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The Forest Of Isle Royale

In Relation To Fire History And Wildlife

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AGRICULTURAL EXPERIMENT STATION

UNIVERSITY OF MINNESOTA

ON THE COVER

Visitors to Isle Royale enjoy watching moose near Washington Harbor at the south-west end of the island. This publication discusses the Isle Royale forest in relation to fire history and the island's wildlife, especially to the moose (Photo is courtesy of National Park Service).

PHOTOS ON THE RIGHT:

Top: This is the view from Lookout Louise at the northeast tip of Isle Royale. Duncan Bay is in the foreground, and the Canadian shore — 15 miles away — can be seen in the background. The island's moose and timber wolves probably came from the Canadian shore. Middle: Screened Adirondack shelters are available at the park. Most of the 22 lakeside and trailside campgrounds have such shelters together with tentsites, toilets, and grills. Bottom: Vistas like this overview of Lake Superior are common at Isle Royale. Hikers can travel on more than 120 miles of foot trails extending throughout the park.



PHOTOS ON OPPOSITE PAGE:

Top left: The lighthouse at Rock Harbor warned 19th century sailing and steam ships of the dangerous, rocky shoreline. Top right: Balsam fir is a main winter browse species for moose. The moose discovered this patch of balsams on Beaver Island in 1961. Middle left: This is typical aquatic habitat for moose. This shoreline sedge mat on Sumner Lake was extensive in 1905. However by 1930, the moose had almost completely trampled it. Middle right: Winter moose habitat has received severe browsing for about 60 years. The balsam fir in the foreground is 3 feet tall and about 30 years old. Bottom left: Beaver are common at Isle Royale. These tireless engineers create ponds that provide aquatic habitat for moose, birds, and trout. Bottom middle: Both early and recent bird lists report that herring gulls are probably the most abundant water birds at Isle Royale. Herring gulls are primarily fish and carrion eaters, keeping the island free of refuse. Bottom right: Gray jays are common permanent residents. These birds have been observed in most cover types, but are most closely associated with coniferous trees. Called "camp robbers," these birds delight visitors by snatching bits of bread from camp tables.



Acknowledgments

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The Forest Of Isle Royale

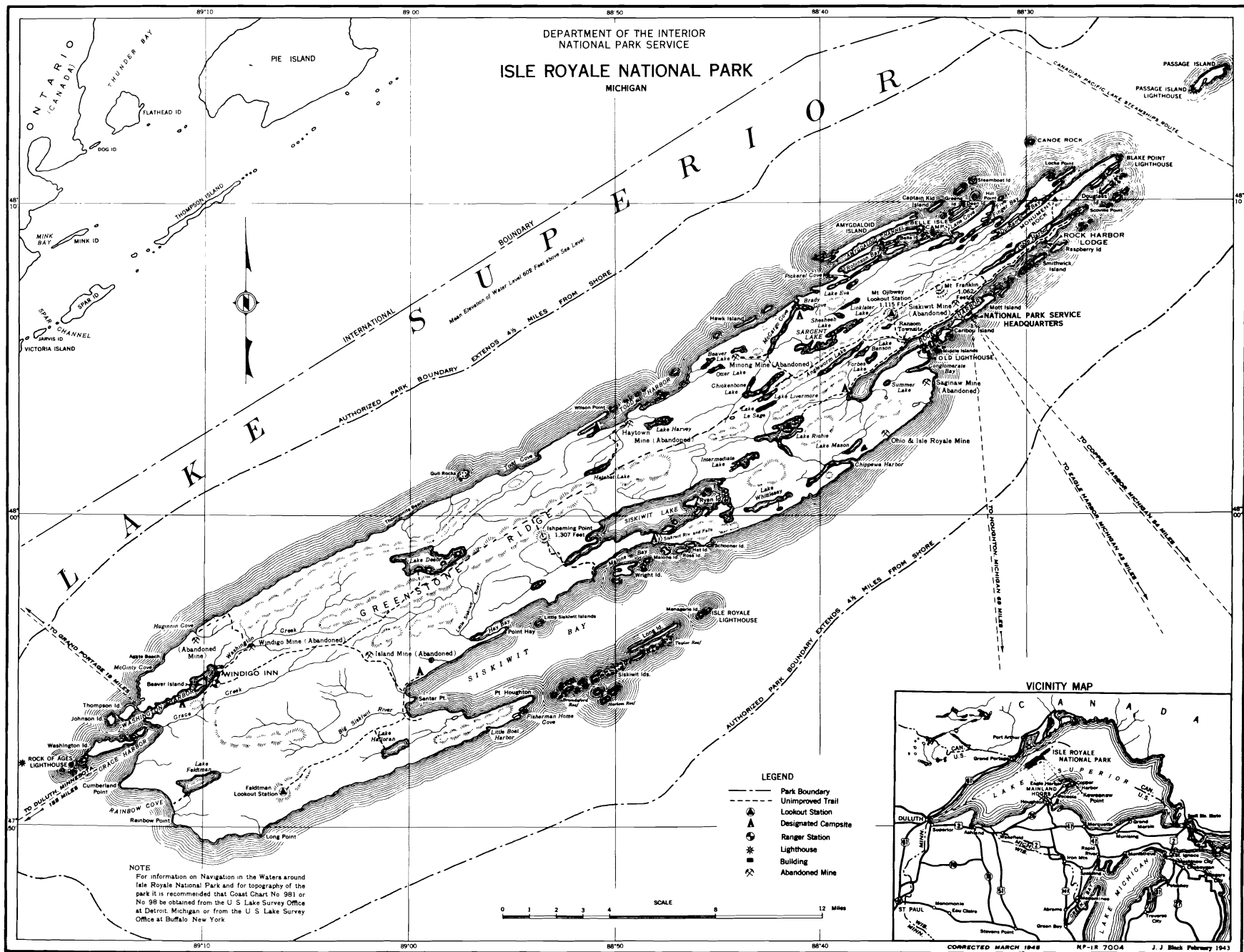
In Relation To Fire History And Wildlife

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ISLE ROYALE IS THE LARGEST island in Lake Superior. It covers about 210 square miles and has an estimated 200 small islands and rock outcrops. The main island is 45 miles long and is 8 miles at its widest point. The island roughly parallels the north shore of Lake Superior. Its closest point to Ontario is 13 miles. Isle Royale is about 18 miles from Minnesota (figure 1).

Its combined isolation, natural beauty, and wealth of prehistoric and early copper mining history make Isle Royale unique. These attractions led to the island's creation as a National Park. There are no year-round residents. National Park Service personnel live on the island from May through October. Winter use is confined to limited visits by park personnel and research workers. The island has no roads. Travel is by foot along the 120-mile trail system. The entire island and its nearby islets are federally owned. A small number of former owners have life-tenure use rights.

Figure 1. Map and location of Isle Royale National Park.



RESEARCH OBJECTIVES

For a long time Isle Royale has been of special interest to a variety of disciplines. Historians and anthropologists have had an early interest in the island. Its copper was mined in prehistoric times. Indians of historic times evidently feared the island. Biologists as early as the mid-1800's explored Isle Royale. They searched for new species and related the island's flora and fauna to its continual isolation by water since postglacial times when it originated as an upthrust of rock folds.

In the early 1900's, scientists of the newly developing discipline of ecology found that Isle Royale was an ideal area for their studies. More recently the animal population, unique as to species because of the island's isolation, has been studied by wildlife biologists. These scientists have been interested especially in species requirements, predator-prey relationships, and distribution anomalies resulting from isolation.

The present study had several objectives. The broad objective was to explore the unique advantages of a large wilderness island as a field laboratory for advancing the knowledge of forest ecosystems. Special reference was placed on forest succession, fire history, browse production, and the role of primary production as the homeostatic control of moose populations. Within this framework were several more specific goals:

1. To identify and describe major forest types according to tree, regeneration, shrub, and herbaceous components. This information is needed for other studies. It's been available only in fragments for the island;

2. To associate primary and secondary successional trends in forest types with their consequences to populations of several wildlife species, especially moose.

ISLE ROYALE — THE STUDY AREA

Climate

Climate has been generally accepted as ultimately determining the broad aspects of natural vegetation. While the vegetation of Isle Royale is related to that of the surrounding mainland, there are some differences in species and type distribution patterns. Therefore, weather records of Isle Royale were compared with reasonably comparable lakeshore stations in Minnesota, Wisconsin, and Michigan. Table 1 summarizes some of this comparative weather information. Data have been obtained from reports and summaries by Stromme (1969). U.S. Department of Commerce climatological data were also used (1941-1972). In comparing mean annual temperatures and high and low temperature extremes, the conditions at Grand Marais, Minn., appear to relate most closely to Isle Royale. However, the average date of the first fall freeze on Isle Royale is 2 to 3 weeks later than that at the other stations. This indicates the strong moderating influence of Lake Superior. Applying Thorntwaite's (1948) classification to Grand Marais records, that station is classified as $B_3C_2sb'_2$;

humid second microthermal, with a moderate summer water deficiency, and a temperature-efficiency regime normal to second mesothermal.

Some general observations can be made. Summer precipitation is well distributed on the island ranging from a minimum monthly mean of 2.12 inches in October to a maximum monthly mean of 3.45 inches in September. The first snowfall usually occurs in late October. Some years patches of snow may still remain in May. Snow accumulation is moderate with depths of 1½ to 2 feet. Accumulation seldom exceeds 3 feet except for drifts on the northwest faces of the ridges. The peak of fall color occurs in late September. Most of the leaves are dropped by mid-October. In winter, ice bridges occasionally form between the island and the Canadian north shore. In recent years, ice bridges were reported solid during late February and March in 1961, 1962, and 1963.

Linn's (1957) intensive studies of the island's microclimatic relationships document a strong lake effect which moderates temperatures and increases air moisture in shoreline areas. He also records warmer, drier conditions on

the southeast compared to northwest exposures. Linn relates these to the sun's more direct angles of insolation on the southeast slopes. These differences have a striking effect on the island's patterns of vegetation and species occurrences.

Postglacial Geologic and Forest History

Isle Royale was subjected to the action of ice sheets during the Pleistocene Age. The ice sheets ground the rocky surfaces smooth and gouged basins that are now lakes. There are 38

named lakes and about as many unnamed ponds. Largest of the lakes is Siskiwit. It is about 7 miles long and 140 feet deep. The drainage is poor within the island's valleys, although there are four important streams: Big Siskiwit River; Washington Creek; Little Siskiwit River; and Tobin Creek. The south shore and the two ends of the main island have sheltered coves and deep fjordlike harbors. These offer good weather protection for boats. In contrast, the north side of the island has few protective harbors.

The island has long been of interest to geologists. An early survey was sponsored by the federal government and reported on by Foster and Whitney (1850, 1851). An important member of that survey team was Edouard Desor. A lake and the highest point of the island were named after him. Bedrock geology was described in a classic report by Lane (1898). Huber (1973) made an excellent report reviewing previous studies and providing geologic information for interpretive programs. This report was a result of a

Table 1. Comparative weather summary on Isle Royale and vicinity.*

	Grand Marais Minn.	Bayfield Wisc.	Ontonagon Mich.	Mott Island ¹ Isle Royale
Highest temperature (F) and median date	82° (July 17)	94° (July 30)	93° (July 18)	89° (July 20)
Lowest temperature (F) and median date	-33° (Jan. 22)	-33° (Jan. 25)	-36° (Feb. 5)	-29° (Feb. 13)
Median date last spring frost	May 15	May 16	May 22	May 17
Median date first fall frost	Sept. 24	Sept. 28	Sept. 17	Oct. 15
Mean annual temperature (F)	39.0°	43.0°	46.6°	38.1°
Total annual precipitation (inches)	24.72	26.68	28.56	30.44

*U.S. Weather Bureau and Isle Royale National Park records.

¹ May through October data available since 1941. Because of some gaps in records, especially for November and April, Isle Royale data are not strictly comparable to other stations.

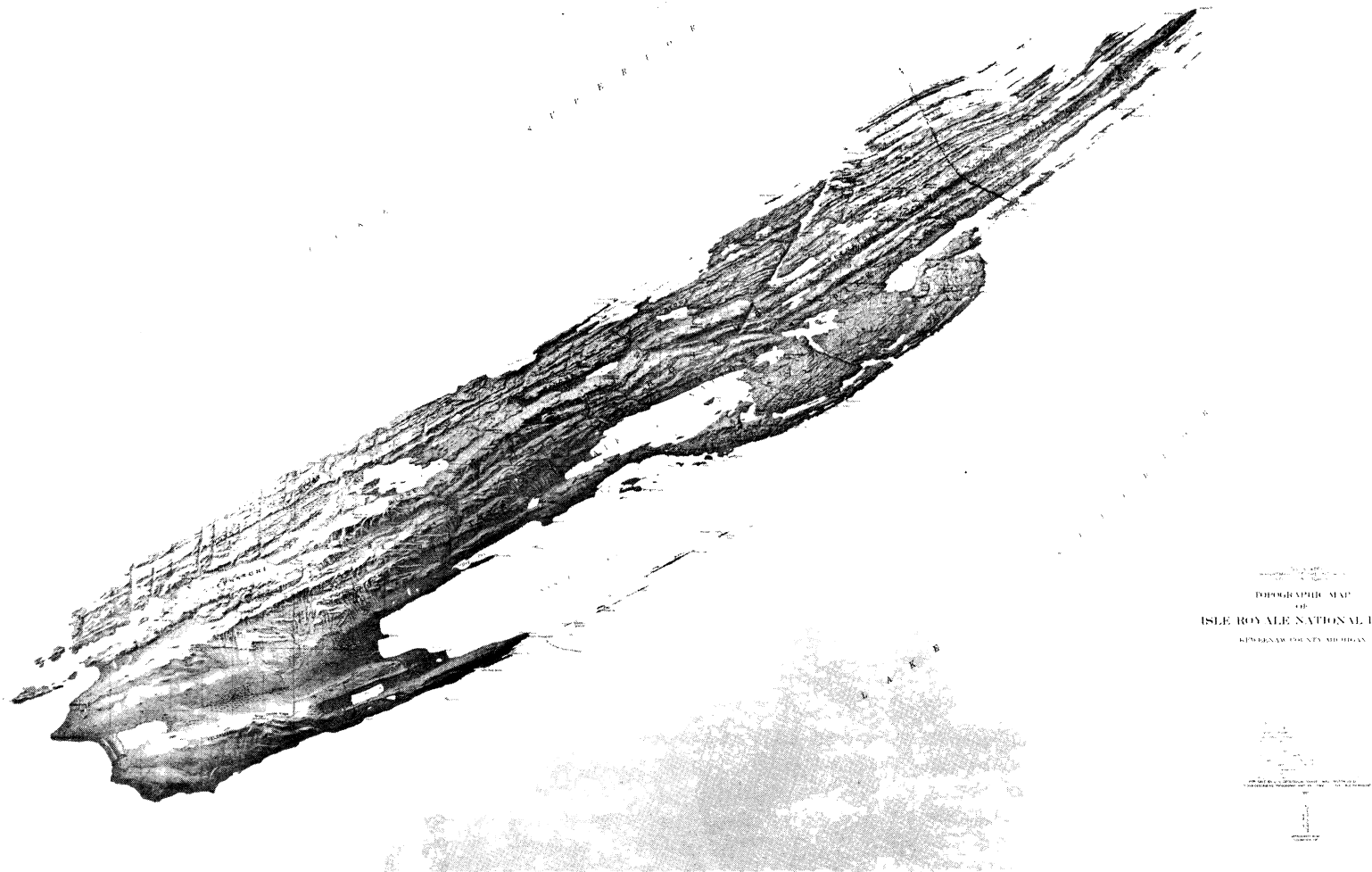


Figure 2. Topographic map of Isle Royale National Park.

cooperative effort between the Geological Survey and the National Park Service. These references are the major source of material presented in the following discussion.

Much of the island is covered by thin rock mantle soils. These were formed from till, talus, and other glacial debris during postglacial times. Ancient beaches and also wave-cut terraces, high on some ridge slopes, document successive stages of subsidence of postglacial lake levels. Since its emergence from postglacial Lake Duluth, Isle Royale has never had a land connection.

The island's basic landform features are a series of ridges and valleys oriented northeast and southwest (figure 2). These were formed in preglacial times by the differential erosion of softer and harder strata in the outcrops of the Keweenaw lava flows.

Occasional valleys cross the strike. These valleys follow fault clefts created by stresses imposed by the weight of the ice mass over the Lake Superior basin. McCargoe Cove is a striking example of this topographic feature.

The most resistant flows formed the Greenstone, Red Oak, and Minong Ridges. All of them are more precipitous on the northwest faces. Their southeast slopes are quite gentle, corresponding to the structural dip of the rock formations. The highest elevation is Mount Desor. It is 792 feet above the level of Lake Superior.

Till is relatively abundant on the west end of the island. This is in striking contrast to the east half where rock outcrops are much more abundant. Except in ravines and valleys, the east half has only a thin soil mantle. This variation in basic soil conditions

accounts for the confinement of the sugar maple–yellow birch forest stands, which require better soils, to the west half of the island.

Isle Royale emerged as a Lake Superior island after the burden of glacial ice was removed from the earth's crust. Because of this, the chronology of its vegetation helps document the general trends of vegetational changes. These vegetational changes reflect the changes in regional climate following the retreat of the glacier.

Pollen samples from nine bogs at various elevations above current Lake Superior enabled Potzger (1954) to describe this vegetational chronology. Predominance of *Abies* and *Picea* pollen from the oldest bogs at the highest elevations – 700 to 800 feet above Lake Superior – date the closing of the boreal fir–spruce association of

between 6,000 and 5,000 B.C. Bog samplings at lower elevations record only more recent pollen depositions. These show the decline of the fir-spruce dominance and record the span of the xerothermic climate period. During this period, *Acer*, *Quercus*, and *Pinus* pollen predominated. Linn (1957) noted that "... bogs at the lowest elevations record only the recent spruce-fir climatic climax; a fact which supports the theory that the island has emerged from Lake Superior waters in successive stages since glaciation."

Vegetation

Early botanical investigations

Botanical investigations were made early in the island's history. Numerous collectors, including Gillman (1873), and Wheeler (1901), and Ruthven (1906) found the island an excellent place for plant explorations. Adams (1909) conducted an early ecological survey. In his report, he included contributions to the knowledge of the flora and fauna made by Gleason (1905), Holt (1905), and Ruthven (1906). During the summers of 1909 and 1910, Cooper (1913) conducted studies leading to his identification and description of the boreal forest climax and the stages in its successional development.

The University of Michigan made a geographical survey of the island during the summers of 1929 and 1930 and in the summer and fall of 1931 (McMurray, ca. 1933). The objective was to determine the components — including ground cover — of the major forest associations in relation to the moose herd. Brown (ca. 1935) gave a general description of the vegetation and accounted for changes due to such factors as insects, fire, and moose. Linn (1957) studied the transition zone between the spruce-fir and the maple-yellow birch climax associations. He did this to determine the nature of the transition zone and the factors related to the site affinities of the two climaxes.

In addition to these systematic studies, some knowledge of the island's vegetation and condition can be found in the descriptive field notes made by Ives (1848) when he made the original land survey and in the description of the Isle Royale forest by Foster and Whitney (1850).

Ecological studies

Ecological surveys were made on Isle Royale in 1904 and 1905 (Adams 1909). Field stations were established at several locations where the habitat was described and collections of the fauna and flora were made. A survey team member (W.P. Holt, p. 224 in Adams 1909) concluded that balsam fir (*Abies balsamea*)* was the most common conifer and appeared to be superseding white spruce (*Picea glauca*), black spruce (*Picea mariana*), and tamarack (*Larix laricina*). In the older clearings and burnings, aspen (*Populus tremuloides*) and paper birch (*Betula papyrifera*) dominated. Undergrowth in these stands was mainly American fly honeysuckle (*Lonicera canadensis*), thimbleberry (*Rubus parviflorus*), blueberry (*Vaccinium* sp.), large-leaved aster (*Aster macrophyllus*), and bunchberry (*Cornus canadensis*). In places there was an abundance of ground hemlock (*Taxus canadensis*). The older uniform paper birch and aspen stands indicated burnings of different ages. Special reference was made to ground hemlock (Holt, p. 236 in Adams 1909) which was described as: "Everywhere abundant in the upland forest of the island. On account of its low, spreading growth it forms one of the greatest impediments in penetrating the island forests. The rankest growth was noted in the lower forest region around Washington Harbor where it attains a height of four to five feet." With reference to forest types present, Holt (p. 226 in Adams, 1909) wrote: "The succession of the burnings and clearings due to the early copper prospectors to clear the land, as well as the results of later forest fires, present an interesting problem; also, the peculiar distribution of hard maple and white pine on the island." H.A. Gleason (pp. 77 and 78 in Adams, 1909), another survey team member, wrote: "From the lake, representing the most primitive habitat, there are three lines of development culminating in the climax association: first, through the tamarack and peat bog; second, through the gravel beach and arbor vitae swamp;

*Botanical nomenclature of tree species follows Little (1953); that of shrubs and herbs, Fernald (1950); and of ferns and allies, with a few exceptions, Tryon (1954).

third, through the rock beach and *Cladonia* clearings."

An early ecological classic, "The Climax Forest of Isle Royale, Lake Superior, and Its Development," by Cooper (1913) was based on field studies made during 1909 and 1910 primarily in the northeast end of the island. This was one of the first studies describing, in a definitive way, a specific climatically determined climax vegetation. The climax described was the general boreal association of fir-spruce-paper birch. The three characteristic species were balsam fir, white spruce, and paper birch. It is significant that these studies did not concentrate on the southwest end of Isle Royale where the maple-birch forest — composed primarily of sugar maple (*Acer saccharum*) and yellow birch (*Betula alleghaniensis*) — also assume climax status. He observed that fires had influenced the forest greatly and described differing effects of fires of varying intensities on the tree, shrub, and herbaceous species. He considered ground hemlock to be the most important species of all the understory vegetation. This is of considerable significance since it is a highly preferred moose browse species. Its abundance since moose occupied the island subsequent to Cooper's studies has been a matter of great interest and concern.

Seventeen years later, Cooper (1928) revisited Smithwick Island along Rock Harbor. He compared paired photographs to indicate the timetable of vegetational change on different sites. As was expected, change was most rapid where a secondary succession was initiated by a burn in 1903 or 1904. In 1909 in depressions on the basic rock formation, considerable herbaceous vegetation, a few shrubs, and occasional balsam fir and white spruce seedlings were found together with sprouting birch and stumps of mountain ash. The vegetation had grown profusely by 1926, and a thin humus was beginning to cover the rock. Almost no change was observed in the crustose and foliose lichens on the rock shore formations. Cooper also noted the rapid increase in the moose population following their "recent" arrival to the island. With some dismay he mentions their effect in converting sedge mat zones around ponds to "mere mud wallows."

In the University of Michigan's geographical survey of the island during the summer of 1929 and 1930 and in the summer and fall of 1931 (McMurray, ca. 1933), aerial photographs were made of the island vegetation. Four associations were recognized: (1) birch—poplar, and birch—poplar—balsam; (2) balsam—spruce—white birch (climax forest); (3) hardwood, and hardwood—conifer; and (4) the swamp forest.

Brown (ca. 1935) in "The Ferns and Flowering Plants of Isle Royale, Michigan" noted that the forest in the northeastern area of the island was composed mainly of balsam fir, white birch, aspen, white spruce, and northern white-cedar (*Thuja occidentalis*). Balsam fir was the most abundant. Pure stands of aspen and paper birch were present, indicating past fires. The central area was most influenced by fire. This part of the island once supported the largest concentration of white pine (*Pinus strobus*). The southwestern area contained the only sugar maple—yellow birch climax forest on the island, some swamp forest type, and large acreages of the spruce—fir—birch climax forest.

Linn (1957), studying the transition forest between the balsam fir—white spruce—paper birch climax at lower elevations and the sugar maple—yellow birch climax at higher elevations, found soil moisture to be the most significant factor determining the location of the various species of these forest types. The relationships of these two climax forests are apparently the result of climatic change occurring after the xerothermic period which maintained sugar maple and northern red oak (*Quercus rubra*) in only the warmer and drier locations. These species now occur on the higher ridges inland from Lake Superior. Mesic sites support sugar maple and yellow birch as codominants; "wet mesic" sites support white spruce and sugar maple. In the transition zone, sugar maple are dominant on the mesic sites. At the lower elevations near Lake Superior, boreal conifers form the balsam fir—white spruce—paper birch climax forest.

Peripheral area vegetational studies

It's not possible, within the limits of this study, to review all the literature describing the vegetation of main-

land areas surrounding Lake Superior. However, reference is made to several publications because of their special relevance as background to the ecology of Isle Royale vegetation.

Maycock and Curtis (1960) conducted an extensive study of the phytosociology of the boreal conifer—hardwood forests of the Great Lakes Region. This study encompassed, but did not specifically include, Isle Royale. This study attempted to describe and explain the nature of that forest belt which is transitional between the boreal conifer forest to the north and the deciduous forest to the south.

The status of this forest has long been a controversial matter. Numerous authors (Sargent, 1884; Cooper, 1913; Weaver and Clements, 1929; Nichols, 1935; Braun, 1950; and Maycock and Curtis, 1960) have attempted to place this forest into a broader classification system. Other authors (Bergman and Stallard, 1916; Grant, 1934; Egger, 1938; Brown and Curtis, 1952; and Butters and Abbe, 1953) have reported on forest studies of more specific portions of the geographic area involved.

The general nature of the controversy is whether the boreal conifer—hardwood forest is a distinct association; a transitional ecotone between distinct boreal and deciduous climaxes; or a portion of a vegetational continuum which defies classification because of no identifiable groups of species. Maycock and Curtis (1960) do not accept the Clementsian notion of discrete climatic climaxes. They consider the entire complex to be part of a continuum. Their data support the assumption that moisture is the primary factor providing a gradient along which the various forest stands can be ordinated. Other environmental characteristics, such as nutrient levels and soil profile characteristics, are shown to be related to moisture classes. The presence, frequency, and importance values of many plant species are also shown to have trends related to the moisture ordination.

Roe (1935) had previously developed a system relating potential forest cover in the Lake States Region to joint soil texture-moisture classes. However, unlike Maycock and Curtis, he recognized northern hardwood and white spruce—balsam fir climax re-

gions. White spruce—balsam fir types were not included in the northern hardwood climax region, and northern hardwoods were included on fresh, moist, and periodically wet sites. In the white spruce—balsam fir climax region, those species were included on moist, periodically wet, and wet sites. Northern hardwood species shared position with these boreal conifers on the best soils under moist conditions.

Because balsam fir is considered to be a climax species on Isle Royale and because its successional role in mixed conifer—hardwood forests is a matter of controversy, the monograph of this species by Bakuzis and Hansen (1965) is felt to be particularly relevant. Using data from northern Minnesota and Wisconsin by Kittredge (1938), from Douglas Lake, Mich., by Gates (1926), and from Algonquin Park, Ontario, by Martin (1959), balsam fir is placed in primary succession schemes leading to northern hardwood climaxes in the areas referred to. The distribution of balsam fir, using the classifications of Halliday (1937) and Rowe (1959) for Canada and Braun (1950) for the eastern United States, has been mapped in this monograph. Isle Royale is shown to be surrounded on the north by subdivisions of the Boreal and Great Lakes—St. Lawrence Regions of Canada and by sections of the hemlock—white pine—northern hardwood region in the Lake States.

The forest cover type classification developed by the Society of American Foresters (1954) has been widely used, particularly for forest inventory. For eastern North America, three broad regions are identified: the Boreal, Great Lakes—St. Lawrence, and Acadian—Appalachian. Within these regions, forest cover types based on the dominant vegetation are arranged on a moisture gradient. Isle Royale would be included within the Great Lakes—St. Lawrence Region rather than the Boreal Region. This is because of the widespread occurrence of the northern hardwoods, species not found within the Boreal Region.

Wildlife

On Isle Royale, only 18 species of mammals occur. The adjacent Canadian mainland supports a larger number (Johnsson and Shelton, 1960). Some of the species never found on

the island include the black bear (*Euarctos americanus*),* raccoon (*Procyon lotor*), fisher (*Martes pennanti*), least weasel (*Mustela rixosa*), striped skunk (*Mephitis mephitis*), gray fox (*Urocyon cinereoargenteus*), bobcat (*Lynx rufus*), woodchuck (*Marmota monax*), least chipmunk (*Eutamias minimum*), eastern chipmunk (*Tamias striatus*), eastern gray squirrel (*Sciurus carolinensis*), northern flying squirrel (*Glaucomys sabrinus*), porcupine (*Erethizon dorsatum*), and several species of voles, shrews, and bats (Johnsson and Shelton, 1960). The list of mammals recorded by Adams (1909) includes: woodland caribou (*Rangifer caribou*), Hudson Bay red squirrel (*Tamiasciurus hudsonicus*), northeastern beaver (*Castor canadensis*), snowshoe hare (*Lepus americanus*), muskrat (*Ondatra zibethicus*), mink (*Mustela vison*), Canada lynx (*Lynx canadensis*), marten (*Martes americana*), and two kinds of mice and weasels plus three kinds of bats. Since Adams' list of mammals, there have been some conspicuous changes in mammal species. The coyote (*Canis latrans*) probably reached the island as early as 1906 and disappeared in 1958 (Krefting, 1969). A second predator, the timber wolf (*Canis lupus*), apparently arrived in the late 1940's (Krefting, 1949; Hakala, 1954). The third predator, the red fox (*Vulpes fulva*), appeared for the first time about 1925 (Johnson, 1969). It became more numerous after the coyote disappeared (Krefting, 1969). The woodland caribou was present in the early 1800's (James, 1830), and in 1840 a solitary herd was reported (U.S. Indian Bureau Ann. Rept., p. 354, 1840). The last caribou were seen in 1926 (Dustin, 1946). In 1912, nine white-tailed deer were introduced, and they were last seen about 1925 (Warren, 1926).

Not only the time of arrival of the moose but also the method of migration is unknown. Some may have arrived in 1905, either by swimming, walking on the ice (Hickie, ca. 1943), or by crossing the ice bridge in the winter of 1912-13 (Murie, 1934).

A total of 197 species of birds have been reported on Isle Royale. Sixty-two species have been bred on the island at least once, 26 are thought to be breeders, and the rest are migrants (Krefting *et al.*, 1966). Although the habitat appears to be suitable for the spruce grouse (*Canachites canadensis**) and the ruffed grouse (*Bonasa umbellus*), they are absent. This is probably because they are incapable of making long flights. The presence of the sharp-tailed grouse is of special interest. This species has been an island resident for a long time (Krefting *et al.*, 1966). A remnant population still occurs on the higher open ridges. The species is dependent on open areas provided by burns.

Because of its isolation from the mainland, the island may be regarded as a separate ecosystem with fewer species of mammals and, therefore, less complex ecological relationships. The principal consumers of the vegetation are the moose, beaver, and snowshoe hare. Currently, the principal predator of the moose and beaver is the wolf; the red fox is the principal predator of the snowshoe hare.

Cultural History

Copper mining

Shiras III (1935) regarded Isle Royale as the most interesting island in the Great Lakes. Others have described it as the wonder island of the north, the enchanted island. Some have likened it to a battleship accompanied by a fleet of destroyers. Indians of the 17th Century feared the island and referred to it as the floating island. Radiocarbon dating of wood recovered from prehistoric mines has shown that aboriginal copper mining on Isle Royale took place at least 3,300 years ago (Drier, 1961). As late as 1850, the Indian tribes of the Great Lakes Region seldom visited this island. They called it "Minong," meaning copper. In the early 1900's, John Linklater, a famous half-breed guide, reported on Indians' dances and appeals to the spirits. These were performed before visiting the island to assure their safety (Hakala, 1955).

In spite of this apparent fear of the island, the Indians exploited the more readily available pure copper lying on the surface. They also chiseled out the seams in the surface layers of bedrock. This copper found its way as far as New England in the form of points, knives, and ornaments (Rakestraw, 1965). Over 1,000 small pits have been located, attesting to this aboriginal activity.

Through a treaty in 1843, the Chippewa relinquished claim to the island. A flurry of exploration and mining ensued. Mining was conducted intermittently from then until about 1890. During that time, the extensive explorations at Washington Harbor involved miles of roads and the development of the Gyllbank Townsite together with houses, storehouses, and other facilities. However, these efforts resulted in little copper production. Rakestraw (1965) recorded the rise and fall of this industry in terms of production figures from the principal mines.

These extensive mining activities influenced not only the landscape, but also the vegetation. Considerable lumber was used to construct homes and buildings and for mine props, fuel, and other purposes. Most, if not all, lumber was obtained locally. The white pine, wherever it was available, was undoubtedly used first for construction lumber. Tamarack would have been preferred for mine timbers where durability and strength was important. This may help explain the current paucity of these species compared to their presence as recorded in the Ives' survey of 1847 and 1848 (Ives, 1848). In addition, to explore for copper seams, forests were burned to expose the surface rock.

Isle Royale — a National Park

The "park idea" first emerged in the early 1920's (Hakala, 1955). For several years, *The Detroit News* carried articles about prominent conservationists, private groups, and conservation agencies who were promoting park status for the island. Proponents of state as well as national park status expounded their point of view. In 1922, Michigan's State Director of Conservation, John Baird, said that failure to get federal status for the area would be regretted in the future. Interestingly, W.T. Hornaday, a prestigious personage of the New York

*Scientific names of mammals follow Miller and Kellogg (1955).

*Scientific names of birds follow the fifth edition (1957) of the American Ornithologists' Union Check List of North American Birds.

Zoological Park, injected a cautionary voice. “. . . There is always a chief drawback to an island as a game preserve and that is that the surplus game is unable to migrate into contiguous territory . . . the surplus game might become embarrassing.” This note of prophesy was to be fulfilled in the 1930's when a totally uncontrolled moose population was decimated by starvation (Hickie, 1936; Titus, 1941).

The agitation for an Isle Royale National Park continued during the 1920's. In 1931, the legislature passed the bill which President Hoover signed. Further delays of several years ensued. Michigan had to arrange for deeding the lands which it owned to federal ownership. Also, the private lands on the island had to be acquired. However by 1941, all lands were in public ownership. The formal dedication was postponed by World War II. It was held Aug. 27, 1946.

Although the park was not formally dedicated until then, National Park Service administration began in 1935. That year four Civilian Conservation Corps camps were proposed. The first was located that year at Siskiwi Bay. Other camps were located at Rock Harbor, Mott Island, and Windigo. These camps, with their hundreds of enrollees and technical staff, were almost totally responsible for the buildings, trails, fire towers, docks, and other facilities used for many years.

Recreational use

Long before the island was considered for a park, its beauties and recreational attractions had not been unnoticed. Hakala's report (1955) says that lodges were operating at four places in the 1910's and 1920's — Singer Island (Washington Island), Tobin Harbor, Belle Isle, and Rock Harbor. In addition, scores of families had summer cottages on the island. Camping parties from Duluth reportedly frequented Isle Royale. Travel, of course, had to be by boat. The boats were either private yachts or such vessels as the “America” which made scheduled runs from Duluth and which now lies on the bottom of the narrow entrance to Washington Harbor.

Some statistical information for 1961-72, taken from file records of the park, is given in table 2. Visitors came from Grand Portage, Minn., Copper Harbor or Houghton, Mich. Travel was predominantly on the several scheduled boat trips from these harbors. Also during this period, 15 percent of the total visitors arrived by private boat. Eight percent came by air from air service points either in Minnesota or Upper Peninsula, Mich.

Several trends in the extent and nature of visitor use are apparent. During the 11-year period, the number of visitors almost tripled from 6,476 in

1961 to 16,116 in 1972. However, the average length of stay has decreased from 3.5 days in 1961 to 3.1 in 1972. Thirty-five percent of the visitors came from Grand Portage, Minn. and 47 percent came from the two Michigan harbors. There were no apparent trend changes.

Two changes in visitor use appear to be of very recent origin. Back-country camping, which includes camping at points other than the designated campgrounds, increased sharply in 1971 and 1972. This reflects a change in park policy in recent years permitting such “free” camping. During 1971 and 1972 there has also been a sharp drop in the “other” use category. This includes use by life lessees and commercial fishermen. Such users represent only a small number of individuals. However, they tend to stay most of the spring, summer, and fall. Therefore, they contribute to the number of use days out of proportion to their small numbers. It is probable that the drop in such use accounts for the small reduction in average length of visitor stay cited previously.

A more detailed analysis of the recreational use of Isle Royale is given in a report by Buckley and Cain (1964) to the Interdepartmental Resource Development Committee (Michigan).

Table 2. Isle Royale visitor use, 1961-1972.*

Year	Number of visitors					Visitor use-days				
	Total ¹ Number	Travel route — percent				Total No. Days	Concessions Percent	Campgrounds — percent		
		Minn.	Upper Penin.	Air	Private Boat			Designated	Back Country	Other Percent
1961	6,476					22,780	29	34		37
1962	5,410					20,692	23	41		36
1963	7,836					29,457	28	45		27
1964	8,189					35,774	23	45	0.2	32
1965	9,477	36	44	7	13	34,559	26	54	0.6	19
1966	10,787	34	42	6	18	38,260	26	49	2.2	22
1967	9,528	29	40	6	24	36,602	24	48	0.9	27
1968	10,065	39	42	8	11	37,117	26	51	2.0	21
1969	10,503	35	43	9	13	37,332	25	50	5.0	20
1970	14,411	36	38	8	17	45,319	25	47	9.0	19
1971	15,868	34	39	10	17	56,033	23	46	28.0	3
1972	16,116	35	44	11	9	51,543	25	57	16.0	2
Average percent 1965-1972		35	42	8	15	Average percent	25	48	7.0	20

* Isle Royale National Park records.

¹ No travel route data for 1961-1964.

INVESTIGATIVE PROCEDURES

Vegetation Survey

To attain the objectives of the study, reasonably accurate description of the island's vegetation was necessary. Because the island vegetation is primarily forest, the backbone of the study is a description of recognizably discrete forest types and their quantification to the greatest possible extent.

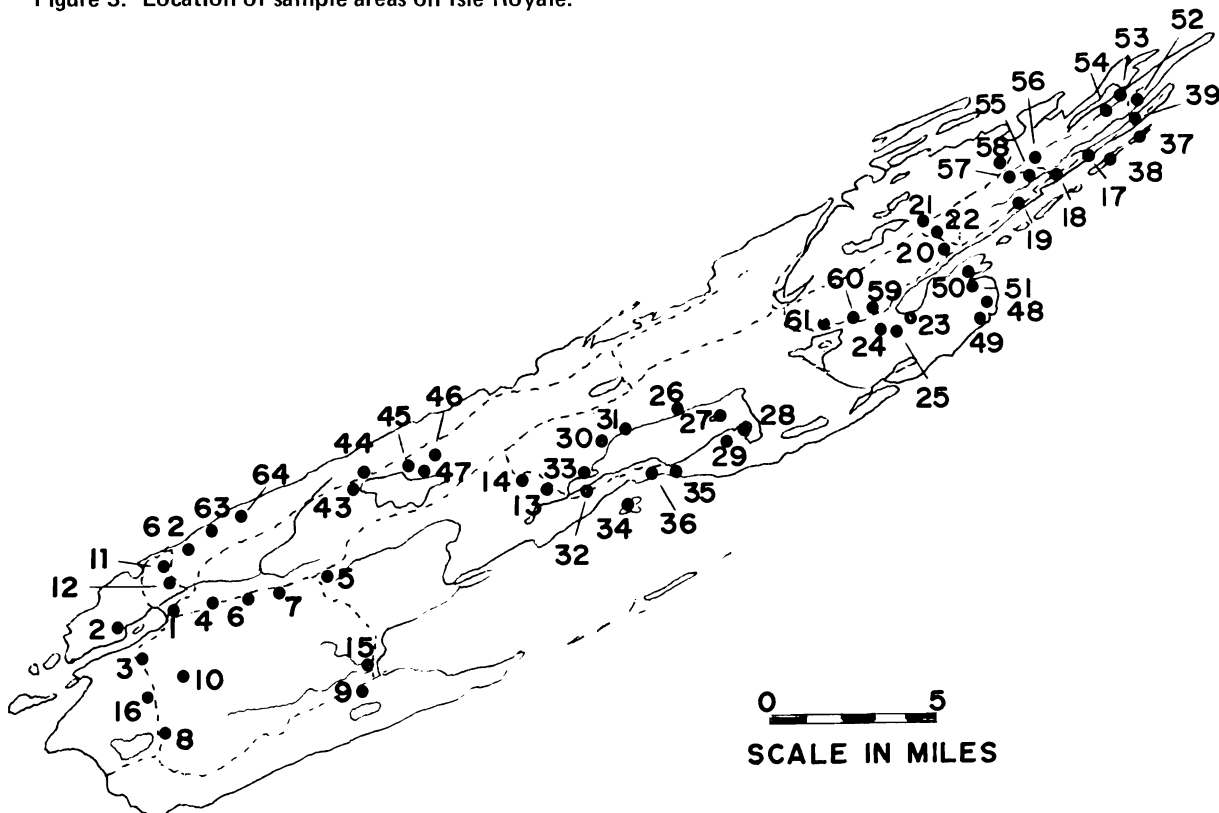
Before performing any vegetational sampling, a reconnaissance was conducted to view the range of ecological conditions, the patterns of distribution of the various forest types, and to become generally familiar with the

island's vegetation. This was done in summer, 1966, by following the island's foot trails, viewing its perimeter by boat, and by several aerial flights. Aerial photos, made from a 1957 survey by the U.S. Geological Survey, were available to help locate the various forest types. In 1964, a systematic interpretation was made of the aerial photos. A type map of the vegetation of the entire island has been published (Krefting *et al.*, 1970). This type map is discussed in detail in a subsequent section.

During the summers of 1967, 1968, and 1969, field surveys were conducted to sample the array of forest types as fully as possible. The rugged topography, difficult access to much of the island, and time limitations made random sampling and strict mechanical sampling an impossibility. Using the types delineated on the cover-type map and the aerial photos as guides, 64 sample stands of the various types were located. These could be reached by aircraft, by trail, or from shore by boat (figure 3). A

42 40
41

Figure 3. Location of sample areas on Isle Royale.



reference stake was driven into the ground. From this stake, a bearing and distance into the stand were determined at random to locate the nest of plots.

Tree data were collected using point sample "Bitterlich" plots. One or more such plots were taken depending on the nature of the stand. The number of stumps per acre was determined on circular 1/100 acre plots. Tree seedling, shrub, and lesser vegetation data were collected through the use of 10 one mil-acre plots.

Collected tree data included species, diameter at breast height, total height, height to the live crown base, age, and crown class. For dead trees, an additional record was kept of whether they were standing, down, or stumps. Six crown classes were recognized. These were open grown, dominant, codominant, intermediate, overtopped, and super-dominant.

Tree reproduction was recorded by species and height classes. In addition, a record was kept of all seedlings which had been browsed. Herbaceous vegetation was recorded using standard Braun-Blanquet cover percent classes.

A tally-sheet form was used. All entries were made on this with numbers. This enabled direct keypunching of data cards usable for computer compilation and programming.

Method of Synecological Coordinates

The core of this study involves the identification, delineation, and description of forest vegetation units which are relatively homogeneous ecologically. Therefore, these units can be expected to respond similarly to disturbance, to have a common climax vegetation, and to be similar in productivity. Such units can be both abstract and specific. They have conceptual characteristics in common with Clements' (1916) notion of the

climax, with the ecosystem concept (Tansley, 1935), and the forest types of Cajander (1926).

The method of synecological coordinates developed by Bakuzis (1959) provided the basic framework for the vegetational studies. This method resembles the techniques used in the construction of ecological models by Rowe (1956), Ellenberg (1950), and Curtis (1955). It is basically patterned after the models developed by Pogrebniak (1930, 1955) and others. The concept of species presence is fundamental to the method. A plant species maintains its position in a natural community only if it is compatible enough with the physical environment to successfully develop and reproduce in competition with other species. Thus in any natural ecosystem, the requirements of an indigenous species may be characterized by an evaluation of the environmental conditions in which it occurs. Conversely if the knowledge of a species' habitat relationships are known, the presence of that species may be a basis to make inferences about the associated environmental factors.

Individual species have been assigned values on a scale of from 1 to 5 relative to the four effective environmental factors of moisture, nutrients, heat, and light. The term "synecological" emphasizes the point that all observations concerning the occurrence of individual species are made under conditions of competition with other species. Species respond quite differently in competition than when competition is absent. Those species occurring predominantly at the lowest intensity of an environmental factor complex receive the lowest coordinate value of 1; the highest intensities are graded as 5, and intermediate coordinates are 2, 3, or 4 depending on their relative position of occurrence along the gradient. This procedure is repeated independently for each of the four factor complexes. Thus, a species

is assigned four values corresponding to its position relative to all other species in its requirements for moisture, nutrients, heat, and light.

The values derived for plants in the total range of Minnesota forest conditions are considered to represent similar conditions in Isle Royale (Bakuzis and Hansen, 1959). Those values have been applied in this study. In the use of synecological coordinates to determine community or forest-stand values, it's assumed a community coordinate represents the average of the individual coordinates of all present species. Contrary to some methods' criteria using the principle of plant indicators, it is assumed that all plant species reflect some characteristics of the environment. Therefore, they are of diagnostic significance. This is in basic agreement with the philosophy of Cajander (1949) who considered the "whole stand" indicative of ecological interrelationships. To apply this method for a specific community, the plants are recorded in the field. The coordinate values for all present species are added. An average is obtained for each factor (moisture, nutrients, heat, light). These resultant averages characterize the environmental relationships of the community. A scatter diagram of such coordinate values — from a sampling of communities representing the range of conditions in a geographic area — constitutes a synecological "field" within any pair of factors such as moisture-nutrients (edaphic field) or heat-light (climatic field). A similar distribution pattern made up of all the coordinate values for communities with a given species is the "ecograph" for that species. When ecographs of major species are superimposed in moisture-nutrient axes, diagrams are obtained similar to the primary succession diagrams developed by the Clementsian school. This provides additional evidence of the edaphic nature of these successional schemes.

FOREST TYPES, SPECIES, AND ECOLOGICAL RELATIONSHIPS

Vegetation Type Map

An Isle Royale map was prepared (Krefting *et al.*, 1970) delineating the locations of the broad vegetational types as interpreted from the 1957 U.S. Geological Survey aerial photographs. The island is almost completely forested except for rock outcrops, water surfaces, marshy meadows, and some shrub types. Consequently, the vegetation is mostly typed as "forest cover." Forest cover types are considered relatively homogeneous assemblages of species which are distinguishable from adjacent types through species, age (size), or developmental differences. They are characterized by the species actually present rather than the "potential" vegetation as described by Kùchler (1964) or the climax formations of Clements (1921). Some cover types, such as aspen and paper birch, are definitely transitional (seral). Others, like sugar maple—yellow birch, are permanent (climax). Within the present climate conditions, climax types are self-perpetuating. Earlier studies by Cooper (1913) and Linn (1957) consider climax on the island to be the northern hardwood type of sugar maple—yellow birch and the boreal forest type of balsam fir—white spruce—paper birch.

It should be noted that, in nature, the possible combinations of species and their relative proportions are almost limitless. In general, however, a cover type is named after the species or combination of species making up over 50 percent of the total tree stand. Table 3 lists these cover types and the acreages they cover. In subsequent

Table 3. Isle Royale vegetation types and acreages.*

Type description	Type symbol	Acres covered	Percent covered
Aspen, paper birch, balsam fir, white spruce	ABFS	32,287	24.03
Aspen, paper birch (burned 1936)	AB(Burn)	25,947	19.31
Birch, balsam fir, white spruce	BFS	21,914	16.33
Black spruce, white-cedar	SC	10,137	7.54
Yellow birch, sugar maple	YM	9,950	7.10
Lakes, 30 named		8,436	6.27
Birch, balsam fir	BF	5,436	4.04
Aspen, paper birch	AB	5,102	3.79
Rock outcrop	R	4,966	3.69
Aspen, paper birch, balsam fir	ABF	1,424	1.06
White spruce	S	1,409	1.04
White-cedar, balsam fir	CF	1,244	0.92
Lowland shrubs	IS	1,186	0.88
Beaver ponds		1,177	0.87
Black spruce, balsam fir, white-cedar	SFC	1,060	0.78
Balsam fir	F	658	0.48
Black spruce	S	513	0.38
Jack pine; jack pine—black spruce	J,JS	436	0.32
Black spruce, tamarack; black spruce—white-cedar—tamarack	SL,SCL	358	0.28
Tamarack	L	266	0.19
Aspen	A	179	0.13
White-cedar	C	179	0.13
Paper birch, yellow birch, sugar maple, balsam fir	BYMF	169	0.12
Paper birch, yellow birch, balsam fir	BYF	160	0.11
Upland shrub	IH	58	0.04
Aspen, balsam fir	AF	48	0.03
Aspen, white spruce	AS	39	0.03
		134,738	

*Determined from vegetation type map of Isle Royale (Krefting *et al.*, 1970).

sections, groupings of these cover types into "type groups" have been made to recognize ecological similarities and successional relationships.

Some conspicuous vegetation patterns should be noted. The conifer climax type occurs at the lower elevations, and the northern hardwood climax type occurs at the higher elevations. This reflects the affinity of the balsam fir and white spruce for the cooler, moister sites nearer Lake Superior. It also reflects the confinement of the more heat demanding sugar maple and yellow birch to the higher sites and where the soils are better developed. Documentation of these microclimatic relationships has been recorded by Linn (1957). Because of this, the Greenstone Ridge Trail, following the highest land on the island, passes through an old virgin stand of sugar maple, yellow birch, and other associated species for about 10 miles. Subclimax forests of paper birch and aspen and other associated species at various transitional stages cover most of the island. The poorly drained areas are covered mostly by black spruce and black spruce-white-cedar types. Jack pine (*Pinus banksiana*) stands occupy small acreages on dry sites, while red pine (*Pinus resinosa*) is a very minor species on a few dry ridges. Scattered red oak are present in limited numbers in the north-eastern section. However, they do not constitute a separate cover type.

A conspicuous feature on the map is the large area in the central and southwest portion of the island typed as burn. The area is the one burned in 1936 in a fire covering over 19 percent of the island (26,000 acres). Successional species, mostly aspen and paper birch, cover most of this area, and there are also areas of rock outcrop. The history of this burn and its consequences are discussed in other sections of this report.

Forest Cover Types in Edaphic and Climatic Fields

The organization aspects of synecological coordinates were used to illustrate the ecological affinities among the sampled stands and among

different forest cover types and to analyze cover types and their component relationships to environmental conditions. In figure 4, the forest cover types, as identified by their species composition, are superimposed on the edaphic and climatic fields of the Isle Royale forest. These fields are outlined by community synecological moisture, nutrient, heat, and light values for all study areas. Each stand location reflects the total plant response to moisture-nutrient and heat-light conditions relative to positions of other stands. Location of these stands is indicated on the map in figure 3.

An outline of the edaphic field depicting the range of moisture and nutrient conditions is shown in figure 4. It resembles a skewed triangle with a long, stretched part of dry, nutrient-poor to moist, nutrient-rich conditions. A narrow, abrupt part tends toward wet, nutrient-poor conditions. With the inclusion of some sphagnum bogs in the study, the field outline would be enlarged toward wetter, nutrient-poorer conditions. A similar outline of the climatic (heat-light) field is also shown in figure 4. It shows large variations in light conditions, ranging from about 1.5 to 4 while variation in heat is quite small, from 1.2 to 2.3.

The limited range of heat conditions — represented by the small variation in coordinate values for that factor — is to be expected. The coordinate values for heat reflect species changes in species occurring latitudinally, going from heat-demanding southern flora to cold-tolerant northern flora. Since the island is relatively small, little such broad latitudinal variation would be reflected. Some variation in heat occurs because of altitude or distance above the cold waters of Lake Superior. This accounts for the positioning of the types containing a predominance of such boreal species as balsam fir, white spruce, and paper birch at somewhat lower heat values. It also accounts for positioning of the types of such characteristic hardwoods as yellow birch and sugar maple at higher heat values in the graph. However, this relationship is somewhat obscured by the transitional forest

types, particularly those on the 1936 burn area where extreme exposure and open stand conditions undoubtedly influence microclimates for the forest stands.

Rock outcrop and jack pine types occupy dry, nutrient-poor, intermediate to warm, and open sites with ample light. Sugar maple and yellow birch-sugar maple types are related to moist, nutrient-rich, intermediate to warm, and shady sites. Black spruce-white-cedar-balsam fir and white-cedar-balsam fir-paper birch types occupy moist to wet, nutrient-poor to intermediate-nutrient, cool, and moderately open to shady sites. The paper birch-aspen-white spruce-balsam fir type is related to intermediate site conditions and occupies a large part of the central portion of both fields. This cover type could be subdivided into dry and moist phases or variants. There is a trend toward decreasing aspen and increasing balsam fir components related to increasing moisture. However, individual stands showed a large variation in the proportions of the four tree cover species. This makes it difficult to combine these differences in the edaphic and climatic fields. Not all stands necessarily contain all four tree species. The shaded area within this type approximates the extent of a relatively recent major disturbance, the 1936 burn.

Species Moisture-Nutrient Relationships

Figure 5 illustrates the distribution of individual tree species and their reproduction in the edaphic field. The graphed distribution pattern of a species is called its ecograph. It indicates species adaptation to environmental factors — in this case to the moisture-nutrient complex — under conditions of competition. Figure 6 shows the adaptations of six shrub and five ground vegetation species to stand and edaphic conditions of the Isle Royale forest.

The species have been selected because of their widespread occurrence on the island, because they are especially characteristic of certain sites, or because of their special value as moose browse. In some cases, com-

parisons have been made with similar ecographs from Minnesota conditions.

Trees and reproduction

Paper birch occurs on a very wide range of site conditions, from dry rock outcrop areas to white-cedar and black spruce swamps. Paper birch is scarce or lacking in shady, well-developed, undisturbed forest communities on moist, nutrient-rich sites (figure 5). Here yellow birch partially takes its place. The range of aspen distribution is narrower than that of paper birch. On moist, intermediate nutrient sites, aspen is present in communities which originated after disturbances in the last 100 years. This time period corresponds approximately with the longevity of aspen. Aspen extends farther into the area of moist, nutrient-rich sites in Minnesota conditions than it does on Isle Royale (Bakuzis and Hansen, 1960). On Isle Royale, these richest sites are most strongly dominated by sugar maple and yellow birch which exclude the intolerant aspen. In some communities of rock outcrop and jack pine types, aspen and paper birch reproduction extends outside of the tree range.

White spruce and balsam fir, considered climax species on the cooler sites of Isle Royale, show a wide range of adaptation to the existing site conditions. They are lacking on the extremes of dry, nutrient-poor and moist, nutrient-rich sites (figure 5). The reproduction of both species is largely confined to the tree range. Black spruce is largely limited to moist or wet, intermediate nutrient conditions except on drier sites where they exist together with jack pine on such microsites as rock crevices. Jack pine, being limited to dry, nutrient-poor sites, occupies a narrow range in the edaphic field. The areal extent of jack pine is also limited, composing only 0.32 percent of the island's total forest complex. In Minnesota, jack pine also extends on moister, nutrient-richer sites as compared to Isle Royale. This is probably due to seed source availability and a greater area of relatively rich, sandy soils.

Sugar maple and yellow birch are present on moist, nutrient-rich sites. On the richest sites, sugar maple completely dominates the stand composition both in the tree and shrub layer. Under Minnesota conditions, sugar maple can be present on sites of

Figure 4. Distribution of forest cover-types and sampled areas in edaphic (moisture-nutrient coordinates) and climatic (heat-light coordinates) fields of the Isle Royale forest.

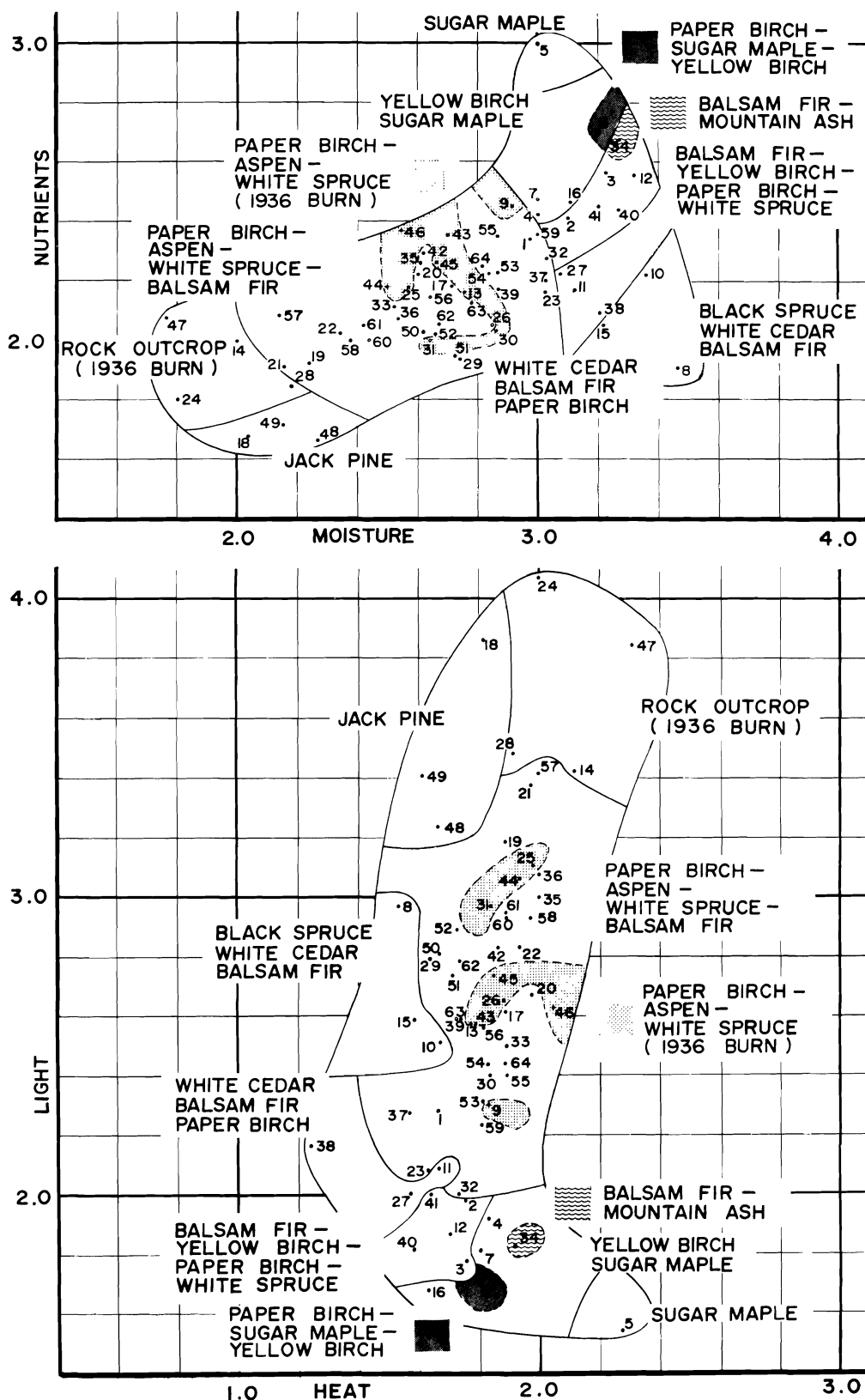


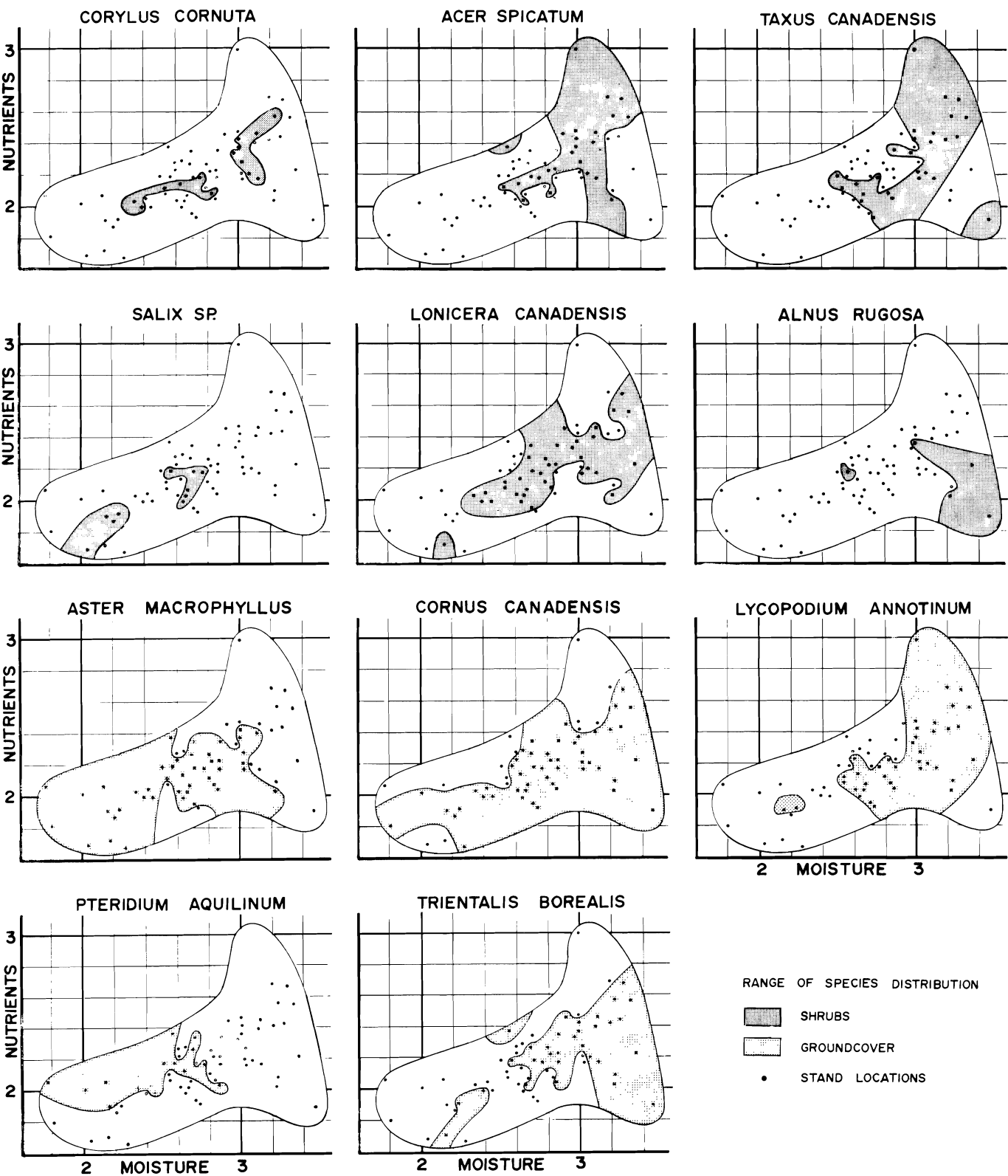
Figure 1 consists of 12 contour plots arranged in a 4x3 grid. Each plot shows the distribution of a specific tree species or tree age across a two-dimensional space defined by Moisture (x-axis, ranging from 2 to 3) and Nutrients (y-axis, ranging from 2 to 3). The plots are titled as follows:

- Row 1: *POPULUS TREMULOIDES*, *ACER SACCHARUM*, *BETULA ALLEGHANIENSIS*
- Row 2: *BETULA PAPYRIFERA*, *SORBUS AMERICANA*, *THUJA OCCIDENTALIS*
- Row 3: *PICEA GLAUCA*, *ABIES BALSAMEA*, *PICEA MARIANA*
- Row 4: *PINUS BANKSIANA*, *TREE AGE DISTRIBUTION*

The legend for the plots is as follows:

- RANGE OF TREE DISTRIBUTION:** Solid black area.
- REPRODUCTION OUTSIDE TREE RANGE:** Hatched area.
- AGE CLASS DISTRIBUTION:**
 - < 40: Dotted pattern.
 - 60-120: Cross-hatched pattern.
 - 120-200: Solid grey pattern.
 - > 200: Solid black pattern.
- STAND LOCATIONS:** Small black dots.

Figure 6. Distribution of shrubs and ground vegetation in the edaphic field (moisture-nutrient coordinates) of the Isle Royale forest.



somewhat lower nutrient status, but the same narrow moisture range prevails. Its reproduction on Isle Royale tends to expand in some occasions to moist, intermediate nutrient sites (figure 5).

White-cedar covers a wide range of moist to wet, intermediate nutrient sites. It forms a connecting ecological bridge between yellow birch–sugar maple and black spruce communities. White-cedar is also reproducing on drier sites and in some recently disturbed areas (1936 burn). Mountain ash (*Sorbus americana*) reproduction is present over a wide range of forest stand and site conditions. It reaches tree size in forest communities on moist, intermediate nutrient sites.

Figure 5 also indicates the tree age distribution based on data from the representative stands studied. The age variation of the stands reflects the fire history of various portions of the island. This indicates a higher fire frequency on the rock outcrop areas and a lesser frequency on the wet sites and on the richer sites occupied by sugar maple and yellow birch.

Shrubs

The range of beaked hazel (*Corylus cornuta*) in the edaphic field (figure 6) on Isle Royale is very narrow as compared to Minnesota. In Minnesota, it is lacking only on very extreme site conditions in terms of moisture and nutrients and under dense shady tree canopies (Bakuzis and Hansen, 1962a). For ground hemlock, the distribution pattern is just the opposite. On Isle Royale, it is present on moist to wet conditions and in the full range of nutrient conditions. In Minnesota, its range is very limited. As indicated by their ecographs, on Isle Royale, mountain maple (*Acer spicatum*) and ground hemlock occur on very similar sites. In Minnesota, mountain maple seems to extend onto somewhat drier, intermediate nutrient sites. Both species are very shade-tolerant and can exist under moderately dense sugar maple and white-cedar canopies. American fly-honeysuckle (*Lonicera canadensis*) is present on intermediate nutrient sites and on a wide range of moisture conditions (figure 6). Speckled alder (*Alnus rugosa*) occupies wet, nutrient-poor to intermediate nutrient sites. Its relationships to site conditions are similar to those in Minnesota (Bakuzis and Hansen, 1962a).

Ground cover species

Large-leaved aster occupies dry to moist, nutrient-poor to intermediate nutrient sites. It is widely present in communities having rather open canopies. Bracken fern (*Pteridium aquilinum*) distribution differs strikingly from most of the ferns because of its xeric character and adaptation to high light conditions. Both species are associated with forest communities which originated after major disturbances in the last 100 years. Bunchberry (*Cornus canadensis*), starflower (*Trientalis borealis*), and bristly clubmoss (*Lycopodium annotinum*) are widely distributed over the edaphic field (figure 6). These, and especially the bristly clubmoss, exceed Minnesota ranges of these species (Bakuzis and Hansen, 1962b). The occurrence of bristly clubmoss is largely related to forest communities undisturbed for the past 100 years.

Comparisons between Isle Royale and Minnesota in distribution patterns of tree, shrub, and ground cover species were made to indicate the changes in species and ecological performance due to overall differences in climatic conditions.

Species ecographs indicate that only a few species are limited to one of the designated forest cover types. Most have a widespread distribution over a range of site conditions.

Cover Type Descriptions

Forest cover type descriptions are based on plot data collected from 64 forest stands in the summers of 1967, 1968, and 1969. The study areas were selected to represent the existing cover types, the range of site conditions, and different stages of forest development. Special attention was given to the vegetation of recently disturbed areas such as the 1936 burn in comparison to forest communities relatively undisturbed for the last 100 to 200 years.

Table 4 is a summary of tree data from the study areas. It shows tree composition, ranges of age, height, and diameter of the main tree species in different forest cover types and indicates associated tree species and reproduction. In this table, the sampled forest stands are arranged along a moisture gradient from dry jack pine and rock outcrop areas to wet white-cedar and black spruce swamps. Eleven

cover types are identified using basal area and number of stems per acre as criteria in determining dominant and associated tree species and considering stand developmental stage and site conditions. While these units are referred to as “cover types,” they reflect environmental relationships and may be considered to be local ecological types. Some of the cover types are combined into broader type groups reflecting successional trends. Three broad age groups are recognized: forest stands in sapling stages; mature stands with 60 to 120 years passed since the last major disturbance; and old growth forest with no noticeable disturbance, at least not in the last 120 years. The ecological relationships of these stands and the various forest cover types have been discussed briefly in a previous section. They are depicted in figure 4.

The following forest cover type groups and cover types have been recognized and described:

Jack pine

Rock outcrop (1936 burn)

Birch–aspen–fir–spruce

Paper birch–aspen–white spruce (1936 burn)

Paper birch–aspen–balsam fir–white spruce

Maple–birch

Paper birch–sugar maple–yellow birch

Sugar maple

Yellow birch–sugar maple

Birch–fir–spruce

Balsam fir–yellow birch–paper birch–white spruce

Balsam fir–mountain ash

White-cedar–fir

White-cedar–balsam fir–paper birch

Black spruce–cedar

Black spruce–white-cedar–balsam fir

Jack Pine

The three stands sampled have open to moderately closed canopies. They are associated with shallow soils. About 70 to 80 years had passed since the last major disturbance. Growth rate of the jack pine has been slow. The trees have reached a maximum

Table 4. Forest cover-types and type groups of Isle Royale, Lake Superior, based on vegetation data of 64 forest stands sampled in 1967, 1968, and 1969.*

Cover type groups	Jack pine	Rock outcrop	Birch—aspens—fir—spruce			Maple—birch		Birch—fir—spruce		White-cedar—fir	Black spruce—cedar
Stand age (years)	80	40 (1936 burn)		60-120			Over 120				
Cover types	Jack pine	Rock outcrop	Paper birch— aspens— white spruce	Paper birch— aspens— white spruce— balsam fir	Paper birch— sugar maple— yellow birch	Sugar maple	Yellow birch— sugar maple	Balsam fir— yellow birch— paper birch— white spruce	Balsam fir— mountain ash	White-cedar— balsam fir— paper birch	Black spruce— white-cedar— balsam fir
Stand number	18,48,49	24,28,47	9, 13, 25, 26, 31, 43, 44, 45, 46	1, 17, 19-23, 29, 30, 32-33, 35-37, 39, 42, 50-64	6	5	4, 17, 16	2, 3, 12, 40, 41	34	11, 27, 38	8, 10, 15
Site conditions	Dry		Moist	Dry to moist				Moist to wet			
Moisture coordinates	2.0-2.3	1.8-2.2	2.5-2.9	2.1-3.0	3.2	3.0	3.0-3.1	3.1-3.3	3.3	3.1-3.2	3.2-3.5
Tree composition	JP	—	PB:WS:A	PB:A:WS:BF	PB:SM:YB	SM	YB:SM	BF:YB:PB	MA:BF	WC:BF:PB	BS:WC:BF
Species basal area ratio no. of stems	10	—	8.5:1.0:0.5	4.5:2.5:1.5:1.5	8.0:1.0:1.0	10	6.5:3.5	6.5:2.0:1.5	6.0:4.0	4.0:3.5:2.5	5.5:3.5:1.0
	10	—	9.5:0.25:0.25	5.5:2.0:1.0:1.5	4.5:4.0:1.5	10	4.0:6.0	9.0:0.5:0.5	6.0:4.0	1.5:3.5:5.0	6.0:3.0:1.0
Basal area average (sq. ft./acre) range	72	—	87	112	143	195	137	133	130	139	113
	35-100	—	35-160	30-250	—	—	100-160	30-240	—	120-170	80-130
Number of average stems/acre range	280	—	2980	300	460	260	130	425	240	570	765
	245-325	—	365-8370	85-875	—	—	100-170	80-390	—	310-890	460-940
Tree age (range — years)	JP:66-80	—	PB:14-32 WS:26-34 A:22-24	PB:15-115 A:18-100 WS:30-165 BF:26-100	PB:54-70 SM:37-80 YB:60-70 WC:95	SM:90-120	YB:66-150 SM:20-235 RM:120 BF:90-110 WC:66-300	BF:50-110 YB:85-150 PB:65-115 WS:35-155 WC:155-190	MA:30-35 BF:98-130	WC:158-220 BF:80-135 PB:30-135 WS:125-155	BS:25-180 WC:45-195 BF:90-125 PB:140-165
Tree height (range — feet)	JP:10-52	—	PB:12-40 WS:20-36 A:38-45	PB:12-87 A:38-98 WS:13-84 BF:23-69	PB:44-64 SM:21-66 YB:55-60 WC:39	SM:32-82	YB:27-70 SM:17-76 RM:64 BF:22-45 WC:28	BF:25-70 YB:49-80 PB:52-83 WS:14-82 WC:44-47	MA:35-50 BF:35-60	WC:32-43 BF:32-66 PB:26-67 WS:36-82	BS:10-67 WC:20-43 BF:14-48 PB:30-42
Tree diameter (range — feet)	JP:3-11	—	PB:1-8 WS:1-7 A:4-6	PB:1-19 A:5-23 WS:6-21 BF:4-16	PB:6-16 SM:1-9 YB:4-11 WC:4	SM:3-16	YB:1-28 SM:1-25 RM:6-15 BF:3-9 WC:5-14	BF:3-10 YB:1-24 PB:3-30 WS:1-17 WC:5-20	MA:6-13 BF:10-11	WC:5-19 BF:4-13 PB:2-23 WS:4-17	BS:1-15 WC:1-11 BF:3-9 PB:5-9
Associated tree species	BS, A	**	MA	MA, WC, BS	WC	—	RM, BF, WC, MA	WS, WC, MA	—	YB, WS, BS	PB, WS
Main reproduction species	BS	PB, A, WC, WS	PB, BF	BF, MA	SM	SM, WC	SM	YB, MA, BF	BF	BF, MA	BS, BF, PB
Associated reproduction species	BF	BS, MA	MA, WS, A, WC, BLA	WS, A, PB, MA	RM, YB	—	MA, WC, BF, YB, RM	WS, PB, WC	—	WC, PB, A, BS, WS, YB	WC, MA

*Sample areas in 1967 = 1-16

Sample areas in 1968 = 17-36

Sample areas in 1969 = 37-64

SPECIES KEY:

JP: Jack pine

PB: Paper birch

A: Aspen

WS: White spruce

BF: Balsam fir

SM: Sugar maple

YB: Yellow birch

WC: White-cedar

MA: Mountain ash

RM: Red maple

BLA: Black ash

BS: Black spruce

**Because of browsing, all species are in shrub stage.

height of 52 feet in 80 years (table 4). One of the stands (No. 18) shows strong microsite variation from extremely dry, rocky surfaces to rock crevices with different plant associations. Jack pine reproduction is scarce. Occurrence of balsam fir, mountain ash, and paper birch seedlings is scattered (table 5). Black spruce seedlings were present in rock crevices.

Predominant shrub species include *Amelanchier* sp. and *Juniperus communis* followed by *Rosa* sp., *Lonicera canadensis*, and *Salix* sp. (table 6). In this type, shrubs did not exceed 3 feet in height. Most commonly occurring herbs are *Aster macrophyllus*, *Maianthemum canadense*, and *Linnaea borealis* (table 7). Major halfshrub species include *Vaccinium angusti-*

folium and *Arctostaphylos uva-ursi* with *Pleurozium schreberi* and *Cladonia* sp. dominating in the moss and lichen layer.

Rock Outcrop (1936 Burn)

Rock outcrop areas are intermingled between flats and swales, the latter having sufficient mineral soil accumulation in which the growth of paper birch and aspen is vigorous. Most rock outcrops in the 1936 burn area face south, resulting in earlier snow melt in the spring than in adjacent swales and flats. The sampled rock outcrops are sparsely covered with stunted, heavily browsed paper birch and aspen. The occurrence of white spruce, northern white-cedar, and mountain ash is scattered.

Paper birch and aspen reproduction show an average of 1,500 and 530 stems over 1 foot in height, respectively (table 5). The prevalent height class of birch and aspen is 3 feet. They are badly stunted. Aspen stems of this height are commonly 2 inches in diameter and over. This indicates continuous browsing and resprouting. Mountain ash and white-cedar reproduction average 30 to 270 stems per acre over 1 foot in height, respectively (table 5). While appreciable white spruce reproduction is present, none is over 1 foot in height. Shrubs predominating on rock outcrop areas are mostly *Salix* sp. with an average of 470 stems per acre over 1 foot in height, followed by *Rhus typhina* and *Rosa* sp. (table 6).

Table 5. Density of tree reproduction by forest cover-types and type groups on Isle Royale.

Species	Forest cover-types and type groups							
	Jack pine	Rock ¹ outcrop	Birch ¹ aspen—spruce	Birch— aspen— fir— spruce	Maple— ² birch	Birch— ³ fir— spruce	White-cedar— fir	Black spruce— cedar
	Number of stems per acre							
<i>Abies balsamea</i>	500 (400)*	—	140 (80)	4,100 (2,100)	100 (0)	2,300 (550)	7,000 (4,600)	3,600 (1,600)
<i>Acer rubrum</i>	—	—	—	10 (10)	2,000 (980)	—	—	—
<i>Acer saccharum</i>	—	—	460 (340)	—	61,000 (24,100)	—	—	—
<i>Betula alleghaniensis</i>	—	—	—	—	430 (50)	650 (270)	—	—
<i>Betula papyrifera</i>	200 (70)	2,100 (1,500)	2,100 (1,600)	600 (220)	—	20 (20)	1,300 (860)	4,600 (3,600)
<i>Fraxinus nigra</i>	—	—	20 (20)	50 (40)	—	—	—	—
<i>Picea glauca</i>	—	400 (0)	20 (10)	150 (60)	—	20 (20)	30 (30)	—
<i>Picea mariana</i>	1,100 (470)	—	10 (0)	20 (20)	—	—	40 (40)	2,000 (540)
<i>Pinus banksiana</i>	30 (0)	—	—	—	—	—	—	—
<i>Pinus strobus</i>	—	—	—	10 (0)	—	—	—	—
<i>Populus tremuloides</i>	70 (70)	900 (530)	60 (40)	830 (730)	—	—	80 (0)	—
<i>Sorbus americana</i>	600 (130)	100 (30)	360 (150)	1,300 (910)	290 (150)	3,600 (1,500)	2,800 (1,100)	290 (130)
<i>Thuja occidentalis</i>	—	600 (270)	230 (150)	410 (50)	300 (180)	20 (20)	570 (430)	1,300 (1,300)
Total	2,500 (1,140)	4,100 (2,330)	3,400 (2,390)	7,480 (4,140)	64,110 (25,460)	6,610 (2,380)	11,820 (7,060)	11,790 (7,170)
Number of stands sampled	3	3	9	31	5	6	3	3

¹ 1936 burn area.

² Includes paper birch—sugar maple—yellow birch, sugar maple, and yellow birch—sugar maple types.

³ Includes balsam fir—yellow birch—paper birch—white spruce and balsam fir—mountain ash types.

*Stems taller than 1 foot in height.

Table 6. Density of shrub species by forest cover-types and type groups on Isle Royale.

Species	Forest cover-types and type groups							
	Jack pine	Rock ¹ outcrop	Birch— ¹ aspen— spruce	Birch— aspen— fir— spruce	Maple— ² birch	Birch— ³ fir— spruce	White- cedar— fir	Black spruce— cedar
	Number of stems per acre							
<i>Acer spicatum</i>	—	—	1,400 (1,300)*	80 (810)	1,600 (1,500)	2,800 (2,500)	4,900 (3,100)	130 (120)
<i>Alnus crispa</i>	—	—	—	50 (50)	—	—	—	—
<i>Alnus rugosa</i>	—	—	1,100 (1,000)	10 (10)	—	—	—	1,900 (1,700)
<i>Amelanchier</i> sp.	1,800 (970)	—	60 (10)	560 (550)	30 (30)	40 (20)	280 (250)	160 (120)
<i>Cornus rugosa</i>	—	—	—	10 (10)	20 (20)	—	—	—
<i>Cornus stolonifera</i>	—	200 (200)	70 (60)	220 (220)	—	290 (200)	—	960 (960)
<i>Corylus cornuta</i>	—	—	960 (960)	1,100 (1,100)	300 (300)	230 (230)	1,600 (1,300)	—
<i>Juniperus communis</i>	1,300 (600)	—	—	10 (10)	—	—	—	—
<i>Lonicera canadensis</i>	200 (130)	—	480 (370)	530 (530)	—	1,200 (1,100)	1,300 (1,200)	160 (120)
<i>Lonicera hirsuta</i>	—	—	—	140 (80)	—	—	—	—
<i>Physocarpus opulifolius</i>	—	—	20 (20)	—	—	—	—	—
<i>Prunus pennsylvanica</i>	30 (30)	400 (100)	180 (170)	20 (20)	—	20 (20)	30 (30)	—
<i>Prunus virginiana</i>	—	—	—	10 (0)	—	—	—	—
<i>Rhamnus alnifolia</i>	—	—	—	110 (110)	—	—	—	—
<i>Rhus typhina</i>	—	430 (430)	—	—	—	—	—	—
<i>Ribes</i> sp.	—	—	100 (40)	180 (50)	—	210 (200)	30 (30)	370 (370)
<i>Rosa</i> sp.	730 (100)	2,100 (300)	90 (30)	490 (170)	—	280 (0)	—	460 (460)
<i>Salix</i> sp.	170 (70)	470 (470)	130 (90)	20 (20)	—	—	—	130 (130)
<i>Sambucus pubens</i>	—	—	90 (90)	10 (10)	—	140 (140)	—	—
<i>Taxus canadensis</i>	—	—	310 (210)	910 (570)	680 (680)	4,500 (3,500)	2,100 (1,200)	700 (700)
<i>Viburnum</i> sp.	—	—	—	950 (920)	—	780 (420)	—	—
Total	4,230 (1,900)	3,600 (1,500)	4,990 (4,350)	6,140 (5,240)	2,630 (2,530)	10,480 (8,280)	10,240 (7,110)	4,970 (4,680)
Number of stands sampled	3	3	9	31	5	6	3	3

¹ 1936 burn area.² Includes paper birch—sugar maple—yellow birch, sugar maple, and yellow birch—sugar maple types.³ Includes balsam fir—yellow birch—paper birch—white spruce and balsam fir—mountain ash types.

*Stems taller than 1 foot in height.

Table 7. Cover of ground vegetation by forest cover-types and type groups on Isle Royale.

Species	Forest cover-types and type groups							
	Jack pine	Rock ¹ outcrop	Birch— ¹ aspen— spruce	Birch— aspen— fir— spruce	Maple— ² birch	Birch— ³ fir— spruce	White- cedar— spruce	Black spruce— cedar
Average cover percent								
<u>Herbs</u>								
Achillea lanulosa	+	0.2	+	+	—	—	—	—
Actaea rubra	—	—	0.1	0.4	0.1	0.2	+	—
Anaphalis margaritacea	0.2	1.5	0.4	0.1	—	+	—	—
Antennaria canadensis	+	0.2	0.4	+	—	—	—	—
Apocynum androsaemifolium	—	—	—	0.1	—	—	—	—
Aralia nudicaulis	—	—	7.5	12.0	0.1	4.0	7.5	0.7
Aster ciliolatus	—	—	0.1	+	—	—	—	+
Aster lateriflorus	—	—	+	—	—	—	—	—
Aster macrophyllus	8.0	—	22.0	24.5	—	+	—	0.2
Aster puniceus	—	—	0.3	—	—	—	—	+
Aster umbellatus	—	0.8	0.6	—	—	—	—	+
Campanula rotundifolia	—	—	—	+	—	—	—	—
Circaea alpina	—	—	—	—	—	2.5	—	+
Clintonia borealis	+	—	3.0	3.5	1.0	12.0	5.5	0.6
Coptis groenlandica	—	—	+	+	—	+	1.5	3.5
Cornus canadensis	0.5	0.5	5.0	7.5	—	1.0	1.5	5.0
Epilobium angustifolium	—	0.5	0.5	0.3	—	+	—	+
Eupatorium maculatum	—	—	+	—	—	—	—	—
Fragaria virginiana	0.2	7.0	2.0	0.4	—	—	—	+
Galium triflorum	—	+	0.3	0.3	0.1	0.6	0.1	0.1
Goodyera sp.	0.1	—	+	0.1	+	—	—	—
Habenaria hookeri	—	—	—	+	—	—	—	—
Habenaria hyperborea	—	—	+	—	—	—	—	+
Habenaria orbiculata	—	—	—	+	—	—	—	—
Halenia deflexa	—	—	—	0.1	—	+	—	—
Hepatica americana	—	—	—	+	—	—	—	—
Heracleum maximum	—	—	+	0.1	—	0.4	—	—
Hieracium canadense	—	—	+	+	—	—	—	—
Hieracium scabrum	+	0.5	—	+	—	—	—	—
Impatiens sp.	—	—	+	+	—	0.4	—	—
Lactuca canadensis	—	0.4	0.2	+	—	0.1	—	—
Lathyrus ochroleucus	—	—	—	0.2	—	—	—	—
Lilium michiganense	+	—	—	—	—	—	—	—
Linnaea borealis	1.0	0.8	0.6	1.0	—	2.0	1.0	0.4
Maianthemum canadense	1.0	1.0	1.5	1.0	0.1	0.7	0.5	0.3
Melampyrum lineare	0.1	0.3	0.1	0.7	—	—	—	+
Mentha arvensis	—	—	+	—	—	—	—	—
Mitella nuda	—	—	0.1	1.0	0.1	7.0	1.0	0.7
Monarda fistulosa	—	2.0	+	+	—	—	—	—
Moneses uniflora	—	—	—	+	—	+	+	+
Monotropa uniflora	—	—	—	+	+	—	+	—
Osmorhiza claytoni	—	—	+	+	+	0.1	+	+
Osmorhiza longistylis	—	—	+	—	—	—	—	—
Petasites palmatus	—	—	0.4	+	—	—	—	—
Polygala paucifolia	—	—	—	+	—	—	—	—
Prenanthes alba	—	—	+	—	—	+	—	+
Potentilla tridentata	0.2	—	—	—	—	—	—	—
Pyrola asarifolia	—	—	—	+	—	—	—	—
Pyrola elliptica	—	—	+	+	—	—	—	—
Pyrola secunda	+	—	0.1	0.2	—	+	—	+
Pyrola virens	—	—	—	+	—	—	—	—
Sanicula marilandica	—	—	—	+	—	—	—	—
Smilacina trifolia	—	—	—	—	—	—	—	0.2
Solidago sp.	0.2	2.0	2.0	—	—	—	—	—

Species	Forest cover types and type groups							
	Jack pine	Rock ¹ outcrop	Birch— ¹ aspen— spruce	Birch— aspen— fir— spruce	Maple— ² birch	Birch— ³ fir— spruce	White- cedar— spruce	Black spruce— cedar
	Average cover present							
<i>Streptopus amplexifolius</i>	—	—	0.1	—	—	—	—	—
<i>Streptopus roseus</i>	—	—	0.3	0.3	1.5	0.2	1.0	0.2
<i>Thalictrum dasycarpum</i>	—	—	+	—	—	—	—	—
<i>Trientalis borealis</i>	0.1	—	0.2	0.3	+	0.3	0.5	0.3
<i>Trillium cernuum</i>	—	—	+	—	—	+	—	—
<i>Uvularia grandiflora</i>	—	—	—	+	—	—	—	—
<i>Vicia americana</i>	—	—	—	+	—	—	—	—
<i>Viola</i> sp.	+	—	0.5	0.6	0.2	0.4	0.4	0.3
<u>Ferns and allies</u>								
<i>Athyrium filix-femina</i>	—	—	0.4	0.2	—	1.5	—	0.8
<i>Botrychium multifidum</i>	+	+	—	—	—	—	—	—
<i>Botrychium virginianum</i>	—	—	+	+	+	+	0.2	+
<i>Dryopteris cristata</i>	—	—	—	—	—	—	—	+
<i>Dryopteris disjuncta</i>	—	—	0.1	0.7	—	2.5	1.0	0.4
<i>Dryopteris phegopteris</i>	—	—	0.5	—	—	—	—	—
<i>Dryopteris spinulosa</i>	—	—	0.2	0.1	0.1	4.0	0.3	0.3
<i>Equisetum arvense</i>	—	—	—	+	—	—	—	0.2
<i>Equisetum palustre</i>	—	—	—	—	—	—	—	1.5
<i>Equisetum scirpoides</i>	—	—	—	—	—	—	—	+
<i>Equisetum sylvaticum</i>	—	—	+	—	—	—	—	11.0
<i>Lycopodium annotinum</i>	—	—	0.1	1.5	4.0	8.0	12.5	0.8
<i>Lycopodium clavatum</i>	0.2	—	0.5	0.7	—	—	—	—
<i>Lycopodium complanatum</i>	—	—	+	+	—	—	—	—
<i>Lycopodium obscurum</i>	—	—	0.1	1.0	0.1	0.1	5.0	0.1
<i>Polypodium virginianum</i>	—	—	—	—	—	+	—	—
<i>Pteridium aquilinum</i>	—	0.5	10.0	3.0	—	—	—	—
<u>Half shrubs</u>								
<i>Arctostaphylos uva-ursi</i>	2.5	6.0	+	0.2	—	—	—	—
<i>Chimaphila umbellata</i>	1.5	—	+	0.5	—	—	—	—
<i>Diervilla lonicera</i>	—	5.0	2.0	4.0	—	—	—	—
<i>Gaultheria hispidula</i>	—	—	—	—	—	—	—	0.5
<i>Ledum groenlandicum</i>	—	—	—	—	—	—	—	0.7
<i>Rubus idaeus</i>	—	—	—	—	—	—	—	—
var. <i>strigosus</i>	—	1.0	4.5	0.1	+	0.4	0.2	—
<i>Rubus parviflorus</i>	—	0.8	12.0	26.5	+	—	0.7	0.1
<i>Rubus pubescens</i>	—	—	3.0	0.3	—	0.1	+	1.0
<i>Vaccinium angustifolium</i>	6.5	5.0	0.3	+	—	—	—	—
<i>Vaccinium myrtilloides</i>	—	—	—	—	—	—	—	+
<i>Vaccinium oxycoccos</i>	—	—	—	—	—	—	—	+
<u>Mosses and lichens</u>								
<i>Cladonia</i> sp.	4.5	10.0	—	+	—	—	—	—
<i>Dicranum</i> sp.	2.5	—	+	0.1	—	—	—	+
<i>Mnium</i> sp.	—	—	—	+	—	0.1	+	0.8
<i>Pleurozium schreberi</i>	14.5	0.8	0.1	0.8	—	+	0.4	5.0
<i>Polytrichum</i> sp.	0.2	1.5	0.1	+	—	0.4	—	+
<i>Sphagnum</i> sp.	+	—	—	—	—	—	—	18.5
Number of stands sampled	3	3	9	29	5	6	3	3

¹ 1936 burn area.

² Includes paper birch—sugar maple—yellow birch, sugar maple, and yellow birch—sugar maple types.

³ Includes balsam fir—yellow birch—paper birch—white spruce and balsam fir—mountain ash types.

Major herb species on rock outcrops are *Aster macrophyllus*, *Fragaria virginiana*, *Solidago* sp., *Monarda fistulosa*, *Anaphalis margaritacea*, and *Maianthemum canadense*. *Arctostaphylos uva-ursi* and *Vaccinium angustifolium* are the predominant halfshrub species (table 7).

Birch—aspens—fir—spruce

These communities comprise the most widespread cover type or type group on the island. They vary in species composition and stand development because of site conditions and stand history. Paper birch is often the dominant species based on basal area measurements and on number of trees per acre. This is especially true on areas burned over in 1936. Paper birch, white spruce, and balsam fir are also components of most other cover types. Cooper (1913) considered these three species to be main constituents of the climax forest on Isle Royale. Aspen is often an associated species in younger developmental stages of this type. Mountain ash is common.

According to past fire disturbance, this broad cover type group was subdivided into two types: (a) paper birch—aspens—white spruce (1936 burn); and (b) paper birch—aspens—balsam fir—white spruce. The latter could still be subdivided based on site conditions, especially moisture availability.

Paper birch—aspens—white spruce (1936 burn)

Paper birch is the dominant tree species on large areas burned over in 1936, forming dense stands with varying mixtures of aspen and white spruce (figure 7). Aspen and white spruce occur groupwise, intermingled in young paper birch communities (figures 8 and 9). Mountain ash occurrence is scattered. Balsam fir is largely absent at this stage of forest development. There could be several reasons for this. Susceptibility to fire, pattern of seed dispersal, seed weight, and site conditions after fire may be of disadvantage to balsam fir as compared to white spruce. Balsam fir is also favored by moose as a winter browse species.

The dominant position of paper birch in the areas sampled is expressed by its high percentage of the total basal area and number of stems per acre (table 4). Table 4 also shows the age, height, and diameter ranges of the

main tree species. The stand age structure shows that the trees are not even aged as might be expected after the 1936 fire. The uneven aged condition may be a result of moose browsing followed by resprouting in the early development of these stands. Paper birch is also the main reproducing species, averaging 1,600 stems per acre over 1 foot in height followed by sugar maple, mountain ash, and white-cedar (table 5).

Of all the shrubs within the type, *Prunus pennsylvanica* is the most uniformly distributed species, occurring on 67 percent of all stands and averaging 170 stems per acre (table 6). Less well distributed but locally more abundant species include *Acer spicatum*, *Ahus rugosa*, *Corylus cornuta*, *Lonicera canadensis*, and *Taxus canadensis*. The shrubs generally range from 3 to 6 feet to a maximum of 12 feet. Herbaceous plants with highest cover densities include *Aster macrophyllus*, *Pteridium aquilinum*, *Aralia nudicaulis*, and *Cornus canadensis*. The most commonly occurring halfshrubs (table 7) are *Rubus parviflorus*, *Rubus idaeus* var. *strigosus*, and *Rubus pubescens*.

Paper birch—aspens—balsam fir—white spruce

Paper birch is the predominant species in this type. At least 80 to 100 years has passed since the last major disturbance. The proportion of balsam fir increases along the gradient from dry to fresh and moist sites. However, the aspen component decreases, indicating a gradient in site conditions of this extensive type (figure 10). Basal area ranges from 30 to 250 square feet per acre, and the number of trees per acre varies from 85 to 875 (table 4). Balsam fir is the predominant reproduction species, averaging 2,100 stems per acre over 1 foot in height (table 5).

The most widespread shrubs are *Lonicera canadensis*, *Amelanchier* sp., and *Taxus canadensis*. *Corylus cornuta*, *Acer spicatum*, and *Viburnum* sp. are abundant in about 20 to 30 percent of the stands. Most of the shrubs are from 1 to 3 feet tall. The predominant herbaceous species are *Aster macrophyllus*, *Aralia nudicaulis*, *Cornus canadensis*, *Clintonia borealis*, and *Pteridium aquilinum* (table 7). Halfshrubs are mainly *Rubus parviflorus* and *Diervilla lonicera*.

Top left: Figure 7. This is a photo of a 33-year-old paper birch stand growing in the area where the 1936 burn took place. Dense stands of paper birch have grown out of reach of the browsing moose. Also, shrubs have been killed because of the resultant shading. Top right: Figure 8. This is a photo of a 36-year-old aspen stand growing in the area where the 1936 burn took place. Aspen is less common than paper birch on the island and is usually confined to smaller areas where site conditions are better for its growth. Bottom left: Figure 9. This is a photo of a 36-year-old white spruce stand growing where the 1936 burn took place. White spruce is one of the first species to become established in the burn area together with scattered white pine and white-cedar. Bottom right: Figure 10. Here is an example of the paper birch—aspens—balsam fir—white spruce forest cover-type on Isle Royale. In this stand, aspen predominates in the overstory. (Photos are by L.W. Krefting. Fish and Wildlife Service, U.S.D.I.)

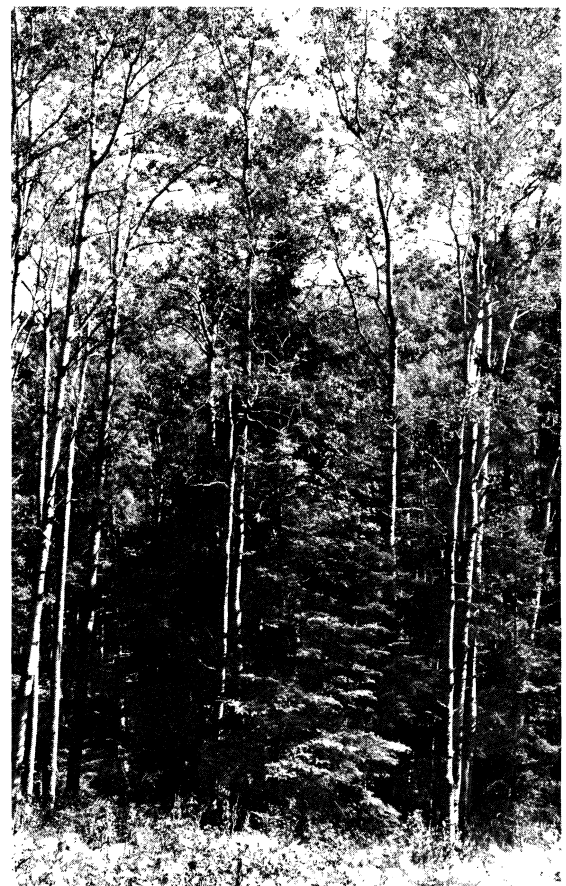




Figure 11. Old growth sugar maple and yellow birch trees up to 28 inches in diameter are present in the sugar maple—yellow birch climax forest. The understory is mostly sugar maple reproduction which is browsed very little by moose in winter. (Photo is by L.W. Krefting. Fish and Wildlife Service, U.S.D.I.)

Maple—Birch

The maple birch forest (figure 11) varies from pure sugar maple to associations of different degree with yellow birch and paper birch, white-cedar, balsam fir, and red maple (*Acer rubrum*). It's primarily located on higher elevations along the Greenstone and Red Oak Ridges in the southwestern part of the island. In general, this maple—birch forest has not been disturbed for at least 120 years. Where sound cores could be obtained from old growth trees, annual ring counts showed sugar maples over 220 years, yellow birches reaching 150 years, and white-cedar about 300 years old.

Paper birch—sugar maple—yellow birch

Along the Greenstone Ridge Trail in the general maple—birch forest there is a locally limited area (stand 6)

which was fire-disturbed about 80 years ago. Paper birch is the dominant tree species. However, sugar maple with some yellow birch have invaded the main canopy. Sugar maple is the dominant reproduction with 46,500 stems per acre followed by yellow birch and red maple with only 250 stems. The most common shrub species are *Acer spicatum* and *Taxus canadensis*, each with 1,800 stems per acre. Predominant species of herbs, ferns, and allies are *Clintonia borealis*, *Lycopodium annotinum*, and *Streptopus roseus*. The cover of herbaceous plants was sparse due to the abundance of sugar maple reproduction.

Sugar maple

Stand 5 is composed exclusively of sugar maple with about 200 square feet of basal area and 260 stems per acre (table 4). This stand has the high-

est nutrient coordinate values of all those studied. It also differed distinctly in nutrient and heat values from all others in the maple—birch type group (figure 4). Sugar maple reproduction of over 50,000 stems per acre dominates the shrub layer and effectively excludes any other tree species. In addition to sugar maple reproduction, a few stems of white-cedar are present. The shade-tolerant *Taxus canadensis* and *Acer spicatum* and *Cornus rugosa* are of infrequent occurrence and low density. There is a sparse cover of *Streptopus roseus*, *Lycopodium annotinum*, and *Clintonia borealis*.

Yellow birch—sugar maple

Yellow birch and sugar maple are the dominant tree species. Basal areas from 100 to 160 square feet and densi-

ties of 100 to 170 stems per acre indicate that the stands are somewhat open. Old growth trees up to 28 inches in diameter are present with a few smaller individuals (table 4). Red maple, balsam fir, and white-cedar are minor stand components. Stands of this type are located on flat to slightly south-facing ridge tops. Sugar maple is by far the most abundant reproduction species, ranging from 53,000 to 82,000 stems per acre within individual communities and with 100 percent frequency distribution. Yellow birch, white-cedar, and mountain ash reproduction is of low density (table 5). Red maple reproduction occurs only in one stand. The common shrubs are *Acer spicatum* and *Taxus canadensis* with *Corylus cornuta* present in two stands. Major species of herbs and ferns and allies include *Lycopodium annotinum*, *Streptopus roseus*, and *Clintonia borealis*. The ground vegetation layer is weakly developed. Only a few raspberry stems representing half-shrubs are present.

Birch—Fir—Spruce

Balsam fir is the major species in association with yellow birch, paper birch, and white spruce. The range of yellow birch is greater than that of sugar maple. Yellow birch is also associated with balsam fir and white spruce. White-cedar is a minor stand component. These are old growth stands; at least 120 years has passed since the last major disturbance. One of the stands in this type (number 34 on Wright Island), although ecologically similar to others, has balsam fir closely associated with mountain ash instead of birch. This stand will be described as a separate type.

Balsam fir—yellow birch—paper birch—white spruce

Balsam fir is the dominant tree species in terms of basal area and number of stems per acre (table 4). White spruce, yellow birch, and paper birch exceed 80 feet in height. The latter two reach diameters of 25 to 30 inches. Balsam fir reaches 70 feet in height. Mountain ash, balsam fir, and yellow birch are the main reproduction species (table 5). There are only a few young paper birch, white spruce, and white-cedar.

The major shrub species are *Taxus canadensis*, *Acer spicatum*, and *Lonicera canadensis*. In one stand,

Corylus cornuta is present. The most common species of herbs and ferns and allies are *Clintonia borealis*, *Lycopodium annotinum*, *Linnaea borealis*, and *Dryopteris spinulosa*. The first two are ground cover species predominating in most forest stands which have been undisturbed in the last 120 years or longer. There is a scattered occurrence of *Rubus* sp.

Balsam fir—mountain ash

A representative stand of this type is located on Wright Island. Balsam fir and mountain ash are the main tree species. There is no indication of disturbance in the recent past since the balsam fir is over 130 years old. No sound cores could be obtained from mountain ash; it reached 13 inches in diameter. Treelike mountain maples are 4 to 5 inches in diameter and up to 48 years old. Balsam fir dominates as reproduction species. However, most of the young stems are less than 1 foot tall (table 5). Mountain ash reproduction is less abundant.

The major shrubs are *Taxus canadensis* and *Acer spicatum*. The prevalent height class of both species is 3 feet. Among the herbs and ferns and allies are *Mitella nuda*, *Clintonia borealis*, *Dryopteris spinulosa*, *Circaea alpina*, *Aralia nudicaulis*, and *Dryopteris disjuncta*. Halfshrubs are mainly *Rubus idaeus* var. *strigosus*.

White-Cedar—Fir

Northern white-cedar occurs on moist to wet sites in association with different tree species. Its distribution extends into sugar maple—yellow birch and yellow birch—balsam fir communities on moist, nutrient-rich sites. It also extends into black spruce—balsam fir communities on wet, intermediate nutrient sites (figure 5). Between these forest types, white-cedar is associated with balsam fir, paper birch, and white spruce.

White-cedar—balsam fir—paper birch

In stands characterizing the local white-cedar—balsam fir—paper birch type, white-cedar composes about 40 percent of the basal area. In number of trees per acre, balsam fir and paper birch exceed that of white-cedar (table 4). White-cedars are largely old growth trees often over 200 years old. Balsam fir, mountain ash, and paper birch are the main reproducing species (table 5). White-cedar new growth averages 430 stems per acre over 1 foot in height.

Many of the young white-cedar stems are reproduced by layering.

The predominant shrub species is *Acer spicatum* with 3,100 stems over 1 foot in height. It's followed by *Taxus canadensis*, *Corylus cornuta*, and *Lonicera canadensis* (table 6). As in preceding cover types, the occurrence of beaked hazel is groupwise not only within a stand but also on the island as a whole. It is not a widely distributed species at present. Herbs and ferns and allies of the greatest cover density include *Lycopodium annotinum*, *Aralia nudicaulis*, *Clintonia borealis*, *Lycopodium obscurum*, *Cornus canadensis*, and *Coptis groenlandica* (table 7). The halfshrubs *Rubus parviflorus* and *Rubus idaeus* var. *strigosus* are of sparse occurrence.

Black Spruce—Cedar

Black spruce occurs on moist to wet soils in association with white-cedar, balsam fir, white spruce; and with paper birch on intermediate nutrient sites; and with balsam fir and paper birch on sites with somewhat lower nutrient and higher moisture levels (figure 5).

Black spruce—white-cedar—balsam fir

Black spruce comprises about 30 to 80 percent of the basal area of stands representing this type. White-cedar and balsam fir basal area ranges from 80 to 130 square feet per acre. Except for balsam fir, the oldest trees exceed 150 years (table 4). No recent major disturbance is noticeable. Paper birch, balsam fir, and black spruce are the most common reproduction species with 3,600; 1,600; and 540 stems per acre over 1 foot tall (table 5). White-cedar reproduction occurs in two of the three stands studied and has an average density of 1,300 stems per acre.

The main shrub is *Alnus rugosa* with 1,700 stems per acre (table 6). Two other species, *Cornus stolonifera* and *Taxus canadensis*, are relatively abundant in one of the three stands. The most common herbs and ferns and allies are *Equisetum sylvaticum*, *Cornus canadensis*, *Coptis groenlandica*, and *Equisetum palustre* (table 7). However, except for Canadian bunchberry, they are not present in all of the stands. The most frequent halfshrubs are *Ledum groenlandicum* and *Gaultheria hispida*.

Figure 12. This is the 1936 burn area on Isle Royale in spring 1937. The extremely hot fire began July 25, 1936. It destroyed the humus layer in addition to the overstory and ground vegetation. The forest that followed made the increased moose population possible. (Photo is by the National Park Service.)



FOREST FIRE HISTORY

Related Fire Chronology in Minnesota

Forest fires have generally played an important role in determining the course of forest succession and, consequently, the nature of the vegetation in an area at any point of time. Therefore, a fire chronology was determined in the study. Such studies have helped reconstruct the history of vegetation and interpret present forest composition at Itasca State Park, Minn. (Frissell, 1968) and the Boundary Waters Canoe Area, Superior National Forest, Minn. (Heinselman, 1969, 1970).

The chronology of fires in the Itasca State Park area has been well documented from 1650 to the present time by fire scars, explorers' records, and more recent official records. In this area, the effect of early agricultural settlement in the mid-1800's, the logging-related fires, and the farmland-clearing fires of the 1890's and early 1900's are clearly evident. The incidence of "natural" fires caused by lightning or set by Indians before 1850 averaged 1 fire every 12 years in this area of about 33,000 acres. In the Boundary Waters Canoe Area, major fires recurred at 5 to 50-year intervals from 1600 to 1920. Some areas burned at intervals of more than 200 years. Heinselman also notes the possible increase in fire incidence since 1800 due to man's activities. At Itasca State Park, the frequency of fires increased from one in 12 years to one in about 6 years when early agricultural development was occurring in the prairies west of the park. During the period of peak logging and farmland clearing, the incidence of fire increased drastically to an average of one in about 3 years.

Similar statistics for Isle Royale are not available. In the two Minnesota areas, a relative abundance of old red pine is present. Their fire scars gave an accurate fire chronology. This species, by virtue of its longevity and the resin flow to scarred areas, preserves fire scars better than any other native species except, perhaps, tamarack. Red pine is rare in the present Isle Royale forest. The main sources of fire information were the excellent notes taken by Ives (1848), surveyor for the General Land Office, and also the National Park Service fire records. The latter were kept since 1935.

The incidence of fire on the island for the past 140 years has been greater than it would be from a natural con-

sequence of lightning. Deliberate burning to expose surface copper has been reported (Rakestraw, 1965) as early as the 1840's. In addition, accidental fires by early mine workers and later campers very likely contributed to the frequency of fire.

Recent Fires on Isle Royale

Table 8 lists the numbers of fires and acreage burned on Isle Royale from 1940 to 1965. The number of fires of lightning origin is listed separately from those of various man-related origins.

From this 25-year record, it is noted there was an average of 1 lightning fire a year. From 1950 to 1965 when individual year data were avail-

Table 8. Recent fires on Isle Royale.*

	Number by origin			Acreage
	Lightning	Other	Total	
1965	—	—	—	—
1964	2	1	3	—
1963	—	—	—	—
1962	1	4	5	0.37
1961	1	—	1	—
1960	—	3	3	—
1959	2	—	2	0.16
1958	5	2	7	1.07
1957	—	2	2	—
1956	—	1	1	—
1955	2	1	3	0.90
1954	2	6	8	6.53
1953	—	—	—	—
1952	—	—	—	—
1951	—	—	—	—
1950	—	—	—	—
1940-1949	11	2	13	1,468.21
Total	26	22	48	1,477.24

*Data from fire reports, National Park Service, Houghton, Mich.

able, lightning fires occurred during 8 of the 15 years. This is about half of the years. Since an active fire protection policy was in effect during this time, the acreage burned has no meaning relative to the area that might have burned due to natural causes if such fires were unchecked.

The 1936 Burn*

On July 25, 1936, a fire started near Siskiwit Bay. Presumably, it was set by a careless camper. This fire was destined to have a more profound effect on the vegetation and animal life of the island than any other single historical event (figure 12). Most of the major forest fires in the history of the Great Lakes Region have been in the fall. However, the extremely low fuel moisture conditions, created by several years of drought, created an unusual situation of extreme fire hazard in mid-summer.

The fire spread quickly. It was aided by slash left from the pulpwood logging at the head of Siskiwit Bay. A crew of 160 Civilian Conservation Corps enrollees and 40 loggers had contained the fire by July 27, but then high winds blew the fire over the control lines. The fire raged furiously and was reported visible from the Michigan mainland, about 50 miles away. Spot fires started new fires in the Lake Desor area. These spread to the north shore of the island, along the Greenstone Ridge, and encircled Siskiwit Lake on the north and east.

A control line from Rock Harbor to Todd Harbor, a favorable wind shift, and a heavy rain on August 18 finally brought the fire under control and saved the resort facilities at the east end of Rock Harbor. Some 1,800 fire fighters — mostly transferred from CCC camps in National Forests in Minnesota, Wisconsin, and Michigan — were involved. The fire covered approximately 26,000 acres or 19 percent of the island (table 3). The ecological consequences in terms of the resultant burn succession and its effect on the moose herd are reviewed in following sections.

*The writers are indebted to Professor Lawrence Rakestraw of Michigan Technological University for this fire information derived from Z.T. Phillips' unpublished reviews of numerous newspaper accounts and official U.S. Department of the Interior fire reports and memoranda.

THE MOOSE HERD

Population Trends

Both the method of migration and the time of arrival of the moose on Isle Royale are unknown. Hickie (ca. 1943) speculated that some moose may have come from the north shore of Lake Superior around 1905. However, Adams (1909) did not report moose in his 1904-05 biological studies. Murie (1934) said that the last moose came in the winter of 1912-13 but that there may have been earlier invasions.

By 1916, the herd was estimated at 250 to 300 moose. By the late 1920's, estimates ranged as high as 5,000 animals (Hickie, ca. 1943). Murie in 1929 and 1930 estimated at least 1,000 and possibly 2,000 or 3,000.

The herd suffered a drastic reduction due to a depleted food supply in the late 1920's and early 1930's (Titus, 1941; Hickie, ca. 1943). Hickie (1936) reported finding 60 dead moose in an area of about one-tenth of the island.

An abundant food supply followed after about 19 percent of the island burned in 1936. That year, the herd was estimated to be about 200 animals (Aldous and Krefting, 1946). Airplane strip count estimates showed an increase to about 500 moose in 1945 and to 600 by 1947 (Krefting, 1951). By the spring of 1948, the estimate was 800. This was followed by a reduction to about 500 animals in the spring of 1950 (Krefting, 1951). In 1960, Mech (1966) estimated there were 600 moose (about three per square mile). His estimates were based on strips paralleling the length of the island. The strips approximated one eighth of a mile, but they overlapped to insure full coverage.

In representative forest cover in 1948, 1950, 1961, 1965, and 1970 (Krefting, 1973), pellet group counts were made on 844 1-1/100th acre plots at 10 chain intervals (660 feet). The findings are shown in table 9. For the period 1948 to 1950, the data

Table 9. Moose population trends on Isle Royale based on pellet group counts.

	Number of 0.01 acre plots	Mean number of pellet groups per acre				
		1948	1950	1961	1965	1970
Entire island	844	82	36	63	83	113
Habitat types:						
Sugar maple—yellow birch	77	44	8	9	8	31
1936 burn:						
Siskiwit Lake	153	125	57	35	30	31
Feldtmann	36	83	50	86	111	122
Aspen—birch—fir— spruce	471	70	33	68	93	125
Birch—fir—spruce	107	98	34	109	150	229

showed that the herd decreased significantly (chi-square = 119, $P < .01$), reflecting the known die-off of the herd (Krefting, 1951). A significant increase followed from 1950 to 1970 (chi-square = 206, $P < .01$). This was in spite of the timber wolf pack known to be present during that time. However, (Jordan *et al.*, 1971) reported the population, based on quadrat airplane counts, remained stable from 1959 to 1969 at about 1,000 moose.

Habitat Preferences

Winter moose movements and habitat selection are influenced by hardness, density, and depth of snow (Peek, 1971; Kelsall and Prescott, 1971). In New Brunswick and Quebec, moose gradually move from more open timber stands to denser cover as the winter advances (des Meules, 1964; Telfer, 1970). In Quebec, moose moved from cutovers to small to medium openings at snow depths of 30 to 34 inches (des Meules, 1964). Uncrusted snow over 36 inches in depth induced more moose use in softwood (conifer) cover types in New Brunswick (Telfer, 1968). In northeast Minnesota, the shift from open to dense cover occurred at lower depths than in New Brunswick and Quebec (Peek, 1971).

The sequence of habitat use in northeast Minnesota showed: aquatic areas and open, poorly stocked stands were used in June; upland aspen and paper birch stands were used throughout the summer period; in late summer and early winter, use centered on upland deciduous stands; and from November to April, the heaviest habitat use occurred (Peek, 1971). Peek found the changes from January to March were influenced by snow quality and weather conditions. During the severest weather, the upland spruce-fir type was used most.

On Isle Royale, snow depth is usually not a hindrance to moose movement. The snow ordinarily does not exceed 3 feet except on northwest-facing ridges. From 1959 to 1961, the depth did not exceed 26 inches in wind-protected areas (Mech, 1966). In 1963, the depths ranged from 18 to 36 inches. For the period 1966 to 1972, the depths exceeded 3 feet for only short periods in 1966,

1969, and 1972 (Park Service records, Houghton, Mich.).

Information on Isle Royale winter habitat use is based on pellet group counts (table 9). Data on the following four cover types show wide differences of use: the sugar maple-yellow birch type; the 1936 burn type; the aspen-birch-fir-spruce type; and the birch-fir-spruce type (Krefting, 1973).

Maple-birch

This type is climax on certain sites because it is self-perpetuating under present conditions. The type covers about 9,950 acres or 7 percent of the island. Most stands in this type have not been disturbed for 120 years or more. The sugar maples are over 220 years, and the yellow birch over 150 years of age.

Pellet group counts (1948 to 1950) (table 9) showed a significant downward trend (chi-square = 40, $P < .01$) and reflect the known die-off of the island's moose during that period (table 9). The counts from 1950 to 1965 were at a uniformly low level of about 8 per acre. However from 1965 to 1970, there was a significant upward trend (chi-square = 34, $P < .01$). The low pellet count data for this type, the lowest of all the types, indicate that the type is unimportant to moose in winter.

Birch-aspen-spruce (1936 burn)

The 26,000 acre burned over area covers 19 percent of the island and contains two separate burns: the Feldtmann burn in the southwest section (3,000 acres); and the Siskiwit Lake burn in the central section (23,000 acres).

In the burn area, paper birch is more widely distributed than is aspen. The aspen and paper birch are not uniform in age because of previous moose browsing. White-cedar and white spruce are scattered in this type. Balsam fir is largely absent.

On the Feldtmann burn, the pellet counts (table 9) showed a significant decrease from 1948 to 1950 (chi-square = 15, $P < .01$). A significant increase occurred from 1950 to 1970 (chi-square = 22, $P < .01$).

The Siskiwit Lake burn also showed a significant decrease from 1948 to 1950 (chi-square = 84, $P < .01$). However, the data showed a significant decrease from 1950 to 1961 (chi-square = 24, $P < .01$), leveling off from

1965 to 1970. These population trends also relate to changes in the availability of browse on the burn area from 1945 to 1970 (Krefting, 1973). This burn was attractive to the moose herd for about 14 years (1936 to 1950). Apparently, the smaller area burned, and the better interspersed of unburned patches of winter swamp cover in Feldtmann burn sustained longer use than the Siskiwit Lake burn.

Birch-aspen-fir-spruce

Due to its fire origin, the type has extensive stands of aspen and paper birch about 80 to 100 years old. It's heavily invaded by white spruce and balsam fir. The type occurs mostly in the northeast end of Isle Royale and covers 43 percent of the island or about 58,000 acres. Balsam fir reproduction has increased strikingly during the past 10 years. Aspen reproduction is scattered, but moose browsing is preventing its establishment.

Pellet group counts from 1948 to 1950 (table 9) indicate a significant decrease in population (chi-square = 198, $P < .01$); from 1950 to 1970 there was a significant upward trend, (chi-square = 358, $P < .01$).

Birch-fir-spruce

Sixteen percent or about 22,000 acres of the island is covered by this type. It consists mainly of three overstory species: balsam fir; paper birch; white spruce; and scattered large aspen. In the absence of fire, it represents the boreal climax stage toward which other plant communities evolve (Cooper, 1913). However, the forest classification by Halliday (1937) and Rowe (1959) suggests that Isle Royale is not typically boreal and that it relates more to the Great Lakes-St. Lawrence Region (Rowe, 1959). Because of more than 60 years of moose browsing, much of the type has become quite open and parklike (figure 13). Balsam firs 30 years old are less than 3 feet tall, and a distinct browse line on the overstory trees still exists from the 1930's. The spruce budworm epidemic in the 1930's also thinned out the older balsam fir. The openness of this type has encouraged more shrub browse than is typical in the boreal type.

The 1970 pellet counts in this type (table 9) averaged 229 per acre, the highest on the island. In 1948, it was

Figure 13. This is Isle Royale's paper birch-balsam fir-white spruce climax forest. Browsing by moose has created open parklike conditions not typical of this forest cover-type. To the right of the photo, the browse line on the overstory balsam fir is 10 to 12 feet high. White spruce on the left is unbrowsed. Mountain ash and beaked hazelnut are sparse because of severe browsing by moose. (Photo is by L.W. Krefting. Fish and Wildlife Service, U.S.D.I.)



second highest (98 per acre). Like the other types, the counts decreased significantly from 1948 to 1950 (chi-square = 72, $P < .01$). There was a significant increase from 1950 to 1970 (chi-square = 214, $P < .01$).

Moose-Wolf Relationships

Wolves were seen on the ice between Sibley Peninsula, Ontario, and Isle Royale in the late 1940's (de Vos, 1950) and in September, 1949. Timber wolf tracks were identified in November, 1950 (Hakala, 1954). Sightings were made the next few years. By 1956, the island supported at least 14 wolves and about 25 by 1957 (Cole, 1957).

Mech (1966) made a study of the timber wolf-moose relationship from 1958 to 1961. He reported a large pack of 15 wolves plus a small pack of three. The number remained about the same each year. His findings showed the wolf pack killed an average of one moose per 3 days, making it possible to stabilize the herd by culling undesirable animals. He concluded: "Indeed, the Isle Royale moose population is one of the best 'managed' big game herds in North America . . .

Apparently the Isle Royale wolf and moose populations have reached a state of dynamic equilibrium . . . Each is relatively stable, so any substantial fluctuation would be absorbed by the other until another equilibrium is reached." Subsequently, Jordan *et al.* (1971) reported the moose population remained stable from 1959 to 1969 and that there was no evidence that any major fluctuations had occurred. However, pellet count data previously discussed have shown there was a significant upward population trend from 1950 to 1970. Mech justified his conclusion that wolves were removing the annual increment of moose by assuming there were 600 animals in the late winter of 1960. He extrapolated data taken over a 2 month winter period to the whole year (Pimlott *et al.*, 1969). If the base population was closer to 1,000 as the more intensive surveys of Jordan *et al.* (1971) indicate, then the pellet group data and the Jordan data do not suggest that wolves were "managing" the moose herd.

More recently, research by Schaller (1972) on predator-prey relations of the lion noted: "The most important influence of predation is this dampening of the tendency of populations to

increase beyond the carrying capacity of their range, an effect that prevents serious oscillations . . . While predation may be a major factor limiting the size of the populations, the primary factor which ultimately exercises control is the habitat."

The habitat has changed substantially since the wolf pack arrived on the island about 24 years ago. Possibly the most significant habitat change has occurred in the 1936 burn area. This covers about one-fifth of the island. It furnished the bulk of the browse supply for the moose. Therefore, it seems apparent that the future moose-wolf relationship is dependent on a major habitat disturbance, such as fire, to increase the browse supply for the moose.

Rutter and Pimlott (1968) summed up their ideas regarding the future of the Isle Royale wolf when they noted: "They are protected. This does not, however, assure their future, since the environment is gradually changing. It is most likely that the end result of the change will be a smaller moose herd that can support fewer wolves or none. Emigration over the ice in winter, disease, or other problems may also eliminate wolves on the island."

OTHER WILDLIFE

Beaver

A history of the beaver shows they were either extinct or uncommon until the 1920's (Krefting, 1963). Only old beaver dams were reported in 1847 (Ives, 1848) and in 1890 (Scott, 1925). As late as 1904, they were believed to be extinct (Adams, 1909). In 1921, they were reported to be common along the south shore of the island (Ferguson, 1922). They kept increasing by the 1930's (Warren, 1926; Murie, 1934; and McMurray, ca. 1933). Beaver increased at a striking rate in the 1940's, and from about 1945 to about 1950 the population was at an all-time peak of 150 to 200 colonies. However, there was evidence that a decline had started in 1948 (Krefting, 1963). The die-off was attributed to a depleted food supply. Predation by the coyote and a tularemialike disease (Stenlund, 1953) from Minnesota and Ontario may have been secondary causes. During 1959 to 1963, the number of active colonies was estimated at 140 or about 900 beavers (Shelton, 1966). From a total of 475 timber wolf scats, 11 percent had beaver in them (fall, 19 percent; spring and summer, 13 percent). In a sample of 438 wolf scats, Mech (1966) reported the occurrence of beaver in

17 percent in 1958, 12 percent in 1959, and 7 percent in 1960. Field observations in 1972 indicated that the population was high, especially in the northeast end of the island.

Snowshoe Hare

Snowshoe hares were abundant and generally distributed over the main island in 1904-1905, 1916-1917, and in the early 1930's (Adams, 1909; Foster, 1917; and Dustin, 1946). Observations suggested the hare population was low from 1941 to 1946. From 1948 to 1953, hares were observed more often, especially in the northeast area. The population was low in 1956. By 1958, it was increasing. This was probably due in part to the disappearance of the coyote (Krefting, 1969), or it may have been related to the general cyclical behavior of hares. The snowshoe hare was the main food in 92 coyote scats collected from 1948 to 1952, especially in the winter months. The frequency of occurrence of hares was 52 percent for winter and spring scats and only 60 percent in summer and fall (Krefting, 1969). Mech (1966) reported hares were scarce in 1958 and that they increased in 1959 and 1960. His analysis of 438 wolf scats showed the percent

frequencies of hares were: 6 in 1958, 3 in 1959, and 2 in 1960. In 195 fox scats, he found the percent of occurrence of hares was 17 in 1958, 46 in 1959, and 52 in 1960. Johnson (1970) examined a total of 448 red fox scats from 1966 to 1968 and found mammals were present in 38 percent. Over 14 percent of these were hares. These data demonstrate that hares are unimportant to the wolf. The red fox depends much more on them for food, especially during the winter months.

Birds

A total of 197 bird species have been observed on the island (table 10), sixty-two species bred at least once, 26 were thought to be breeders, and the rest are migrants (Krefting *et al.*, 1966). Four species are winter residents only. Of the 106 summer residents, only 35 species are common. Fourteen species are permanent residents, and six of these are common: hairy woodpecker (*Dendrocopos villosus*); downy woodpecker (*Dendrocopos pubescens*); gray jay (*Perisoreus canadensis*); blue jay (*Cyanocitta cristata*); black-capped chickadee (*Parus atricapillus*); and red-breasted nuthatch (*Sitta canadensis*). The sharp-tailed grouse (*Pedioecetes phasianellus*) is uncommon now. This is because brush habitat covers only a small area which is mostly rock outcrop openings. The ruffed grouse and spruce grouse are absent, apparently because of the island's wide water barrier.

Table 10. Bird distribution and habitats on Isle Royale.*

Habitat	Characteristic birds
Sugar maple—yellow birch type	Red-eyed vireo, oven bird, black-throated blue warbler, and wood peewee.
Spruce—fir—birch climax type	Chipping sparrow, oven bird, red-eyed vireo, gray jay, blue jay, black-capped chickadee, Swainson thrush, golden and ruby crowned kinglet, red-breasted nuthatch, and several kinds of warblers.
Aspen—birch, fir—spruce type	Rose-breasted grosbeak, red-eyed vireo, and hermit thrush.
1936 burn, aspen—birch type	Flicker, starling, sparrow hawk, and oven bird.
Swamp and bog forest	White-winged crossbill, purple finch, and yellow-bellied flycatcher.
Rock outcrop and grass openings	Nighthawk, horned lark, lapland longspur, sharp-tailed grouse, white-throated sparrow, and mourning warbler.
Riparian brush	Song sparrow, parula warbler, Canada warbler, yellow throat, American redstart, and water thrush.
Lake Superior, inland lakes, shorelines, and beaver ponds	Grebes, shorebirds, ducks, marsh birds, and gulls.

*From the Birds of Isle Royale in Lake Superior by Krefting *et al.*, 1966.

SUMMARY OF VEGETATION CHANGES AND THEIR IMPLICATIONS FOR WILDLIFE

Clements' (1916) pioneering investigations and conceptualization, leading to his formalization of the climax concept, recognized the existence of climatically determined vegetational associations which are self-perpetuating within a stable climate. He also emphasized the dynamic processes of vegetational succession leading toward the climax. Furthermore, Clements' concepts made it clear that, given sufficient knowledge of the nature of the existing vegetation and the competitive processes, successional trends are predictable even though the timetable is less definitive in many specific situations.

The ecosystem concept defined by Tansley (1935) considers the interrelationships of all organisms and their environment within a physical-biological "system" in a space-time relationship. This system can be of any size depending on the space requirements of the organisms being examined. The identification of the system nature of ecology provides the framework within which the various levels of organization and interdependence can be studied. In this study, the relationships of vegetation to the physical

factors of the environment, the interactions of animal organisms and their habitats, and the control exerted by the habitat on the animal populations is of special interest.

Forest Succession on Isle Royale

This study was not designed to test the validity of the various phytosociological concepts relating broadly to natural vegetation. However, the authors consider the polyclimax concept to be the most useful as a basis for the classification and interpretation of the forests of Isle Royale and also for making predictions as to the future trends existing vegetation will take.

The northern hardwood type — dominated strongly by sugar maple and yellow birch — is well represented on the island on mesic, high nutrient level sites. It has all the attributes of a self-perpetuating climax. On such sites, where secondary successions have been initiated by fires at various past intervals, the trends toward this climax are evident in the successful reinvasion by tolerant hardwoods.

The constituent species of the boreal conifer type as identified by

Cooper (1913) are present on most of the island. They are in various combination patterns. However, "typical" boreal stands of balsam fir, white spruce, and paper birch, with few intrusions of more southern species such as yellow birch, red maple, white-cedar, and mountain ash, are found only on Passage Island and on microsites with evidently cooler, more moist environments than generally prevail on the island. Several factors may explain this situation. The general climate may favor the more heat-demanding non-boreal species. These can compete favorably with the balsam fir and spruce on all but the coolest moist sites. Furthermore, the moose herd during its years of great abundance had drastically altered forest composition by heavy browsing, especially on balsam fir, a favored winter food. This has opened up the normal dense canopies. It allowed an abundance of shrubs and herbaceous vegetation to enter and favored some of the more heat-demanding hardwoods over the boreal conifers. This supports the conclusion that Isle Royale is more closely related to the Great Lakes-St. Lawrence Region than to the Boreal

Region in the Canadian classification system developed by Halliday (1937) and Rowe (1959).

The forest types of Isle Royale have been broadly oriented with climatic and edaphic coordinates as discussed previously. Two major lines of succession are evident. One leading to the sugar maple–yellow birch climax, and the other leads to the paper birch–balsam fir–white spruce climax. A minor line of succession involves the general swamp forest in all its variations of black spruce, tamarack, and white-cedar. The ecological conditions on which these climaxes exist are depicted in figure 4. The site affinities of the key tree species in the principal forest types are shown as ecographs in figure 5. These graphic presentations help to explain the site affinities or ecological “preferences” of the forest types as well as their associated shrub and ground cover species.

This information, coupled with a knowledge of the silvical characteristics of the tree species, provides the basis for making successional predictions. Of particular importance are the silvical characteristics relating to the species’ competitive ability to invade new areas, to dominate its associates, and to establish and perpetuate itself as a climax.

Tolerance to shade conditions enables a species to invade a stand of less tolerant species, to overtop them, and to shade them out. Such climax species as sugar maple and balsam fir are the most tolerant species in the area. Because of rapid juvenile height growth, light seed easily disseminated by wind, ability to reproduce by root suckers or stem sprouts, or special seed bed adaptations, other species are better equipped to follow such major disturbances as fire, logging, insect attacks, or blowdown. Jack pine, aspen, and paper birch are classic examples of such post fire disturbance species. Still other species, such as tamarack and black spruce, are able to occupy sites too extreme in moisture or in other aspects for species to invade.

Wildlife Implications

The preference by moose for various habitats during different seasons and in various parts of Canada and Minnesota has been reviewed in a previous section. Also discussed was

the history of moose population trends on Isle Royale and their relative winter preferences for the four major cover types as documented by pellet group counts from 1948 to 1970. From table 9, it is evident that the winter use by moose is minimal in the sugar maple–yellow birch type. Since this is a climax type and self-perpetuating, no change is predicted that will affect the low winter moose use of the approximately 10,000 acres this type occupies. However, moose use this type more in spring and fall. An increase in the area of this type will occur on portions of the 1936 burn containing some sugar maple and yellow birch regeneration as those species expand their dominance there. However, this is a very slow process taking at least another generation of tree growth – possibly several hundred years.

Since beaver and the snowshoe hare are not typically climax forest species, their abundance is not particularly related to the future of this sugar maple–yellow birch type. Those bird species which prefer this forest type will, of course, continue in it. As the type expands to occupy its former area in the 1936 burn, these birds will increase to the same extent.

The other major line of successional development is toward the boreal climax. These balsam fir are the dominant species together with birch and spruce associates. This type, with its seral predecessors, is estimated to occupy over 50 percent of the forest area on the island. Its future condition will greatly affect wildlife.

In this climax, balsam fir is the essential tree species dominating the type. A monograph on balsam fir (Bakuzis and Hansen, 1965) reported that moose distribution in eastern North America coincides reasonably well with the general limits of balsam fir distribution except for its southern extension along the Appalachian Mountains. In the same monograph, Cook and Robeson are cited as calling the snowshoe hare the characteristic lagomorph of the northern coniferous forest of North America. Four subspecies are reported (Miller and Kellogg, 1955) as occurring within the general range of balsam fir.

Numerous authors report the importance of balsam fir in the moose’s winter use patterns (Murie, 1934;

Aldous and Krefting, 1946; Pimlott, 1953; and others). In Newfoundland, Pimlott (1955, 1961) reported balsam fir, paper birch, and aspen to be key browse species for moose. He observed that, as the moose population increased, utilization of balsam fir became the most important food in the diet. Table 9 records that pellet group counts in 1961, 1965, and 1970 indicate heavier winter use of the paper birch–balsam fir–white spruce climax type than of any other type sampled. Only in the 1948 and 1950 counts, when the regrowth on the 1936 burn was still available to moose, did the use of any other forest type exceed that of the boreal climax.

A third line of successional development should also be recognized relating to the swamp forest stands. These are composed of various combinations of three key species: tamarack; black spruce; and white-cedar. The edaphic relationships of white-cedar and black spruce are graphed in figure 5. While tamarack is not included because it is presently a very minor species, its site affinities are essentially like those of black spruce or even more restricted to the wettest sites. White-cedar occurs on somewhat less wet but higher nutrient sites than do tamarack or black spruce. Most of these swamp stands, except the wettest, contain some balsam fir and paper birch, especially in the border areas adjacent to the upland sites. While these swamp types occupy a relatively small area, they provide important winter habitat. As mesification processes continue, these stands will undoubtedly be invaded by balsam fir. On those sites presently having white-cedar, the succession will possibly be toward the sugar maple–yellow birch climax. Even in these stands, balsam fir is abundant in the reproduction. For the predictable future, balsam fir will undoubtedly increase its dominance.

Preclimax Disturbance Successions

Factors initiating secondary successions have been predominantly fire and the spruce budworm. The extent of logging has been minor, and the influence on the moose herd has been insignificant. Tree destruction by wind has occurred. However in most cases, blowdown has resulted after insects or diseases have killed the trees, making

them more easily broken off or blown down by heavy wind. While major destruction by wind has not been recorded, observations indicate that blowdowns have occurred and benefit the moose.

Insect epidemics

Little is known of the extent to which insects have affected the forests of Isle Royale. It is almost certain that the larch sawfly (*Pristiphora erichsonii*) epidemic, which devastated huge areas in Ontario and northern Minnesota in the early 1900's, also occurred on Isle Royale. Very likely, tamarack mortality from this epidemic accounts for the present scarcity of the species as compared to its relative abundance as noted in Ives (1848) survey notes. However, tamarack is not a tree of particular importance to the moose, hare, or other major animal species.

The role of the spruce budworm (*Christoneura fumiferana*), since it is the most destructive insect of balsam fir, is of much greater significance. Outbreaks of epidemic proportions have been reported by various observers (Bakuzis and Hansen, 1965) from nearby Ontario and Minnesota locations in about 1880, from 1909 to 1913, from 1937 to 1955, in 1954, and in 1956. If extensive enough, they can benefit moose. In Minnesota (Batzer and Bean, 1962), the area affected by the spruce budworm increased from 96,000 acres in 1960 to 240,000 acres in 1961.

Although the attacks sometimes kill young balsams, an important winter browse plant, the destruction of the overstory permits light to reach the forest floor. This enhances the growth of browse. When budworm-killed stands are burned, the successional growth provides excellent moose habitat (Simkin, 1963). He noted that such species as aspen, beaked hazelnut, junberry, mountain ash, willow, and paper birch increased greatly.

On Isle Royale, the budworm attack in the early 1930's killed 75 to 100 percent of the balsam stands along the entire south shore of the island (Brown, ca. 1935). Hickie's (1936) observations showed 90 to 100 percent of the balsams were killed. The overstory stands needed for winter cover were destroyed. The budworm-killed trees probably provided additional fuel for the 1936 burn. The fire reduced succession to the early seral

stage and was partly responsible for the marked increase in the moose herd (Krefting, 1973).

The spruce budworm outbreaks are a natural event which will undoubtedly continue to affect the forest types having large proportions of balsam fir. However, the future incidence of these outbreaks is difficult to predict as to extent, periodicity, or severity. The role of the spruce budworm outbreaks must be considered beneficial to moose.

Fire

Undoubtedly, fire has been the major agent for secondary successions on Isle Royale in the historic past. The recent fire history of the island, and particularly the extensive 1936 burn, has been discussed previously. This discussion has emphasized that there is ample evidence for the occurrence of "natural" fires in the past. Just as do insect epidemics and logging, fires produce second growth stands that many species, including moose, deer, snowshoe hare, and beaver, prefer.

The most dynamic forest types on Isle Royale are those which have been burned over and on which second growth stands occur and on which post fire successional processes are underway. The more recent the fire, the more fluid is the stand's developmental stage. The vegetational succession leading to the sugar maple-yellow birch climax or involving only the swamp species, i.e. black spruce or tamarack, are considered of less importance to the major wildlife species. This is either because the tree species do not have significant importance to the animals, or because the areas involved are minor. Similarly, the jack pine type covering only a few hundred acres has little overall significance to wildlife. By far most of the island is occupied by stand mixtures in varying proportions of aspen, paper birch, balsam fir, white spruce, and white-cedar together with various minor species. These stands are generally ordinated along a line of succession leading toward the paper birch-balsam fir-white spruce climax. In most cases, they have a fire history which may be as recent as the 1936 and 1948 burns or as old as 100 years or more. Some forest types, such as the white-cedar-balsam fir-paper birch, show no evidence of fire. They probably represent a later stage in the

succession toward the same climax. In all cases, balsam fir is the key species which, because of its aggressiveness and relative shade tolerance, dominates the successional process.

The most important habitats for the moose are produced in the early stages of plant succession within the boreal forest (Peterson, 1955). Because of forest succession, the habitats are constantly changing. The moose populations vary accordingly. Normally, the subclimax types have the highest moose densities, and the populations decrease as the forest reaches maturity.

This study documents the importance of depressions in rock outcrop sites in providing oases of revegetation sources following forest fires. This was previously noted by Cooper (1928). On such microsites, the successional processes are far more rapid and vegetation is more abundant than on nearby sites. Many sites on the 1936 burn area are still bare of vegetation.

Like the moose, beaver prefer the early seral stages of plant succession. Aspen is the most preferred and nutritious species (Shelton, 1966). On large areas of the island, aspen will be eliminated and replaced by balsam fir and white spruce as the stands reach maturity. These species will also shade out tree reproduction and shrubs needed for food. Snowshoe hares also thrive best during the early seral stages of plant succession. This is particularly so when there is an abundance of preferred woody species such as aspen, willow, and white-cedar. Along with the moose and beaver, the snowshoe hare is best adapted to a fire induced ecosystem. It is not a climax forest species.

The pellet group counts show that the climax of paper birch-balsam fir-white spruce have heavier moose use than do the preclimax types. This can be explained by the atypical open condition of this general "boreal" climax on the island as compared to its dense stocking in the typical condition. The open condition is undoubtedly a result of heavy browsing by moose. This browsing has greatly restricted growth of the balsam fir and has permitted the growth of woody browse not found in denser stands.

Some of the effect of the heavy browsing on the general birch-fir-

Table 11. Density and browsing of some preferred species in the birch—fir—spruce type on Isle Royale as compared to nearby islands.

Species	Isle Royale		Raspberry, Smithwick, and Wright Islands		Passage Island ¹	
	Number of stems per acre and percent browsed ²					
	Number	Percent	Number	Percent	Number	Percent
<i>Abies balsamea</i>	1,420 ³	73	6,100 ³	0	100	0
<i>Cornus stolonifera</i>	130	72	0	—	1,100	0
<i>Sorbus americana</i>	890	79	730	50	600	0
<i>Taxus canadensis</i>	210	75	7,400	0	3,470	10
<i>Viburnum</i> sp.	310	73	0	—	4,700	10

¹ Clipped by snowshoe hare. There are no moose on Passage Island.

² Stems over 1 foot in height. Browse tallies made in 1968 and 1969.

³ Mostly small seedlings below the general snow cover.

spruce forest type can be seen in table 11. Here the type is compared in its occurrence on Isle Royale where it has been heavily browsed, on several nearby small islands with less browsing pressure, and on nearby Passage Island which has no moose. The paucity of ground hemlock — probably the most highly preferred moose food — on Isle Royale and its abundance on the small islands is very striking. The few balsam fir seedlings, also highly preferred browse, on Passage Island is also related to the difference in browsing history. On Passage Island, this boreal climax has developed without browsing. Its stand density, as measured by tree numbers and basal area, is much greater than on Isle Royale. It's too dense to permit seedling regeneration. On the main island, however, the early history of very heavy browsing on the balsam fir opened up the overstory. This permitted a considerable amount of seedling regeneration.

The effect of future succession on these types as related to moose habitat depends both on the future extent of burning and spruce budworm attacks and on the abundance of moose and their browsing pressure. If there are no setbacks by fire, insects, or moose browsing, the balsam fir and other species will grow out of reach. The production of available browse will decrease. However, excessive browsing can selectively reduce the ratio of balsam fir to less preferred species and greatly restrict its height growth.

The interactions of moose and their forest habitats are further complicated by the activities of beaver. By their

tree-cutting and dam-building activities, beaver also influence moose habitat. They compete with moose for such species as aspen, paper birch, willow, and other shrubs. Beaver make more browse available for the moose when they cut down large aspen and paper birch. Their dams also provide aquatic plant-feeding areas. The water levels of many lakes are maintained by dams, and beavers provide the habitat for many species of birds.

The vegetation tallies in the 1936 burn area show that paper birch predominates. Willows form part of the food supply for the beaver, but these are repeatedly browsed by the moose. Willows are also easily shaded out as the stand matures. Aspen is in limited supply and develops best on the better sites.

In the birch—fir—spruce type, large aspens are uncommon in the overstory. However, old-cut stumps attest to their former use by beaver. Aspen is poorly distributed because of its intolerance to shade and severe browsing by the moose. The best beaver habitat is in the aspen—birch—fir—spruce type in the northeast end of the island since it still contains large available aspen. However even in this area, the supply is dwindling. Young aspen reproduction is in short supply and is being overbrowsed by moose.

Bird life will also be greatly affected by successional changes due to fire or other causes. Sharp-tailed grouse are of special interest because they are known to have been present for a century or more. Their habitats are closely associated with natural brushy openings and burned-over

areas. Populations increase when fires burn extensive areas, such as occurred in 1936. After the fire, sharptails became fairly common, but they have gradually decreased. If sharptails are to be maintained, even at a remnant level, it will be necessary to reintroduce fire into the ecosystem.

As previously discussed, the general succession of most of the upland forest types will be toward the birch—fir—spruce climax. Bird life will change accordingly. The extent of the aquatic habitat produced by beaver dams which benefit birds will fluctuate with the level of the beaver population. Moose browsing will tend to keep open, parklike stands. However in the absence of disturbance, the forest will ultimately become denser.

Two major lines of successional development on Isle Royale have been identified leading to the sugar maple—yellow birch and the paper birch—balsam fir—white spruce climax associations. Of these, the paper birch—balsam fir—white spruce climax, together with its preclimax successional stages, covers most of the island. They are of great significance as wildlife habitat, particularly for moose. Fire, the spruce budworm, and wind have initiated secondary successions that have greatly affected the nature and development of the vegetation and consequently its quality as animal habitat. These seral stages are generally the habitats preferred by moose, beaver, snowshoe hare, and some bird species. The frequency and extent of such disturbances will effectively determine the animal relationships in future years.

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This rocky shoreline is on the north side of Isle Royale and has a characteristic paper birch, balsam fir, and white spruce forest. The main island is 45 miles long and is 8 miles at its widest point.

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