various points along this stretch of shore.

The study was undertaken at the suggestion of Dr. HENRY C. COWLES of the University of Chicago. I wish to express my appreciation of his invaluable assistance and co-operation, freely given at all times during the progress of the investigation. I desire also to extend my thanks to Dr. M. L. FERNALD of the Gray Herbarium of Harvard University, who determined all doubtful spermatophytes and pteridophytes, and to Miss EDITH A. WARNER of Brooklyn, N.Y., who determined the mosses collected upon the island, about 80 in number. The nomenclature of the pteridophytes and spermatophytes is that of the seventh edition of GRAY'S *Manual.*

PREVIOUS BOTANICAL WORK UPON ISLE ROYALE

A limited amount of botanical work of taxonomic and ecological nature has been done upon Isle Royale. In 1848 W. D. WHITNEY, acting as naturalist for a government exploring party, made a brief list of plants found upon the island, which was published in the report of the expedition (**24**) in 1851. In 1890, according to ADAMS (**4**), F. E. WOOD made a collection of plants in the vicinity of Rock Harbor and presented them to the University of Michigan. In 1901 W. A. WHEELER (**58**) published a list of noteworthy species, reporting for the first time the strange occurrence of *Fatsia horrida* (devil's club) upon the island.

In 1904 and 1905 Isle Royale was visited by parties from the Museum of the University of Michigan, both equipped for ecological work among plants and animals. The first, under the leadership of Dr. A. G. RUTHVEN (**3**), spent three weeks upon the island, after a month's work in the Porcupine Mountains of the northern peninsula of Michigan. Their explorations were confined to the southwestern end of the island. In respect to the vegetation the results of this expedition consist in scattered ecological notes and a list of plants including only 91 species (**49**).

The second party, headed by Dr. C. C. ADAMS, devoted all its time (about six weeks) to Isle Royale, and the resulting report is incorporated in a volume of more than 400 pages (**4**). The botanical work was done by HOLT (**33**), whose report comprises a ten-page account of the plant societies, and an annotated list of lichens, mosses, ferns, and seed plants, including 364 species. There is also much of ecological value to be found in the sections by ADAMS, and the report by GLEASON upon the ecology of the invertebrates (**29**).

Two papers by the present writer (**12, 12*a***) should also be mentioned, as they were suggested by observations upon Isle Royale.

TOPOGRAPHY AND PHYSIOGRAPHIC HISTORY

Isle Royale is situated in the northwestern part of Lake Superior in lat. 48° N., long. 89° W., about 25 km. distant from Thunder Cape, which is the nearest point of the Canadian mainland. The island is elongated, extending northeast and southwest, and its dimensions are 72 km. by 14 km. at the widest part. It is formed of several parallel ridges which are made by the resistant centers of successive outcrops of a series of Keweenawan lava flows. These dip southeastward at angles varying from 5° to 40°. The southeast slopes of the ridges are gentle, corresponding with the dip of the beds, while the northwest faces are steep and broken, often precipitous. Several of them extend into the lake at either end of the island as promontories or rows of small islands (fig. 1). The largest, the Greenstone Range, stretches the whole length of the island, and is continued northeastward in Passage Island and Gull Rocks. At several points it reaches an altitude of more than 150 m. above the lake level. Between the ridges are narrow valleys, corresponding with the less resistant peripheral portions of the flows and the sedimentary layers that are interbedded with them. These contain many lakes, and where submerged at the ends of the island form narrow fiord-like harbors and channels. The drainage is well adjusted to structure, the streams flowing along the strike of the less resistant beds, entering the lake at the ends of the valleys, or occasionally through narrow cross valleys, most of which are due to faults.

The quaternary history of Isle Royale is briefly as follows: At the beginning of the glacial period the topography, produced during a long period of subaerial erosion, was essentially as now. The ice completely covered the island, moving southwestward nearly with the strike of the beds, but wrought only slight modifications in the topography. Rock basins were excavated in the

Fig. 1.—Southeast across Scovill Point and the outer islands from the slope of the Greenstone Range: Tobin's Harbor in the foreground; Rock Harbor beyond; Lake Superior in the distance.

valleys and many surfaces were smoothed and striated. *Roches moutonnées* are common. Of the little drift that was left behind most was dropped upon the southwest end, and practically all has been rehandled by the waters of the successive postglacial lakes.

Upon the retreat of the ice, Isle Royale was left entirely submerged beneath the waters of Lake Duluth. The remaining history records a gradual emergence corresponding with the repeated changes of the water level as the lake found successively lower outlets. That this emergence was frequently interrupted is shown by the beaches, sea cliffs, and wave-cut terraces that occur at various altitudes, corresponding with similar ones along the mainland coast. These indicate periods when the water level was stationary for a considerable time. According to LANE (36) the present shore line is more strongly marked than any at higher levels. "Nor is it surprising," LANE remarks, "that the lake level should now be tolerably constant, for Lake Superior now drains over a rock threshold." In comparatively recent post-glacial time (since the formation of the very recent Nipissing beach) tilting occurred in the Lake Superior region, with uplift northward. This must have modified more or less the drainage conditions upon Isle Royale. It is important to bear in mind the self-evident fact that never since its first emergence from the waters of Lake Duluth has Isle Royale been connected with the mainland.

For further geologic and physiographic details the reader is referred to LANE'S report (36), to which I am indebted for the material for this brief sketch; and also to ADAMS (4), who discusses the physiographic history of the island with considerable fulness. ADAMS also gives much valuable data concerning the influence of the lake storms and surface currents upon the biota of the island.

PHYSIOGRAPHIC AGENCIES NOW AT WORK

The agencies that are now modifying the surface of the island, which are of course the same that have been active throughout its history, may be considered under two heads.

Among the DESTRUCTIVE agencies, *weathering* is of the greatest importance in its influence upon vegetation. It is most evident upon the steep northwest slopes of the higher ridges. Here there are somewhat extensive talus piles lying at the bases of cliffs, or in some cases occupying the whole slope, the cliff having been buried by the accumulation of fragments. In many places the talus is fully clothed with climax forest, in others the fragments are bare or merely lichen covered. The results of weathering are evident also upon the bare rock shores, where scales and plates are seen to have been split from the rock surfaces through the agency of temperature changes. Very important, though effectually concealed, is the chemical action which is going on beneath the humus carpet that covers most of the island's surface. Between the humus and the bed rock there is nearly everywhere a layer of small rock fragments mixed with organic matter. Most of these fragments are so decomposed that they can be cut easily with a knife. The bed rock itself frequently shows the effect of chemical action. Vegetation is here seen as an important physiographic agent.

Stream erosion is of trifling importance upon Isle Royale because of the small size and low gradient of most of the streams and their freedom from transported materials, necessary as agents of abrasion.

Wave erosion is the most conspicuous of destructive agencies. The surf is actively cutting into the land, and the shore features at the present lake level are very pronounced. At many points along the southeast coast the normally gentle slope of the shore has been transformed into terrace and cliff. In some parts of the abrupt northwest shore the waves are undermining the climax forest itself. In connection with erosion by waves should be mentioned the work of ice, the precise effects of which could not be determined in summer study.

Under the head of CONSTRUCTIVE agencies come deposition by streams, waves, currents, and vegetation. The only notable instances of stream deposition are the few deltas, the materials for which were derived largely from the glacial drift and the products of wave erosion at former levels. The subject is treated further under the head of "Delta swamp succession." The fragments eroded by waves are deposited in the form of beaches and bars, in coves and harbors. Shore currents are effective in transporting the material, and in sweeping the finest into sheltered bays, where it is dropped in the quiet waters. The work of vegetation consists in the formation of peat and humus. Plant life here again appears as a physiographic agent of great importance.

CLIMATE

ADAMS (**4**, pp. 41–44) has described in some detail the climate of the general region, his data being obtained from the records of the Weather Bureau at Port Arthur. The following summary (table I) is derived partly from ADAMS' account and partly from more recent data from Port Arthur obtained through the courtesy of the Canadian Weather Service.

TABLE I

NORMAL TEMPERATURE AT PORT ARTHUR FOR THE 20 YEARS 1888–1907

	Jan.	Feb.	March	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Yr.
° C.	−13.9	−13.7	−7.2	1.7	7.7	13.6	16.8	15.6	11.6	5.3	−2.8	−9.8	2.1

The average maximum temperature for the ten years 1896–1905 was 30.1° C.; the average minimum for the same period was −34.9° C. The mean monthly temperature was below 0° C. for five months, and the mean monthly minimum below 0° C. every month except June, July, and August. The growing season is thus short, including about four months, or even less, between the middle of May and the middle of September. The long northern period of daylight compensates somewhat for the short season.

TABLE II

NORMAL PRECIPITATION AT PORT ARTHUR FOR THE 20 YEARS 1888–1907

	Jan.	Feb.	Mar.	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Year
cm.	1.77	1.31	2.44	4.18	5.56	7.67	9.82	7.77	8.23	6.49	3.15	1.77	60.16

It is here seen that the greater part of the precipitation takes place during the growing season; 39.05 cm., or more than three-fifths of the total, occurs during the months May–September. The snowfall is rather light; during the six years 1900–1905 the average was 61.03 cm. Reduced to water this amounts to a precipitation of 6.1 cm., which is about one-tenth of the average total for that period.

The evaporation rate is doubtless low because of the low temperature, but there are no data available. This and the relatively abundant precipitation during the growing season seem adequate to account for the extreme mesophytism of the forests of the region.

Since 1906 temperature and precipitation records have been kept during the season of navigation by Captain MALONE at the lighthouse on Menagerie Island. This is one of the Isle Royale archipelago situated 4 km. distant from the nearest point of the main island. During the summer of 1910 I kept thermograph and rain gauge records at Park Place. There is therefore opportunity for a partial comparison of the insular climate with that of the mainland. Summarization of the records for Port Arthur, Park Place, and Menagerie Island gives the following results:

TABLE III

TEMPERATURES ° C.

		June	July	August
Port Arthur	Mean maximum	23.4	23.9	21.3
	Mean minimum	10.4	11.7	10.0
	Mean daily range	13.0	12.2	11.3
Park Place	Mean maximum	....	21.4	21.4
	Mean minimum	....	12.4	12.9
	Mean daily range	....	9.0	8.5
Menagerie Island	Mean maximum	17.0	18.8	19.4
	Mean minimum	7.1	10.5	13.1
	Mean daily range	9.9	8.3	6.3

From this table we see that the maxima upon Isle Royale are lower than upon the mainland, during the summer at least. Menagerie Island, most under the lake's influence, is the lowest, and Park Place, upon the main island, is intermediate. We may infer that as a result of lower temperatures the evaporation is less upon Isle Royale. ADAMS (4, p. 44) suggests that insular location and imperfect drainage probably operate to reduce evaporation. The table also shows that the Isle Royale climate is characterized by less pronounced daily temperature changes than is that of the mainland. The daily range is shown to be uniformly greatest at Port Arthur, intermediate at Park Place, and least at Menagerie Island.

A further comparison (table IV) brings out the fact that the proximity of the lake retards the opening of the growing season, but also that the same factor prolongs it into the fall.

TABLE IV

MEAN MONTHLY TEMPERATURES (° C.) MAY–NOV.; AVERAGE 1906–1909

	May	June	July	August	Sept.	Oct.	Nov.
Port Arthur	7.9	13.6	16.9	15.9	11.6	5.7	−1.7
Menagerie Island	4.3	8.9	11.6	14.4	12.6	6.8	1.9

Evidencing the retardation of the season is the fact that ice frequently remains in sheltered places on the northwest coast of the island into July. I have seen a deserted mine shaft filled solid with ice on July 4. FOSTER and WHITNEY report ice "under the shade of crags, and among the thick evergreen swamps of white cedar."

In precipitation there is apparently not much difference between Port Arthur and Isle Royale, at least during the growing season. As far as the records go the mainland has a slight advantage.

TABLE V

AVERAGE PRECIPITATION MAY–NOV., 1906–1909

Port Arthur	48.00 cm.
Menagerie Island	43.74 cm.

From the foregoing data, which unfortunately are rather fragmentary, it appears that there is at present no ground for concluding that the island climate is effective in producing a more mesophytic type of vegetation than that of the mainland, or vice versa. The lower evaporation rate upon the island, due to lower temperature, is balanced by a less precipitation during the growing season; and the growing season, although retarded in its commencement upon the island, is apparently as long as upon the mainland. The question cannot fully be settled without fuller precipitation records from Isle Royale and a determination of the actual evaporation rates in the two localities. The data presented, however, indicate, so far as they go, that the insular position of the field of study does not seriously affect its value as a fair sample of the region dominated by the northeastern conifer forest.

Part I.—The climax forest

The forest that completely clothes the surface of Isle Royale, with the exception of a part of the bog areas, some limited stretches of xerophytic character, and the small portion dominated by the maple, is made up largely of three trees: *Abies balsamea* (L.) Mill (balsam fir), *Betula alba* L. var. *papyrifera* (Marsh) Spach (paper birch), and *Picea canadensis* (Mill) BSP (white spruce). The studies embodied in the present paper show that this type is the climax forest of that portion of the northeastern conifer region under consideration; in other words, that upon Isle Royale it is the final and permanent vegetational stage, toward the establishment of which all the other plant societies are successive steps. It is the "climatic" forest of the region, permanent while the climate remains essentially as now.

The evidence in support of this conclusion lies along four lines: (1) extreme mesophytism of the forest; (2) its uniformity of development; (3) all successions lead to it; (4) maintenance of equilibrium. These lines of evidence will now be considered in order.

1. MESOPHYTISM.—The balsam-birch-white spruce forest is the most mesophytic of all the plant societies of the island. The truth of this statement will appear during the discussion of other points and so no further treatment is necessary here.

2. UNIFORMITY OF DEVELOPMENT.—In all places where it occurs, whether upon rock surfaces or reclaimed bogs, upon the part most recently emerged from the lake or upon the highest ridge, the dominant forest is essentially uniform in character. The tree species are the same, and they bear everywhere the same relations to each other.

3. ALL SUCCESSIONS LEAD TO THE BALSAM-BIRCH-WHITE SPRUCE FOREST.—In a later portion of this paper the various successions are treated in detail, and it is shown that all end with the establishment of the balsam-birch-white spruce forest. In other words, those phases of the vegetation that are not uniform in character with the main forest mass are plainly tending toward uniformity. The successions upon Isle Royale may be classified as follows:

A. Primary successions
  - I. Xerarch[1] successions
    1. The rock shore succession
    2. The beach succession

[1] The terms *xerarch* and *hydrarch* are here used for the first time, for the purpose of indicating a natural and important classification of plant successions. The former is applied to those successions which, having their origin in xerophytic habitats, such as rock shores, beaches, and cliffs, become more and more mesophytic in their successive stages; the latter to those which, originating in hydrophytic habitats such as lakes and ponds, also progress toward mesophytism.

II. Hydrarch successions
1. The bog succession
2. The delta swamp succession

B. Secondary succession
The burn succession

4. Maintenance of equilibrium.—It has been possible to state with brevity the three points that have so far been presented; indeed, to one visiting the island they are almost self-evident. The validity of the fourth is not so plainly to be seen.

Both observational and experimental studies have shown that the balsam-birch-white spruce forest, in spite of appearances to the contrary, is, taken as a whole, in equilibrium; that no changes of a successional nature are taking place within it. Superficial observation would be likely to lead to exactly the opposite conclusion. In the presence of the other good evidences of permanence outlined in the preceding paragraphs, it became necessary to seek for an explanation of the seeming condition of rapid change that was apparently so plain in the forest. The solution was found in the course of a detailed study which included (1) the characteristics and life history of each tree species and of certain of the lower forms which were of importance, and (2) all the processes and changes brought about through the interrelations of the forest species, discovered by intensive study of a number of limited areas of definite size (quadrats), with every available source of evidence laid under contribution; in other words, an attempt at a thorough investigation of the dynamics of the forest. In the following discussion the results will be given under three heads: I. Description of the forest; II. Studies of individual species; III. Quadrat studies.

I. Description of the forest

For the sake of concreteness I have selected a definite locality for description, bearing in mind, however, that such a thing as a piece of forest of limited extent which is "typical" of the growth of a region hardly exists.

Smithwick Island (sec. 4, T. 66 N., R. 33 W.) was the selection for this description and for particular study, because the outer row of small islands inclosing Rock Harbor had the appearance of having been least disturbed by accidental conditions such as fires; and of these islands Smithwick was the most conveniently situated. So primeval and luxuriant is the aspect of the forest here that at first it seemed almost safe to assume that the island had never been burned over since its emergence from the lake. I found, however, in one place, at a depth of one-third of a meter, a layer of carbonaceous material with fragments of charcoal. It is certain then that fire, to an unknown extent, has entered into the history of the island, notwithstanding the many indications to the contrary. Nevertheless, granting that the island may have been burned over at some time, it is plain that the forest has long since returned to its natural condition and may fairly be taken as a suitable area for the study of the climax state. We may be sure that the forest on Smithwick Island has not been disturbed for many hundreds of years at least, and this is not often the case on the main Isle Royale.

There is one somewhat abnormal feature of the conditions surrounding these outer islands that should be mentioned, namely, that the exposure to the strong lake winds is greater than on the main island, and that the death-rate among the trees is thereby increased, and not always proportionally among the different species. On the whole, though, this added exposure merely intensifies certain processes that are in operation everywhere, and thus renders them easier of observation.

The average elevation of Smithwick Island is about 7 m. The southwest one-third was thoroughly burned over about 15 years ago. The forest covers the unburned portion almost completely, being bordered along most of the Rock Harbor side by a narrow shingle beach, and on the lakeward edge by a belt of bare sloping rocks, frequently interrupted by broken or precipitous sea cliffs.

Seen from Rock Harbor the forest has the following appearance, and this description will apply fairly well to the climax forest of Isle Royale in general (fig. 2). The first impression is of great density, the thick foliage extending to the ground at the edge of the forest, allowing no view into the interior. The sky line is ragged, made up of an irregular combination of sharp points and rounded curves, due to the mixture of broad-leaved trees and conifers.

Above the general level of the treetops tower occasional very old white spruces, conspicuous features in spite of or rather on account of their fewness. The paper birches make considerable show by reason of their thick tops, often appearing to compose at least half of the forest, but in reality not much more abundant than the spruces. The balsams are plainly very abundant, and are actually even more so than they seem, since many small ones are hidden by other trees. There are a few large specimens approaching the spruces in size, and thick groves of medium-sized trees are just

FIG. 2.—Exterior view of the climax forest upon one of the row of islands bounding Rock Harbor on the southeast: two tall white spruces at the right; a group of balsams at the left; several large birches.

visible, their spirelike tips appearing in dense clusters among the birch tops. The forest toward the harbor is bordered by a belt where *Alnus crispa* (Ait.) Pursh (green alder) is common, filling in the gaps between the trees. In this region *Pyrus americana* (Marsh) DC (mountain ash) is also frequent, and *Thuja occidentalis* L. (arbor vitae) is occasional.

Upon entering the forest we seem in many places to be in the midst of a dense growth of nearly pure balsam. The individuals of this species are of all sizes, and there is a pronounced tendency among them to grow in close groups. The small trees (roughly those 7 m. high and under) are greatly in excess of the larger ones. There are also numerous dead and dying specimens, almost always small ones, some of the dead trees showing evidence of having succumbed very recently, the needles not yet having dropped off. The occasional large trunks of the birches are conspicuous objects, but young ones are not numerous. It is often difficult to find a single spruce, unless one has carefully estimated from the exterior the position of one of the conspicuous old specimens. Young spruces are exceedingly rare, so that a long search will be necessary to discover one. The shade in most parts, especially under the closely placed balsams, is dense, though there are frequent partial openings, caused principally by windfalls (fig. 3). Standing dead trees of large size are very rare, but fallen trunks in all stages of decomposition are numerous, the greater number being balsams, though the dead birches are more conspicuous on account of their greater size.

FIG. 3.—Illustrates conditions resulting from a windfall in the climax forest: fallen trunks and young balsams; Smithwick Island.

Shrubby growth is not abundant. The areas of not too dense shade are often thickly populated with *Taxus canadensis* Marsh (ground hemlock). Other large shrubs that are more or less frequent are *Alnus crispa* (Ait.) Pursh (green alder), *Viburnum pauciflorum* Raf. (high bush cranberry), *Sambucus racemosa* L. (red-berried elder), *Lonicera canadensis* Marsh (bush honeysuckle), *Fatsia horrida* (Sm.) B. & H. (devil's club), the last abundant in one restricted area.

The herbaceous growth is sparse except in partial openings.

Most prominent is the association of about eight herbs which is so characteristic of the northeastern conifer forest, and in part of similar forests over a much wider range. The group includes the following: *Cornus canadensis* L. (bunch-berry), *Trientalis americana* (Pers.) Pursh (star-flower), *Linnaea borealis* L. var. *americana* (Forbes) Rehder (twin-flower), *Maianthemum canadense* Desf. (two-leaved Solomon's seal), *Clintonia borealis* (Ait.) Raf., *Mitella nuda* L. (mitrewort), *Aralia nudicaulis* L. (wild sarsaparilla), *Coptis trifolia* (L.) Salisb. (goldthread). These species are found in every part of the Isle Royale climax forest, and many of them in the bog forest, bogs, and along the rock shores as well. Others, less characteristic and abundant, still occur commonly: *Lycopodium annotinum* L. (stiff club moss), *L. obscurum* L. (ground pine), *Phegopteris Dryopteris* (L.) Fée (oak fern), *Aspidium spinulosum* (O. F. Müller) Sw. (shield fern), *Polypodium vulgare* L. (polypod), *Cystopteris fragilis* (L.) Bernh. (fragile fern), *Moneses uniflora* (L.) Gray (one-flowered Pyrola), *Ribes prostratum* L'Her (fetid currant), *Epipactis repens* (L.) Crantz var. *ophioides* (Fernald) A. A. Eaton (rattlesnake plantain), *Oxalis Acetosella* L. (wood sorrel), *Habenaria obtusata* (Pursh) Richards, *Comandra livida* Richards.

By far the most important part of the herbaceous vegetation, both quantitatively and ecologically, is the moss contingent. This forms a nearly continuous carpet, being absent only where the shade is very dense. Three species are chiefly concerned, and these are quite equally distributed, one usually being dominant in a given spot. *Calliergon Schreberi* (Willd.) Grout (*Hypnum Schreberi* Willd.) is perhaps the most abundant, and grows in the drier places alone, as well as mixed with the other two in general. *Hylocomium proliferum* (L.) Lindb. usually covers the areas of well decomposed humus; while *Hypnum crista-castrensis* L. seems to prefer rotten wood. Next to these in abundance is *Hylocomium triquetrum* (L.) Lindb.

The humus soil, which is composed largely of moss remains, tree waste, and rotten wood, varies in depth from 0.25 to 6 dm., the average being perhaps about 3 dm. It rests directly upon the smooth rock surface or is separated from it by a loose layer of decomposed fragments.

Returning to the trees, the first conclusion would naturally be that we have here a stage in the succession approaching but not having reached the final or climax condition. The spruces and birches appear like relicts, and the balsams, which seem to be of all ages, but mostly younger than the trees of other species, are apparently succeeding them. The seeming probability is that before long the birches and spruces will have died out, leaving a pure growth of balsam which in the future will succeed itself. Appearances of this kind have sometimes been considered sufficient to prove that succession is in active progress, and there are undoubtedly many cases where the phenomena are not deceptive. In no case, however, should the mere appearance of rapid succession be admitted as valid evidence until verified by surer methods of study. The results of an attempt to use such methods are detailed in the two following sections.

II. STUDIES OF INDIVIDUAL SPECIES

ABIES BALSAMEA (balsam fir).—If it be objected that the forest is after all a practically pure stand of balsam, with a mere scattering of other species, the following facts will be sufficient answer. It is true that in number of individuals, all sizes considered, the balsam is greatly preponderant. Of the 254 trees included in the six quadrats soon to be described, 78.7 per cent are balsam. But if we take account only of those trees which may be considered as forming the mature stand, the percentage of balsam becomes much smaller. Size, not age, is here the proper criterion. Considering those trees which are 1.25 dm. and more in diameter, which is a rather low limit to set, the proportion is only 56.7 per cent. Among the larger trees the balsams are still less numerous, making only 33.3 per cent of those 2.5 dm. and more in diameter (fig. 4). The same facts are shown when age is considered instead of size, though in a somewhat less striking manner (fig. 5).

Two causes are responsible for the preponderance of balsam in the young growth. First, the seedlings make a successful start in almost any sort of situation, provided sufficient light be available. Very young seedlings were seen commonly in such diverse situations as the following: natural openings in the forest caused by windfall, in moss and humus (by far the commonest situation); windfall opening in cedar swamp, in moss; rotten logs in forest

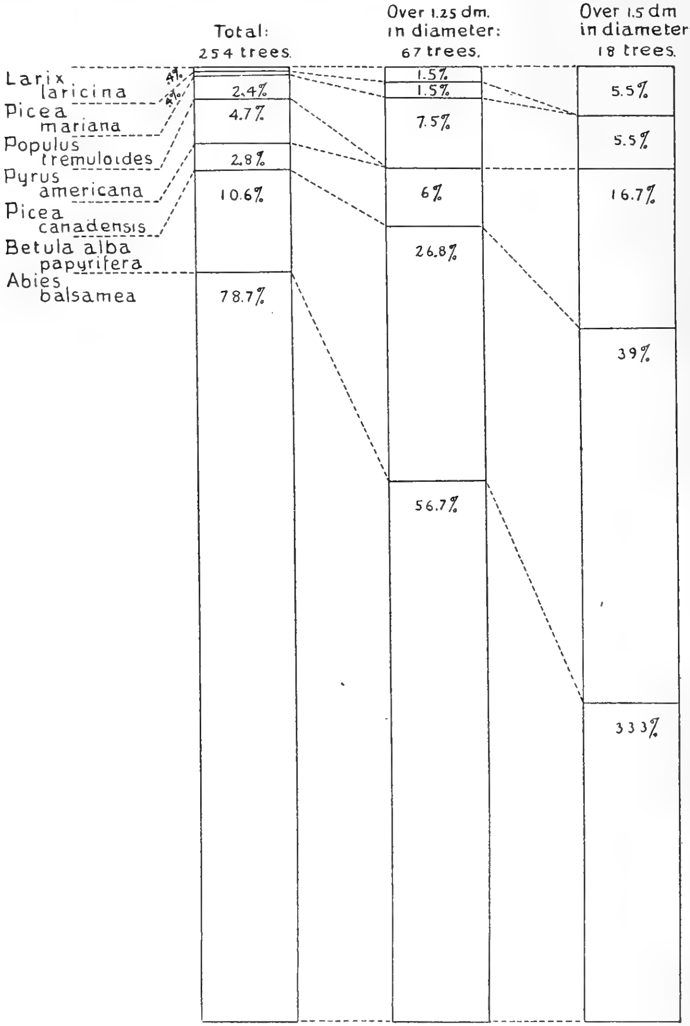


FIG. 4.—Composition of the climax forest; according to size of trees

(infrequent in this region); open bogs in sphagnum; crevices and humus-filled depressions on rock shores; burned areas, both forested and bare, not abundant; upper beach among large shingle, in partial shade and entirely open, abundant in one locality; sand bar across mouth of small stream, abundant. The entire absence

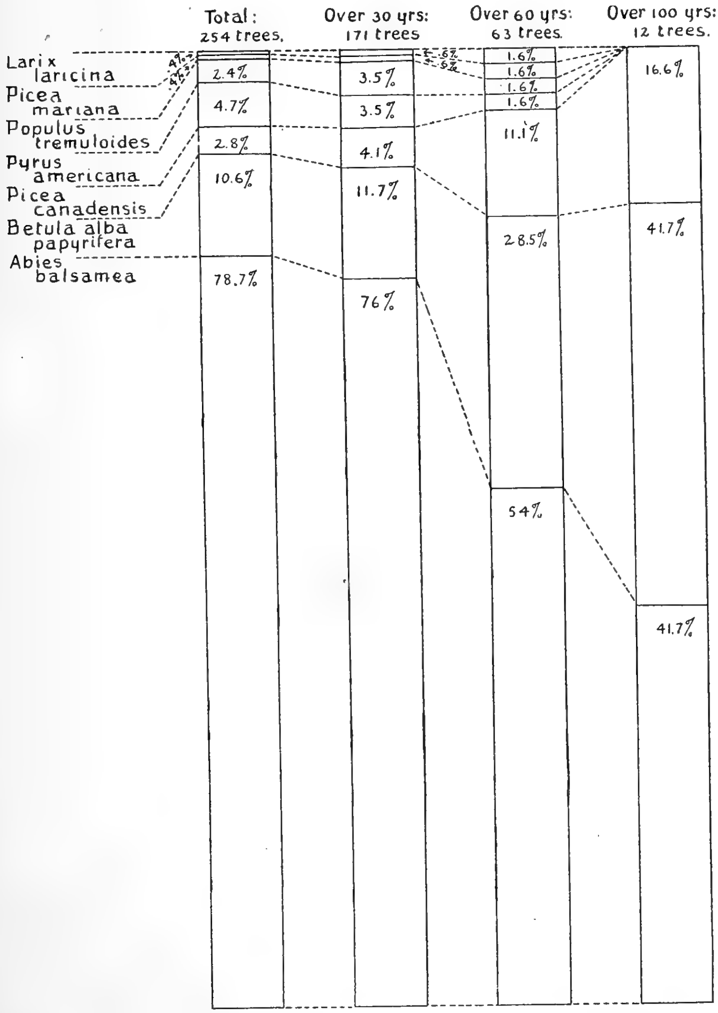


FIG. 5.—Composition of the climax forest; according to age of trees

of very young seedlings wherever the shade is even moderately dense is noteworthy. Later in life the young trees can endure severe shading, but for a successful start abundant light seems to be a necessity. The possibility must be admitted that light (or rather radiant energy) is only indirectly the important factor, its influence lying in its effect upon the seed bed. Densely shaded soils upon Isle Royale are nearly everywhere more or less of the nature of peat, low in temperature, soggy with unavailable water, and probably like peat deficient in certain types of bacterial and fungal life. The obvious effects of abundant access of radiant energy would be to partially cure the sogginess of the soil and thus increase its oxygen content, and to bring about a high soil temperature; both of which changes would result in greatly increased activity among the various types of soil organisms. Plans to carry out some experiments with a view toward determining the germination conditions of the balsam and other trees were frustrated by the total failure of the seed crop in 1910.

A second cause, which easily accounts for a considerable part of the young growth of balsam, is found in the habit of layering, by which that species reproduces abundantly. All the other conifers of Isle Royale except the pines possess the habit too, but to a much less degree. In a previous paper (**12**) I have described in detail the layering habit of the balsam and other conifers, and therefore a few words here will be sufficient. In the forest one frequently comes upon small groups of young balsams, composed often of about half a dozen individuals of various sizes. Upon superficial inspection these would easily pass for a cluster of seedlings, but if the group be carefully dug up it will be found that the young trees are all connected with each other just below the surface of the ground. The group comes into existence in the following manner. One or more of the earliest branches of a young tree (which is sometimes hardly beyond the seedling stage) comes to be slightly covered with humus and litter, and produces roots. The tips then become erect, and taking on radial symmetry are transformed into miniature trees. By successive layering of branches as many as five generations produced in this manner may be included in a single group. Large drooping branches of mature individuals may layer in the same way, and it is not uncommon to find an old trunk surrounded by a circle of daughter trees developed from layered branches. The young shoots soon come to depend entirely upon their own root systems for sustenance, and there is evidence that a considerable number of them become independent through the decay of the connecting branch. The habit is so common in the Isle Royale forests that a large proportion of the apparent balsam seedlings may be accounted for in this way.

The preponderance of balsam in the young tree growth being accounted for, it is now necessary to explain its rapid decrease when greater size and age are considered. Several causes combine to bring this about. Abundant germination is itself a disadvantage, since it results in severe competition, much of the stand undergoing suppression and finally death. The species is very susceptible to fungus attacks and to diseases of many kinds. Rotten-hearted trees are very common. Witches' brooms caused by a rust (*Peridermium*) are familiar objects. According to MOORE and ROGERS (41), the liability to fungus attack is greater in pure stands than where trees are scattered. The common group habit of the species is therefore a disadvantage in this respect. The prevalence of heart rot, together with the natural brittleness of the wood, cause extreme liability to windfall, and broken trunks are a common sight, while uprooted balsams are rare. It is not surprising, in view of these facts, that in spite of its prolific power of germination the balsam never reaches the position of dominance in the mature stand. In a word, its high birth-rate is balanced by a high rate of mortality.

BETULA ALBA var. PAPYRIFERA (paper birch).—The prominence of this species in the mature stand and in the general aspect of the forest has been noted, and also its comparative scarcity in the young growth. It is certain that the germination of the birch in this region is far from prolific. Very young seedlings were frequently seen, and in situations almost as varied as those inhabited by the balsam, but never in abundance as in the case of that tree. I quite frequently found very small seedlings in dense shade, but they were never more than five or six years old, indicating that conditions (probably light supply for photosynthesis) were not favorable for continued growth. Opportunity for successful reproduction comes usually, as in the case of the balsam, after windfalls (fig. 8). On account of its much less prolific germination the birch is far less abundant in such situations than the balsam. Its growth under the same conditions seems to be somewhat faster, however, and so the few birches of the windfall area, or some of them, soon overtop the balsams and cause the suppression of many of the latter, at the same time, with the aid of the balsams, temporarily preventing further reproduction of either species. Paper birch has comparatively few and ineffective fungus enemies (DANA 18) and is not particularly susceptible to damage by wind, on account of its elastic branches and extensive though shallow root system. Even when it is broken off in severe storms, as occasionally happens, it has a means of recovery in its ability to send up vigorous sprouts from the stump. Occasional clumps of immense birch sprouts scattered through the forest are evidence of this power. The most effective obstacle to its increase is competition with the balsam in its early stages, and here its greater rate of growth gives it a slight but important advantage. On the whole it may be said with certainty that its low birth-rate is compensated by a very low mortality, and it is thus able to maintain itself in making a good proportion of the mature stand (figs. 4, 5).

PICEA CANADENSIS (white spruce).—This species is ecologically much less important than the first two, occurring only sparingly in most places; but it attains a greater size than the other trees, and is one of the most conspicuous features of the forest. On account of its scarcity little could be discovered concerning its life-history upon Isle Royale. From the few seedlings that were observed it seems probable that abundant light is necessary for its successful reproduction. According to the United States Forest Service (**22**) it is not a prolific seed bearer, and has definite seed years, which in New England are about eight years apart. All the young trees seen were growing in situations where at least fairly abundant light was available. It seems probable therefore that the white spruce is also largely dependent upon windfalls for its successful reproduction in the virgin forest. It is able to withstand severe winds without breaking, as is shown by individuals towering conspicuously above the general forest level. It is not particularly liable to fungus injury. Birth-rate and mortality are both low, and the species is able to maintain its small proportion in the forest.

OTHER TREES.—*Pyrus americana* (Marsh) DC (mountain ash), though fairly common, is of little importance ecologically, since it is very short-lived, never reaches any great size, and produces little shade. Its life history in most respects is similar to that of the birch, and it has the same habit of producing sprouts from the stump. *Pinus Strobus* L. (white pine) is scattered thinly through many parts of the forest, generally towering high above the other trees. Its ecological status seems to be similar to that of the white spruce. There is no indication that in recent times at least it has ever been abundant upon Isle Royale. *Picea mariana* (Mill) BSP, *Larix laricina* (DuRoi) Koch, and *Populus tremuloides* Michx., which are found here and there in the climax forest, will be sufficiently treated in connection with quadrats 5 and 6. *Populus balsamifera* L. also occurs sparingly.

TAXUS CANADENSIS.—The most important of the lower plants of the forest—more important indeed than many of the trees—is the ground hemlock. Its influence lies in the completeness with which it occupies and shades the ground, preventing tree reproduction over large areas. This effect will be noted in connection with quadrats 5 and 6, and quadrat 1 includes part of a ground hemlock area in which trees are practically absent. *Taxus* can endure considerable shading, but is never found in the dense shade cast by the balsam groups. Balsam in its turn is excluded from large areas by *Taxus*, so that the competition between these two species is exceedingly keen. *Taxus* spreads abundantly by underground stems, and in this way invades new areas of forest when conditions are favorable, at the same time dying out in the older portions of the growth, thus allowing other plants to start in such places.

III. QUADRAT STUDIES

The method of investigation whereby a knowledge of the dynamics of the forest was gained was as follows. A rectangular area was laid off, made up of one or more units of 5 m. square, the usual size being a quadrat of 10 m. square, or four units. In the diagram of this area the position and kind of every tree, down to the smallest seedling, was plotted and its diameter noted. Cuts were next made with an ax to the centers of the large trees, and the small ones were felled. The age of every tree was then determined by counting the annual rings, and note was made in each case of the degree of soundness of wood, width of rings, and periods of suppression indicated thereby. The cuttings were made at the height of about 0.3 m. An element of error is introduced here, making the age as determined a few years too low. It seemed inadvisable, considering the many quadrats to be studied, to use up much valuable time in making the counts absolutely accurate. This would have involved the cutting of every tree at the surface of the ground, a very difficult and slow process. A saw might have been used instead of an ax, but when the rings are at all obscure it is impossible to count them from a sawed surface. I believe that the error introduced does not affect the validity of the results, since it is approximately the same in nearly every instance. The method on the whole gave excellent results, in the study of the rock shores and bogs as well as of the climax forest. Its use was made easy by the comparatively small size of the Isle Royale trees. Sixteen quadrats were studied in all, comprising 74 units of area, and involving the determination of the ages of about 900 trees. If objection be raised that the method is unduly destructive, it may be answered that the cutting over of these small areas produces exactly the same effect as does windfall, a process that is continually taking place, and thus makes possible a new crop.

In addition to the statistical study of the trees, careful notes were taken of the lower vegetation and the physical factors of the habitat. Less detailed studies of many other localities were also made for comparison with the quadrats.

The results of the quadrat studies so far as they concern the climax forest will now be given in detail. The first four described were located on Smithwick Island; quadrats 5 and 6 were upon the main Isle Royale.

Quadrats on Smithwick Island

QUADRAT 1 (fig. 6).—This quadrat exhibits most clearly the relations which the different tree species hold to each other and to the physical conditions of the habitat. It includes but one spruce, an aged giant 250 years old, long past maturity, with sparse foliage, giving practically no shade. Two healthy birches (105 and 107 years old), close together, produce considerable shade in their vicinity. There are several rather old balsams (64–90 years) well

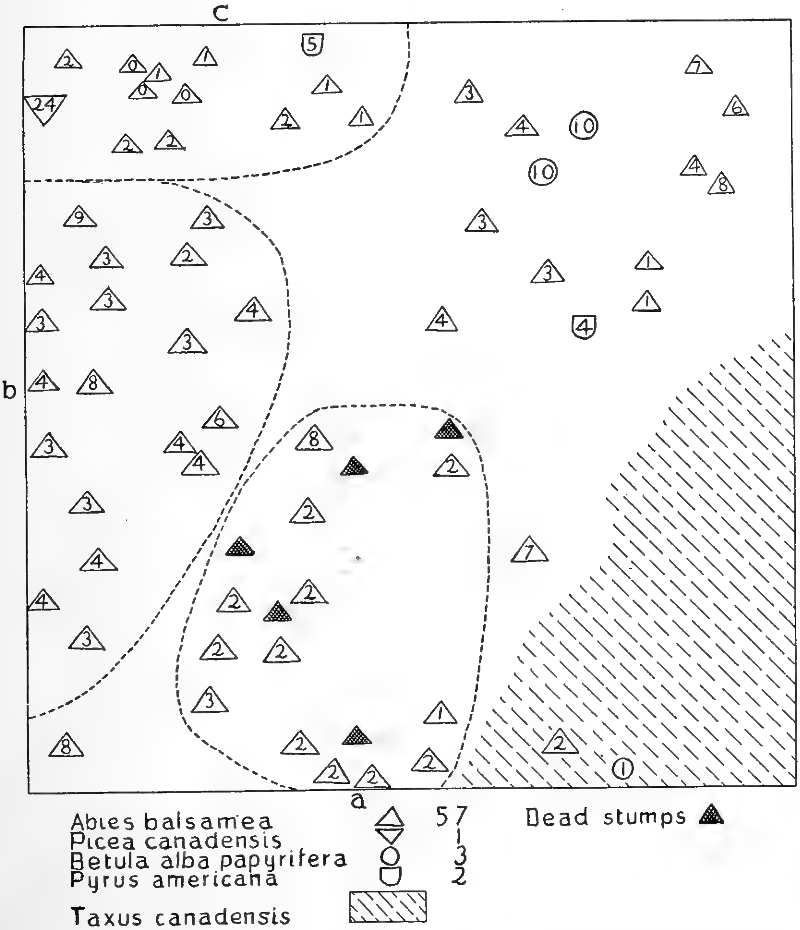


FIG. 6.—Quadrat 1, Smithwick Island: the symbols indicate the species; the numbers within them the ages of the trees by tens; for example, a tree marked *6* is between 61 and 70 years of age.

scattered over the quadrat, and usually more or less isolated from the smaller growth. The young trees are practically all balsams, the only representatives of other species being two mountain ash (one a clump of three stump sprouts) and a 20-year old birch in the lower right-hand corner. The young growth is not evenly distributed, but shows a tendency toward grouping, which tendency will be seen in each of the succeeding quadrats. The larger number of trees of each group are approximately even-aged. For example, the rather scattered group *a* that surrounds the 5 balsam stumps contains 13 balsams, 10 of which are 23–28 years old. Of the 18 trees in group *b*, 14 are between the ages of 30 and 50, not so uniform as the last, but decidedly of a single generation. Of the 13 trees in group *c*, all but the mountain ash and the large spruce are under 30 years.

Group *a* illustrates in a striking manner the way in which these even-aged clusters come into existence. Within its limits were 5 large rotten balsam stumps from which the trees had been broken a meter or more above the ground. The group evidently constitutes a windfall, probably caused by a single storm, one tree in its fall carrying others with it. Such windfalls of various ages are exceedingly numerous throughout the forest, the balsams, on account of their brittleness and susceptibility to fungus attack, being the ones most frequently destroyed. This particular windfall is of special interest because it was possible to determine the time at which it occurred. One of the large balsams in falling pinned to the ground a young tree of the same species, which, in spite of unnatural position and dense shade caused by the branches of the fallen one, has continued to live up to the present. The younger tree was 49 years old, and the first 12 rings were exceptionally wide, showing that up to the age of 12 years it was an unusually vigorous sapling. At this point a sudden change becomes evident, for the remaining rings are so close that in counting them a magnifying glass was an absolute necessity. This change could have been brought about only by some sudden and violent cause, and this cause is evidently to be found in the fall of the older tree. The windfall is therefore to be dated about 37 years ago. Returning to the trees composing group *a*, we find that they are all balsams; one is 85 years old, another 38, a third 14, and 10 range from 23 to 28; 11 then are subsequent to the windfall, and 10 began life within a period of six years, 9–14 years after the windfall occurred. There is only one that clearly antedates it.

Upon inquiring as to the cause of these facts, the factor of radiant energy immediately suggests itself (see p. 20). The older balsams, now fallen, when living were close enough to cast a dense shade over the area which they controlled, and there can have been no young trees beneath them, since if there had been, the present generation would antedate the windfall. It was not until 10 years after that event that young balsams began to appear in the area. Radiant energy being the principal factor involved, this interval of a number of years is entirely to be expected, since some time would elapse before the disintegration of the tangle of branches with their persistent needles would allow a large amount of the energy to reach the ground. Evidence in support of this hypothesis was found in every quadrat and in every considerable part of the forest. In no other case was it possible to determine the exact age of the windfall, but the general relation between the older and younger generation was usually plainly to be seen. Frequently the only sign of windfall is in the rotting moss-covered logs, but the close group of even-aged trees, sometimes 50 years old or more, tells the story plainly.

In quadrat 1 two other windfall areas are shown, one (*c*) quite recent, the other (*b*) older. The greater range of age among the trees in these areas suggests that those of the former generation did not all fall together. This type of windfall is commoner than that represented by group *a*. The fall of the first trees gives the wind a better chance to reach others. This slow process may be extended over a long period, even until the new generation has begun to fill in the gaps first made. In contrast to the dense grouping just described is the remaining area of the quadrat, where the individuals are less closely placed and are on the average much older. The part not included in the three groups comprises two-thirds of the area of the quadrat, yet it contains only 18 trees, 7 of which are over 60 years; while the other third of the quadrat contains 45, only 5 of them being over 60 years. The fewer trees in the larger part nevertheless produce a dense shade, and there is very little young growth beneath them.

There is a difference that should be noted between the shade-producing capacity of the balsam and that of the birch. The former, with its many whorls of short branches close together and its opaque leaves, casts an exceedingly dense shadow which does not influence a large area. A moderately close stand of large balsams allows extremely little light to reach the ground. The birch (in its primeval forest form) influences a large area, but its shade is not dense, because of its comparatively thin crown and translucent leaves. Under the shade of large birches there is frequently a scattering of young growth, while under thrifty balsams there is rarely to be found any at all. Both conditions are well shown in the diagram of quadrat 1.

The effect of shading is seen also in the undergrowth. In the dense shadow of the balsams there is a mere sprinkling of herbs, and mosses are usually absent entirely, the ground being covered with a layer of tree waste. It is in shade of moderate density and in openings that the greatest luxuriance of mosses and herbs is found. The ground hemlock is excluded from most of the quadrat for the same reason, but in the lower right-hand corner there is an area completely occupied by a dense growth of it, which effectually prevents the establishment of any other species.

QUADRAT 2 (fig. 7).—This quadrat shows the same features as the last. Group *a* contains a great number of young trees of similar age, mostly balsams, which have started as a consequence of one or more windfalls. Of the 40 balsams in the area, 33 are between the ages of 20 and 35 years, and within these limits, as shown by the diagram, there is a tendency for those of similar age to be neighbors. Numerous fallen trunks represent the former generation. The large balsam marked "12," which was 121 years old—an unusual age for this species—was past maturity, and like the big spruce in the preceding quadrat was ineffective in producing shade. At *b* there is a part of an older group, 5 of the 7 balsams being between 44 and 53 years old. The upper left-hand corner is dominated by a few old and large trees, balsams and birches, with practically no young ones—only a few beneath the birches. The shade in this area was dense and the undergrowth sparse, even the ground hemlock being nearly absent. No spruce grew in this quadrat, but there were occasional large ones near.

QUADRAT 3 (fig. 8).—This small quadrat of one unit area shows a group of even-aged trees, among which are several young birch

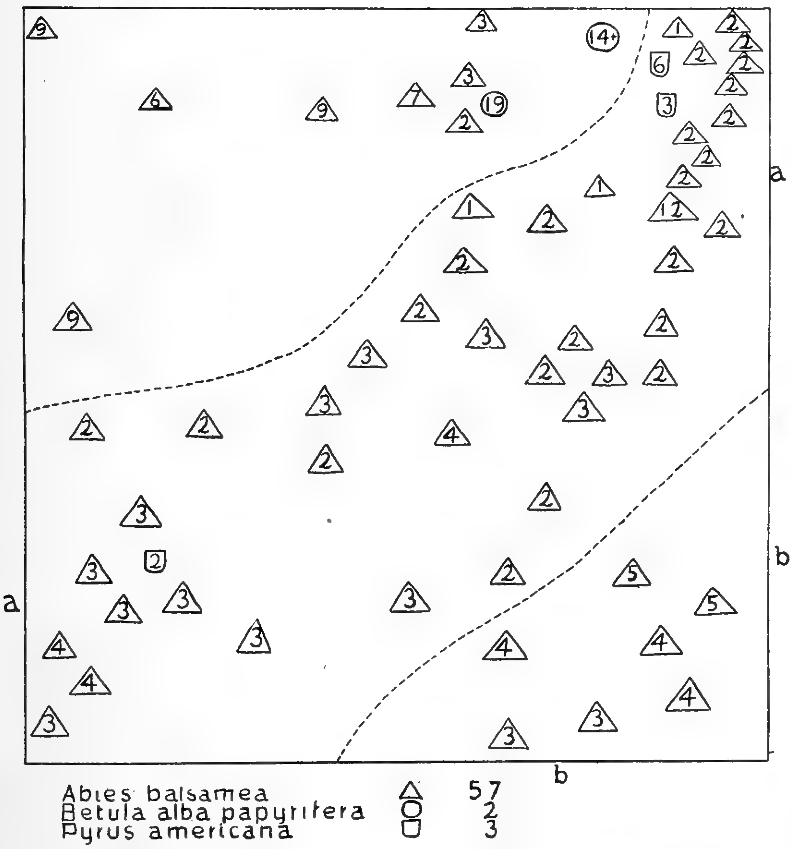


FIG. 7.—Quadrat 2, Smithwick Island; for explanation of symbols see fig. 6

and mountain ash as well as balsam. No living trees of a former generation are present within the limits of the quadrat, but several were seen near. Decayed trunks were frequent and were mostly birch. Of the 37 trees, 26 were within the ages of 26 and 35 years, and the others were very close to these limits. Evidently then all three species started growth at practically the same time, and the immediate cause was a windfall. The birches are tall and spindling, but now slightly overtop the balsams in spite of a somewhat later start. Having gained the advantage as to light supply, their tops will spread fast, and these trees, or more likely one or two of them, will doubtless finally develop the thick-stemmed, spreading, round-topped form characteristic of mature specimens in the virgin forest. The balsams which are within the sphere of influence of the birches will be suppressed. This process in fact has already begun. The last 5–10 rings of those balsams which were close to the birches were found to be noticeably narrower than the earlier ones, while the rings of those growing isolated from other trees were uniformly spaced. Undergrowth was practically lacking, the shade being everywhere very dense. Even the ground hemlock was entirely absent.

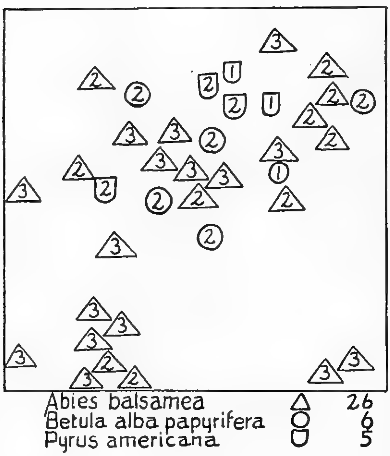
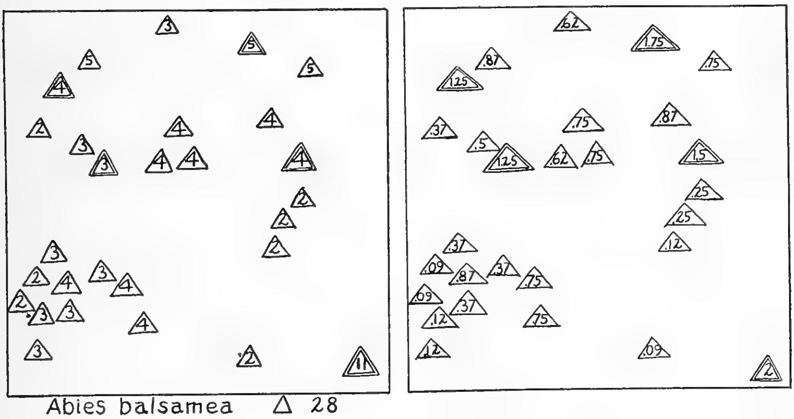


FIG. 8.—Quadrat 3, Smithwick Island; for explanation of symbols see fig. 6.

In this quadrat the mountain ash showed an interesting habit of growth. Several saplings were seen among the closest groups of balsams which were so slender and weak as to closely resemble lianes. One specimen was 4.3 m. high and 2.25 cm. thick at the base, unbranched, with a single tuft of leaves at the top. It was supported entirely by the balsams against which it leaned, and its upper portion had penetrated among the interlacing balsam branches close to the trunk of a near-by tree. It was 16 years old, and had evidently started before the balsams had begun to shade the ground thoroughly, but was left behind in the severe competition for the available light supply.

QUADRAT 4 (figs. 9, 10).—This quadrat, also of one unit area, includes two generations of balsam and no other species. Several large birches were near by and a large spruce. The older generation is represented by one individual in the lower right-hand corner, well isolated from other trees, 115 years old. The younger generation illustrates competition between individuals of a single species which began life at about the same time. Fig. 9 shows the age of each tree, and fig. 10 its diameter, which, it may be noted, maintains a pretty constant proportion to height. It will be seen from the latter that 4 trees (marked by double symbols) have attained a much greater size than the others; and if comparison be made with fig. 9 it will be evident that these 4 are not noticeably older than



9 10

Figs. 9, 10.—Fig. 9, quadrat 4, Smithwick Island: age of trees; for explanation of symbols see fig. 6; fig. 10, quadrat 4, size of trees; the numbers indicate the diameters of the trees in decimeters.

their neighbors. The annual rings of these 4 trees were found in every case to be wide and evenly spaced, while those of their less favored companions were either very narrow from the beginning or plainly showed recent suppression. This illustrates an important principle in forest study, namely, that no reliance can be placed upon the size of a tree in fixing its age or in determining its place where two or more generations are concerned. These 4 individuals in some way gained the advantage early in life and caused the suppression of their neighbors. Evidence of the severity of the shading was shown by the presence among the living balsams of 20 dead specimens, averaging a meter in height, and in length of life from 14 to 38 years. Some had been dead for a long time, while others showed evidence, in needles still clinging, of having been alive until very recently. All had undergone severe suppression. In consequence of the deep shade the undergrowth was extremely sparse, except in the lower left-hand corner where there was a partial opening. Here was a luxuriant growth of mosses, including *Hylocomium proliferum* (dominant), *Hypnum crista-castrensis*, *Calliergon Schreberi*, and *Dicranum undulatum*. The close group of young balsams occupying this locality was largely due to layering. Quadrat 4 then includes in the main a group of balsams of very different sizes, giving an appearance of gradual reproduction, but in reality essentially even-aged, and belonging distinctly to a single generation.

Quadrats on the main Isle Royale

It has been said that the conditions on Smithwick Island include one that is somewhat abnormal for the region as a whole, namely, that the exposure to wind is greater. Two quadrats in sheltered localities on the mainland of Isle Royale were studied for the purpose of comparison. They probably represent the opposite extreme so far as exposure is concerned.

QUADRAT 5 (figs. 11, 12) was located a few hundred meters back from the southeast shore of the Blake Point peninsula in sec. 23, T. 67 N., R. 33 W. The locality is thoroughly sheltered from northwest winds by the main ridge, and from the lake winds by the islands to the southeast. On the diagram several points of difference from the preceding quadrats are readily seen. Most noticeable are the greater average age of all species and the absence of very young growth. Two new trees appear: *Picea mariana* (Mill) BSP (black spruce) and *Larix laricina* (DuRoi) Koch (tamarack), each species being represented by one individual. The whole stand is remarkably even-aged, 22 of the 38 trees being between the ages of 82 and 98 years. There is some tendency toward grouping of trees of similar age, though not so noticeably as on Smithwick Island. The group *a* is a very marked one, however. Of the 9 individuals of 4 species composing it, 7 are between 83 and 92 years, and 5 between 89 and 92. The effect of shelter from wind is very evident in the greater height of the trees. The protection which this area enjoys does not by any means prevent windfall, but merely lessens its intensity, and allows the trees to reach a greater height before they are overthrown. Several

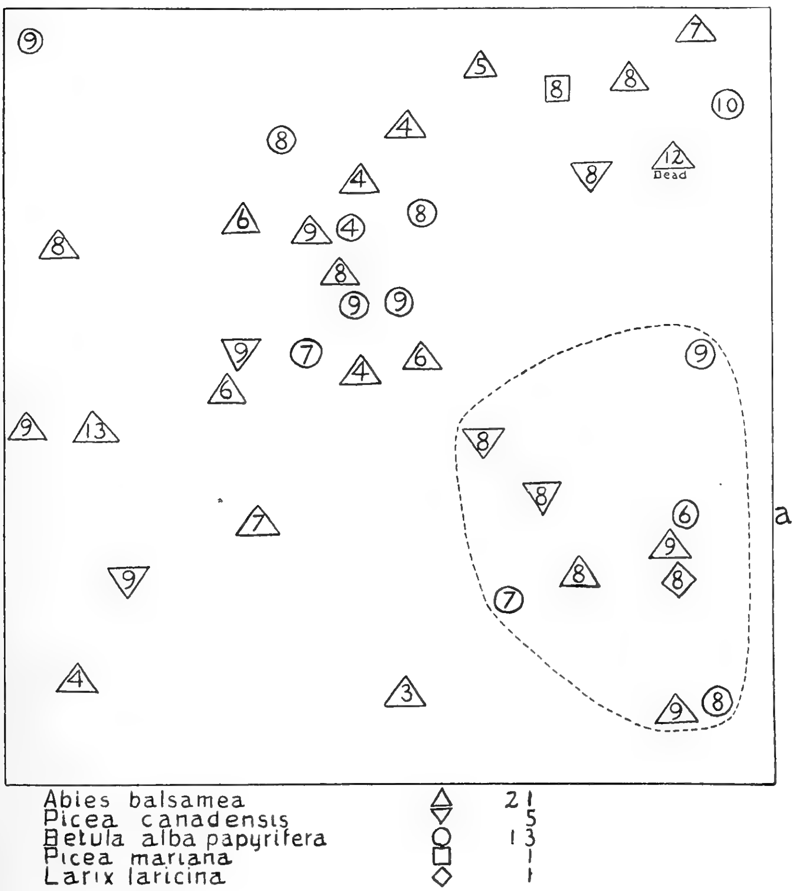


FIG. 11.—Quadrat 5, Blake Point Peninsula: age of trees; for explanation of symbols see fig. 6.

standing dead balsams were seen on this quadrat and they were frequent through the neighboring forest. On the outer islands the balsams almost never die a standing death. Quadrat 5 (fig. 12) also shows suppression of part of the stand, the larger trees being indicated by double symbols. The absence of very young growth is explained by the fact that the forest floor was covered by a thick mass of ground hemlock.

Black spruce and tamarack are found occasionally throughout the forest. Since they are both very intolerant of shade, they probably make a successful start only where an extensive windfall

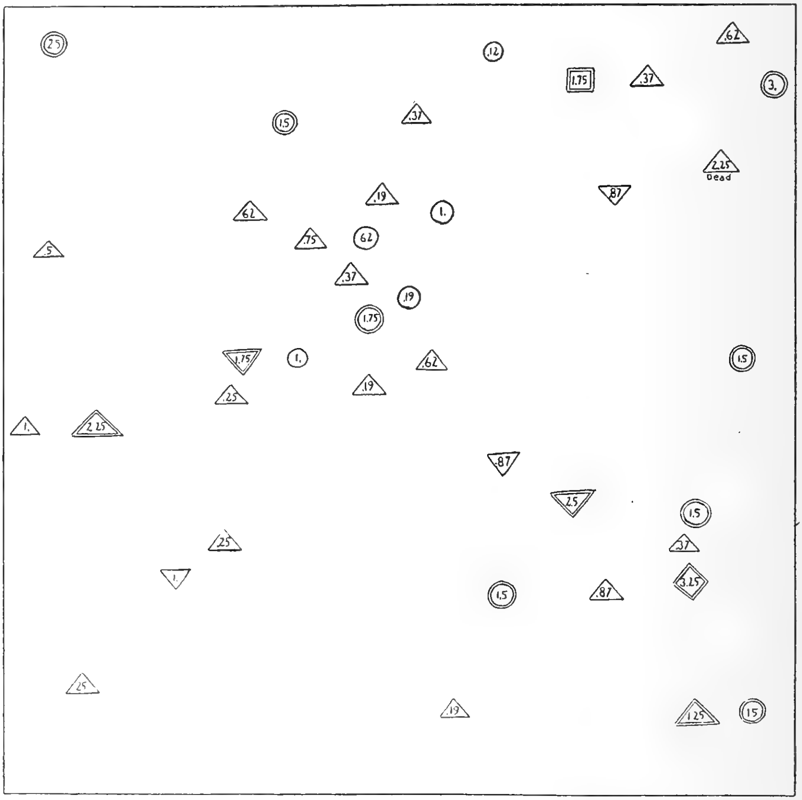


FIG. 12.—Quadrat 5: size of trees; for explanation of symbols see fig. 10

has let in abundant light. The black spruce as a member of the upland forest is abundant in one locality on the southeast shore of Isle Royale and in certain other places. The evidence seems to show that this species in abundance in the upland forest indicates a transitional stage approaching the climax. The subject will be treated again in the consideration of the rock shore succession.

QUADRAT 6 (fig. 13).—The conditions here as to shelter were similar to those of the last. The quadrat was located near the shore of Tobin's Harbor in sec. 33, T. 67 N., R. 33 W. The small number and large size of the trees are noticeable, and also the entire

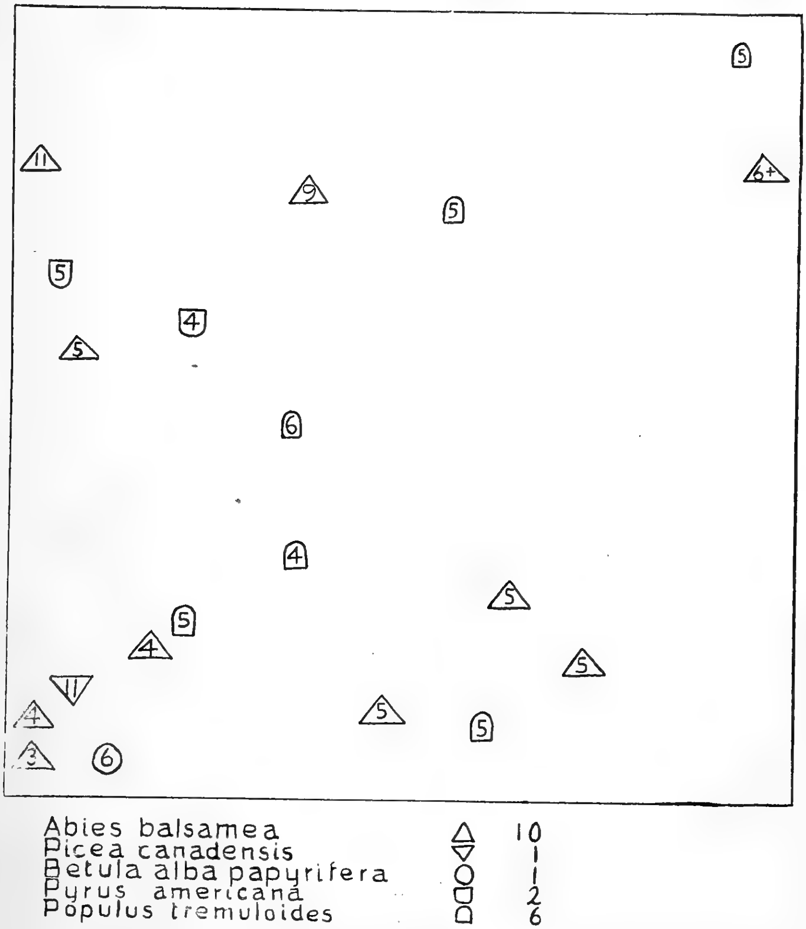


FIG. 13.—Quadrat 6, near Tobin's Harbor; for explanation of symbols see fig. 6

absence of young growth, in spite of the comparative lightness of the shade. These conditions were plainly due to the mat of ground hemlock which practically covered the quadrat. The ground hemlock therefore, rather than any tree species, dominates and controls this area. The surrounding forest was found to be essentially similar to the sample, except that the cover of ground hemlock was not continuous, and where it was absent the usual conditions of windfall reproduction, especially of balsam, prevailed. The large number of good-sized trees, balsams being specially noticeable, owe their continued existence to the protected position of the area. The presence of *Populus tremuloides* Michx. (aspen) in considerable abundance is noteworthy. This species seems to be ecologically equivalent to the birch, except that it does not to any great extent possess the power of sprouting from the stump, at least in this region.

A similar situation was noted in a narrow valley near Duncan Bay (sec. 28, T. 67 N., R. 33 W.), which was protected by abrupt ridges on both sides. Here the trees of all species are very large, the shade is not dense, and windfalls are relatively scarce. Ground hemlock is exceedingly abundant and large, and is plainly responsible for the lack of young tree growth and the resulting openness of the forest. Some scattered groups of small balsams were plainly related to windfalls.

The foregoing studies show that the climax forest is a complex of windfall areas of differing ages, the youngest made up of dense clumps of small trees, and the oldest containing a few mature trees with little or no young growth beneath, those of a single group being approximately even-aged. This mosaic or patchwork changes continually in a manner that may almost be called kaleidoscopic when long periods of time are considered. The forest as a whole, however, remains the same, the changes in various parts balancing each other.

EXTENT OF THIS TYPE OF FOREST AS THE CLIMAX OUTSIDE OF ISLE ROYALE

Attempts to obtain information relating to the nature of the climax forest of other portions of the northeastern conifer region have not been attended with much success. The distributions of the various trees have been determined by BELL (8) and others with considerable accuracy, but practically nothing of an ecological nature has been published. From the data I have been able to discover, the impression has been gained that the same association of balsam, paper birch, and white spruce, which is the dominant forest type of Isle Royale, is found in the most mesophytic habitats throughout northeastern Canada. The probability is that it is the climax type over much of the region, though there is not sufficient evidence to justify a confident statement to that effect. It is not necessary that the component species bear the same relations to each other in all parts of the region, or even that the species themselves be everywhere the same. One or even two of the climax trees may be lacking in certain places, species that are ecologically equivalent may be substituted, or others added. Analogous differences occur in the deciduous forest. The two climax trees that are almost omnipresent are the maple and the beech, and yet there is a belt along the northern edge of the region where the maple alone forms the climax forest, unless the yellow birch (*Betula lutea*) may possibly take the place of the beech. Again, in the Great Lakes region a third climax tree, the hemlock (*Thuja canadensis*) is present; and in the southern Appalachians the number of species composing the climax forest reaches a dozen or more. Similarly, in northeastern Canada the climax forest may vary from place to place.

Of northern Quebec MACOUN (**39**) says: "In the country around Lake Mistassini it [balsam] grows mixed with aspen, birch, and white spruce, and on the lower part of the Rupert River it is found growing with the same trees all the way to James Bay." The correspondence of this to the Isle Royale forest is striking. In reports of the Department of Lands and Forests of Quebec (**45, 46**) expressions such as the following are frequent, the region described being the country north of Lake St. John, west to Lake Abitibi: "well timbered, mostly with spruce, fir, and white birch, with some scattered white and Banksian pine on the high ridges." In the "Report of the survey and exploration of northern Ontario" (**43**) there is much detailed information concerning the distribution of the trees in that region, though the data presented have little ecological value. However, in reading the reports of the various parties one frequently comes upon such statements as the following: "chiefly small poplar [*Populus tremuloides*], spruce, white birch, and balsam, and a few balm of Gilead [*Populus balsamifera*]"; "spruce, balm of Gilead, poplar, balsam, and white birch"; "white birch, balsam, and a few large spruce"; "the white variety of spruce of good size was seen continually along the rivers and on

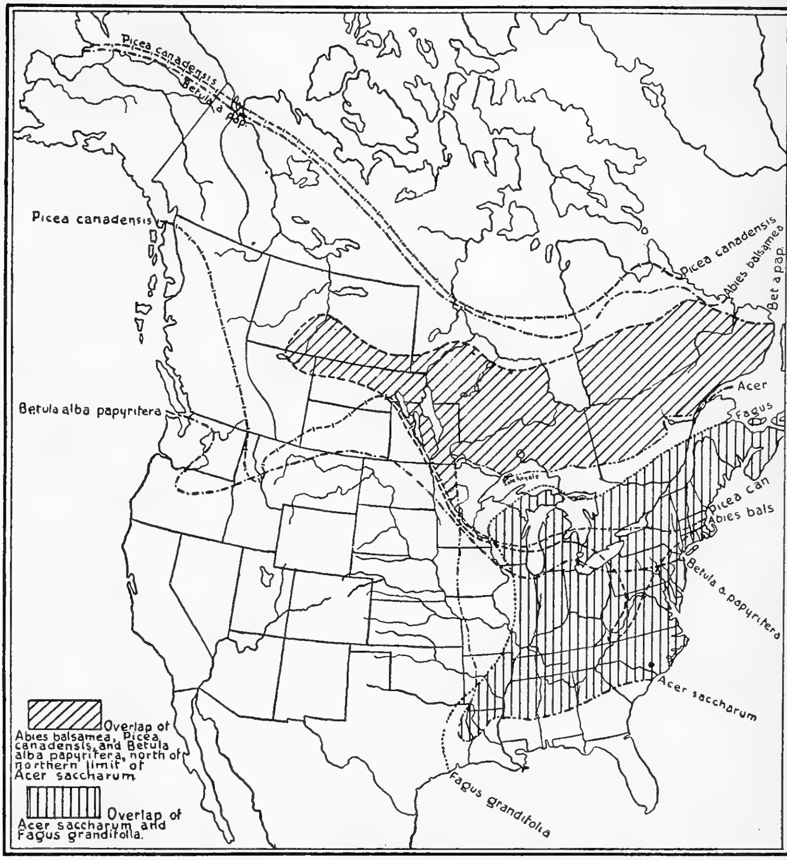


FIG. 14.—Ranges of the climax trees of the northeastern conifer forest and the eastern deciduous forest.

ridges back from them. Black spruce, generally scrubby, clothes the muskegs. . . . . Birch and balsam are also common on high lands." The black and white spruces are not usually distinguished in these reports, but it is clear that the former is the principal tree upon the extensive muskeg lands, while the latter is confined to the higher grounds, where it usually has the balsam and birch as its companions.

The data here presented, though very unsatisfactory, are sufficient in my opinion to establish the probability of the generalization that the climax type of the whole of the northeastern conifer region is of the general character described for Isle Royale, with local variations due to the elimination or addition of species, or to the substitution of others that are ecological equivalents.

Important confirmation has recently been received from Dr. Robert Bell of Ottawa, the best authority upon the distribution of Canadian trees, who writes: "The same type of upland forest which you describe on Isle Royale extends from the Great Lakes to James Bay and east and west of it, with modifications in parts."

On the map (fig. 14) the area shaded with oblique lines represents the region over which the ranges of the balsam, paper birch, and white spruce overlap, *north* of the range of the sugar maple (data largely from Transeau **55**). It is in this region that the type of forest described is thought to be the climax. Beyond the limits of the balsam, which has the narrowest range of the three, some other species must be substituted for it, or else the climax forest is composed of the remaining two species alone.

COMPARISON WITH THE CONIFER FOREST OF THE SOUTHERN APPALACHIAN SUMMITS

In connection with the study of the Isle Royale forest it will be worth while to make comparison with another region that has come under my observation, where the forest is extremely similar to that described in the present paper. On the highest summits of the mountains of North Carolina, eastern Tennessee, and southwestern Virginia, there are isolated areas of dominantly coniferous forest, which seem like detached portions of the great northeastern forest (see detailed description by Harshberger **32**). The species are different, the balsam being *Abies Fraseri* (Pursh) Poir., the spruce *Picea rubra* (DuRoi) Dietr., and the birch *Betula lutea* Michx. f. In general aspect this forest is surprisingly like that of Isle Royale. Because of the predominance of the first tree mentioned many of the mountains themselves are locally called "Balsams." The results of studies upon three of these summits in western North Carolina may be briefly summarized as follows, the localities being Richland Balsam, Plott Balsam, and the Black Mountains (Mount Mitchell).

The coniferous forest covers the mountain slopes from about 1600 m. to the summits, the highest of which is about 2010 m. *Abies Fraseri* is on the whole the most abundant species except along the lower edge of the coniferous region, where *Picea rubra* is of somewhat greater importance. *Betula lutea* is scattered more or less thickly throughout and grows to a great size, specimens having been noted that were 1.3 m. in diameter. As on Isle Royale, birch and spruce are sparsely represented in the young growth, which is predominantly balsam. The shrubby vegetation consists almost entirely of *Rhododendron catawbiense* Michx., which is very abundant. It is interesting to note that the balsam seedlings are practically absent under the shade of the rhododendrons, and scarce in shade in general, but are exceedingly abundant in partial openings. The ground is covered by a luxuriant moss carpet, almost identical in composition with that of the Isle Royale forest, and the herbaceous growth includes most of the characteristic group of northern forest plants which has been listed (p. 16).

The similarity between Isle Royale and the North Carolina "Balsams" is thus a striking one. In the latter region there is even an ecological equivalent to the ground hemlock. *Rhododendron catawbiense*, in spite of its very different habit, is equally effective in densely occupying and shading the ground and thus in temporarily preventing reproduction of the forest trees over wide areas. I believe that the conclusions which have been reached concerning the Isle Royale forest will also hold, with minor modifications, for the forests of the North Carolina summits. The conifer-birch forest of the mountains is to be regarded as the climax type of its own limited area (not including, of course, the lower slopes dominated by deciduous trees), and at the same time as an extension or outlier of the northeastern climax forest.

THE MAPLE FOREST OF ISLE ROYALE AND ITS RELATIONS

Wherever the sugar maple occurs it forms a part of the climax forest, and is usually the dominant species therein. Between the two great eastern forest regions there is a transitional belt several hundred kilometers wide where the three climax trees of the conifer, and the two of the deciduous forest all occur (see map, fig. 14). This belt extends from northern Wisconsin through the upper peninsula and the northern part of the southern peninsula of Michigan and eastward to New Brunswick. WHITFORD (**59**) studied the successions in a portion of this belt, and found that the climax forest in northern Michigan (both peninsulas) is the beech-maple type. The balsam, birch, and spruce are very abundant, but here they belong to preliminary stages in the successions. GANONG (**26, 27**) gives an excellent summary of the plant formations of New Brunswick. He states that the climatic forest type is the "mixed maple-birch-spruce-fir association." There is no indication in his paper that the maple ever supersedes the other trees, but the presence of such a possibility must be admitted. The conclusion from the studies of WHITFORD and others seems to be that the maple and beech, where not climatically excluded, are able to supersede the climax trees of the northeastern forest.

Coming now to Isle Royale, we find upon the southwestern end, occupying the summit of the highest ridge, a mixed growth of *Acer saccharum* Marsh (sugar maple), *Betula lutea* Michx. f. (yellow birch), and *B. lenta* L. (sweet birch); with the characteristically northern trees as a minor element (see ADAMS **4**, pp. 30–31, and HOLT **33**, p. 224). The maple is decidedly the dominant species and reaches a large size.[1] At the northern edge of this northernmost outpost of the maples we may draw the line that separates the true northern forest from the transitional belt (fig. 14). South of this line the representatives of the southeastern deciduous forest, though not necessarily forming the bulk of the stand, yet have the upper hand; north of it the supremacy of the conifers and the paper birch is undisputed.

[1] It is of interest to note that the maple is common on the southern side of Michipicoten Island, near the eastern shore of Lake Superior.

Since glacial times there has been a continual northward advance of the forest, with the conifers as the pioneers, closely followed by the hardwoods. The problem as to whether the extension of the latter is still going on might be studied to good advantage in such localities as the southwestern end of Isle Royale, and Michipicoten Island. The large size and thriftiness of the maple at its northernmost limit would seem to indicate that it has not reached its climatic limit (BELL **8**). The manner and causes of "climatic successions," or the invasion of one climax forest by another, are still to be worked out.

SUMMARY.—THE CLIMAX FOREST

I. The dominant forest of Isle Royale is composed of *Abies balsamea*, *Betula alba* var. *papyrifera*, and *Picea canadensis*, with a few other species occasionally present. *Abies*, all sizes and ages considered, is by far the most abundant, but the greater number of individuals are small. *Betula*, although conspicuous, is not abundant, and young trees are scarce. *Picea* is rare, though occasional specimens tower high above the other trees. Shrubs and herbaceous growth are sparse except in partial openings. The most important element in the latter is the moss contingent, which is responsible for the formation of great amounts of humus.

II. Studies of individual species gave the following results. *Abies* is preponderant in the young growth because (1) the seedlings make a successful start in almost any situation provided sufficient light be available; (2) the species reproduces abundantly by layering. Its rapid decrease when greater size and age are considered is due to (1) competition because of abundant germination; (2) fungus attacks, and (3) brittleness of wood, both resulting in extreme liability to windfall. Its high birth-rate is balanced by a high rate of mortality. *Betula* does not germinate abundantly in the forest, but, because it is not liable to disease and windfall, holds its own with *Abies*. Even when broken off by severe winds it has a means of recovery in its ability to produce stump sprouts. Its more rapid growth gives it an advantage in competition with *Abies*. Abundant light is necessary for successful reproduction. Low birth-rate is compensated by a very low mortality. *Picea* is ecologically unimportant on account of its scarcity. Germination in the forest is less abundant than in the case of *Betula*. It is not liable to fungus attacks and withstands severe winds. Birth-rate and mortality are both low. *Taxus canadensis* is the most important species of the undergrowth, its influence lying in the completeness with which it occupies and shades the ground, preventing tree reproduction over large areas.

III. Intensive study of selected areas (quadrats) yielded the following facts concerning the dynamics of the forest.

The forest is a complex of windfall areas of differing ages, the youngest made up of dense clumps of small trees, and the oldest containing a few mature trees with little young growth beneath. The history of a windfall area is as follows. After the débris has disintegrated sufficiently to allow abundant light to reach the ground, a new generation of trees springs up, approximately even-aged, composed of the three dominant species, *Abies* always greatly preponderant. During the continued development of this group most of the individuals are at various times eliminated, *Abies* suffering most for the causes enumerated in section II. Because of the dense shade no new individuals can start beneath them, and the final outcome is a group composed of a few large trees, approximately even-aged, in which *Abies* has nearly or quite lost its position of dominance to *Betula*. In situations sheltered from wind all species live to a greater age and windfalls are less frequent. The processes though less rapid are nevertheless the same as in more exposed situations. The result in the forest in general is a mosaic or patchwork which is in a state of continual change. The forest as a whole remains the same, the changes in various parts balancing each other.

IV. The following evidences that the dominant forest of Isle Royale is also the climax have been derived from the studies summarized above and from those dealing with the successions.

1. The dominant forest is the most mesophytic of the plant societies.

2. It is uniform upon all soils and upon areas that have passed through very different lengths of subaerial history.

3. All the successions culminate in the establishment of this as the final stage.

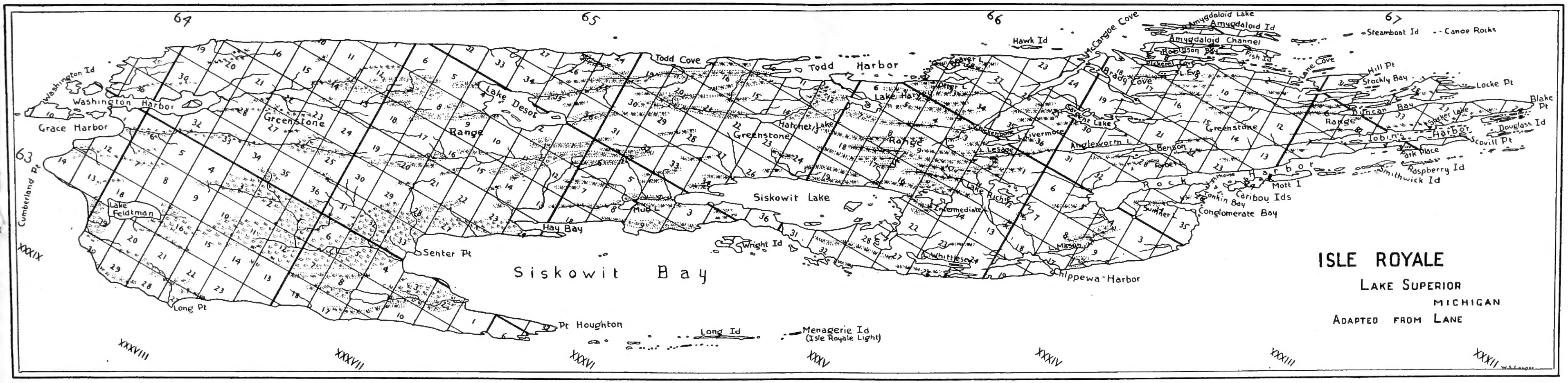
4. The character of the forest as a whole is stable, though any given area is continually changing in composition and relative proportions of the various species.

V. The same type of forest, with local differences in some places, is probably the climax throughout the northeastern conifer region.

VI. Comparison with the conifer-birch forest of the southern Appalachian summits shows a striking equivalence of species and marked correspondence between the two in ecological characteristics, indicating that the forest dynamics are essentially the same. The mountain forest may logically be considered as a southward extension or outlier of the northeastern climax forest.

VII. *Acer saccharum* is dominant upon the main ridge at the southwestern end of Isle Royale, reaching here its extreme northern limit in this region. Southward it is probably able to supersede the conifers and birch, while north of its northern limit the supremacy of the latter trees is undisputed.

PALO ALTO, CALIFORNIA


ISLE ROYALE
Lake Superior
Michigan
Adapted from Lane
Siskowit Bay
Siskowit Lake
Washington Harbor
Grace Harbor
Washington Id
Cumberland Pt
Lake Feldtman
Long Pt
Pt Houghton
Long Id
Menagerie Id
(Isle Royale Light)
Senter Pt
Hay Bay
Mud L
Wright Id
Lake Desor
Greenstone
Range
Todd Cove
Todd Harbor
Hatchet Lake
Lake Harvey
Otter L
Beaver L
Hawk Id
McCargoe Cove
Amygdaloid Lake
Amygdaloid Id
Amygdaloid Channel
Robinson Bay
Pickerel Cove
L. Eva
Fish Id
Brady Cove
Sargent Lake
Chickenbone
Livermore
L. Lesage
Lake Richie
Intermediate
Whittlesey
Angleworm L
Benson
Forbes
Sumner L
Mason
Chippewa Harbor
Rock Harbor
Conglomerate Bay
Tonkin Bay
Caribou Ids
Mott I
Smithwick Id
Raspberry Id
Tobin's Harbor
Duncan Bay
Lane Cove
Stockly Bay
Hill Pt
Locke Pt
Blake Pt
Douglass Id
Scovill Pt
Steamboat Id
Canoe Rocks
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