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THE SPRUCE-FIR FORESTS OF THE COAST OF MAINE

A Thesis

Presented to the Faculty of the Graduate School

of Cornell University for the Degree of

Doctor of Philosophy

by

Ronald Barnard Davis

February 1961

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BIOGRAPHICAL SKETCH

Ronald Barnard Davis was born to Pearl and Daniel Davis at Brooklyn, New York, on August 6, 1931. He resided there until twenty-two years of age. He attended the public school system, graduating from James Madison High School in 1949.

Until 1952 he attended New York University. He graduated from Grinnell College, Iowa, in 1954, with a major in biology. He received a Master of Science degree from the University of New Hampshire in 1956. His thesis was an ecological study of a tidal marsh.

Study continued at Cornell University where he concentrated on ecology, limnology, and science education. Here he met and married Shirley Lou Hoenstine in 1957. He held teaching assistantships in zoology from 1954-1958.

During the past few summers he worked at Acadia National Park as a Ranger-Naturalist, specializing in intertidal ecology. His other interests include hiking, canoeing, skiing, nature photography, philosophy, and music.

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ACKNOWLEDGEMENTS

Many individuals and several institutions contributed directly or indirectly to this thesis. It is only possible to acknowledge certain of these here.

I express sincere appreciation to Professor LaMont C. Cole who directed my graduate study at Cornell University. Dr. Cole helped assemble equipment for this study and edited the paper. Also I thank the other members of my advisory committee, Professors Clifford O. Berg and Verne N. Rockcastle, for their counsel.

Fellowship funds made available by Cornell University supported this research. During the academic year of 1958-1959 I held the Schyler-Gage Fellowship in Animal Sciences. During 1959-1960 Cornell Woodrow Wilson funds were provided.

The staff at Acadia National Park facilitated this study in several ways. I am particularly indebted to Park Naturalist Paul G. Favour, Jr., who gave freely of his time and knowledge.

The staff and facilities at the Jackson Memorial Laboratory, Bar Harbor, were most helpful during certain phases of the research.

Several taxonomic specialists generously identified collections. These individuals are mentioned in appropriate sections of the text. Estate owners who granted permission

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to study their forests are named in text Table 5. Correspondents too numerous to name helped locate stands suitable for study.

Among the many individuals who contributed their time, knowledge, and/or resources are: A. E. Brower, Entomologist, State of Maine; G. Gordon Bruce, Chief Ranger, Acadia National Park; Kenneth V. Goodman, United States Soil Conservation Service; Louis T. Ibbotson, Librarian, University of Maine; John M. Kingsbury, Botany Department, Cornell University; D. J. Lathwell, Soil Analysis Laboratory, Cornell University; Richard G. Smith, Bar Harbor, Maine; Joan Staats, Librarian, Jackson Memorial Laboratory; E. S. Whitaker, Landscape Architect, Acadia National Park; and George M. Woodwell, Botany Department, University of Maine.

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Finally, I acknowledge that throughout this study my wife, Lee, was a devoted co-worker. She helped in the field, in the preparation of text figures, and by typing and editing drafts. To Lee this thesis is affectionately dedicated.

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INTRODUCTION

In the non-montane regions of eastern North America, sizable areas of spruce-fir forests reach their southern limit on the coasts of Maine and Nova Scotia. Certain aspects of the Maine coastal forests have been treated in the literature, but up to this time no detailed general description and analysis has appeared. The major purpose of this study is to fill this gap.

The ecological importance of the coastal forests results not only from their unique geographic position, but also from the particular configuration of their distribution on the Maine coast. This irregular coast is composed of a multitude of islands and elongate peninsulas extending seaward into the cool waters of the Gulf of Maine. It will be contended that spruce-fir forests approach climax status locally on peninsula and insular outliers in the western portion of the coast, and more generally from Penobscot Bay eastward. Furthermore, this dissertation will attempt to demonstrate that the distribution is distinctly correlated with intensity of marine influence and latitude.

When considered in the light of the overall trend of postglacial history in eastern North America (Dillon, 1956), the coastal forests may be interpreted as constituting a large relict community. As such, they present a fortunate circumstance in the field, analogous to experimental "con-

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trol" in the laboratory. One set of biota-environment correlates, the coastal spruce-fir ecosystem, stands out rather distinctly from adjacent climax systems. By the very nature of the case, such extensive and relatively clear-cut juxtaposition is harder to find nearer the center of ranges of such systems. Assuming an essential degree of biological equivalence between the spruce-fir forests of the Maine coast and spruce-fir forests elsewhere, the results of the "natural experiment" on the coast may be valuable for interpreting the ecology of spruce-fir forests in general. The argument behind this approach is expanded upon by Clements (1934), and Dansereau(1957), under the headings "relict" and "preclimax and postclimax".

The Scope and General Approach of the Study

In order to make this study, I spent the period from September 1958 to January 1960 along the coast of Maine. Mount Desert Island, where I resided, constituted the base of operations. This location was chosen because a considerable portion of the island is included within the boundaries of Acadia National Park. Such public preserves are excellently suited for ecological studies. Of the eighteen spruce-fir stands chosen for study, six are located in the park, while others are scattered over the entire coastal region. Several types of data obtained in

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the forests on Mount Desert Island were not obtained elsewhere.

The spruce-fir stands studied were all of the "upland" variety in the sense that none occurred on very poorly drained or boggy areas. Throughout this paper, unless otherwise stated, the term "spruce-fir" will exclude bog forests. This latter type is encountered infrequently in the coastal area. When it occurs it is usually readily distinguishable by the presence of black spruce, Picea mariana.

The selection of the aspects of forest ecology to be investigated was based in large part on relevance to the general problems discussed in the opening paragraphs. Thus, a major consideration rested on the availability in the literature of comparable data from other spruce-fir areas. The categories finally chosen were: macroclimate; forest microclimate; soils; floristic and vegetational quantities (excluding thallophytes); and selected faunal groups, including carabid beetles and vertebrates.

Macroclimatological data from various stations in Maine were obtained primarily from United States Weather Bureau records. These were utilized for description and comparison of inland and coastal localities.

Forest microclimate investigation was concentrated on Mount Desert Island, but it is felt that considerable gen-

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eralization to other areas is justifiable. This investigation consisted of three studies. The first was designed to measure temperature differences between forest and open sites, at coastal and inland localities. The latter portion of this comparison dealt with considerably shorter distances than those discussed under macroclimates. For these purposes maximum-minimum thermometers were used. As it was possible to read these only at weekly intervals, the temperature-integrating property of the soil was put to use by taking readings at a depth of seven inches. A second study attempted to measure differences between precipitation within and outside of the forest. To accomplish this, twenty home-style precipitation gauges were placed in a "typical" stand, and the results compared to precipitation at an adjacent open area. Considerable time and effort was invested in a third microclimatological study. Its aim was the automatic recording of forest temperature stratification throughout weekly periods during different seasons. However, because of the bulk of data and their indirect application to the major problems at hand, they are withheld for a later paper.

Soils were studied in detail only on Mount Desert Island. Time considerations required that only limited attention be paid to this important aspect of forest ecology.

In order to determine the distribution and relative

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concentration of the spruce-fir forest type at various coastal localities, the entire coastal area was inspected by flying along parallel lines in a small airplane. The map which resulted is included in the rear pocket.

At fourteen stands the vegetation was studied in some detail. Presence data were acquired for corticolous bryophytes and lichens, ground surface bryophytes and lichens, pteridophytes, herbs, shrubs, and trees. Coverage data for ground surface bryophytes and lichens were obtained by a transect method. Vascular plant frequency and density, as well as size-class distribution and basal area for tree species, were determined by quadrat methods. As an aid in investigating matters of growth, succession, and climax, increment borings were taken from various sized trees at each stand.

Carabid beetles were studied only on Mount Desert Island. In order to determine kinds and estimate relative numbers, both ordinary collecting and trapping were employed. The traps consisted of twenty-four baited #10 tin cans (ca. 0.8 gallon) sunk into the ground, their open tops flush with the ground surface. These were placed not only in spruce-fir stands, but also in adjacent habitats to determine the degree of "fidelity" (as in Cain and Castro, 1959) of the various species.

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To capture small mammals, lines of snap traps were set out at fourteen locations. As in the beetle study, traps were placed in both spruce-fir stands and adjacent habitats. Trapping totaled 7,570 trap nights.

Breeding-bird populations were sampled in fourteen stands by a sample count method similar to the one used by Bond (1957).

Various other less systematic methods were used to collect information on aspects of the forests considered to be less important than the ones discussed above.

Orientation Map for Readers

An index map showing the numerous localities which are referred to in this thesis has been included as the next page (Figure 1). On the first three text pages whenever a locality is mentioned, it bears a number and letter in parentheses. These refer to the numbered and lettered rows and columns on the index map.

Taxonomic Nomenclature

Latin binomials are used in the text the first instance a species is mentioned. Thereafter, those species bearing a well-known common name will be indicated by it only. Latin nomenclature will follow the authorities listed below, ex-

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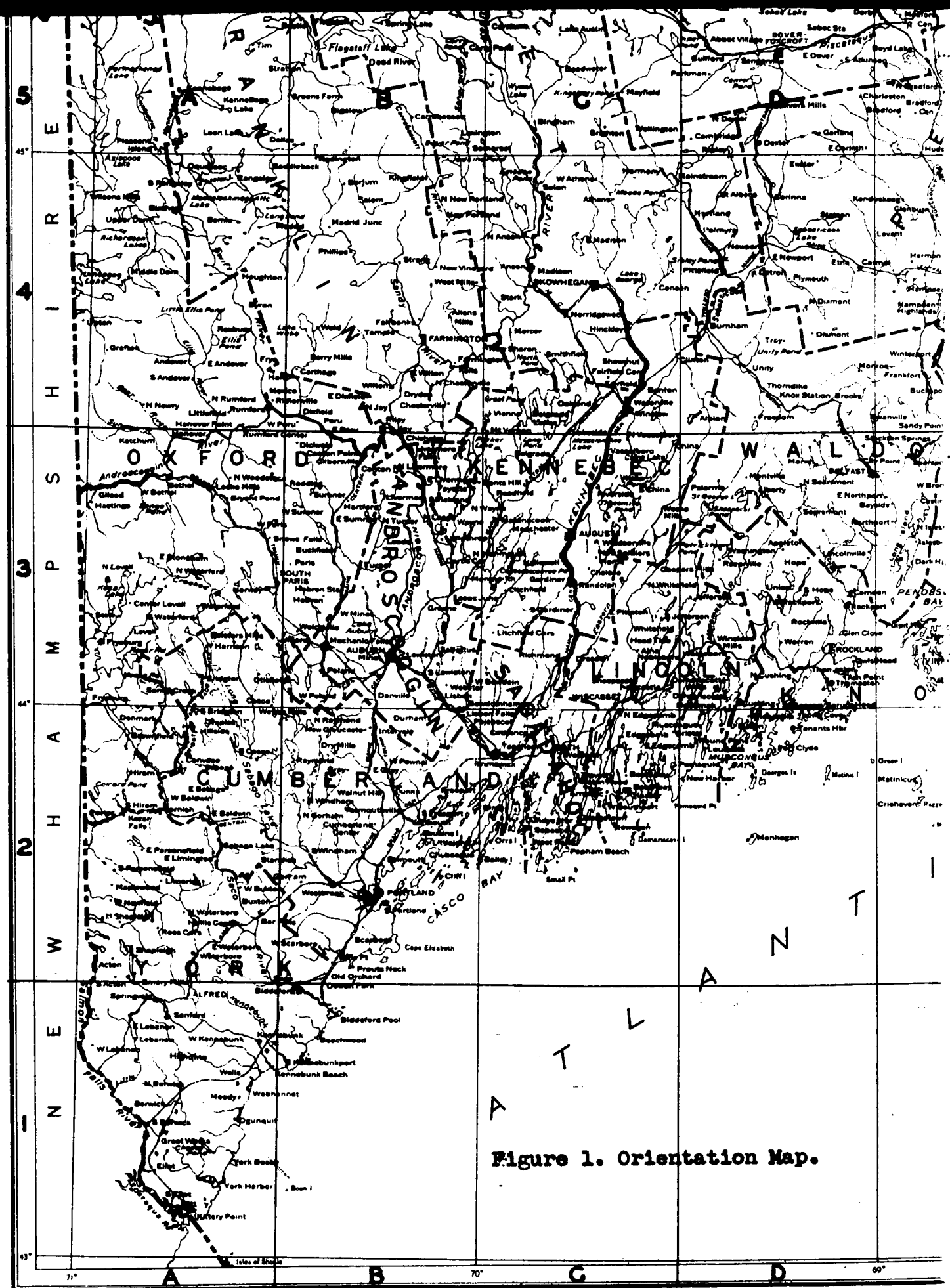


Figure 1. Orientation Map.

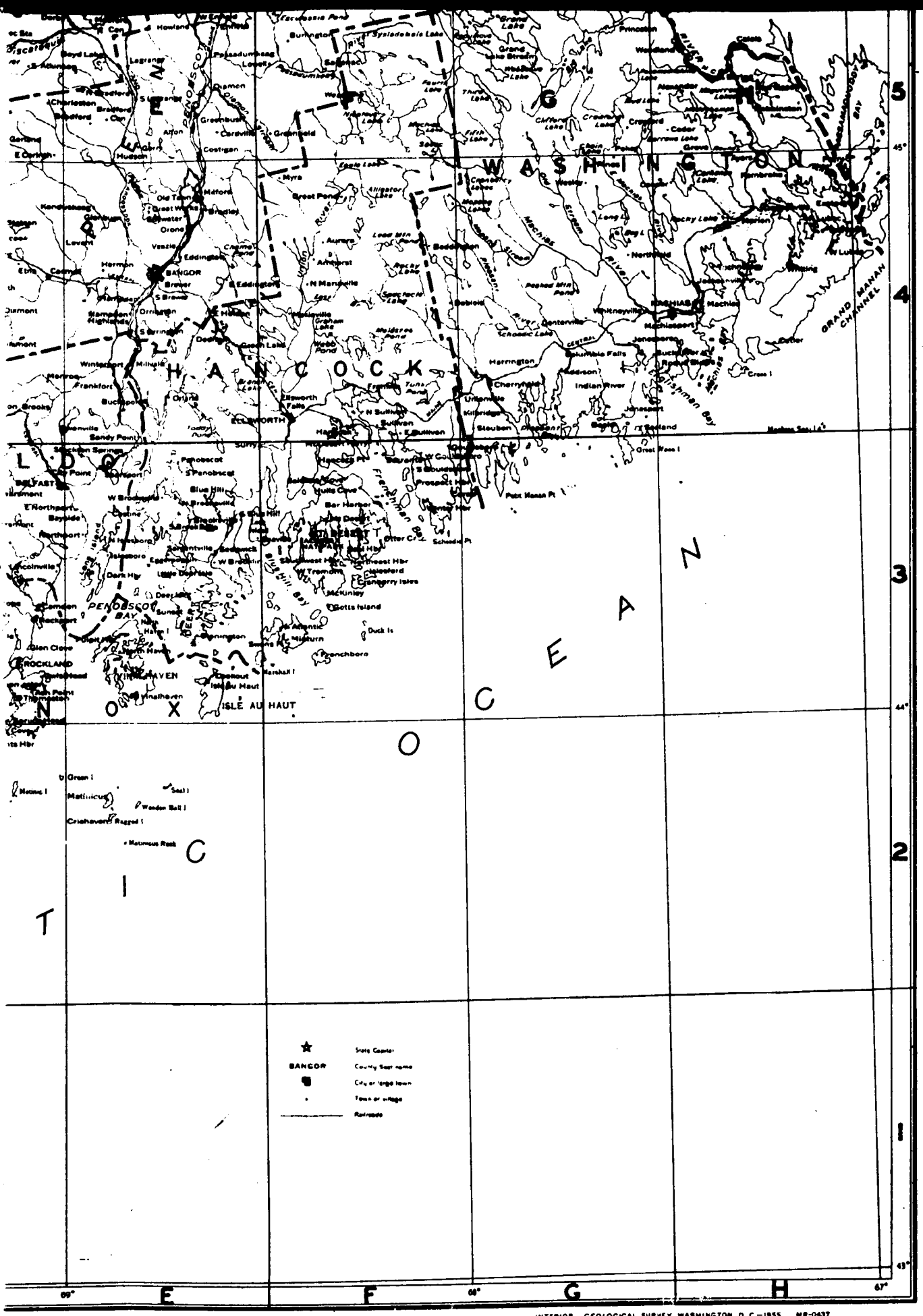
J. G. Staack, Chief Topographic Engineer
A. F. Hassan, Cartographer
Compiled in 1921-1922

Scale 1/1000000

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10 0 10 20 30

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INTERIOR—GEOLOGICAL SURVEY, WASHINGTON, D. C.—1955 MR-0437

Scale 1/1000000

10 0 20 40 Miles

10 0 20 30 40 50 Kilometers

Modified polyconic projection. North American datum

Edition of 1922
reprinted 1955

OLOGICAL SURVEY, WASHINGTON 25, D.C.

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cept for their capitalization of specific names.

Lichens: Hale and Culberson, 1956

Bryophyta:
Hepaticae: Evans, 1940
Sphagnaceae: Andrews, 1940
Other Musci: Grout, 1940

Tracheophyta: Fernald, 1950

Carabidae: Leng, 1920

Amphibia and Reptilia: Schmidt, 1953

Aves: American Ornithological Union, 1957

Mammalia: Anderson, 1947

Literature on Maine Coastal Spruce-fir Forests

The only literature reviewed in this section is that published within the past sixty-five years, and which applies directly to the biology of the coast of Maine spruce-fir forests. Earlier literature pertaining to the coastal forests, matters concerning physical habitat, references consulted primarily for methodology, and literature on other geographic areas used for comparison are cited in appropriate sections on later pages.

Considering the ecological and biogeographic importance of these forests, it is surprising to find that so little has been written about them in the scientific literature. The majority of publications reviewed in the following paragraphs contain information on the spruce-fir forests as

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only a portion of their subject matter or as incidental notes. A high proportion of all biological work on the coast of Maine has been concentrated at Mount Desert Island (3F). (Because of the frequent reference to this location it will henceforth be abbreviated MDI.)

Flora

Floristic studies on the Maine coastal region consist of several score papers published in the periodicals of various northeastern natural history societies and in taxonomic journals. These usually consist of short annotated lists which often single out species because of their taxonomic or biogeographic interest. The reader primarily interested in the floristics of the coastal region should consult the indices of such publications as The Acadian Naturalist, The Maine Naturalist, Bulletin of the Torrey Botanical Club, and especially Rhodora.

One of the most thorough floristic studies on a Maine coastal area is that of Hill (1919), on the vascular plants of the eastern Penobscot Bay region (3E). The list is annotated with considerable habitat information. Another long list is Rand and Redfield's (1894) on MDI and adjacent islands. In its annotations, emphasis is placed on rare and unusual species, while none but the most general habitat data are given for important common species. These authors'

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publications on the small offshore islands to the south of MDI (Redfield, 1885; and Rand, 1900) indicate the highly disturbed state of the vegetation then. In an 1886 paper, Redfield points out that such islands commonly had large portions cleared for sheep pasturage. However, the forested areas then, as today, were dominated by red spruce (Picea rubens), white spruce (Picea glauca), balsam fir (Abies balsamea), and paper birch (Betula papyrifera).

I have found that in the coastal area the most effective approach for solving problems on vascular plant identification is the combined use of Wherry's excellent book on the Wild Flowers of Mount Desert Island, Maine (1928), and Fernald's Gray's Manual (1950). Behind the rather casual-sounding title of Wherry's book, the reader will find a considerable amount of ecological information on the MDI (3F) flora.

Helpful references on flora, which cover the entire state of Maine are Ogden's book (1948) on ferns, Hyland and Steinmetz's book (1944) on woody plants, and Ogden, Steinmetz, and Hyland's (1948) checklist of vascular plants.

Vegetation

Hill's (1923) study of the Penobscot Bay region (3E) is one of two major vegetational studies on Maine coastal areas. He covered all the non-marine seral and climax association

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types. Qualitative description of the spruce-fir forests was presented in considerable detail. These forests, so characteristic of islands and seaward peninsulas in that area, were thought to constitute a "physiographic climax", rather than being representative of the broader climatic climax which Hill recognized for northern New England. On these matters he subscribed to the theory of Nichols (1923).

The other important paper on the terrestrial ecology of a coastal area is the monograph on MDI by Moore and Taylor (1927). My observations lead me to believe that both Hill's and Moore and Taylor's major conclusions are in large part applicable to the entire coastal stretch from eastern Casco Bay (2B) to Eastport (4H). Both papers cover a number of vegetational types and detail is necessarily limited. Description is primarily qualitative. A map showing the vegetation of the entire island is included by Moore and Taylor. Red spruce was thought to be the most numerous tree species, and spruce-dominated forests to cover some 70% of the island at that time. Matters pertaining to succession and climax constitute the major theme of the paper. The authors were not preoccupied with theories pertaining to extensive regional climaxes as was Hill. Thus, it was with little qualification that spruce forests were said to constitute the climax for most of the island, with a northern hardwoods-

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spruce type limited to a few central areas.

Johnson and Skutch (1928) included a description of a portion of the spruce-fir forest at Otter Point, MDI, as a part of their study of the shore vegetation there. They listed species and commented on common forms.

Kuchler's maps (1956a,b) of southeastern MDI (3F) show the coverage of various vegetational types. They were prepared from aerial photographs, supported by ground checks. Comparison to Moore and Taylor's 1927 map dramatizes the havoc wrought to the forests by the famous Bar Harbor fire of 1947. Kuchler's maps have obvious ecological value, but they should be used with caution. Because of the unavoidably limited number of descriptive categories and combinations, the characterization of any one patch in the mosaic on the maps is usually only roughly correct. Thus, for example, at my study area at Pemetic Mountain, I found the forest to be composed by basal area of 75% red spruce, 13% hemlock (Tsuga canadensis), 6% paper birch, 3% red maple (Acer rubrum), and lesser species (see Tabular Results, Part III). Kuchler omitted hemlock from his characterization, and attributed less than 1% cover to paper birch and red maple. I found 16% bryophytic ground cover, and Kuchler 25-50%.

Knowlton (1915) described eight plant "societies" at

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Roque Bluffs (4H), among which he included the "Canadian forest". It was not possible to ascertain whether the stand in which I counted birds at that area coincided with one of his, as he gave no specific locations. The forest was described as being dark and mossy, and dominated by evergreens. His list of vascular plants is similar to mine for nearby Roque Island (4G) and Cutler (4H). However, the relative importance of his various species cannot be judged, as no quantities were given. Knowlton found that "Such rich woods trees as the maples and yellow birch are rare near the shore, even in the undergrowth." According to my observations, this is still true.

Specialized Forest Studies

Biotic Relationships:

Economically important phytophagous insects, their forest tree hosts, degrees of infestation, and control were discussed for various parts of Maine by Nutting (1957). "Witches brooms", caused by dwarf mistletoe (*Arceuthobium pusillum*) were mentioned as occurring on white spruce and "black spruce" (*Picea mariana* and/or *P. rubens* ?) at a number of coastal locations from Casco Bay (2B) eastward (Nutting, 1957; Norton, 1907).

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Tumors:

White (1958) and White and Millington (1954) discussed the structure, development, and geographic distribution of tumors on white spruce. These tumors are a common and striking characteristic of this species in coastal Maine. According to White and Millington (1954), affected trees are strongly concentrated in locations most exposed to marine influence.

Growth and Reproduction Studies:

The environmental correlates, seasonal periods and rates of height growth of balsam fir, white, and red spruce were studied by Baldwin (1931) in New Hampshire and Maine. On MDI, as elsewhere, he found that about 90% of growth occurred in the first six-week period of summer, and concluded that temperature was probably the most important factor.

In an important series of papers (1917a,b; 1922; 1926) Moore described the effects of various soil conditions and light on the reproduction of red spruce, white spruce, balsam fir, and other conifers on MDI.

Lichen Ecology:

Succession, the effects of evaporation and light on distribution, and the correlation between lichen flora and forest type have been studied on MDI by Plitt (1924, 1927) and Plitt and Pessin (1924). One of Plitt's study areas co-

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incides with one of mine: the spruce-fir stand at Otter Point.

Forest Fauna

Carabidae:

So far as I have been able to ascertain, there exist few publications of any note regarding the Carabidae of the Maine coast. The foremost of these is Procter's annotated list of the insects (most recent revision, 1946) of the MDI region. In his 1943 discussion of Carabidae of mountains and islands, Darlington utilized an earlier edition of Proctor for his MDI data.

Mammals:

The paper with the greatest general information coverage on the mammals of Maine is probably Palmer's 1937 thesis. The geographic distribution of "wildlife" in the state was discussed by R. L. Day (1953, not seen).

Information on the mammals of the Portland area (2B) was assembled and reviewed by Norton (1930). A paper on the mammals of the Brunswick area (2C) was published by Pope (1922). Manville's notes on the mammals of MDI include several spruce-fir forest species. More recently, a number of trap lines were run on MDI in conjunction with Calhoun's North American Census of Small Mammals (1948-1959), some of them in spruce-fir forests.

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The deer populations of MDI have been the subject of a number of studies (Banasiak and Peppard, 1956; Banasiak, 1956; Favour, 1957). Among other things, these studies point out the winter shelter value of spruce-fir stands, but the lack of deer food in such stands. Favour discussed the degree to which various plant species in the area are browsed. Such relationships may have an important effect on forest succession and composition, and are discussed later.

Birds:

Until 1949, Knight's book on the birds of Maine (1908) constituted the major ornithological reference on the state. Palmer's more recent and concentrated treatment of the state's avifauna (1949) has largely replaced the earlier stand-by. Palmer includes a considerable amount of habitat data. More general works of value in studying the birds of Maine are Forbush's volumes on the New England states (1925-1929), and Bent's monumental series on the life histories of North American birds (1919-1953).

A number of short papers and annotated lists, including information on the birds of the coastal forests, have been published in the Bulletin of the Maine Audubon Society (now the Maine Field Naturalist), the Journal of the Maine Ornithological Society, and the Maine Naturalist. Only the most pertinent of these are considered here.

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Walch's annotated list for the Brunswick area (2C) (1926) includes observations in the forests of eastern Casco Bay (2B). Montgomery's annotated list (1890) covers the area just to the east of the former, from Bath to Boothbay (2C). Cruickshank's studies of Lincoln County birds were concentrated at the Muscongus Bay area (2D) (1938, 1950). Allen's (1908) paper on Monhegan Island (2D) mentions several species of the spruce-fir growth there.

The MDI area is represented by two publications, both including specific habitat information. These are Tyson and Bond's booklet (1941), and Bond's more recent annotated list (1958). Probably the paper most applicable to the extreme eastern portion of the Maine coast is that of Pettingill (1939) on the birds of the Grand Manon archipelago (4H+), just over the international boundary. His discussion of the "Canadian Life Zone" in that area is referred to later under Fauna, Part III.

A number of papers have been published on the wood warblers (Parulidae) of the spruce-fir forests of the Maine coast. My results indicate that this bird family is by far the one best represented in the coastal spruce-fir forests, by total numbers and variety of species. Bond (1947) discussed the habitats of the various species. Cruickshank (1956) tabulated the nesting heights above the ground for

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those species found in the forests at Hog Island and vicinity (2D). In 1937 Bond discussed the status of the Cape May warbler (Dendroica tigrina) in Maine, mentioning its occurrence on MDI. Mendall (1937) noted that the bay-breasted warbler (Dendroica castanea) bred on the coast at least as far southwest as South Thomaston (3D). He also discussed the other spruce-fir species of that area. The excessive population fluctuations of these last two species were discussed by MacArthur (1958) in his excellent study on the population ecology of warblers in northeastern spruce-fir forests. A considerable portion of this study was concentrated on MDI, in particular at Bass Harbor Head which was also one of my study areas. MacArthur's results are discussed later.

Cruickshank and Cadbury have run breeding-bird censuses at a thirty acre mature red and white spruce tract on Hog Island in Muscongus Bay (2D) for a number of years (1936-42, 1946, 1947, 1949-58). In 1946 they mentioned that since 1942 many dozen trees had been blown down, but that the habitat (up to that time) remained "...virtually unchanged". During storms in the next four years an area of blow-down widened to four acres. Then, following the 1954 census, twelve more acres of forest were blown down. The changes in breeding-bird populations in years following these events

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were recorded in the series of reports. This bit of history is related here because such events may be typical of exposed second growth spruce stands on the coast of Maine, as is discussed later.

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Part I

FOREST DISTRIBUTION AND ENVIRONMENTAL CORRELATES

Forest Distribution Survey and Map

No published maps were found which indicated the extent and configuration of distribution of the coastal spruce-fir forests except in the most general outline form. One of the more up to date outline maps is that of Westveld, et al. (1955). A slight modification of that map is reproduced in the upper left corner of the map in the rear pocket. Reference to it will reveal two major coastal portions of the "Spruce-Fir-Northern Hardwoods" zone. The first occupies the region between the northwest shore of Casco Bay and Rockland (3D). The second, and larger area, extends from the islands of Penobscot Bay (3E) eastward. In easternmost Maine this forest becomes indistinguishable as a coastal zone. For the purposes of this study more detailed knowledge of forest distribution was needed, and a survey was undertaken.

Preliminary Ground Survey

Exploration of the entire coastal area at first took the form of hundreds of miles of travel by automobile, and scores of miles by boat and on foot. Such exploration revealed, first, that only a very small portion of the non-

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urban coastal area to the east of Casco Bay, probably less than 10%, was utilized for agriculture, and that the remainder was mostly covered by forests in various stages of development. (The discussion and percentages which follow refer to the forested areas only.) Second, it was not possible to distinguish any distinct large forest zones. Rather, the closer one came to the sea, the more frequent became the occurrence of nearly pure spruce-fir stands. Also, the closer one came to the sea, the higher became the proportion of spruce and fir trees in mixed forests. This suggested a causal connection between the sea and the forest. In order to analyze such a relationship it was thought necessary to have a better idea of the relative concentrations of spruce-fir forests at various distances from, and positions relative to, the sea. To obtain such information an aerial survey was undertaken.

Aerial Survey

In early November, 1959, the entire coastal area was systematically observed from a small airplane. The craft consisted of a two-seater with pilot in front. Because of the high cost of such transportation, careful planning was necessary to take full advantage of time spent in the air. A preliminary flight revealed those characteristics of the

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vegetation which required consideration in the formulation of an observation technique.

Tree Identification:

Tree identification from the air was made easier because the flights took place after most of the leaves had been dropped by the deciduous trees. Those that still remained bore a color other than green. Little effort was made to distinguish the various deciduous species, though this was often an easy matter and proved helpful. For example, the presence of white barked birch (Betula papyrifera and/or B. populifolia) provided a valuable clue to forest history.

Prior field experience in the area proved indispensable in the identification of various coniferous species. Distinguishing conifers at a distance depends on the observer's sensitivity to a variety of clues, many of which are quite subtle and involve both the trees themselves and their environment. Among the more obvious of these are the relatively broad-ended and horizontally well-developed limbs of certain pines; the weakly developed leaders of hemlocks; the light green color, frequently specialized habitat, and often open growth of the cedars; and the narrowly tapering conical shape, rigid and pointed appearance of spruces and firs. Unfortunately, it was not possible reliably to distinguish spruce from fir. Thus, throughout the remainder of Part I

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the symbol "S-F" will be used to mean total spruce and fir, even when one or the other is absent.

Relatively pure white spruce stands could be distinguished readily from adjacent S-F stands which lacked a strong white spruce admixture. This was done on the basis of color. The distinction was clearest with the most direct lighting, when the small shadow of the airplane passed over the area under scrutiny.

Throughout the flights it was necessary from time to time to take a low altitude "turn-about" to check tree identification. Such departures from flight lines were minimized, however, by prior knowledge of areas obtained in the ground survey.

Vegetational Pattern:

In formulating a technique for estimating the percentage of S-F, I had to consider the pattern of vegetation. The vegetation was perceived as a mosaic consisting of variously shaped patches ranging in size from one to several score acres. Each patch was distinguishable from adjacent ones by its relatively homogeneous composition of hardwoods, evergreens, or a mixture in certain proportions and its roughly uniform tree size and density. Such patches were called stands. Stands could be roughly categorized into three types: relatively pure S-F; mixed, containing varying amounts of S-F; and relatively pure non-S-F. For rapid coverage from

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the air, a larger sample unit was needed. Stands were grouped into areas called tracts. These were of various shapes, anywhere from several score acres to two or three square miles in size. They were chosen so as to be readily distinguishable by topographic or other features of the landscape, and at the same time had to be units within which the total percentage of S-F could be estimated readily. Examples of tracts are: an island; a group of islets; a tip of a peninsula; a valley; a group of small hills; a mountain; or an area between a road and a lake. Tracts included anywhere from six to about thirty-five stands. Where the countryside was covered with many small stands, as in sections heavily utilized by man, a small tract had to be chosen for the sampling unit; and conversely, large tracts could be chosen in relatively undisturbed areas such as certain of the more inland portions of southeastern Washington County (4H).

Flight Procedures:

Prior to each flight a series of roughly parallel flight lines were laid out on U. S. G. S. topographic maps (1:62,500 "quadrangles"). A flight line might follow such features as a river, a road, a series of lakes, or an elongate peninsula or bay. An altitude of 1500 feet above the ground surface and a speed of ninety miles per hour were found to constitute the most satisfactory compromise between breadth of view,

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detail of observation, and speed of coverage. The extent and delimitation of tracts were determined while in flight and outlined directly on topographic maps.

While in flight, attention was directed ahead and to one side of the flight line. A tract would be chosen and scanned to estimate the relative proportions of the two pure stand types. A mental note was made of this. Then, the average percentage of S-F crown-cover in the mixed stands was judged. This was combined with the former estimate, in proper proportions, and a final appraisal for the tract, to the nearest 5%, was penciled onto the map. Then, in order to obtain full coverage, before half the tract had been traversed, attention was shifted from it to the next tract being approached on the other side of the flight line. Thus, in rapid sequence tracts on both sides of the flight line were delimited and their percentages of S-F estimated. This resulted in irregular strips of such tracts, which were later pieced together to make a final map.

From Kittery Point (1A) to Yarmouth (2B), and on the western shore of Penobscot Bay, it was only necessary to fly two flight lines, one going and one returning parallel to the coast for, as far as the eye could see, S-F was limited to small isolated areas within a narrow strip near the shore.

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Each time the airplane took off from the Bar Harbor Airport, I "recalibrated" myself against areas on MDI where I had earlier obtained detailed knowledge by field work on the ground.

In the laboratory the data from the topographic sheets were entered onto a large map of coastal Maine. In doing this, however, the twenty-one 5% appraisal classes were lumped into five categories. This seemed advisable because of the approximate character of the data. Thus, a number of adjacent tracts often merged into a single category which formed a relatively large patch on the final map.

Results; Percentage Categories and Their Interpretation:

The results of this survey are incorporated into the map in the rear pocket (its plastic overlay will be explained later).

The five percentage categories are interpreted in the following paragraphs. This interpretation is here prefaced with a word of caution: The designation on any patch on the final map cannot be used by the reader to deduce the percentage S-F for any specific location within. Rather, each patch is to be viewed as a gross estimate for the entire heterogenous area it encompasses.

1. "5%": usually extensive areas with or without widely scattered S-F; sometimes including occasional small

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areas with a light admixture of S-F; and the rare occurrence of small nearly pure S-F stands. Almost the entire territory to the southwest of Yarmouth (2B) is in this category, except for the most marine-exposed locations. Conversely, from the islands of Penobscot Bay eastward, this becomes an exceptional category near the coast. Most of these exceptional isolated patches were investigated on the ground and found to be results of severe disturbances such as fire. An outstanding example is the northeastern third of MDI, which was burned over in 1947. The Jonesport peninsula (4G) is covered in large part by heath and bog. The peninsula just to the west of Cutler (4H) has recently been cleared completely of timber for a military installation.

2. "5-10%": usually extensive forest areas with a light admixture of S-F (ca. one in twenty trees); often with lesser areas of stronger admixture; and scattered small stands of nearly pure S-F. Except for the most marine-exposed locations between Yarmouth (2B) and Rockland (3D), the major part of the coastal territory in that area is covered with forests in this category. From the islands of Penobscot Bay eastward to the "barrens" this becomes primarily an inland category, with higher categories between it and the coast. East of the barrens this category usually occupies disturbed areas, such as the Lubec (4H) and Calais

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(5H) vicinities. In such eastern areas the hardwood element is often dominated by paper birch.

3. "11-32%": areas mostly covered by a mixed forest with less than 20% S-F; with smaller areas of stronger admixture; and a few nearly pure S-F stands. Where this category occurs near the coast to the east of MDI, it usually consists of forests in the process of recovery from earlier disturbances. However, in the inland areas between Penobscot Bay and Columbia Falls (4G), well-developed mixed forests are often included.

4. "33-63%": when inland, usually consisting of tracts composed of large stands of mixed forest, side-by-side with smaller areas of either white-birch dominated forests or nearly pure S-F stands. In Washington County (4H) where this percentage was frequently encountered, it often included fairly large stands of nearly pure S-F on poorly-drained areas. Between Penobscot Bay and Machias (4H) it forms an irregular strip, interposed between a more inland 11-32% category and the more coastal category below.

5. "64-100%": of three major types, the first two of which are composed mostly of nearly pure S-F tracts. The first consists of well-developed S-F tracts occupying islands and seaward peninsulas. To the west of Muscongus Bay (2D) such areas are infrequent and small, and when they occur

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there it is only at the most strongly marine-influenced locations. Eastward this type becomes common on the coast, there typifying the "spruce-fir forests of the coast of Maine." The second type is confined to poorly drained areas such as bogs and the flat shores of rivers and lakes. Some of these areas are large enough to appear on the map as distinct series of black patches in the inland stretch from Tunk Lake (4F) eastward. Although no ground checks were run in these areas, their overall appearance from the air leaves little doubt that they are dominated by black spruce. The third type is represented by a large patch of black in the center of inland southeastern Washington County (4H). This is an area of many small hills, bordered to the south and west by lake country. Except for a few nearly pure S-F bogs and areas along lake and river shores, the tracts composing the black patch are mostly mixed stands of roughly one-half S-F, with lesser areas of white birch. A synthesis of the data barely put these tracts into the 64-100% category.

White Spruce Distribution:

One of the most striking distributional phenomena encountered during the flights was the distinct border formed by a concentration of white spruces along the shore. The border varied in width from a few trees to some hundred yards or more. This phenomenon was not rare or occasional but was

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the usual distributional pattern along the immediate shore from Sheepscot Bay (West Southport, 2C) eastward. On scores of islands and peninsulas the border appeared almost as regular as a hem around the edge of a garment.

Except for this border, the predominant species in most heavy spruce areas was red spruce. Large mature stands dominated by white spruce were not the rule, but young and often open-growth stands dominated by this species sometimes extended considerable distances in from the shores on large islands. A special case of white spruce abundance was encountered where land surfaces were exposed to the full force of the winds from the open sea. Here the landscape became dotted with slow-growing white spruces, the overall aspect being similar to alpine meadows or balds being overgrown by forests. Such an area near Cutler (4H) was commented upon by Kennedy (1902), who found white spruces fruiting abundantly while only ten to fifteen feet high. Where white spruce reached high concentrations inland, it was usually in the form of small old-field stands.

From Georgetown (2C) southwestward, coastal spruce-fir areas lacked the white spruce border. In the eastern Casco Bay area, white spruce did not constitute a significant percentage of the trees. However, a few small old-field stands containing considerable percentages of white spruce were

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still found there (during an earlier ground survey). According to Norton (1913), white spruce was abundant on the islands east of the Georges group (2D), while westward it became less abundant and at Casco Bay decidedly rare, though a few trees were found at Trundys Reef, Cape Elizabeth (2B). My results are in essential agreement, though I would qualify the description in terms of the white spruce border west to Sheepscot Bay (2C), and would call the species uncommon rather than rare in the eastern Casco Bay area. Southwest of Casco Bay I encountered the species only rarely. It was found to occur naturally as far southwest as Kennebunk (1B). Here, open growth individuals were found in association with substantial percentages of red spruce in stands on the Parsons Estate.

Summary:

The regions of 5% or more S-F on the coast of Maine correspond closely to the "Spruce-Fir-Northern Hardwoods" area on the map of Westveld et al. (1955). However, small S-F areas were found further southwest near the shore on southward-facing irregularities of the coast. From Casco Bay to Rockland (3D), and from the islands of Penobscot Bay to the Columbia Falls area (4G), the percentage of S-F is greatest near the coast and diminishes inland.

These forests did not form a distinct zone. On the

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other hand, the decrease in S-F away from the coast did not have the form of a smooth shading or gradual mixture of forest elements. Discrete units, the stands, were present in reality. The vegetation consisted of an irregular mosaic of these, each patch containing a certain percentage of S-F. The frequency of nearly pure S-F stands decreased away from the coast, but such stands existed even in areas containing less-than 5% S-F.

For practical reasons, stands were grouped into larger observational units called tracts, and the percentage S-F crown-cover in these was categorized by five ranges. Thereby, an unreal zonal character appeared in the final map. If it had been possible to record the stands separately, and enter each of them on the large map of coastal Maine, the subsequent great reduction in size would probably have completely concealed their mosaic character. Unreal smooth shading, rather than unreal zoning, would have resulted.

From Columbia Falls (4G) eastward and northward, spruce-fir forests become of general distribution, with high S-F percentages no longer limited to the coast. Here, the coastal spruce-fir forest merges with the more extensive spruce-fir areas of eastern and Northern Maine, and New Brunswick.

Red spruce is the most abundant spruce in the coastal region of Maine. However, at the immediate shore, white

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spruce becomes most common. From Sheepscot Bay (2C) eastward, white spruce forms a distinct seaside border in most places, with red spruce usually attaining dominance just landward. In its distribution on the Maine coast, white spruce is more restricted than red. It is not found in high quantities as far to the southwest as red spruce. In eastern Maine, where red spruce becomes important inland, white spruce remains more concentrated near the shore. This is with the exception of small inland old-field stands where white spruce may locally dominate.

Physical Environment and Forest Distribution

The purpose of this section is to describe the topographic, edaphic, and climatic characteristics of the Maine coastal section, and to discuss their possible effects on the forest distribution.

Topography

Most of the countryside in the coastal section is made up either of small irregular hills or gentle slopes. This terrain is mostly well-drained. In comparison to territories further north, swampy and boggy areas are small and infrequent, and there are few extensive poorly-drained flats. In four areas small ranges of mountains, with peaks attain-

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ing altitudes of 1000 to 1600 feet above sea level are found. These are the Camden Hills (3D), the mountains just northwest of Branch Lake (4E), MDI, and the mountains just northwest of Tunk Lake (4F).

The coast line itself is famous for its extreme irregularity. The straight line distance between Portland (2E) and Eastport (4H) is about 200 miles, while if all the coastal irregularities are followed, the distance is some 2000 miles. To the east of Cape Elizabeth (2B) the shore is mostly jagged and rocky, and is bordered by impressive cliffs in many places.

Edaphic Factors

Bedrock and Glacial Drift:

Geological maps of various Maine coastal areas were located by reference to Boardman and Watson's geological map index of the state (1949). Other references were found by using Rand's (et al., 1958) bibliography on Maine geology. Most maps and geological descriptions of the coastal area are very general, and only a few small areas have been mapped in any detail. These latter include Smith, Bastin, and Brown's map (1907), and Bastin's map (1908), both of the Penobscot Bay area, and Chadwick's map of MDI (1939). Except for such areas, little can be said on the effect of bedrock on specific stands or tracts. However, broad areas

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can be compared by using Keith's preliminary geological map of the entire state (1933).

Keith's map shows that an elongate area of granite and highly metamorphosed rocks, some twenty to sixty miles wide, forms a coastal zone from Casco Bay and the Kennebec River (3C) eastward almost to Eastport (4H). Within this zone, a series of large patches of granite alternate with large patches of banded micaceous gneisses and schists. These patches are themselves elongate, some twenty to sixty miles long and about ten to forty miles wide, each oriented with its long axis roughly perpendicular to the coast. The spruce-fir area between Casco Bay and Rockland is mostly underlain by a large patch of the metamorphic type, while from Penobscot Bay eastward spruce-fir forests grow on both rock types.

The only sizeable areas of mildly metamorphosed sediments are found between Kittery (1A) and Cape Elizabeth (2B), including portions of Casco Bay; between Rockland and Lincolnville (3D); along the northern shore of Penobscot Bay; and then not again until the Eastport area. Limestone and its metamorphic derivatives are limited to two small deposits: one immediately west of Rockland, and the other west of Camden (3D) (W. F. Stickney, Geologist, State of Maine; personal communication). The Eastport area consists of a com-

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plex of many rock types.

According to Flint, et al. (1945), the entire Maine coast was glaciated, and all but the highest portions were subject to interglacial and interstadial marine submergence. Perkin's map of the glacial deposits in Maine (1934) shows four extensive "wash plains". One runs inland several miles between Kittery (1A) and eastern Casco Bay; another covers the Muscongus Bay area; another the stretch from Gouldsboro (3F) to Machias (4H); and the last in the Cutler region. These are composed of both marine and fresh water deposits. Except for steep slopes, much of the coastal region, not indicated as being covered by glacial deposits on Perkin's map, is probably overlain by relatively thin, unstratified till. Such material was found in the lower layers of the soils investigated on MDI (see Forest Soils, Part III.) Because the bedrock types described above extend twenty to sixty miles inland, it is likely that most of the till in the coastal section is composed of schistose, gneissic, and granitic material.

Soils:

United States Department of Agriculture soil survey publications are available for only three coastal counties. These are York (Goodman, et al., 1952), Cumberland (Duyne, et al., 1915), and Waldo (Goodman, et al., 1955). These in-

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clude the least S-F of all the coastal counties. This is not surprising since such surveys are undertaken primarily as an aid to agriculture, and those counties with the least S-F have the most agriculture.

Waldo County comes closest to the spruce-fir area (3D-E), and certain portions of the southern part coincide with the area I surveyed. According to Goodman, et al. (1955), the soils of Waldo County are transitional between podsols and brown podsolics.

Soil study was undertaken as a part of this research, but the detailed presentation of results is postponed until Part III. All spruce-fir stands which were studied had well-developed, though not always typical, podsols.

Correlations, Edaphic Factors and Forest Types:

The only notable correlations between forest and bedrock, over areas broad enough to be distinguished by these methods, are the low concentrations of S-F on the west and northwest shores of Penobscot Bay, and from Kittery to Casco Bay. These are the two longest coastal stretches dominated by substrata other than gneisses, schists, or granite. The first of the areas is underlain mostly by quartzites and slates and includes the previously mentioned limestone deposits. The second area is almost completely covered by glacial outwash, under which are mostly quartzites, phyllite,

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and slates. However, not only do these areas differ from the remainder of the coast in the nature of their rock materials, but also as follows: Both exhibit a less-southerly and decidedly more easterly marine exposure. Along these stretches, those few coastal irregularities and islands which have a greater exposure to the sea on the south and southwest are usually covered by a greater percentage S-F. For example, Long Island (Islesboro) (3E) has heavy S-F growth. It is included by Keith (1933) in the same bedrock area as Rockland, and on Perkin's map (1934) its glacial deposits are not differentiated from the adjacent mainland.

The stretch to the southwest of Casco Bay is already beyond the southwestern limit of appreciable S-F growth but, even there, those coastal irregularities which have a more southerly exposure often support outlier stands including a considerable percentage of S-F.

It is difficult to evaluate the effect of soils on vegetation. The characteristics of the soil are to a certain degree dependent on parental materials, but at the same time they are both independent and dependent variables in relation to vegetation. Furthermore, both vegetation and soils are profoundly affected by climate. Thus, soil descriptions are included in the forest description section, Part III.

Fortunately, the shoreline of Long Island (Islesboro)

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(3E) was irregular enough so that during the survey flights a relatively detailed record of S-F percentages was obtained because of the necessity of recording many small tracts on the topographic map. Thus it was possible to make a somewhat detailed comparison between percentage S-F and the soil types recorded on the maps in the Waldo County publication (Goodman, et al., 1955). Spruce-fir stands were found to occur on no less than thirteen different soil series. On the other hand, less detailed comparisons made elsewhere--as on the adjacent mainland which is less exposed to marine influence, and southwest of Casco Bay--suggest correlation with soil factors.

At Gerrish Island, Kittery, for example, a small outlier spruce-fir area occurs on a Shapleigh stony loam, known often to be a thin podsol, frequently found on pegmatite and coarse gneiss and associated with the Canaan, Glaucester, and Herman series on glacial till (Goodman, et al., 1952). At Cape Elizabeth, several of the Casco Bay islands, and on the Harpswell Points (2B-C) a shallow phase of Gloucester loam, developed mostly on slate and schist, appears to be associated with spruce-fir growth (Duyne, et al., 1915). On the mainland in southern Waldo County, podsols on granite, especially those in the Canaan, Adams, and Herman series are associated with spruce-fir growth, according to Goodman, et

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al. (1955).

Thus, although the evidence is somewhat limited, it might tentatively be concluded that on the borderline of appreciable S-F growth, as in parts of southern Waldo County, those few small S-F dominated areas which do exist tend to be limited to poor, shallow soils, mostly derived from non-calcareous highly metamorphosed and granitic rocks.

In other portions of the coastal region, however, edaphic factors appear to be less effective. From Casco Bay to Rockland, and from the Penobscot Bay islands to Columbia Falls, the ostensible zonation of S-F percentages runs roughly parallel to the coast. High percentage S-F areas are limited to a narrow coastal strip. On the other hand, forests dominated by species other than S-F are found on the same bedrock types a short distance inland. Furthermore, the strong coastal orientation of S-F does not appear to be upset, nor in any noticeable way modified, by the irregular distribution of glacial deposits. It should be emphasized, however, that these conclusions are applicable to individual stand types only in terms of the probability of occurrence within relatively large map areas. The fact that tracts of more than 64% S-F occur only at the most marine-exposed locations in the Penobscot Bay area, for example, does not mean that stands strongly dominated by hardwoods

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do not occur within such tracts. These methods yield little information about distributional relationships between stand types and edaphic factors.

Climate

Because it is suspected here that climate constitutes the most important set of factors determining the presence and specific distribution of spruce-fir forests on the coast of Maine, it will be described in some detail in this section. Fobes' discussion (1946) and Lautzenheiser's summary (1959) of Maine's climate have been helpful along these lines. Fobes' "Coastal Section" corresponds closely to the area I have studied.

As Fobes' and Lautzenheiser's data are not complete enough for the purposes of this thesis I have gone directly to United States Weather Bureau tabulations (1879, ff.). All U. S. W. B. stations whose data are utilized here are listed in Table 1, where the reader may obtain information on their official designations and locations.

All stations said to be in the coastal section are within five miles of sea water. However, few of these are located where they might receive the strongest effects of marine influence. Thus, it may be assumed by the reader that the marine effects to be illustrated with these data are in reality greater for a large portion of the coastal forests.

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Table 1. United States Weather Bureau Stations: Location Data. Designations and locations as of U. S. W. B., 1959. Tabulation in order from west to east.

Off. Designation	USWB No.	USGS Quad. 1/62,500	Alt. ASL	North Lat.	West Long.	Miles to the Sea North	East	South	West
Wolfeboro Falls,N.H.	9865	Wolfeboro	520	43°36'	71°12'	+100	49	+100	+100
Portland Airport	6905	Portland	61	43°39'	70°19'	+100	3	8	+100
Portland	6900	Portland	65	43°40'	70°15'	< 1	< 1	< 1	+100
Lewiston	4566	Lewiston	182	44°06'	70°15'	+100	58	27	+100
Brunswick	0934	Bath	70	43°53'	69°56'	+100	10	5	+100
East Winthrop	2539	Augusta	173	44°19'	69°54'	+100	51	33	+100
Rockland	7250	Rockland	40	44°06'	69°07'	+100	<1	4	+100
Belfast	0480	Belfast	20	44°24'	69°00'	2	<1	7	+100
Old Town	6420	Orono	108	44°56'	68°39'	+100	74	46	+100
Ellsworth	2620	Ellsworth	24	44°32'	68°26'	+100	28	3	+100
Southwest Harbor	8301	Swans Island	20	44°14'	68°18'	2	<1	<1	2
Bar Harbor	0371	Bar Harbor	40	44°23'	68°12'	<1	<1	6	9
Jonesboro	4183	Columbia Falls	185	44°40'	67°35'	+100	9	3	+100
Machias	4878	Machias	40	44°43'	67°28'	+100	3	8	+100
Woodland	9891	Calais	140	45°09'	67°24'	+100	63	33	+100
Eastport	2426	Eastport	80	44°55'	66°59'	<1	<1	1	1

Climatic Description and Comparisons Within the Coastal Section:

Table 2 lists monthly temperature means for various coastal stations. This table tells us that average temperatures at these stations during the summer months vary within the cool range of 55-68°F, and in the winter from 22-32°F. In the summer months stations in coastal spruce-fir areas are from 2-8°F cooler than elsewhere in the coastal section. In the winter months temperatures in spruce-fir and other coastal areas are quite similar. In interpreting these figures, one should remember that not only is the spruce-fir region more easterly and strongly coastal, but that it is also more northerly. The average annual temperature in the coastal section is about 44.6°F, with the spruce-fir stations averaging about 2°F cooler than the others.

Table 3 indicates that the average yearly precipitation in the coastal section is about forty-four inches, with about four inches per month in winter and three per month in summer. In the coastal spruce-fir area, precipitation is higher in the fall and winter and lower from April through August than elsewhere in the coastal section. The annual total in the spruce-fir areas is about two inches higher than elsewhere in the coastal section. These data are from various periods averaging thirty-nine years in duration, and

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Table 2. Temperature Means (°F), Coastal Section. Based on data available for various periods up to and including 1959 (United States Weather Bureau, 1901 ff.). Stations are arranged in order from west-southwest to east-northeast. Symbols: MF = hardwood & mixed forests predominate; S = more than one-third forest area is predominantly S-F.

Area	Yrs. Rec.	J	F	M	A	M	J	J	A	S	O	N	D	Mean Annual
Portland,MF	53	21.7	23.6	32.2	43.0	52.7	62.0	68.2	66.5	58.6	49.1	38.5	26.2	45.2
Brunswick,MF	8	22.4	25.0	32.2	43.5	53.2	62.2	68.4	66.6	59.0	49.2	39.7	27.6	45.7
Rockland,MF	15	22.6	24.2	32.2	42.1	51.8	61.0	67.3	66.4	58.7	49.2	38.8	27.1	45.1
Belfast,MF	14	22.6	23.6	32.2	43.0	52.6	61.4	68.2	66.4	59.0	49.5	39.4	27.2	45.4
Bar Harbor,S	51	22.7	23.1	31.9	41.5	52.0	60.3	66.3	64.9	58.4	48.7	38.7	26.7	44.6
Jonesboro,S	11	21.8	22.1	29.8	41.5	50.4	59.2	65.3	63.3	55.4	46.3	36.9	26.3	43.5
Eastport,S	45	22.3	22.4	30.6	39.7	48.0	55.3	60.6	60.8	56.2	48.2	38.0	26.2	42.4
S Mean		22.3	22.5	30.8	40.9	50.1	58.3	64.1	63.0	56.7	47.7	37.9	26.4	43.4
MF Mean		22.3	24.1	32.2	42.9	52.6	61.7	68.0	66.5	58.8	49.2	39.1	27.0	45.4
Overall Mean		22.3	23.4	31.6	42.0	51.5	60.2	66.3	65.0	57.9	48.6	38.6	26.8	44.6

Table 3. Precipitation Means in Inches, Coastal Section. Based on data available for various periods up to and including 1948, with the exception of Eastport, 1900-1959 (United States Weather Bureau, 1879 ff.). Stations are arranged in order from west-southwest to east-northeast. Symbols: MF = hardwood & mixed forests predominate; S = more than one-third forest area is predominantly S-F.

Area	Yrs. Rec.	J	F	M	A	M	J	J	A	S	O	N	D	Annual
Portland,MF	40	4.38	4.05	4.27	3.75	3.13	3.23	3.04	2.93	3.24	2.89	3.10	4.04	42.05
Brunswick,MF	39	3.48	2.87	3.78	3.58	4.29	3.71	3.47	4.17	3.18	3.63	4.95	4.13	45.18
Rockland,MF	15	3.76	3.52	3.80	3.76	3.82	3.40	3.24	2.41	3.58	3.40	5.46	3.95	44.10
Belfast,MF	24	4.47	3.60	4.05	3.19	3.84	3.12	3.05	2.96	3.19	3.38	4.75	4.22	43.83
Ellsworth,MF	44	3.64	3.02	3.55	3.68	3.08	3.22	3.12	3.02	3.86	3.98	4.04	3.60	41.78
Bar Harbor,S	69	4.64	3.82	4.59	3.66	3.55	3.29	3.30	3.23	3.78	4.27	4.80	4.39	47.32
Machias,S	22	4.68	3.90	4.08	3.86	3.43	3.69	3.15	3.13	4.41	3.96	5.28	4.40	47.97
Eastport,S	60	3.67	3.11	3.39	2.88	3.64	2.95	2.83	2.91	3.03	3.28	3.41	3.46	38.56
S Mean		4.33	3.61	4.02	3.47	3.54	3.31	3.09	3.09	3.74	3.84	4.50	4.08	44.62
MF Mean		3.95	3.41	3.89	3.59	3.63	3.34	3.18	3.10	3.41	3.46	4.46	3.99	43.41
Overall Mean		4.09	3.49	3.94	3.55	3.60	3.33	3.15	3.09	3.53	3.60	4.47	4.02	43.85

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possess the advantage of long-term coverage. So that the relative precipitation between various coastal stations could be more reliably compared, Table 4 was prepared. It includes precipitation for an identical period for every station listed (1949-1959). In general, the results are the same as in Table 3. However, this period was considerably more moist over-all, and the summer precipitation at the spruce-fir stations did not fall to lower values than elsewhere in the coastal section.

Comparisons of the Coastal Section to Adjacent Regions of Maine:

Comparisons of the coastal section to areas several score miles inland were made by Fobes (1946). As would be expected, his tabulations indicate that the coastal region has the warmest winters, the coolest summers, the narrowest ranges between temperature extremes, and the longest frost-free season. The summer temperature pattern is illustrated in Figure 2, a map of isotherms of mean July temperature (after Fobes, 1946).

The relationship between coastal temperatures, inland temperatures, and sea water temperatures is clearly shown in Figure 3. This figure was prepared by selecting four low-altitude inland stations, thirty to fifty miles from the sea, and comparing them to four coastal stations, each less than

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Table 4. Comparable Precipitation Means in Inches, Coastal Section. Based on eleven years, 1949-1959 (United States Weather Bureau, 1949 ff.). Stations are arranged in order from west-southwest to east-northeast. Symbols: MF = hardwood & mixed forests predominate; S = more than one-third forest area is predominately S-F.

Area	J	F	M	A	M	J	J	A	S	O	N	D	Annual
Portland,MF	4.20	3.39	4.44	3.62	3.13	2.66	2.55	2.69	3.44	3.37	4.72	3.69	41.90
Brunswick,MF	4.40	3.82	5.18	4.01	3.16	2.64	2.69	3.23	3.87	3.90	4.50	4.49	45.89
Rockland,MF	5.28	4.53	4.99	4.13	3.13	2.91	3.68	3.37	4.04	4.37	5.69	4.67	50.79
Belfast,MF	5.02	4.00	4.38	3.91	3.12	3.02	3.61	3.22	3.77	4.43	6.43	4.80	49.71
Ellsworth,MF	4.66	3.79	3.83	3.45	2.78	2.46	3.36	3.08	3.68	3.88	5.10	4.56	44.63
Southwest Hbr.,S	4.76	4.00	4.47	3.75	3.26	2.90	2.89	2.94	3.69	3.64	5.09	4.24	45.63
Bar Harbor,S	5.47	4.19	4.41	4.14	3.59	3.17	3.05	3.43	4.27	4.44	6.09	4.79	51.04
Jonesboro,S	5.49	3.72	4.04	3.97	3.18	3.27	2.92	3.57	4.05	3.56	5.64	4.53	47.94
Machias,S	5.81	4.84	4.16	4.19	3.42	3.73	3.46	3.90	4.42	3.79	6.27	5.19	53.18
Eastport,S	4.82	4.05	3.42	3.52	2.90	3.54	3.14	3.71	2.94	3.13	5.29	4.38	44.84
S Mean	5.27	4.16	4.10	3.91	3.27	3.32	3.09	3.51	3.87	3.71	5.68	4.63	48.52
MF Mean	4.71	3.91	4.56	3.82	3.06	2.74	3.18	3.12	3.76	3.99	5.29	4.44	46.58
Overall Mean	4.99	4.04	4.33	3.87	3.16	3.03	3.13	3.31	3.81	3.85	5.49	4.54	47.55

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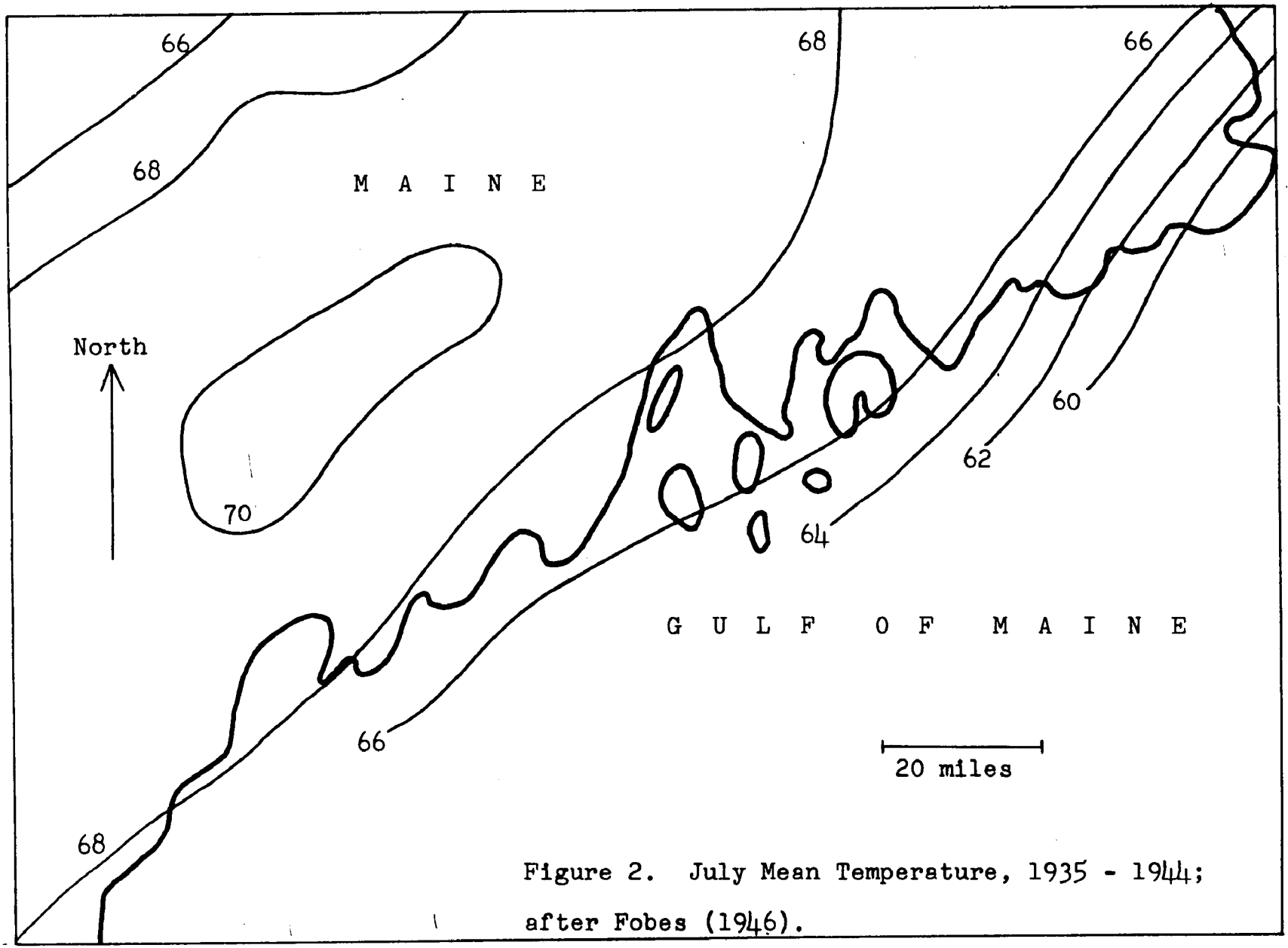


Figure 2. July Mean Temperature, 1935 - 1944; after Fobes (1946).

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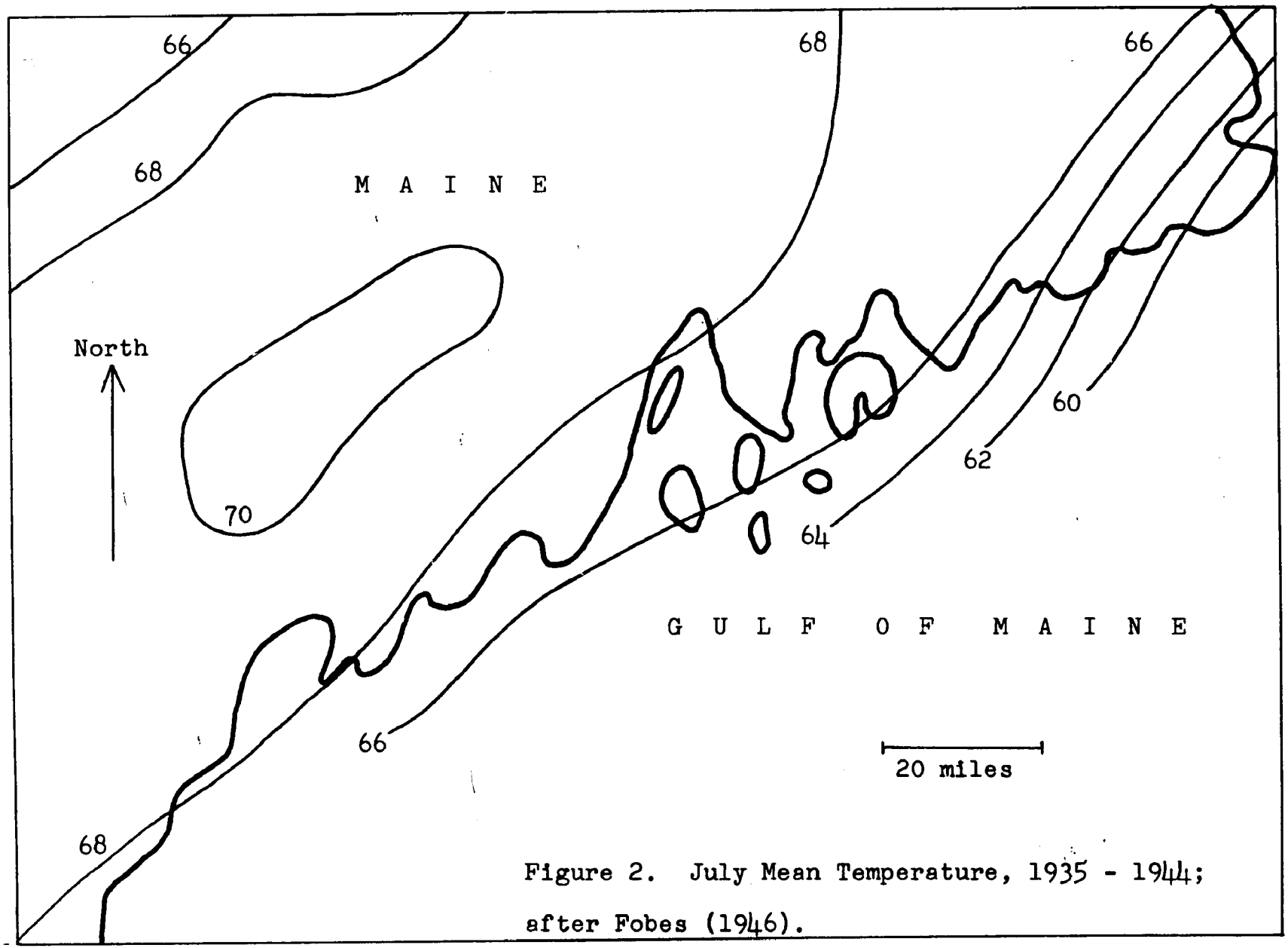


Figure 2. July Mean Temperature, 1935 - 1944; after Fobes (1946).

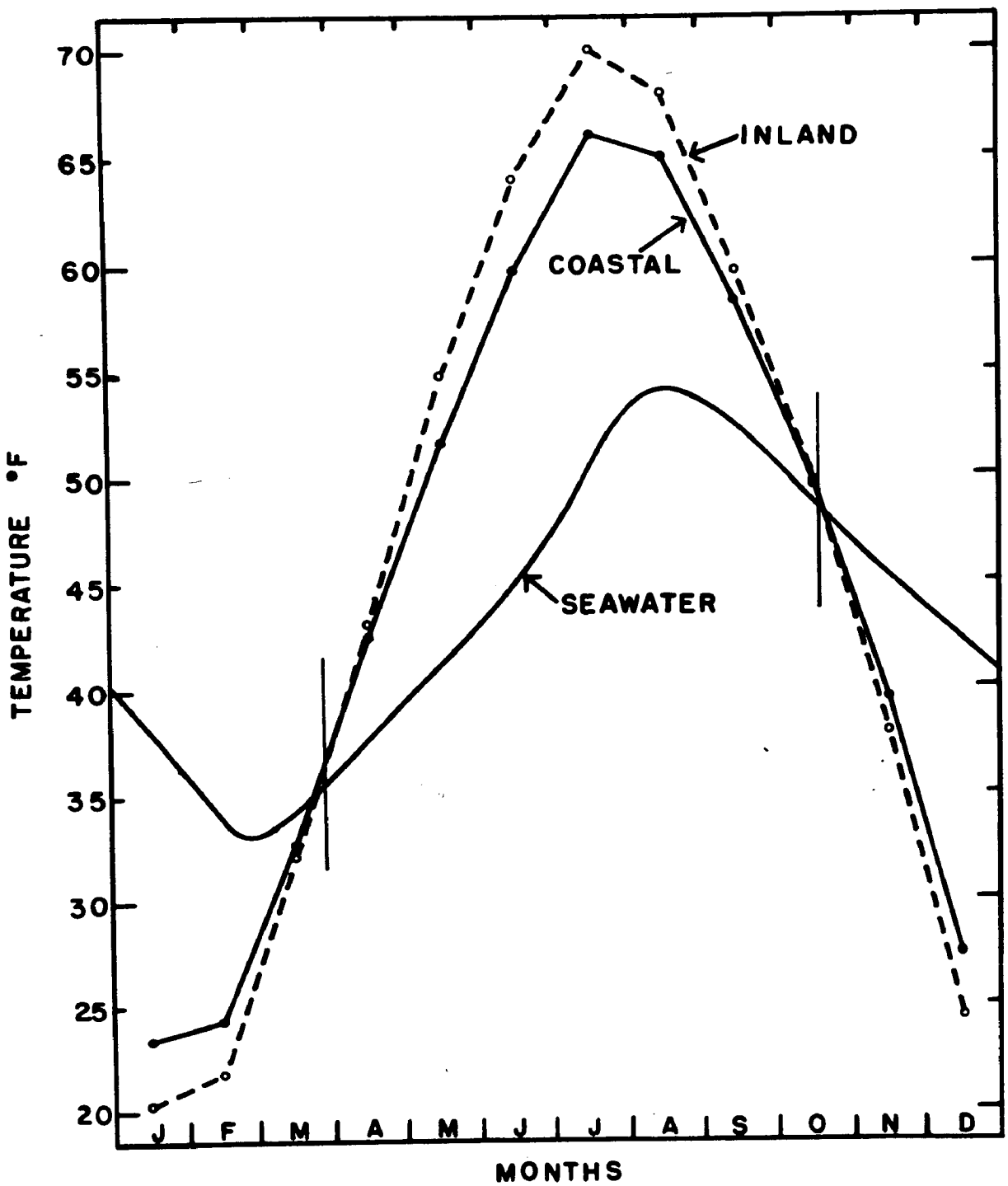


Figure 3. Inland and coastal temperatures compared. U.S.W.B. data used for derivation of mean monthly temperatures. Curve of sea water temperatures adapted from Bigelow (1924).

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one mile from the sea, and each at a latitude corresponding to one of the inland stations. The curve of sea surface temperatures is derived from data obtained during the years 1915, 1920, 1921, and 1923, as presented by Bigelow (1924). Changes that may have taken place since those years are probably insignificant so far as these comparisons are concerned. In the winter, the degree to which coastal air temperatures are higher than those inland is directly proportional to the difference between inland air temperature and sea water temperature. In the summer the entire relationship reverses. This relationship is closely linear. If twelve monthly points are plotted, with mid-monthly sea surface temperature minus mean monthly inland temperature on the ordinate, and coastal mean monthly temperature minus inland mean monthly temperature on the abscissa, a straight line with a high coefficient of correlation is obtained (a=.7254; b=4.9516; r=.9935).

Fobes' (1946) comparisons reveal that although the annual precipitation is from three to seven inches higher in the coastal section than in the remainder of the state, the summer precipitation is actually lower. As Lautzenheiser (1959) points out, this is due to the suppression of thunderstorm activity by cooling maritime effects in the summer. Both the local sea breezes and the more general winds con-

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tribute. In the winter precipitation is much heavier on the coast as a result of the coastal storms called "Northeasters".

Precipitation is usually dependable throughout the year and prolonged droughts are infrequent (Lautzenheiser, 1959), but when they occur it is usually in late summer and early fall ("fire season"). At such times the duff on the floor of spruce-fir forests may become extremely inflammable. The first snows ordinarily come in late fall, but repeated thaws completely melt whatever falls. It is usually not until January that a snow-cover becomes more persistent, but even during the remainder of the winter thaws commonly free the ground of snow one or more times, according to Lautzenheiser. The total snowfall in the coastal section averages from fifty to seventy-five inches a year, the lowest in the state.

During the summer months, winds blow from the southwest through south about 50% of the time. These winds are considerably warmer than the surface waters of the Gulf of Maine over which they must blow before reaching the coast. This produces frequent cool summer fogs, which dissipate rapidly just a few miles inland. From Cape Elizabeth eastward, United States Coast Guard fog signals operate from 200 to 500 hours during July and August (based on six-year average; U. S. Coast and Geodetic Survey, 1950).

Data are not available on the degree to which this sum-

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mer fog decreases evaporation and thereby compensates, or possibly more than compensates, for the infrequency of thunder-storms near the coast. Because of the great frequency of fog, there can be little doubt that its effect is appreciable. Another consequence of fog, not so well known, but mentioned by White (1788), Cooper (1917), Oberlander (1956), and McIntosh (1958) is fog-drip. I have frequently observed this phenomenon in exposed coastal locations, where heavy precipitation was occurring under isolated trees or in heavily-thinned stands, but no rain was falling in the open. However, in the usually dense coastal forests noticeable fog-drip appears to stop at the edges. Oberlander's study supports this latter observation, as he found fog-drip to be appreciable only under trees fully exposed to blasting fog-laden wind.

Fog-drip is not the only way fog may supply water directly to the forest community. Bryophytes and lichens, both important in these forests, readily absorb moisture directly from the atmosphere (Barkman, 1958). As for the actual effects of fog on tree distribution, it might be mentioned here that Cooper (1917) accounted for the presence and distribution of the redwoods (Sequoia sempervirens) in low-rainfall areas of California in terms of decreased evaporation and fog-drip caused by ocean fogs.

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Marine Salts:

Sea winds, while differing in temperature and moisture content from land winds, also differ chemically. It is possible that this latter difference affects forest distribution. Unfortunately, few data directly applicable to the Maine coast have been located in the literature. However, some pertinent study has been pursued elsewhere.

It is known that salt spray can be an important factor in coastal ecology (Wells and Shunk, 1938). White (1958) and White and Millington (1954) proposed that salt spray may be an important factor in the development of tumors on white spruces near the seashore in Maine.

Moss (1940) found that following the 1938 hurricane in Connecticut, deciduous vegetation was injured by salt spray as far inland as forty-five miles. On the other hand, certain species of conifers, viz. pines (Pinus spp.), Colorado blue spruce (Picea pungens), and junipers (Juniperus spp.), were almost completely unaffected even when only a few yards from the ocean. Of course, such evidence might in part account for a rarity of deciduous species on certain coasts, but it thereby would only incompletely explain an abundance of conifers. In southwestern Maine and southern New England, deciduous trees are abundant near the shore. It appears unlikely that their lesser abundance on the shores of eastern

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Maine results from salt spray phenomena distinctive to that region.

Recently Krajina (1959) has suggested that salt spray may be an important factor determining the strongly coastal distribution of Sitka spruce (Picea sitchensis) in the Pacific Northwest. He stated, "....Sitka spruce, requiring great amounts of available Mg, establishes pure stands under the influence of oceanic spray;...."

No such considerations were found in the literature on red or white spruce, or any of the other common tree species in the spruce-fir forests of the coast of Maine. Furthermore, all the species common in these forests have extensive ranges in non-maritime regions. Therefore, there is little reason to suspect that marine salts are responsible for their coastal distribution.

Summary and Evaluation in Terms of Thornthwaite's Methods:

In summary, the climate of the coastal forests may be said to be cool, moist, and maritime. It will be recalled from the discussion of topography that the coast line is exceedingly irregular. This serves to increase greatly the land area subject to marine influence.

In terms of Thornthwaite's early system (1931, 1941), this climate is classified as "superhumid". Except for the

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high portions of the Appalachians, the remainder of the eastern two-fifths of the United States is classified as merely "humid". In his later system, in which "potential evapotranspiration" is substituted for evaporation in the precipitation-evaporation formula, the Maine coastal spruce-fir area is again classified in the most humid category, this time called "perhumid" (1948). In reference to this category, Thornthwaite stated:

> Perhumid climates are not extensive in the United States. They occur along the coasts of Washington, Oregon, and northern California and on the western slopes of the Cascades and the Sierras. There is a single small island in the high rockies of Colorado, and other islands on the high elevations in the Appalachians. A narrow belt along the Maine coast is perhumid.

As for temperature relationships ("thermal efficiency"), Thornthwaite's early system placed the coast of Maine in the "microthermal" category, and the later system called it "warm microthermal". According to the 1948 paper, and a later discussion of climate-forest correlations (Thornthwaite and Hare, 1955), both categories are one step warmer than taiga regions. Thus, the temperatures of the coast of Maine might be interpreted as being representative of the northern portion of what is ordinarily considered to be the transitional forest zone.

Both moisture and temperature are thought to play important roles in the forest distribution on the coast of

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Maine. The correlation between spruce-fir forests and high moisture does not in itself explain the absence of well-developed hardwood forests. At this point, no overall theory which accounts for the presence of the spruce-fir forests will be formulated. Rather, this is gradually developed as information on the composition, reproduction, and biogeographic relationships of the forests is presented.

Forest Distribution Theory

Thus far, no general theory accounting for the distribution of S-F percentages has been presented. It does not appear likely that either bedrock or soils are major factors determining this distribution, although their effects may be locally important (as discussed earlier). On the other hand, there are a number of factors which suggest that climatic characteristics are major causes.

From Machias (4H) southwestward there appears to be a correlation between proximity to sea water and quantity of S-F. The coverage of spruce-fir growth probably is increased greatly by the extreme irregularity of the coast which exposes greater land areas to marine influence. S-F quantities are greatest where the shore is exposed to the fullest sweep of sea winds, especially those from the south through west, as about 60% of all winds during the growing

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season blow from this quadrant (U. S. Coast and Geodetic Survey, 1950).

Figure 4, a simplified version of the large forest distribution map, shows these relationships. Shores indicated by A and C have the least S-F growth; B, D, and E have the most. Over the entire coast, development of S-F is typically correlated with southwestern marine exposure. A re-examination of the larger map will reveal additional more-detailed cases of this same relationship.

In addition to marine exposure, from south to north greater quantities of S-F are found farther from the coast. This latitudinal effect, however, does not obscure the patterns discussed above, until the area near Machias is reached.

Test of Theory

If the factors just discussed can be incorporated into a simple mathematical formula, an objective test may be made in order to determine the degree of correspondence between the real forest distribution and one predicted on the basis of the formula itself.

The formula utilized for this purpose was that of a multiple regression with two independent variables:

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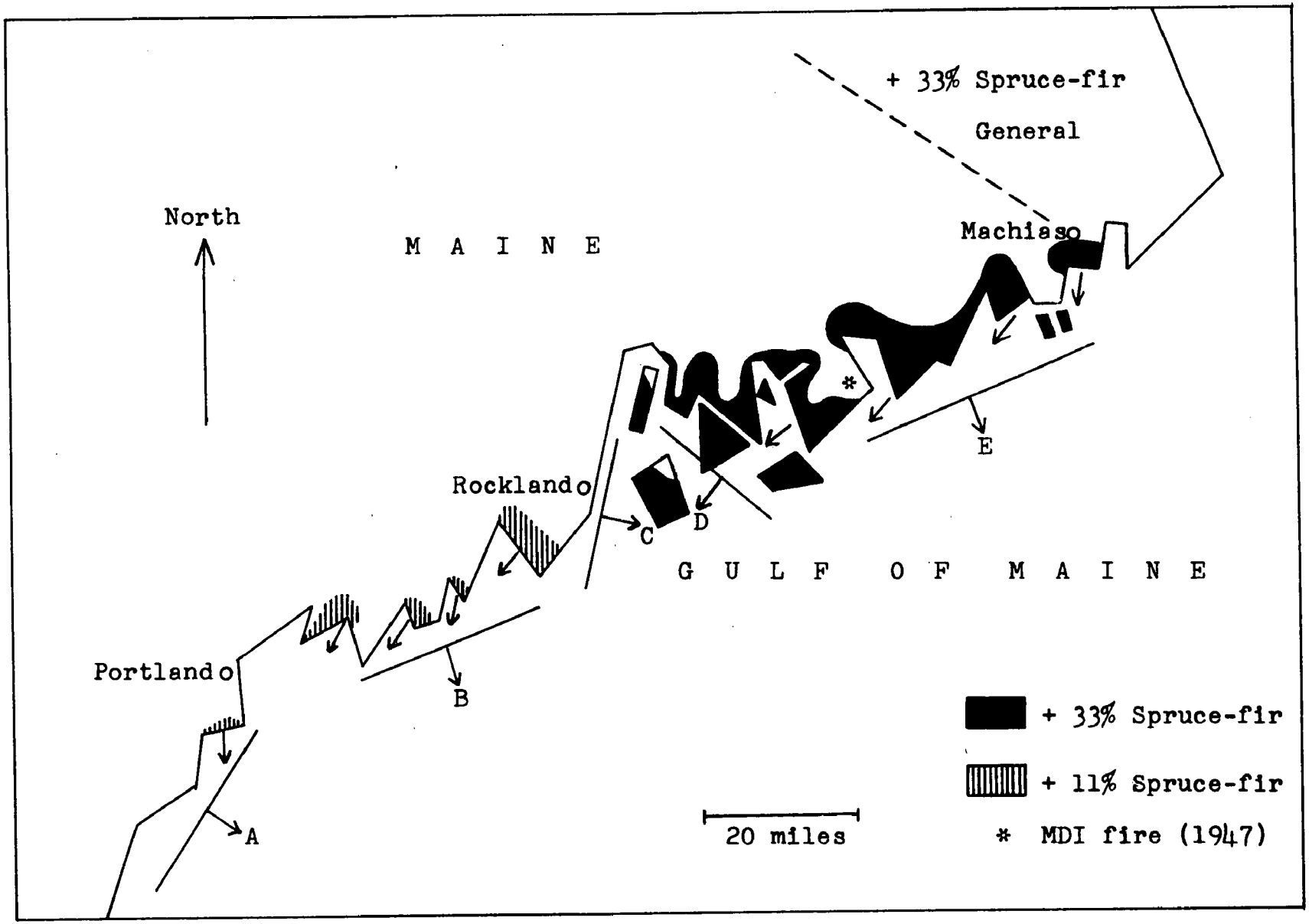


Figure 4. Simplified map showing distribution of spruce-fir percentages on coast of Maine.

$$Y = a + bX + cZ$$

Y = % S-F at any point

X = marine exposure value

Z = latitude

Procedures:

The constants a, b, and c were calculated from data obtained by sampling large numbers of points on the forest distribution map.

The first step in procuring these data was to rule off a grid on an outline map of the coast of Maine, forty spaces between each degree of latitude and twenty-eight between each degree longitude. The points where the lines crossed were each assigned a marine exposure value based on two factors: (1) wind domination (direction and frequency) and (2) proximity to the seashore, and extent of the sea beyond the shore.

Data for (1) were obtained from the United States Coast Pilot (U. S. Coast and Geodetic Survey, 1950). The relative time that winds blew from each of the eight major compass directions during the months of April through November was calculated.

Marine exposure values for each point on the map were obtained by using a transparent overlay, on which were drawn the eight compass lines, radiating from a central point,

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each representing twenty miles on the map scale. The radii were subdivided into ten units of two miles each, weighted from ten nearest the center, nine, eight,.....to one at the circumference. To determine the marine exposure for a point, the overlay was centered over it, and bodies of sea water intersected by the radii were tallied and weighted according to which portions of a radius covered them. The eight sums thus obtained were then multiplied by the corresponding wind dominance values, and the products were summed. This result, a marine exposure value, was recorded on the map beside each point.

The real forest distribution was then entered onto the outline map, using transparent lightly colored areas (five colors) corresponding to the five S-F percentages. Data were obtained in each S-F percentage category (Y) by a complete enumeration of paired X and Z values for all the points falling in that particular color. A total of 601 points were thus sampled.

The data were then used to obtain values for a, b, and c. These values, and coefficients of partial correlation ($r_{xy.z}$ and $r_{zy.x}$) were computed by means of the "L" statis-

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tics described by Cole (1959).* Standard partial regression coefficients were calculated by means of the following formulae:

$$b' = b\sqrt{\frac{L_x}{L_y}}$$

$$c' = c\sqrt{\frac{L_z}{L_y}}$$

and the multiple correlation coefficient by:

$$R = \sqrt{r_{xy.z}b' + r_{zy.x}c'}$$

Next, using the regression formula with its numerical constants, formula-derived boundary lines between the five spruce-fir percentage categories were mapped. In order to do this, values for Y were calculated and entered on the map at the grid points. Lines were then drawn between equal values of Y ("isolines") corresponding to the four boundaries. These lines were transcribed onto a transparent overlay and

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*Typographic errors in two of the computational formulae in that publication were corrected by the author via personal communication. Corrected forms for the two erroneous formulae are as follows:

$$a = \frac{Sy - bSx - cSz}{n}$$

$$r_{xy.z} = \frac{L_zL_{xy} - L_{xz}L_{yz}}{\sqrt{(L_xL_z - L_{xz}^2)(L_yL_z - L_{yz}^2)}}$$

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could then be compared directly to the real forest distribution. The congruence between the formulated and the real forests may be studied directly if the reader will refer to the map and overlay in the rear pocket.

Results:

$Y = -2057.4 + (.01776)X + (46.48)Z$

$b' = .8112$

$c' = .6475$

$r_{xy.z} = .6437$

$r_{zy.x} = .4453$

$R = .90$

The three latter figures demonstrate reliable correlation (<1% L.S.), according to the table for these statistics in Snedecor (1956). However, the distribution of marine exposure values (X) relative to Y appears to satisfy the assumption of linearity in the regression formula somewhat better than does latitude (Z) against Y.

The standard partial regression coefficients (b' and c') are similar, with b' a little higher, suggesting that marine exposure makes a slightly greater contribution to the determination of S-R percentage.

The boundaries predicted by the formula and entered on the overlay show good correspondence to the actual forest distribution. However, certain departures of the formula-

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predicted forest from the underlying one are present. The most important of these are listed below.

On the basis of the formula we would expect:

1. No S-F at Gerrish Island, Kittery.

2. More extensive development of S-F on Cape Elizabeth.

3. A higher percentage and greater coverage by S-F on the Small Point-Sebasco (2C) peninsula (Phippsburg).

4. A higher percentage and more inland development of S-F along the western shores of Penobscot Bay.

5. Not so extensive a development of 64-100% S-F on the seaward portions of the islands and peninsulas of Penobscot Bay to (and including) MDI.

6. Between Belfast (3D-E) and Cherryfield (4G) more extensive distribution of 11-32% S-F inland to the borders of the survey.

7. 11-32% S-F on the "Barrens" north of Cherryfield.

8. 33-63% S-F on the Jonesport peninsula (4G).

9. Lesser development of S-F in the Northfield area (4G), north of Machias.

10. Greater coverage by 64-100% S-F in the Lubec (4H) and Eastport vicinities.

11. Greater coverage by 33-63% S-F in the Calais (5H) region.

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Discussion:

It was concluded that in its general form there is good correspondence between the real and formulated forest distributions. Careful examination of the map will also reveal correspondence in a surprising number of details. However, a number of important exceptions suggest that additional factors, not incorporated into the formula, also affect the real distribution of S-F.

A number of exceptions easily lend themselves to interpretation in terms of recent disturbance of the forests by man. Good cases could be made for numbers 2, 3, 7, 8, 10, and 11; and other cases were incorporated into the discussion under Aerial Survey, Part I. Number 2, Cape Elizabeth, has in the past few decades become heavily populated, some portions virtually constituting a suburb of Portland (2B). Only where the forests have been specially protected, as on the Sprague Estate, have they been spared strong modification or destruction by man. Longfellow's descriptions (1853) suggest that forests containing red spruce were once more extensive on the Cape.

Areas indicated by numbers 7 and 8 support what are locally called "blueberry barrens". There can be little doubt that large portions of these areas have been repeatedly and intentionally burned for many decades. Many sec-

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tions of them, which in recent years have been left undisturbed, are now becoming overgrown by shrubby hardwoods often dominated by birches (Betula spp.).

Cases 10 and 11 refer to areas with a relatively high human population, as compared to adjacent areas. They appear to have been more heavily agriculturalized, lumbered, and burned in recent years than adjacent areas.

Cases 6 and 9 are interpreted as having resulted from the assumption of linearity in the regression formula. The abrupt increase in S-F percentage to the northeast of Columbia Falls, suggests a curvilinear rather than linear relationship between Z and Y. The large number of points sampled in the northeastern area had the effect of an overall steepening of the regression of Z on Y, thereby overemphasizing the importance of latitude in the area between Belfast (3D-E) and Columbia Falls (Case 6). The reverse effect of linearity is illustrated by the underemphasis in Case 9. Nevertheless, a highly significant $r_{zy.x}$ was obtained.

Number 4, the prediction by the formula of much higher percentage and more extensively distributed S-F than actually exists on the west shore of Penobscot Bay, is judged to be the most important departure from the formulated forest distribution. The causes behind this low development of

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S-F may be multifold. In the preceding section on edaphic factors in the physical environment, the possible effect of bedrock and soils was discussed. In Part II the effects of fire will be considered in some detail.

Conclusions to Part I

In this portion of the thesis the overall distribution of S-F in the coast of Maine forests has been described. The description has been in terms of the percentage crown-cover which spruce and fir contribute to the forests of which they are a part.

A distinct seaside border is formed by high concentrations of white spruce along the immediate shore, with red spruce percentages higher just inland. Surveys revealed that red spruce is the most common species composing the spruce-fir element of the coastal forests.

Forests containing the greatest percentages of S-F were found nearest the sea, especially where the shore faced the southwest. Winds prevail largely from this general direction in the growing season. During their passage over the waters of the Gulf of Maine the winds are cooled and frequently become fog-laden. A distinctly maritime climate is thus created.

Through analysis by multiple regression, with marine-

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exposure and latitude as independent variables, it was found that S-F percentage was closely correlated with both, and that they each affect the percentage about equally. When an idealized forest distribution is computed and mapped by means of the multiple regression formula, it is found to be closely congruent with the real forest distribution.

Therefore, it is reasonable to expect that factors held in common by marine exposure and latitude are in large part responsible for the forest distribution. The most prominent of these is a cool growing season coupled with an adequate moisture supply. Additional information will be presented in subsequent sections which will support this proposition.

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Part II

FORESTS OF THE PAST ALONG THE COAST OF MAINE

If forests were stable in time and space there would be no need for a discussion such as this. However, there is a considerable body of evidence which indicates that the character of the coastal forest hundreds and thousands of years ago was quite different from its character today. This is the time scale, and the story begins with the end of the most recent glacial period.

Forest Since Glaciation

The deposition and preservation of plant remains (especially pollen) in the sediments of lake bottoms and bogs since the last glaciation has enabled a number of workers to piece together the history of vegetation since that time. Much of this literature has been reviewed for North America by Dillon (1956), and a concise summary presented for the northeastern regions by Sears (1948).

There is general agreement that at the height of glaciation a broad belt of spruce-fir forests existed across northern United States. As far south as West Virginia, 70% of the pollen in lowest bog layers was composed of spruce and fir (Darlington, 1943). Lesser quantities of such pollen,

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presumably deposited at the height of the last glaciation, have been found as far south as northern Florida and Louisiana (white spruce) (Brown, 1938; Davis, 1946), and in Texas (white spruce, black spruce, and balsam fir) by Potzger and Tharp (1954).

Since glaciation, the spruce-fir forests have been gradually replaced by more southern vegetational types. As the ice melted and its southern border receded northward, the spruce-fir belt followed. This has been the overall trend. However, it has not been a smooth trend. A number of workers postulate a warm and/or dry ("xerothermic") period, as revealed by mid-profile pollen spectra. Thus, for example, Transeau (1941) found that a number of prairie species had temporarily invaded Ohio. Brooks (1949) dated this period 3000-5000 years ago. Zumberge and Potzger (1955), by means of radiocarbon dating in the Lake Michigan area, placed this period some time more recent than 4000 years ago. Since that time the climate appears to have become somewhat cooler and/or more moist.

The applicability of this general picture in the Maine area is substantiated by the studies of Auer (1933), Potzger and Friesner (1948), and Deevey (1951). Auer's borings, taken from bogs in nearby New Brunswick and Nova Scotia, indicate spruce and balsam fir pollen in deepest layers, fol-

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lowed by their decline and the increase of more southern species. This is followed by a recent increase in spruce and fir, said to result from "climatic deterioration".

Potzger and Friesner's paper is reviewed in some detail here because of its important bearing on the history of the coastal forests. The authors obtained borings from six bogs in the mid-coastal area of Maine. Three of these were near the western shore of Penobscot Bay, another a few miles east of Ellsworth (4F), and two on northern MDI. All six yielded consistent results, indicating early dominance by white spruce, black spruce, and jack pine (Pinus banksiana). White pine (Pinus strobus) and/or red pine (Pinus resinosa), hemlock, birch, oak (Quercus spp.), and other species were present in small but significant quantities.

In early mid-profile a great increase in certain species occurred. Especially high quantities of white pine and/or red pine, and substantial amounts of birch and oak were found. A corresponding decrease in white spruce, black spruce, and jack pine took place. White spruce pollen reached very low numbers in this "xerothermic" period, and for a long time bordered "....on relic status.", according to the authors. It is tempting to speculate that during the period it became limited to the most seaward locations, as no refuges for such a species were likely to have existed im-

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mediately inland.

In late mid-profile a marked increase in hemlock (suggesting moister and/or cooler conditions) took place, along with a gradual increase in spruce. In upper layers the increase in spruce accelerated and reached high proportions, while hemlock became less abundant. White and black spruce were present, as were intermediate sized pollen grains. The size of red spruce pollen overlaps both the former and many of these intermediate sized grains were probably from this species. White pine and/or red pine and hemlock showed a corresponding decline, but still maintained moderately high numbers. Jack pine showed little recovery, but maintained the low but significant amounts to which it had been reduced in mid-period. Birch generally held moderately high amounts in the upper layers and a sudden increase appeared at most locations in the uppermost layer. Other hardwoods were present in low quantities. In the uppermost stratum, oak increased significantly to the west of Penobscot Bay, but was still low. Balsam fir maintained very low percentages throughout all levels in the bogs. On first impression, the general picture which the upper bog layers present appears similar to what might be expected on the basis of the present day forests.

Potzger and Friesner's profiles and interpretations

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possess certain puzzling features. The presence of southern species in the lowermost layers is difficult to explain. The authors proposed that the pines, hemlocks, and oaks were able quickly to populate the coast because of the moderating influence of an early maritime climate. On the contrary, it seems to me that with all the glacial ice water flowing into the sea, the growing season near the shore must not have been any more conducive to the southern species than the climate just inland, and probably less so.

In the uppermost layers of the three bogs west of Penobscot Bay, Potzger and Friesner found substantial quantities of spruces. This was not to be expected on the basis of present day forests there, unless high percentages of such pollen are carried greater distances than is supposed.

The substantial quantities of hemlock in the uppermost layers were surprising. The contemporary forests in this region include only a very small percentage of this genus. In my experience it represents well under 1% of the trees in the area. This estimate is supported by Hill's (1919, 1923) and Moore's (1927) comments.

Perhaps the most perplexing aspect of the uppermost layers in all six bogs is the low but significant quantity of jack pine pollen. In the light of the present day distribution of this species, this would not be expected. The

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most southwestern stand of jack pine on the Maine coast is a small outlier grove on Cadillac Mountain, MDI. If the species occurs naturally near the coast to the south and southwest, it is almost certainly rare; and although occasionally used as a decorative shrub, few if any stands have been planted. This was substantiated by Hyland and Steinmetz (1944).

Potzger and Friesner concluded their discussion with the following:

> If accurate data on the rate of peat accumulation were available it might be found that the upper foot-level of peat accumulated since civilized man began his lumbering activity in Maine some 300 years ago. Increase of Picea in that case would, perhaps, mean greater abundance of Picea in response to lessened competition from more tolerant trees.

I believe this interpretation to be untenable, as is brought out in the paragraphs which follow in this section and in later sections.

This entire matter is clarified if it is assumed that Potzger and Friesner's cores were incomplete on top and bottom. This was precisely what Deevey (1951) said about them. Deevey studied lake sediments as well as bog cores in northern (Aroostook Co.) and southern (Kennebec Co.) Maine. In reference to Potzger and Friesner's bottom layers, Deevey cited Leavit and Perkins (1935) and Stone (1899) to the effect that in early postglacial time the entire low-lying

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coastal region was flooded by the sea. I earlier cited Perkin's map (1934) and Flint, et al. (1945) on this same conclusion. It was thus some time before forests could invade the coastal region. Forests already may have populated the inland sections before that time.

On the basis of fossiliferous postglacial deposits on MDI, 120 feet above present sea level, Raisz (1929) claimed that the conditions in that sea were then subarctic. The "rock flour" which Potzger and Friesner found under the peat in their bogs may have come from glacial runoff brought to the sea by rivers and deposited there. Deevey pointed out that the unusually high proportions of grass and other non-arboreal pollen which Potzger and Friesner tabulated for these layers (but failed adequately to interpret) suggested that, rather than a forest, a tundra-like vegetation existed adjacent to the cold sea in earliest postglacial times. Relicts of such vegetation are found today.*

By the time the land surfaces rose out of the sea and peat bogs developed at Potzger and Friesner's sites, hem-

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*In their 1910 paper Fernald and Wiegand stated: "....a narrow coastal subarctic strip extends (westward) along the outer mainland and islands to Great Cranberry Island (3F), and in less pronounced development to Monhegan (2D) and even beyond...." (my parenthetical additions). These authors were in particular referring to the species of exposed, non-forested headlands and offshore islands. Black crowberry (Empetrum nigrum) is an example. Hill (1919) reviewed the literature on this matter.

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lock and hardwoods, including oak, had entered the area. Boreal species declined in ensuing periods. Then, some time after 4000 years ago perhaps, the climate grew gradually cooler and/or moister. According to Deevey (1951) this "...deterioration of climate...", along with an increase in spruce, started about 2000 years ago. Various arguments on the dating and existence of these trends may be found in Brooks (1949).

It appears likely that the increase in pollen of boreal species in the upper layers of Potzger and Friesner's bogs has been occurring for a longer time than the past 300 years. At the point where their records stopped, perhaps 1000 years ago, the pollen spectra were as I have described on preceding pages. Spruce was increasing, and at the time, appeared to have reached considerable percentages just inland to the west of Penobscot Bay. Jack pine was present in low amounts throughout. Birch was common and showed a recent increase in most areas. Oak was uncommon, but showed a recent increase especially to the west of Penobscot Bay.

Forest Descriptions by Early European Explorers

Shortly after 1600 the English and French began intensive exploration of the Maine coast. Contrary to popular conception, these early explorers did not invariably encounter the "forest primeval" described by the poet. Rather,

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their original descriptions indicate that considerable portions of the forests had been modified by the Indians. Day, in his excellent article on this subject (1953), should have dispelled any misconceptions on this matter.

In the following paragraphs I review and comment on a number of early writings, in order to piece together a description of the forests as they were in about 1600. Early English and French plant names often differ from contemporary names. Where this is known to be the case, I have inserted what I judge to be the proper name in parentheses. In these changes I largely follow Ganong (1909). All other parenthetic inclusions within quotations have also been added by me. The following descriptions are presented in order, from west to east.

The Western Coast, as far Eastward as Cape Elizabeth

Samuel Champlain (1613) observed (in his 1605 voyage) that near Biddeford (1B) the Indians "...till and cultivate the soil...," an activity which, it is important to note, he had not observed further eastward along the coast. As he put it, "Their permanent abode (the Indians), the tillage, and the fine trees led us to conclude that the air here is milder and better than that where we passed the winter (St. Croix, 5H+), and at the other places we visited on the coast (eastern Maine)." Champlain continued, "The forests of the

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interior are very thin (along the Saco River, 1B), although abounding in oaks, beeches, ashes, and elms; in wet places there are many willows."

On Richmond Island, just off Cape Elizabeth, Champlain (1613) found in 1605, "...fine oaks and nut trees, the soil cleared up, and many vineyards bearing beautiful grapes in their season, which were the first we had seen on all these coasts from Cap de la Heve (Nova Scotia)." In their 1607 voyage Popham and Gilbert (Unknown, 1892) observed large trees on Cape Elizabeth, "...being for the most part of ocke & wallnutt (probably Juglans cinerea and/or Carya spp.) growinge a greatt space asoonder on from the other as our parks in England and no thickett growinge under them..."

As Day (1953) pointed out, Indian practice favored nut trees, and they may have planted them. The deliberate use of fire by the Indians was correlated with fixed habitation and agriculture at least as far northeast as the southwestern region of Maine. No doubt fires sometimes got out of hand and extensive areas were burned.

An abundance of species capable of sprouting ("coppice growth") may have resulted from repeated burning. According to Brown (1960), who has recently been studying the effect of fires on forest composition in Rhode Island, "The tolerant species and those reproducing by seed are eliminated

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or greatly reduced by fires, including hemlock, beech, yellow birch, black birch and white pine." The oaks were said to be the typical occupants of burned tracts in that area.

Formal study of the effects of fire on forest composition has not been pursued in detail in coastal Maine. However, Hill (1923) pointed out for the Penobscot Bay region that the deciduous forests are not nearly as easily destroyed by fire as the coniferous ones. When incompletely burned, surviving deciduous trees may reproduce by sprouting. Species of the coastal area which are known to be able to sprout include the oaks, red maple, beech (Fagus grandifolia), hickory (Carya spp.), and the ashes (Fraxinus spp.) (Harlow and Harrar, 1958). Spruce-fir forests are highly inflammable and when dry are likely to be completely destroyed once a fire starts. Then they are usually succeeded by deciduous growth, at least temporarily. However, where pine seed sources are available in abundance, they may seed in rapidly, in some burned areas. Paper birch and poplars (Populus spp.) replace burned spruce areas more commonly.

White pine, now so abundant on the coast southwest of Casco Bay, was not mentioned by Champlain or Popham and Gilbert. Heavy fires prior to 1600 may have localized the pines to small protected areas in that coastal stretch.

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Casco Bay to Camden (3D)

East of Cape Elizabeth the early explorers usually indicated that the coastal forests were better developed, less disturbed, and more extensive than along the coast to the west. However, all available observations (two) made a short distance inland noted forests which may be interpreted as being highly disturbed.

Popham and Gilbert (Unknown, 1892) found in 1607 that in Casco Bay the "...Illands are all overgrowen with woods very thicke as ocks wallnet pyne trees & many other things growinge as Sarsperilla hassell nuts & whorts (blueberries) in abundance." They found Small Point (2C) to be "...full of pyne trees & ocke." However, two years earlier, Champlain sailed more inland along the shores of the Kennebec (2C), and there found "...a great many small oaks, and very little arable land." The Indians told him that corn used to be planted in that coastal section until enemy raids made the practice unprofitable.

The information presented by the Indians and the forest descriptions suggest that the area was in the process of recovery from earlier repeated burnings. The thickness of the woods and prominance of pine (likely white pine) in the early descriptions imply that this recovery had progressed to a substantial degree. These are the first and most westward

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references to pine. Today it is abundant in that area, as well as farther southwest.

According to Captain John Smith (1616), the irregular coast between eastern Casco Bay and Penobscot Bay was "...overgrowen with all sorts of excellent good woodes..." Levett (1847) did not appear completely to share this opinion for, in describing the coast between the Sheepscot and Damariscotta Rivers (Boothbay area, 2C), he stated that (in 1623) "...little good timber" was present. That this comment indicated lack of value for the species present, and not that the forests were in general poorly developed, is implied by Champlain's (1613) statement about this area. According to Champlain, "All the islands and coasts are covered with extensive woods, of the same sort as that which I have reported as existing on the other coasts (eastward)." As is pointed out in the following section (Penobscot Bay and Eastward) this "sort" differed markedly from the forests to the west and included spruce and/or fir.

However, the most southwestern location at which spruce and/or fir was actually called by name was the Muscongus Bay area. In Rosier's (1887) relation of Weymouth's 1605 voyage, Monhegan was referred to as "...woody, growen with Firre (possibly fir and/or spruce), Birch, Oke and Beech as far as we saw along the shore; and so likely to be within." It

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should be pointed out that the early explorers often did not distinguish fir from spruce, and early usage of word equivalents for the modern "fir" or "spruce" are likely to mean either or both, and sometimes may even include hemlock. Thus, as Ganong (1909) pointed out, Champlain used the word "Sapin" (French, originally for European Fir) "...to include all trees which the English commonly group under Spruce, viz., the three true species of Spruce, the Balsam Fir, and probably also the Hemlock; but they sometimes separated out the Prusse, the large timber spruce, just as the English sometimes separate out the Fir from their "Spruce,"..."

Rosier (1887) did not indicate the relative abundance of the various species on Monhegan in 1605, though it might be assumed that those he mentioned first were perceived most prominently. In more recent times the forests of Monhegan have been described. Allen (1908) found in the early twentieth century a mostly low growth of red and white spruce, including a scattering of yellow (Betula lutea) and paper birch and other hardwoods, with some areas covered by alders (Alnus spp.). A somewhat similarly situated off-shore island is Matinicus (2E), where McAtee (1916) found white and red spruce to be abundant. He added, "Corroborative testimony is to the effect that most of the cleared portions of the island were once covered by a dense stand of yellow birch

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and rock maple. Only one maple (doubtfully native) now remains." (The parenthetical addition here is McAtee's).

Nearer the mainland, on the Georges Islands (2D), Rosier (1887) found in 1605 "...wood of sundry sorts, some very great, and all tall: Birch, Beech, Ash, Maple, Spruce, Cherry-tree, Yew (probably hemlock), Oke very great and good, and Firre-tree,..." Near the shore the forest was either open and/or free from undergrowth as they were found to "...hindereth not..." In 1959 I found that the majority of these islands were forest covered, though some open areas were present. About half of the forests were strongly dominated by red and white spruce, while the remainder included hardwoods in various proportions.

Along the shores of the St. George River (3D), Rosier (1887) found in 1605 "The wood she beareth is not shrubbish (,) fit only for fewell, but goodly tall Firre, Spruce, Birch, Beech, Oke, which in many places is not so thicke..." Except for a contemporary prominence of white pine, Rosier's description roughly applies to present day forests in that area.

Further inland, to the west of what is now called Rockland, Rosier found the woods on the shores of the river to be "...very thinne, chiefly oke and some small young birch..." Exploring further north, on foot, probably as far as the

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southern slopes of the Camden Hills (3D), Rosier noted a predominance of park-like areas with isolated oaks, and small "...Birch, Hazle and Brake..." These descriptions strongly suggest that the area had been heavily burned.

Penobscot Bay and Eastward

Captain Smith (1616), gazing over the islands of Penobscot Bay, commented that "...as far I could see Eastward of it is nothing but such high craggy Cliffy Rocks and stony Iles, that I wondered such great trees could growe upon so hard foundations." Of eastern Maine in 1605, Champlain (1613) marveled at the numerous "...islands, banks, reefs, and rocks, which in places extend more than four leagues out to sea...most of which are covered with pines, firs, and other trees of an inferior sort."; of the forests on MDI, "The woods consist of pines, firs, and birches only."

However, when Champlain headed inland from Penobscot Bay, up the Penobscot River (4E), he saw "...only a few firs, but numerous pines on one side of the river; on the other only oaks, and some copse wood which extends far into the interior."

Just as in western coastal Maine, in the east there was correspondence between the ways of life of the Indians and the state of forest development. For the Abnakies of southeastern Maine (Penobscots and Passamaquoddies), the motives

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for burning--clearing the underbrush for ease of travel, driving game, and agriculture--were in large part absent (Day, 1953 - after Speck, 1940). Travel during the warmer months was mainly over the numerous water routes by canoe, and during winter on the ice or on snowshoes. Big game hunting was not usually done by driving. Agriculture, though practiced to a limited degree at inland river villages (e.g. Old Town, 4E), was not practiced along the coast. Here the Indians spent the summers harvesting foods provided by the sea (Speck, 1940). Even in southeastern Maine, however, it seems probable that the Indians were responsible for numerous forest fires. As in Nova Scotia (Schierbeck, 1911) the Indians probably burned heavily forested areas to promote shrubby growth which provided food for game. Villages and agricultural plots on the rivers had to be cleared, as did the summer encampments at the seashore. Campfires probably sometimes escaped.

The degree to which the way of life of these Indians was related to the forests about them is reflected by their heavy use of birch bark (Betula papyrifera) laced together with spruce roots, out of which they made their canoes, utensils, and shelters (Butler and Hadlock, 1957). Paper birch must have been common. This intolerant species cannot long endure encroachment by heavy spruce-fir forests; there-

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fore, the forests must have been opened by some means (not necessarily by man).

The effects of Indians upon the forests of coastal Maine were probably not limited to the centuries immediately preceding 1600. As early as 1400 to 2000 B.C. the use of fire was practiced by local peoples near Ellsworth (4F) (Hadlock and Byers, 1956).

Synthesis

The degree to which the forests were affected by the local peoples 500, 1000, or more years ago is conjectural. A re-examination of the pollen spectra of Potzger and Friesner (1948), as well as those of other authors, reveals that reasonable theories can readily be proposed explaining certain oscillations in terms of the effects of aboriginal peoples. However, overall trends in forest composition probably reflect climatic trends.

The most recent fluctuation in Potzger and Friesner's spectra, an increase in oak and birch, might be explained as having resulted from a series of disastrous fires started by the Indians (or by other means). However, climate cannot be completely disregarded, as such a series of fires is more likely to occur during dry years than wet ones.

The sixteenth century, just prior to arrival in Maine by the Europeans, was said by Brooks (1949) to have been ex-

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ceptionally dry. Continental climates appear to have been the rule in the whole north temperate zone. Warm dry summers tend to favor a higher development of forests with species such as oak, both directly and indirectly through a greater frequency of fire.

In Part I, under Forest Distribution Theory, the effects of winds on the contemporary distribution of coastal forests was discussed. Coastal stretches exposed to cool southwestern sea winds were shown to have developed high percentages of spruce and/or fir in the forests. It was proposed that temperature and moisture are probably causally related. Now that the effects of fire have been discussed, a certain qualification must be added to that theory.

It may be assumed that during the 1500's winds prevailed from a generally westerly direction (Brooks, 1949). This was probably especially so during the early autumn, the so-called "fire season". Fires would usually tend to be driven toward the east. When this effect is considered together with the particular configuration of the coast, the results are immediately apparent. Reference to the sketch map (Figure 4) will help the reader unfamiliar with the coast. Fires might not stop until they reached the shore. The western shore of Penobscot Bay is a logical barrier to fires coming from the west, as is the shore from Casco Bay southwest-

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ward.

The areas described by early explorers, which I interpret as having been heavily burned, are precisely those areas most exposed to fires. Even today the correlation is apparent. It will be recalled that when a theoretical distribution of percentages of spruce and/or fir was mapped (overlay on map in rear pocket), the most significant departure of the theoretical from the real forest was found on the western shores of Penobscot Bay. As was pointed out, this may be related to bedrock and soils. Here it is suggested that fire may be important.

The coastal stretch between Casco Bay and Rockland, and the stretch from the islands of Penobscot Bay eastward are relatively protected from extensive fires, both by virtue of their less easterly orientation and by their irregularity. The numerous indentations of the coast by bays and estuaries form a series of efficient fire barriers. Fires tend to be limited to relatively small patches where they start. In discussing the "relation of climax vegetation to islands and peninsulas," Harper (1911) also emphasized this natural fire protection. For an island to burn, the fire must originate there. For a narrow peninsula to burn completely the fire must come from a single direction.

The tendency toward greater development of spruce-fir

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forests on the southwestern facing sides of islands and peninsulas may be another example of the relationships of fire, wind, and the lay of the land. With the winds most frequent from the south through west, a stand on a southwestern shore is unlikely to burn unless the fire starts on that shore. A fire starting in the middle of a peninsula or island would more often burn to the east or northeast than to the west or southwest.

This argument appears to be contradicted by the high percentages of spruce and/or fir in southeastern Washington County. This area is further from the extreme southern limit of spruce-fir forests than is mid-coastal Maine. The balance between spruce-fir forests and other forest types is not as precarious as in the central coastal region. A lower frequency of man-initiated fires may also contribute.

Conclusions to Part II

1. During the height of the last glaciation a belt of spruce-fir forests covered much of northern United States.

2. This belt moved northward with glacial recession and was replaced over its former range by more southerly vegetation.

3. Following glaciation, much of the coastal section of Maine was covered by a sea initially of subarctic char-

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acter. By the time the land had emerged, the spruce-fir-jack pine forests which occupied inland areas had already been invaded from the south by small percentages of white and/or red pine, hemlock, and oak. This was the forest which appears initially to have overgrown the coastal section.

4. During a "xerothermic" period which followed, spruce and jack pine were reduced to low numbers. Much of the coastal region was probably occupied by forests of white and/or red pine, birch, and oak. White spruce then may have been confined to the most seaward locations.

5. Upper pollen spectra suggest that during the past 2000 to 4000 years there has been a return to cooler and more moist climates, and a corresponding expansion of spruce-fir forests in the coastal region.

6. Shortly after 1600, explorers to the coast of Maine found forests with an overall pattern similar to present day forests. However, a lesser proportion of spruce and fir may have been the rule then.

7. The forests to the southwest of Casco Bay appeared to have been strongly modified by the Indians in that region, especially by means of fire.

8. The forests in 1600 along the outer coast from Casco Bay to Penobscot Bay were probably well developed and prob-

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ably included considerable spruce and fir. However, the forests just inland in that stretch appeared as if they had been heavily and repeatedly burned.

9. The early descriptions of the forests near the western shore of Penobscot Bay are also suggestive of strong modification by repeated fires.

10. Indian tribes to the east of Penobscot Bay probably made much less extensive use of forest burning than the Indians to the southwest. Correspondingly, the forests there in 1600 were better developed than southwestward.

11. Spruce and fir were common along the eastern coast in 1600 but pine appears to have occupied a more prominent position than it does today. Paper birch was common.

12. The prominence of paper birch in the early descriptions and the important role that the species played in the Indian culture in southeastern Maine suggest that the forests were disturbed.

13. Repeated fires in the coastal forests are thought to favor certain hardwood types. The spruce-fir type is particularly vulnerable to destruction by fire.

14. It is argued that the pattern of fire destruction to be expected from prevailing westerly winds and the specific configuration of the Maine coast, conforms to the pattern of spruce-fir forest distribution.

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15. The high development of spruce-fir forests on islands and peninsulas may result in part from lesser disturbance by fire.

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Part III

FOREST DESCRIPTION

In this section the spruce-fir forests are described. The objective of Part III is to characterize such forests where they reach their highest and most extensive development in the coastal region of Maine. The black areas on the forest distribution map usually coincide with such areas. The successional trends on most sites in these areas appear to be towards a climax dominated by red spruce, as surveys during the early stages of this study revealed. Both Hill (1923) and Moore and Taylor (1927) recognized the climax status of these forests, though Hill added that they were "...merely a physiographic climax", thus remaining consistent with the "climatic climax" (extensive regions) theory to which he ascribed.

As the vegetation in the coastal region exists in various stages of successional development, and the forests are subject to a number of disturbances which alter their structure and composition, it was necessary to define exactly which areas were to be studied. To put this in statistical terms, the population to be sampled had to be defined.

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Vegetation

Sampling Procedures

The Forests, Defined as a Population of Stands:

It was stated in Part I that the coastal forests were perceived as a mosaic of stands. Stands were distinguishable from adjacent vegetational units by the relatively homogeneous size and physiognomy of the plants composing them, and the relatively homogeneous distribution of the floristic components within. This is not meant to imply absolute homogeneity within a stand, but merely to indicate its discontinuity from adjacent vegetation. Stands usually were clearly distinguishable in the coastal region because of the history of disturbance by man. Such disturbance, commonly in the form of lumbering or burning, took place in patches.

All stands which were considered to qualify as units of the population to be sampled had to meet the following requirements:

1. At least 50% of the trees contributing to the canopy cover were to be red spruce, and/or white spruce, and/or balsam fir. Signs that this dominance was in the process of changing would disqualify a stand.

2. The stands were to be located within ten miles of sea water.

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3. Each stand had to be at least five acres in area, with the shortest dimension no less than 300 feet.

4. Blow-down areas might be included within a stand, but they were not considered to contribute to the required five acres.

5. Stands were not to be located on sites so poorly drained that characteristic bog species were present in substantial numbers.

6. No lumbering was to have occurred during the life of the present trees. Light thinning may have taken place when the stand was young. But only when it was judged that the thinning had not initiated permanent changes in stand structure and composition could it be sampled. (Such cases are specified in the stand descriptions.)

7. A stand was disqualified if there was any evidence that fires had occurred during the lifetime of the present trees.

8. The average age of the trees composing the upper story had to be sixty years or more.

Selection of Stands:

During the early survey stages of this study a few stands were located which satisfied the requirements outlined above. In an effort to locate as many stands as possible, numerous letters of inquiry were sent to biologists

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and foresters throughout the state. Scores of stands were named in their replies, but on checking these the large majority had to be rejected. Either cutting, fire, or extensive blow-down had occurred since the correspondent had observed the area, or the requirements were not satisfied in some other way. Except when specially preserved, stands of mature spruce-fir lead a very fleeting existence in the coastal region. Their most common fate is pulpwood, and this often befalls them when the trees barely reach eight inches DBH.

Finally eighteen eligible stands were found. These were located from Gerrish Island, Kittery, to Cutler. Of these, five were borderline cases so far as meeting the stand qualifications was concerned. Of the five, only Gerrish Island was used for formal vegetational sampling, because of its important geographic position. The other four were used for bird population study only. Data on the location of the eighteen stands is included in Table 5. The stands in Acadia National Park (MDI) are likely to remain relatively undisturbed in future years. So that they may be relocated, maps indicating their positions (Figure 5) are included. The rectangular area on these maps indicates the approximate central portion of the stand, where certain observations were concentrated. So that the reader may ascer-

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Table 5. Forest Study Areas: Location Data. Tabulation in order from west to east.

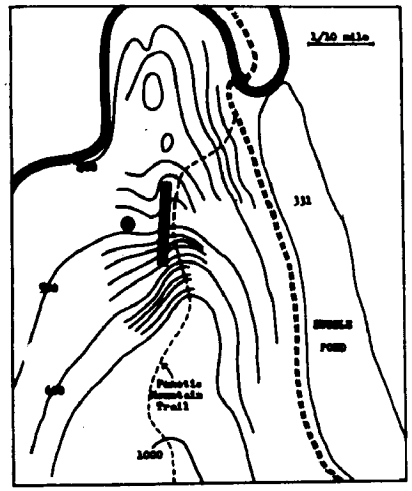
Area Designation	abbr.	USGS Quad. 1/62,500	Alt. ASL	North Lat.	West Long.	Miles to the Sea North	East	South	West
Gerrish Island, Delano Estate, Kittery, York Co.	GI	York	30	43°04'	70°41'	1.0	0.3	0.2	0.9
Cape Elizabeth, Sprague Estate, Cumberland Co.	CE	Portland	50	43°33'	70°15'	5.5	1.3	0.4	0.6
Cundys Harbor, D. Pulsifer Estate, Cumberland Co.	CH	Bath	40	43°48'	69°55'	0.2	0.9	0.7	0.1
Hog Island, Audubon Society Camp, Lincoln Co.	HI	Monhegan	40	43°58'	69°25'	0.9	0.1	0.1	0.4
Gay Island, Knox Co.	GayI	Monhegan	20	43°57'	69°18'	0.1	0.3	0.2	0.1
Western Mountain, Acadia National Park, MDI, Hancock Co.	WM	Mount Desert	1000	44°18'	68°22'	6.2	3.0	4.1	2.1
Whitney Farm, Oak Hill, Somesville, MDI, Hancock Co.	WF	Mount Desert	100	44°22'	68°22'	1.6	1.5	8.8	1.6
Beech Hill, Acadia National Park, MDI, Hancock Co.	BH	Mount Desert	500	44°19'	68°20'	7.3	1.3	6.3	3.9
Bass Harbor Head, Acadia National Park, MDI, Hancock Co.	BHH	Swans Island	100	44°13'	68°20'	17.0	0.2	0.1	0.2
Pemetic Mountain, Acadia National Park, MDI, Hancock Co.	PM	Bar Harbor	500	44°21'	68°15'	4.4	3.4	3.5	3.0

Table 5. continued

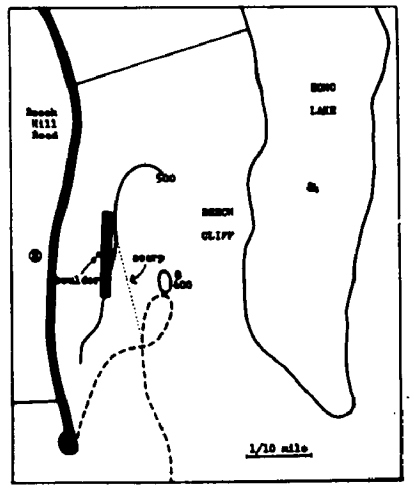
Area Designation	abbr.	USGS Quad. 1/62,500	Alt. ASL	North Lat.	West Long.	Miles to the Sea North	East	South	West
Black Woods, Acadia National Park, MDI, Hancock Co.	BW	Bar Harbor	125	44°18'	68°12'	6.1	0.2	0.2	4.7
Otter Point, Acadia National Park, MDI, Hancock Co.	OP	Bar Harbor	110	44°19'	68°12'	4.4	0.1	0.4	0.2
Ironbound Island, Frenchman Bay, Hancock Co.	II	Bar Harbor	40	44°23'	68°08'	1.2	0.4	0.4	0.3
Tunk Lake, Hancock Co.	TL	Tunk Lake	220	44°36'	68°03'	+100	25	19	+100
Dyer Neck, Washington Co.	DN	Petit Manon	20	44°25'	67°57'	+100	0.2	0.9	0.5
South Addison, Washington Co.	SA	Columbia Falls	80	44°30'	67°43'	0.9	0.2	0.4	0.6
Roque Island, Gardner Homestead, Washington Co.	RI	Columbia Falls	20	44°35'	67°37'	0.4	<0.1	0.9	0.3
Roque Bluffs, Washington Co.	RB	Machias	30	44°38'	67°29'	+100	1.4	1.5	0.9
Cutler, Washington Co.	C	Cutler	50	44°40'	67°12'	+100	0.2	0.3	2.3

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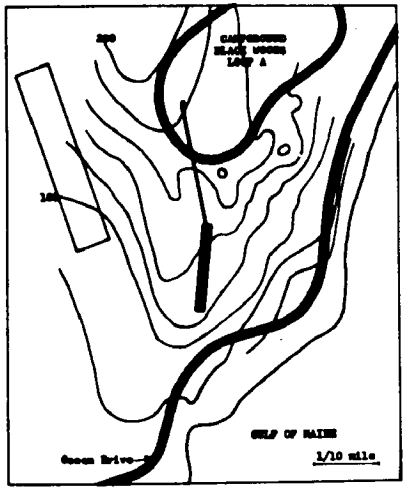


Pemetic Mountain

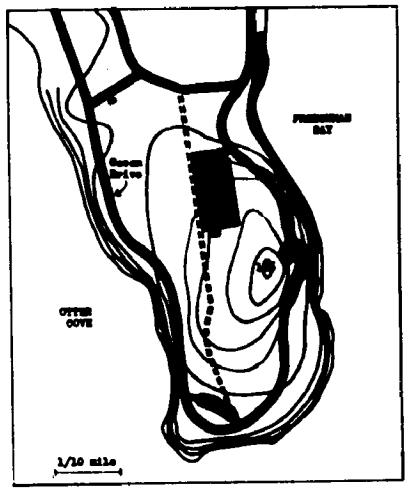


Beech Hill

Black Woods



Otter Point



Bass Harbor Head

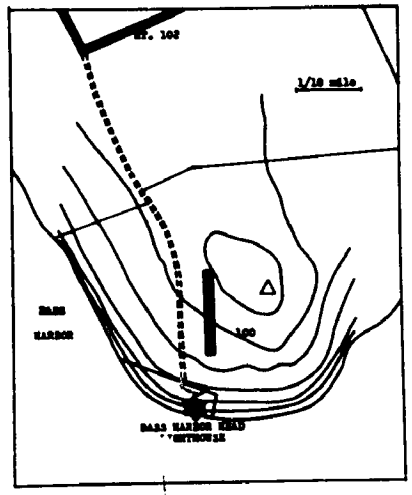


Figure 5. Study Areas; Acadia National Park, MDI. Cross-hatched rectangles indicate portion of stand about which most observations were centered. Contour lines are at twenty foot intervals. Maps based on the U.S.G.S. quadrangles listed in Table 5.

tain the position of the stands relative to the overall forest distribution, they are labeled on the large map (in rear pocket).

It is impossible to state with certainty how many qualified stands existed which were not located. No doubt, there were a few on relatively inaccessible and poorly known islands. However, the thoroughness with which the inquiry to locate them was pursued, and the low number finally located, suggested that not many additional qualified stands existed. Therefore, it is judged that the sample of eighteen represents a large proportion of the population of which it is a part.

The Intra-Stand Sample:

Each stand was sampled by a quadrat method, in some respects similar to that used by Oosting and Billings (1951). Quadrat pairs, each consisting of a 10 X 10 meter plot with a 1 x 4 meter plot placed in one corner were used. Five of these pairs were run at each of fourteen stands. Quadrats were distributed by first ascertaining the approximate shape and dimensions of the stand to be sampled. A plan was made for distributing the quadrats as evenly and widely as possible throughout the stand. This plan was then faithfully followed, using a system of sighting and pacing which assured objective placement of the quadrats. Then, a system

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of coin spinning and sighting was used to position objectively the corners of the large quadrat and the placement of the small one within.

In the 10 X 10 meter quadrat all live woody plants one inch or more DBH were counted and their DBH measured. Tree reproduction, shrubs, and herbs were counted on the 1 X 4 meter quadrat. Reproduction was considered to include any sapling less than one inch DBH, plus established tree seedlings. Then, the corner where the small quadrat had been placed was used as the vertex for an L-shaped transect along two ten-meter sides of the large quadrat. A measuring tape which had been placed along those sides was used to measure ground-cover by bryophytes and lichens. Each species and the distance (to the nearest decimeter) that it was intersected by the tape were tallied.

Next the large quadrat was searched for the presence of any plant species (excluding thallophytes) not already recorded there, and these were tabulated. All species of doubtful identity found throughout the sampling procedures were collected and assigned identification numbers. The general vicinity of the large quadrat was explored to discover any species present in that portion of the stand, but not in the quadrat. By means of an Abney Level and measuring tape, the height of a number of trees was measured to

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determine the general height of the canopy there. Then, a collection of as many species of breast-height corticolous lichens and bryophytes as could be found in that portion of the stand was made. A series of breast-height increment borings taken from the north sides of spruces in each four inch DBH size class was obtained before moving on to the next quadrat.

After these procedures were repeated for all quadrats and their vicinities, the entire stand was re-explored to record any species as present that might have been missed. Soil observations were made in all stands, but systematic collections of samples were taken only from stands on MDI. The description of methods and presentation of results of all soil observations are reserved for a separate section.

Problems of Species Identification and Reference Collections:

When in doubt as to the identity of any species, collections were made and specimens sent to experts for identification. At least one specimen of each lichen species was identified by Mason E. Hale. These specimens are now deposited in the collection of the Smithsonian Institution in Washington, D. C. (United States National Museum, collection numbers 225054, 225608, and 227956). I possess a duplicate collection which is available for examination.

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At least one specimen of each species of bryophyte was checked by one or more of the following persons: Lewis E. Anderson of the Department of Botany, Duke University, Durham, North Carolina; A. LeRoy Andrews (especially Sphagnaceae) at the Department of Botany, Cornell University, Ithaca, New York; Henry S. Conard of Grinnell, Iowa; Howard Crum of the National Museum of Canada, Ottawa; and A. J. Sharp, D. H. Norris, and R. E. Hatcher of the Department of Botany at the University of Tennessee, Knoxville. Various specimens of the species cited in this thesis are distributed among the personal collections and respective institutional collections of these individuals. A representative set of the common species is deposited at Acadia National Park, Bar Harbor, Maine; and a nearly complete set is in the collection at Cornell University. I assume all responsibility for the accuracy of bryophyte identification. I possess a duplicate set of specimens which is available for examination.

Vascular plants usually presented no identification problems, but a few troublesome specimens were identified by C. D. Richards at the University of Maine in Orono.

Tabular Results and Vegetational Quantities

The results of vegetational sampling are presented in Tables 6-23. In this section these tables are interpreted

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and summarized. In the text, unless otherwise specified, a standard error expression following an overall mean (applicable to all stands) is the standard error of the group means (n = 14).

Trees:

In Tables 6-19 each stand is characterized according to those of its tree species which were tallied during the quantitative phases of sampling. Reproduction, size class distribution, frequency, density, and basal area are all included. These data are tabulated separately for each stand not because it is my primary purpose to characterize individual stands in detail (sampling procedures were inadequate for this); rather, these tables are presented to illustrate the nature of variability between stands in the coastal forests. Overall means and statistical expressions of error fail to do this.

It will be noted that standard errors (n = 5) in Tables 6-19 are frequently high. The number of quadrats was small. Nevertheless, these forests were uniform enough so that the average of the standard errors of the fourteen basal area means (all species) was 10.9%, and for the basal areas of spruce only, 13.5%. Reproduction means, on the other hand, bear standard errors averaging 36%. Reproduction appeared to be distributed with considerable contagion, and the small

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Tables 6 to 19. Tree Data. Reproduction density (#/m^2 ± SE) and frequency (%F) are based on five 1 x 4 meter quadrats. Numbers of trees found in five 10 x 10 meter (500 m^2) quadrats are arranged by size class, inches diameter at breast height ("DBH). Sizes not represented in quadrats, but present in stand, are indicated by P. This is followed in the tables by standard percentage frequency and relative frequency in parentheses, based on the large quadrats. Data are totaled and summarized in terms of basal area in square feet per acre (ft^2/acre ± SE) and importance value (%IV). The latter term is explained in the text.

Table 6. Gerrish Island, Trees.

Species	Reproduction			Size Classes ("DBH)									Summary				
														Density		Basal Area	
	#/m^2 ± SE	% all spp.	%F	1-	2-	4-	8-	12-	16-	20-	24-	28-	Freq %	Sum 1"+ / 500 m^2	% all spp. 1"+	ft^2/ acre ± SE	%BA all spp.	% IV
Picea rubens Sarg. red spruce	3.90 ±.67	17	100	2	12	41	10	2					100 (38)	67	77	133 +14	85	60
Acer rubrum L. red maple	18.90 ±8.32	83	100	1	4	5	1						100 (38)	11	13	18	11	31
Betula papyrifera Marsh. paper-birch	-	-	-		1	2							40 (15)	3	3	4	3	5
Vaccinium corymbosum L. highbush blueberry	-	-	-	6									20 (8)	6	7	1	1	3
Sum all species	22.80	100		9	17	48	11	2						87	100	156 ±11	100	99

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Table 7. Cape Elizabeth, Trees. See legend, Table 6, page 103.

Species	Reproduction			Size Classes ("DBH)									Summary					
													Freq %	Density		BasalArea		% IV
	#/m² ±SE	% all spp.	%F	1-	2-	4-	8-	12-	16-	20-	24-	28-		Sum 1"+ 500 m²	% all spp. 1"+	ft²/ acre ±SE	%BA all spp.	
Picea rubens Sarg. red spruce	3.05 ±1.62	68	60	9	12	45	17	5	P	P	P	P	100 (71)	88	96	191 22	98	86
Acer rubrum L. red maple	1.15 ±.67	26	80				1						20 (14)	1	1	4	2	9
Abies balsamea (L.) Mill. balsam-fir	.30	7	20	3									20 (14)	3	3	-	-	5
Sum all species	4.50	100		12	12	45	18	5						92	100	196 ±20	100	100

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Table 8. Cundys Harbor, Trees. See legend, Table 6, page 103.

Species	Reproduction			Size Classes ("DBH)								Summary					
													Density		BasalArea		
	#/m² ±SE	% all spp.	%F	1-	2-	4-	8-	12-	16-	20-	24-	Freq %	Sum 1"+ 500 m²	% all spp. 1"+	ft²/ acre ±SE	%BA all spp.	% IV
Picea rubens Sarg. red spruce	3.55 ±1.57	68	80	P	6	30	6	3	P			100 (29)	45	59	102 ±11	47	50
Pinus strobus L. white pine	.50	10	40			3	1	4		1		80 (24)	9	12	65	30	21
Thuja occidentalis L. arbor vitae	--	--	--	1	3	6	3	1				60 (18)	14	18	28	13	12
Tsuga canadensis (L.) Carr. hemlock	.85	16	80		2	1		1				40 (12)	4	5	11	5	9
Betula papyrifera Marsh. paper-birch	.05	1	20		1	1		1				40 (12)	3	4	11	10	7
Acer rubrum L. red maple	.25	5	40		1							20 (6)	1	1	--	--	2
Sum all species	5.20	100		1	13	41	10	10		1			76	100	218 ±26	100	100

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Table 9. Hog Island, Trees. See legend, Table 6, page 103.

Species	Reproduction			Size Classes ("DBH)								Summary					
													Density		Basal Area		
	#/m² ±SE	% all spp.	%F	1-	2-	4-	8-	12-	16-	20-	24-	Freq %	Sum 1"+ / 500 m²	% all spp. 1"+	ft²/ acre ±SE	%BA all spp.	% IV
Picea rubens Sarg. red spruce	4.95 1.97	87	100	12	4	17	14	8	1			100 (42)	56	67	175 50	83	72
Abies balsamea (L.) Mill. balsam-fir	.55	10	80	14	3	1						100 (42)	18	22	4	2	16
Picea glauca (Moench) Voss white spruce	.20	4	40			6	1	2				40 (17)	9	11	31 19	15	12
Red and white spruce	5.15 1.87	(91)	100	12	4	23	15	10	1			(100)	(65)	78	206 37	98	79
Sum all species	5.70	100		26	7	24	15	10	1				83	100	211 ±37	100	100

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Table 10. Western Mountain, Trees. See legend, Table 6, page 103.

Species	Reproduction			Size Classes ("DBH)								Summary					
													Density		BasalArea		
	#/m² ±SE	% all spp.	%F	1-	2-	4-	8-	12-	16-	20-	24-	Freq %	Sum 1"+ 500 m²	% all spp. 1"+	ft²/ acre ±SE	%BA all spp.	% IV
Picea rubens Sarg. red spruce	16.54 4.50	97	100	20	17	15	8	7	3	P		100 (50)	70	65	171 19	94	80
Abies balsamea (L.) Mill. balsam-fir	.55	3	80	29	4	3						80 (40)	36	34	9	5	17
Betula lutea Michx. f. yellow birch	--	--	--			1						20 (10)	1	1	2	1	3
Sum all species	16.99	100		49	21	19	8	7	3				107	100	182 ±22	100	100

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Table 11. Beech Hill, Trees. See legend, Table 6, page 103.

Species	Reproduction			Size Classes ("DBH)								Summary					
													Density		Basal Area		
	#/m² ±SE	% all spp.	%F	1-	2-	4-	8-	12-	16-	20-	24-	Freq %	Sum 1"+ 500 m²	% all spp. 1"+	ft²/ acre ±SE	%BA all spp.	% IV
Picea rubens Sarg. red spruce	6.20 ±1.15	95	100	1	15	28	21	4	3			100 (45)	72	89	222 ±42	90	82
Betula papyrifera Marsh. paper-birch	--	--	--			1	2	1				20 (9)	4	5	19	8	6
Tsuga canadensis (L.) Carr. hemlock	--	--	--		1		1					40 (18)	2	2	5	2	5
Thuja occidentalis L. arbor vitae	--	--	--		2							40 (18)	2	2	1	-	4
Abies balsamea (L.) Mill. balsam-fir	.30	5	20		1							20 (9)	1	1	-	-	3
Sum all species	6.50	100		1	19	29	24	5	3				81	100	247 ±28	100	100

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Table 12. Bass Harbor Head, Trees. See legend, Table 6, page 103.

Species	Reproduction			Size Classes ("DBH)								Summary					
													Density		BasalArea		
	#/m² ±SE	% all spp.	%F	1-	2-	4-	8-	12-	16-	20-	24-	Freq %	Sum 1"+ 500 m²	% all spp. 1"+	ft²/ acre ±SE	%BA all spp.	% IV
Picea glauca (Moench) Voss white spruce	.65	15	40			21	16	5	P	P		100 (38)	42	65	147 28	83	57
Picea rubens Sarg. red spruce	3.45 ±2.00	78	60	3	1	7	2	1	P			80 (31)	14	22	29 21	16	33
Abies balsamea (L.) Mill. balsam-fir	.30	7	40	7								60 (23)	7	11	1	1	9
Alnus crispa mollis Fern. green-alder	--	--	--	2								20 (8)	2	3	--	--	2
red and white spruce	4.10 ±2.20		60	3	1	28	18	6	P	P			(56)	86	177 19	100	
Sum all species	4.40	100		12	1	28	18	6					65	100	177 ±18	100	100

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Table 13. Pemetic Mountain, Trees. See legend, Table 6, page 103.

Species	Reproduction			Size Classes ("DBH)								Summary					
													Density		BasalArea		
	#/m² ±SE	% all spp.	%F	1-	2-	4-	8-	12-	16-	20-	24-	Freq %	Sum 1"+ 500 m²	% all spp. 1"+	ft²/ acre ±SE	%BA all spp.	% IV
Picea rubens Sarg. red spruce	1.90 .77	76	60	3	7	31	21	2	P			100 (31)	64	70	147 18	75	65
Tsuga canadensis (L.) Carr. hemlock	--	--	--	1	4	10	2					100 (31)	17	18	26	13	15
Acer pensylvanicum L. striped maple	.45	18	80		1	2						40 (13)	3	3	4	2	8
Betula papyrifera Marsh. paper-birch	.15	6	40			2	2					40 (13)	4	4	12	6	7
Acer rubrum L. red maple	--	--	--		1	1	1					20 (6)	3	3	6	3	3
Amelanchier sp.	--	--	--			1						20 (6)	1	1	2	1	2
Sum all species	2.50	100		4	13	47	26	2					92	100	197 ±7	100	100

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Table 14. Black Woods, Trees. See legend, Table 6, page 103.

Species	Reproduction			Size Classes ("DBH)								Summary					
													Density		BasalArea		
	#/m² ±SE	% all spp.	%F	1-	2-	4-	8-	12-	16-	20-	24-	Freq %	Sum 1"+ 500 m²	% all spp. 1"+	ft²/ acre ±SE	%BA all spp.	% IV
Picea rubens Sarg. red spruce	4.35 2.32	93	80	10	46	77	18	P				100 (45)	151	94	221 23	97	85
Betula papyrifera Marsh. paper-birch	--	--	--		1	4						40 (18)	5	3	7	3	5
Abies balsamea (L.) Mill. balsam-fir	.35	7	40	3								40 (18)	3	2	--	--	5
Viburnum cassinoides L. witherod	--	--	--	1								20 (9)	1	1	--	--	2
Amelanchier Medic sp. shadbush	--	--	--	1								20 (9)	1	1	--	--	2
Sum all species	4.70	100		15	47	81	18						161	100	229 ±21	100	100

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Table 15. Otter Point, Trees. See legend, Table 6, page 103. The sample size differs here, in that 6 1 x 4 meter quadrats were sampled for reproduction, and 7 10 x 10 meter quadrats for trees.

Species	Reproduction			Size Classes ("DBH)									Summary					
														Density		BasalArea		
	#/m² ±SE	% all spp.	%F	1-	2-	4-	8-	12-	16-	20-	24-	28+	Freq %	Sum 1"+ 500 m²	% all spp. 1"+	ft²/ acre ±SE	%BA all spp.	% IV
Picea rubens Sarg. red spruce	3.83 ±.82	67	83	4	5	1	5	9	4	1	P	P	100 (33)	29	25	130 35	53	46
Abies balsamea (L.) Mill. balsam-fir	1.79	31	50	37	31	6							100 (33)	74	55	17	7	27
Picea glauca (Moench) Voss white spruce	--	--	--			4	10	7	2	P			86 (29)	23	20	100 32	40	26
Amelanchier Medic sp. shadbush	.08	1	17		1								14 (5)	1	1	--	--	1
red and white spruce	3.83 ±.82		83	4	5	5	15	16	6	1	P	P	(100)	52	45	230 29	93	72
Sum all species	5.70	100	100	41	37	11	15	16	8	1				127	100	248 ±30	100	100

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Table 16. Ironbound Island, Trees. See legend, Table 6, page 103.

Species	Reproduction			Size Classes ("DBH)								Summary					
													Density		BasalArea		
	#/m² ±SE	% all spp.	%F	1-	2-	4-	8-	12-	16-	20-	24-	Freq %	Sum 1"+ 500 m²	% all spp. 1"+	ft²/ acre ±SE	%BA all spp.	% IV
Picea rubens Sarg. red spruce	4.00 ±2.67	57	80	3	14	16	10	12	3	1	P	100 (26)	59	43	243 ±25	86	60
Acer rubrum L. red maple	2.25 ±.57	32	80	2	1	5	5					100 (26)	13	9	31	11	18
Abies balsamea (L.) Mill. balsam-fir	.75	11	80	54	2							60 (16)	56	41	6	2	14
Amelanchier Medic sp. shadbush	--	--	--	4								40 (10)	4	3	--	--	3
Thuja occidentalis L. arbor vitae	--	--	--		2							20 (5)	2	1	1	--	1
Acer pensylvanicum L. striped maple	--	--	--		1							20 (5)	1	1	--	--	1
Acer spicatum Lam. mountain-maple	--	--	--	2								20 (5)	2	1	--	--	1
Viburnum alnifolium Marsh. hobblebush	.05	1	20	1								20 (5)	1	1	--	--	1
Sum all species	7.05	100	100	66	20	21	15	12	3	1			138	100	282 ±30	100	100

Table 17. Tunk Lake, Trees. See legend, Table 6, page 103.

Species	Reproduction			Size Classes ("DBH)								Summary					
													Density		Basal Area		
	#/m² ±SE	% all spp.	%F	1-	2-	4-	8-	12-	16-	20-	24-	Freq %	Sum 1"+ 500 m²	% all spp. 1"+	ft²/ acre ±SE	%BA all spp.	% IV
Picea rubens Sarg. red spruce	.25 ±.11	29	60	P	1	23	22	2	P			100 (21)	48	49	147 18	67	47
Acer rubrum L. red maple	.30 ±.14	35	60	7	3	8	2					80 (17)	20	20	23	11	19
Tsuga canadensis (L.) Carr. hemlock	.05	6	20	1		5	2					60 (12)	8	8	17	8	8
Thuja occidentalis L. arbor vitae	.15	18	60	1	5	1						60 (12)	7	7	4	2	8
Pinus strobus L. white pine	--	--	--			1	2	1				60 (12)	4	4	19	9	7
Abies balsamea (L.) Mill. balsam-fir	.10	12	40	5	1							60 (12)	6	6	1	--	6
Betula papyrifera Marsh. paper-birch	--	--	--			4						40 (8)	4	4	6	3	4
Fagus grandifolia Ehrh. beech	--	--	--			1						20 (4)	1	1	2	1	1
Sum all species	.85	100		14	10	43	28	3					98	100	219 ±20	100	100

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Table 18. Roque Island, Trees. See legend, Table 6, page 103.

Species	Reproduction			Size Classes ("DBH)								Summary					
													Density		BasalArea		
	#/m² ±SE	% all spp.	%F	1-	2-	4-	8-	12-	16-	20-	24-	Freq %	Sum 1"+ 500 m²	% all spp. 1"+	ft²/ acre ±SE	%BA all spp.	% IV
Picea rubens Sarg. red spruce	10.80 2.95	82	100	10	5	12	22	8	4	2		100 (36)	63	60	288 63	95	74
Abies balsamea (L.) Mill. balsam-fir	2.25 ±1.32	17	80	34		1						60 (21)	35	33	5	2	15
Acer pensylvanicum L. striped maple	--	--	--	2								40 (14)	2	2	--	--	3
Acer rubrum L. red maple	.15	1	40				1					20 (7)	1	1	4	1	2
Betula papyrifera Marsh. paper-birch	--	--	--			2						20 (7)	2	2	3	1	2
Betula lutea Michx. f. yellow birch	--	--	--			1						20 (7)	1	1	2	1	2
Amelanchier Medic sp. shadbush	--	--	--	1								20 (7)	1	1	--	--	2
Sum all species	13.20	100		47	5	16	23	8	4	2			105	100	303 ±58	100	100

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Table 19. Cutler, Trees. See legend, Table 6, page 103.

Species	Reproduction			Size Classes ("DBH)								Summary					
													Density		BasalArea		
	#/m² ±SE	% all spp.	%F	1-	2-	4-	8-	12-	16-	20-	24-	Freq %	Sum 1"+ 500 m²	% all spp. 1"+	ft²/ acre ±SE	%BA all spp.	% IV
Picea rubens Sarg. red spruce	5.60 3.12	35	100	1	21	62	21	P				100 (31)	105	81	200 28	79	61
Abies balsamea (L.) Mill. balsam-fir	10.55 ±1.20	65	100			4	5					80 (25)	9	7	28	12	24
Picea glauca (Moench) Voss white spruce	--	--	--				4					80 (25)	4	3	18 4	7	8
Betula papyrifera Marsh. paper-birch	--	--	--		10	1						60 (19)	11	9	6	2	6
red and white spruce	5.60 3.12		100	1	21	62	25	P					109	84	217 25	86	
Sum all species	16.15	100		1	31	67	30						129	100	251 ±15	100	100

samples proved inadequate for any but the grossest estimate of the quantity. Tests (t) at the 10% level of significance failed to distinguish between any but the most extreme reproduction means.

The final column in these tables lists importance values (IV) for each species. These are derived as follows:

$$\%IV = \frac{\%R + r\%F + \%D + 2(\%BA)}{500}$$

where %R equals relative reproduction, r%F equals relative percentage frequency, %D equals relative density, and %BA equals relative basal area. The relative percentage frequency is used as in Curtis and McIntosh (1951). The importance value here differs from theirs in that I have included a value for reproduction and have weighted relative basal area twice. Reproduction was used because in some cases it indicated significant trends which were taking place within the stand. Basal area was weighted twice as it is believed to be strongly correlated with crown cover. This latter expression is a good indicator of what is ordinarily called "ecological dominance" (Cain and Oliveira Castro, 1959).

In Table 20 the importance values are summarized for all stands. In addition, tree species recorded as present but not tabulated quantitatively are listed. The five most important tree species, in order of greatest importance, are

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Table 20. Trees, Summary. This table includes both presence and importance data for each tree species in each stand. See Table 5 for meanings of stand abbreviations. The species are listed in order of greatest mean importance.

SPECIES	GI	CE	CH	HI	WM	BH	BHH	PM	BW	OP	II	TL	RI	C	$\overline{\%IV}$
Picea rubens Sarg. red spruce	60	86	50	72	80	82	33	65	85	46	60	47	74	61	65
Abies balsamea (L.) Mill. balsam-fir	-	5	P	16	17	3	9	P	5	27	14	6	15	24	10
Picea glauca (Moench) Voss white spruce	-	-	-	12	-	-	57	-	-	26	-	-	-	8	7
Acer rubrum L. red maple	31	9	2	P	P	P	P	3	P	P	18	19	2	-	6
Betula papyrifera Marsh. paper-birch	5	P	7	P	P	6	P	7	5	P	P	4	2	6	3
Tsuga canadensis (L.) Carr. hemlock	-	-	9	-	-	5	-	15	-	-	-	8	-	-	3
Pinus strobus L. white pine	P	P	21	P	-	P	P	P	P	P	P	7	-	-	2
Thuja occidentalis L. arbor vitae	-	-	12	-	-	4	-	P	P	P	1	8	-	-	2
Acer pensylvanicum L. striped maple	-	-	P	-	P	P	-	8	P	P	1	P	3	-	1
Amelanchier Medic sp. shadbush	P	P	-	-	-	P	P	2	2	1	3	P	2	P	1
Pyrus cf. americana (Marsh.) D.C. American Mountain-Ash	-	-	-	-	P	P	P	P	P	P	P	-	P	P	0

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Table 20. continued

SPECIES	GI	CE	CH	HI	WM	BH	BHH	PM	BW	OP	II	TL	RI	C	%IV
Betula lutea Michx. f. yellow birch	-	-	P	-	3	-	-	P	-	P	P	P	2	-	0
Quercus rubra L. red oak	P	P	P	-	-	-	-	-	-	P	-	P	-	P	0
Acer saccharum Marsh. sugar maple	-	-	-	-	-	P	-	-	-	P	-	P	-	-	0
Acer spicatum Lam. mountain-maple	-	-	-	-	-	-	-	-	-	-	P	P	P	-	0
Fagus grandifolia Ehrh. beech	-	-	-	-	-	P	-	-	-	-	-	P	-	P	0
Pinus resinosa Ait. red pine	-	-	P	-	-	-	-	-	-	-	-	P	-	-	0
Betula populifolia Marsh. gray birch	-	-	P	-	-	-	-	-	-	P	-	-	-	-	0
Fraxinus americana L. white ash	-	-	-	-	-	-	-	-	-	P	-	-	-	-	0
Populus grandidentata Michx. large-toothed aspen	-	-	-	-	-	-	-	P	-	-	-	-	-	-	0

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red spruce, balsam fir, white spruce, red maple, and paper birch.

Overall mean quantities for all species and for spruce alone are as follows:

Basal Area, $ft.^2$/acre at breast height:

222.4 ± 10.9 all species

192.6 ± 13.3 spruce

Density, number of stems (+1"DBH) per 100 m^2:

19.86 ± 1.43 all species

14.07 ± 1.56 spruce

Other Vascular Plants:

In Table 21 shrub, herb, and pteridophyte densities and frequencies are listed. Subtotals for these groups are included. Importance values for each species were determined as follows:

$$\%IV = \frac{\text{mean \% density + mean frequency + constance}}{\text{Sum \%IV all species}} \times 100$$

The five most important shrub species are low sweet blueberry (Vaccinium angustifolium), witherod (Viburnum cassinoides), mountain holly (Nemopanthus mucronata), sheep laurel (Kalmia angustifolia), and sour-top-blueberry (Vaccinium myrtilloides). Shrubs were not randomly distributed, but were often found concentrated where the canopy was least dense. In overall density, shrubs contributed little to

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Table 21. Vascular Plants, Excluding Trees. Species are grouped in the following categories: Shrubs, taller than 10 cm. at maturity; Herbs, including dwarf shrubs; and Pteridophytes. Each species is followed by two rows of numbers. The upper row indicates density per square meter, based on five 1 x 4 meter quadrats per stand. The lower row indicates relative frequency (%), based on five 10 x 10 meter quadrats per stand (except six at OP). Species which were present in stand, but not on the sample plots are indicated by a P. Data are summarized in terms of mean absolute density, mean relative density, mean frequency (%F), and constance (%C). Constance is based on the percentage of stands in which the species was tallied in the first 500 square meters sampled. For each species, a relative importance value (%IV) is derived, based on mean relative density, plus mean frequency, plus constance.

SPECIES	STANDS														SUMMARY				% IV
	GI	CE	CH	HI	WM	BH	BHH	PM	BW	OP	II	TL	RI	C	Density /m²	Density %	%F	%C	
Shrubs:																			
Vaccinium angustifolium Ait. low sweet blueberry	.10 40	.265 100	.10 80	.15 100	.05 80	.15 60	P 40	P	.05 20	.17 83	P 60	P 20	P	P 20	.24	45	50	86	26
Viburnum cassinoides L. withered	.45 60	P 20	.05 80		.20 60	P	.05 80	.05 20	.05 40	.04 33	.05 80	P 60		P 20	.07	13	40	79	19
Nemopanthus mucronata (L.) Trel. mountain-holly		P	P 40		.05 80	.05 40			P	P 33	P	.30 60	P 20		.03	6	20	43	10
Kalmia angustifolia L. sheep-laurel	P 40	.25 20			P 60	P 20				P		.70 40	P	P	.07	13	13	36	9
Vaccinium myrtilloides Michx. sour-top-blueberry					P 20		P				P 20	P 20	P 20				6	29	5
Taxus canadensis Marsh. American yew											P 20	130 20			.09	17	3	14	5

Table 21. continued

	GI	CE	CH	HI	WM	BH	BHH	PM	BW	OP	II	TL	RI	C	Dens M²	Dens %	%C	%F	%I	V
Alnus crispa (Ait.) Pursh green alder							P (60)			P (17)	P	P (20)		P	0	0	21	7	4	
Ilex verticillata (L.) Gray black alder	.45 (60)	P (20)	P											.03	6	14	6	4		
Vaccinium corymbosum L. highbush blueberry	.01 (60)	.05 (20)		P											0	0	14	6	3	
Viburnum alnifolium Marsh. hobblebush		P									P (80)	P (40)			0	0	14	9	3	
Gaylussacia baccata (Wang.) K. Koch black huckleberry				P (20)						P (17)			P		0	0	14	3	2	
Lonicera canadensis Bartr. fly-honeysuckle										P	P (20)		P (20)		0	0	14	3	2	
Spiraea latifolia (Ait.) Borkh. meadow-sweet				P			.05 (20)			P					0	0	7	1	1	
Lyonia ligustrina (L.) DC. maleberry		P (20)				P									0	0	7	1	1	

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Table 21. continued

	GI	CE	CH	HI	WM	BH	BHH	PM	BW	OP	II	TL	RI	C	Dens M^2	Dens %	%C	%F	%IV
Prunus pensylvanica L. f. fire-cherry							P			P (17)					0	0	7	1	1
Prunus virginiana L. choke-cherry			P (40)				P								0	0	7	3	1
Rubus L. sp. bramble										P (17)					0	0	7	1	1
Hamamelis virginiana L. witch-hazel		P										P			0	0	0	0	0
Sambucus pubens Michx. red-berried elder							P			P					0	0	0	0	0
Diervilla lonicera Mill. bush-honeysuckle										P (17)			P		0	0	0	1	0
Alnus rugosa (Du Roi) Spreng. speckled alder												P			0	0	0	0	0
Chimaphila umbellata (L.) Bart. pipsissewa												P			0	0	0	0	0
Comptonia peregrina (L.) Coult. sweet fern										P					0	0	0	0	0

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Table 21. continued

	GI	CE	CH	HI	WM	BH	BHH	PM	BW	OP	II	TL	RI	C	Density /m²	Density %	%C	%F	%IV
Myrica pensylvanica Loisel. bayberry										P				0	0	0	0	0	
Rhododendron canadense (L.) Torr. rhodora					P									0	0	0	0	0	
Rubus idaeus L. raspberry													P	0	0	0	0	0	
Total Shrubs/m²	1.01	2.95	.15	.15	.30	.20	.10	.05	.10	.21	.05	2.30	0	0	.53				
Herbs:																			
Maianthemum canadense Desf. false lily-of-the-valley	.85 80	P 60	2.75 100		1.07 80	P 60	1.05 100	P	P	12.67 100	3.67 80	1.65 100	3.15 80	3.90 100	2.91	35	79	67	13
Trientalis borealis Raf. star-flower	4.35 100		.05 80	P 40	.70 60	.15 40	5.75 80	P 20	P	.21 100	.15 80	.10 40	.05 60	.15 80	.83	10	86	56	11
Coptis groenlandica (Oeder) Fern. goldthread	34.90 100		P 60		.45 40	P 20					P 20	P 80	P	P 60	2.52	30	50	27	8
Cornus canadensis L. bunchberry	6.85 80	P 20			.55 80	P 20			P	.08 50	.05 80	.10 40	P 20	P 60	.54	6	64	32	7
Aralia nudicaulis L. wild sarsaparilla	2.25 80		P 40			P	P 20	P	P 20	.50 67	P	.10 60		P	.20	2	43	20	5

Table 21. continued

	GI	CE	CH	HI	WM	BH	BHH	PM	BW	OP	II	TL	RI	C	Mean Density /M²	%	% C	% F	% IV
Aster acuminatus Michx. cut-leaf aster					P	P (20)	P (20)	P		P (33)	P (20)	P (20)	P (40)	P (40)	0	0	50	14	5
Monotropa uniflora L. Indian-pipe			P		P (80)	P (20)	P (20)				P (20)	P (20)	P (40)	P	0	0	43	14	4
Linnaea borealis L. twinflower			P				P (60)			188 (50)	P (20)	P (20)	P (40)	P	.13	1	36	14	4
Clintonia borealis (Ait.) Raf. bluebead-lily	P (20)	P	.05 (20)		P (20)						.70 (80)	P (20)	.60 (60)		.10	1	43	16	4
Gaultheria hispidula (L.) Bigel. creeping snowberry		.15 (20)	P (20)		310 (80)						P (20)	P	P (40)		.23	3	36	13	4
Oxalis montana Raf. common wood-sorrel			P (20)		P (20)						.90 (60)		230 (80)	P (20)	.23	3	36	14	4
Vaccinium vitis-idaea L. mountain-cranberry					140 (80)	P (20)				P (33)	P (60)		P	P	.10	1	29	14	3
Cypripedium acaule Ait. common lady's-slipper	15 (40)	P (20)	P (40)									P (40)			.01	0	29	10	3
Carex L. sp. sedge						P (20)	P (20)			P (17)			P (40)		0	0	29	7	3
Gaultheria procumbens L. teaberry		335 (60)	P			P						155 (60)			.35	4	14	9	.2

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Table 21. continued

	GI	CE	CH	HI	WM	BH	BHH	PM	BW	OP	II	TL	RI	C	Mean Density /M²	%	% C	% F	% IV
Mitchella repens L. partridge-berry	.35 (40)	P (--)	P (40)									.20 (40)			.04	0	21	9	2
Medeola virginiana L. Indian cucumber-root		P (20)	P (20)			P						.20 (40)			.01	0	21	6	2
Deschampsia caespitosa (L.) Beauv. tufted hairgrass		P (20)			P (20)					P (33)			P		0	0	21	5	2
Viola L. spp. violets				P (40)		P	P (20)						P		0	0	14	4	1
Festuca rubra L. fescue-grass		P (20)				P				P (50)					0	0	14	5	1
Trillium undulatum Willd. painted trillium						P					P (20)	P (40)			0	0	14	4	1
Epigaea repens L. trailing arbutus		110 (60)										.25 (20)			.10	1	14	6	1
Carex deflexa Hornem. sedge							.70 (40)			P (17)					.05	1	14	4	1
Aster umbellatus Mill. flat-top aster							P (20)			.25 (17)					.02	0	7	3	1
Polygala paucifolia Willd. fringed polygala												P (20)	P		0	0	7	1	1

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Table 21. continued

	GI	CE	CH	HI	WM	BH	BHH	PM	BW	OP	II	TL	RI	C	Mean Density /M²	%	% C	% F	% IV
Streptopus roseus Michx. twisted-stalk			P (20)									P (20)			0	0	14	3	1
Prenanthes L. sp. rattlesnake-root											P		P (20)		0	0	7	1	1
Danthonia spicata (L.) Beauv. poverty-grass							P (40)			P (17)					0	0	14	4	1
Solidago rugosa Ait. wrinkled goldenrod							.55 (20)								.04	0	7	1	1
Erechtites hieracifolia (L.) Raf. fireweed				.10 (20)											.01	0	7	1	1
Monotropa hypopithys L. Pine-sap									P (20)						0	0	7	1	1
Viola conspersa Reichenb. American dog-violet										P (17)					0	0	7	1	1
Pyrola secunda L. one-sided pyrola											P (20)				0	0	7	1	1
Carex communis Bailey sedge							P (20)								0	0	7	1	1
Festuca ovina L. sheep's-fescue grass							P (20)								0	0	7	1	1

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Table 21. continued

	GI	CE	CH	HI	WM	BH	BHH	PM	BW	OP	II	TL	RI	C	Mean Density /M²	%	% C	% F	% IV
Agrostis alba L. redtop grass							P (20)								0	0	7	1	1
Goodyera pubescens (Willd.) R. Br. downy rattlesnake-orchid			P									P			0	0	0	0	0
Hieracium L. spp. hawkweed			P							P					0	0	0	0	0
Carex pensylvanica Lam. sedge						P				P					0	0	0	0	0
Veratrum viride Ait. false hellebore				P											0	0	0	0	0
Hieracium aurantiacum L. orange hawkweed										P					0	0	0	0	0
Viola adunca Sm. violet										P					0	0	0	0	0
Viola fimbriatula Sm. pasture violet			P												0	0	0	0	0
Aster macrophyllum L. large-leaved aster										P					0	0	0	0	0
Fragaria virginiana Duchesne wild field strawberry										P					0	0	0	0	0

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Table 21. continued

	GI	CE	CH	HI	WM	BH	BHH	PM	BW	OP	II	TL	RI	C	Mean Density /M²	%	% C	%F	% IV
Moneses uniflora (L.) Gray one-flowered pyrola													P		0	0	0	0	0
Melampyrum lineare Desr. cow-wheat												P			0	0	0	0	0
Circaea alpina L. dwarf enchanters-nightshade													P		0	0	0	0	0
Lycopus uniflorus Michx. bugleweed													P		0	0	0	0	0
Erigeron L. sp. fleabane													P		0	0	0	0	0
Carex brunnescens (Pers.) Poir. sedge													P		0	0	0	0	0
Carex trisperma Dew. sedge													P		0	0	0	0	0
Panicum lanuginosum Ell. panic-grass			P												0	0	0	0	0
Total Herbs/m²	9.70	460	285	.10	727	.15	1805	0	0	1559	547	415	6.10	405	842				
Pteridophytes:																			
Osmunda cinnamomea L. cinnamon-fern	115 (100)	P (20)	P (20)	P (20)		P					P (20)	P	P	P (20)	.08	53	43	14	33

Table 21. continued

	GI	CE	CH	HI	WM	BH	BM	HP	M	BW	OP	II	TL	RI	C	Mean Density /M²	% C	% F	% IV
Dryopteris spinulosa americana (Fisch.) Fern. mountain wood-fern					.35 (20)		P (40)				P (17)	P (20)	P (40)	P	P	.02	13	29	10	16
Pteridium aquilinum (L.) Kuhn bracken		.20 (40)	P	P (20)		P				P	P		.15 (20)			.02	13	21	6	12
Dennstaedtia punctilobula (Michx.) Moore hay-scented fern				.10 (40)		.25 (20)								P (20)		.02	13	21	6	12
Dryopteris spinulosa intermedia (Muhl.) Underw. evergreen wood-fern			P	P	P		P (17)				P	P				0	0	21	6	8
Polypodium virginianum L. rock-polypody fern			P			P (20)					P (33)		P (20)			0	0	21	5	8
Lycopodium clavatum L. common club-moss						.20 (20)										.01	7	7	1	4
Lycopodium obscurum dendroideum (Michx.) D. C. Eat. round-branch ground-pine						P				P (20)			P			0	0	7	1	2
Osmunda regalis L. royal fern	P (20)															0	0	7	1	2

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Table 21. continued

	GI	CE	CH	HI	WM	BH	BHH	PM	BW	OP	II	TL	RI	C	Mean Density /M²	%	% C	% F	% IV
Osmunda Claytoniana L. interrupted fern										P (17)					0	0	7	1	2
Lycopodium annotinum L. interrupted club-moss						P						P			0	0	0	0	0
Lycopodium lucidulum Michx. shining club-moss			P										P		0	0	0	0	0
Dryopteris Phegopteris (L.) Christens. long beech-fern											P				0	0	0	0	0
Equisetum sylvaticum L. wood horsetail											P				0	0	0	0	0
Total Pter./m²	1.15	.20	0	.10	.35	.45	0	0	0	0	0	.15	0	0	.15				

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this forest type, and they did not form a distinct stratum. An overall mean density of .53 ± .21 stems per square meter was found.

An herb stratum sometimes was present, although it was usually sparse. As was the case for shrubs, herbs were distributed with contagion. The overall mean density of herbs and pteridophytes was 8.57 ± 3.59 stems per square meter. The most numerous species were small-sized herbs, and their density must be evaluated with this in mind. The five most important were false lily-of-the-valley (Maianthemum canadense), star-flower (Trientalis borealis), goldthread (Coptis groenlandica), bunchberry (Cornus canadensis), and wild sarsaparilla (Aralia nudicaulis).

Ground Cover Bryophytes and Lichens:

A prominent feature of most coastal spruce-fir stands is a mat of bryophytes and lichens which covers much of the ground. The species composing this mat are listed in Table 22, where their percentage cover and quadrat frequency are indicated for each stand. Species are listed in order of their importance values. In this case importance value was derived for each species as follows:

$$\%IV = \frac{10(\text{mean \% cover}) + \text{mean frequency} + \text{constance}}{\text{Sum \%IV all species}} \times 100$$

The five most important species were Calliergonella schreberi, Bazzania trilobata, Ptilidium pulcherrimum (incl. P. ciliare),

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Table 22. Ground cover Bryophytes and Lichens. Major substrata indicated: h, humus; w, rotten wood; t, treebase; r, rock. Cover data are based on 20-meter L-shaped transects, each on the edge of a 10 x 10 meter quadrat. For each species at each stand two figures are entered in the table. The upper one represents relative ground-cover (%), and the lower one the frequency of occurrence (%) in the quadrats. P = present in stand but not tallied in sample units. Data are summarized in terms of: $\bar{\%c}$ = mean relative cover; $\bar{\%F}$ = mean relative frequency; and %C = constance. Constance is based on only the first four quadrats sampled in each stand, except Gerrish Island where only three were run. Frequencies based only on tallies, subsequent to the fourth quadrat are underlined. % I.V. = relative importance value, defined in text. An asterisk (*) precedes each lichen name.

SPECIES	Substratum	RELATIVE COVER AND FREQUENCY (%) Stands and Number of Samples in Each														SUMMARY			%IV
		GI 3	CE 5	CH 4	HI 4	WM 5	BH 5	BHH 5	PM 6	BW 6	OP 9	II 5	TL 4	RI 5	C 4	$\bar{\%c}$	$\bar{\%F}$	%C	
Calliergonella schreberi (Bry. Eur.) Grout	h		2.1 80	3.6 100	9.2 100	38.0 100	.2 100	29.8 100	.2 100	12.2 100	23.0 100	9.4 80	.1 75	17.4 100	26.9 100	12.29	88	93	16.9
Bazzania trilobata (L.) S. F. Gray	h	.2 100	.1 100	P 50	.9 50	20.0 100	.8 80	P 40	5.5 100	5.8 100	P 33	19.6 100	2.8 100	12.8 100	.9 50	4.95	79	100	8.1
Ptilidium pulcherrimum (Web.) Hampe (inc. P. ciliare (L.) Nees)	h, t, w	.1 67	1.2 100	.9 100	11.1	9.4 100	8.4 100	3.6 100	.2 83	2.2 100	12.3 100	.2 80	.1 100	.3 100	3.3 100	3.81	95	100	6.9
Dicranum scoparium Hedw.	h, w	P 100	1.3 100	.4 100	2.3 100	.6 100	.4 80	6.4 100	1.0 100	3.5 100	3.9 100	1.8 100	2.3 75	6.5 100	7.2 100	2.69	97	100	5.6
Hylocomium splendens (Hedw.) Bry. Eur.	h		P	P	.3 25	2.8 60	P 20	3.2 100	P 17	2.0 100	.8 78	7.4 100	P 75	7.4 100	17.2 100	2.94	55	79	5.1
Dicranum rugosum (Hoffm.) Brid.	h		3.1	P	4.4	1.6	P	2.4	P	3.9	2.8	1.0	3.4	4.4	.1	1.95	68	86	4.2

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Table 22. continued

SPECIES		GI	CE	CH	HI	WM	BH	BHH	PM	BW	OP	II	TL	RI	C	%c	%F	%C	%IV
Hypnum imponens Hedw.	h,t r,w	P 100	.1 80	.1 100	5.2 100	.4 80	.2 100	.7 80	6.7 100	.9 100	.11 56	1.5 100	.2 100	2.8 100	.6 75	1.39	91	100	3.9
* Cladonia squamosa (Scop.) Hoffm.	h	P 100	.4 100	.5 100	3.6 100	.41 100	1.0 100	.7 100	.8 83	.3 83	.3 89	.2 100	.5 100	.4 80	P 100	.66	95	100	3.1
* Cladonia chlorophaea (Flk.) Spreng.	h,w	.12 100	2.0 100	.3 100	.2 100	P 100	.4 100	.4 100	P 83	.3 100	.2 78	.1 40	.1 50	P 80	.1 75	.29	86	100	2.6
Dicranum montanum Hedw.	w,h t	P 100	P 60	P 100	.1 100	.4 100	.4 100	.2 100	.5 83	.2 100	.2 89	.4 80	.2 75	.1 80	P 75	.20	89	100	2.5
Lepidozia reptans (L.) Dumort.	w,h	P 33	.4 100	.1 100	P 50	P 100	P 100	.1 60	.4 100	.4 100	.1 67	.6 100	P 75	.3 100	.3 100	.19	85	100	2.4
Leucobryum glaucum (Hedw.) Schimp.	h,w	P 67	.2 100	.4 100	P 100	.3 40	P 100	.2 80	P 50	.2 83	P 11	.4 60	.2 100	.1 60	P 25	.14	70	100	2.2
Tetraphis pellucida Hedw.	w	P 67	.1 60	P 50	P 75	P 80	P 100	.1 40	P 67	P 33	.1 78	.2 40	P 75	.2 80	.1 100	.06	68	100	2.1
* Cladonia rangiferina (L.) Web.	h		.1 40	P	P 75	P 60	.1 60	P 20	.11 33	.5 67	.8 67	P 40	P 50	P 20	P	.19	38	79	1.6
Dicranum flagellare Hedw.	h	P 100	.3 40	P 50			.1 80	P	P 50	.4 67	.1 22	P 20	.7 75	.1 20	.5 50	.16	41	79	1.6
Lophocolea heterophylla (Schrad.) Dumort.	w,h t	P 67		.1 100	P 25	P 60	P 80	P	P 80	P 83	P 22	P 40	P	P 80	P 75	.01	51	79	1.6
Dicranum fuscescens Turn.	h			.1 100	P 25	P 80	P 40	.3 20	.3 83	P 83	.2 22	.1 20	.1 75	.4 60		.11	43	71	1.5

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Table 22. continued

SPECIES	Substratum	GI	CE	CH	HI	WM	BH	BHH	PM	BW	OP	II	TL	RI	C	%c	%F	%C	%IV
Polytrichum commune Hedw.	h		P 20	.2 50	1.1 100	.1 80	P 40	.2 100		P	P 33	P	.1 50		1.1 50	.20	37	64	1.4
Jamesoniella autumnalis (DC) Steph.	r		P	P	P		P	P	.1	P	P	P	P	P	P	.01	33	79	1.3
	h,w		40	50	25		40		83	33	33	20	75	40	25				
Nowellia curvifolia (Dicks.) Mitt.	w					P 60	P 60		P 17	P 83	P 11	.3 80	P 25	.2 100	P 75	.04	37	64	1.3
* Cladonia cristatella Tuck.	h,w		.1 40	P 75	.3 50	P 20	P 40	P 20	P 17		P 33		P	P 40	P 25	.03	26	71	1.2
* Cladonia gracilis (L.) Willd.	h		.2 40	P	.2 25	.1 40	P 40		.1 17	.1 83	.3 33	P 20		P	P 25	.07	23	64	1.1
Hypnum reptile Michx.	t,h	P		P		P	P	P	P		P	.1	P	P		.01	23	57	1.0
	w	33		50		20	80		67		22	20	25						
Sphagnum girgensohnii Russow	h					2.5 40	P 20			P		P 20	P	.4 40	1.0 50	.28	12	36	0.9
Brotherella recurvans (Michx.) Fleisch.	h,w		P 20	.6 50		P 40	P 40		P 50	P	P 11		P 75		P 25	.04	22	50	0.9
Plagiothecium turfaceum (Lindb.) Lindb.	w,h	.1 67		P 50		P 20	P			P 33		.1 20		P 20	P 75	.01	20	50	0.8
Hypnum fertile Sendt.	t,w							P	P	P	P	.6		P	P	.04	12	43	0.7
	h								33	17	11	40		40	25				
Plagiothecium denticulatum (Hedw.) Bry.Eur.	w,h		P 60	P 75	P 25	P	P 20	P	P 33		P 22	.1 60		P		.01	21	36	0.7

Table 22. continued

SPECIES	Sub-stratum	GI	CE	CH	HI	WM	BH	BHH	PM	BW	OP	II	TL	RI	C	%c	%F	%C	%IV
Cephalozia Dumort. sp.	w					P 20	P		P 17	P 17	P	P	P 25	.1 40	P 25	.01	10	43	0.6
Drepanocladus uncinatus (Hedw.) Warnst.	w,h			P 25	P 25			P	P 17	P	P 11	P 20		.2		.01	8	43	0.6
Cephalozia catenulata (Huben.) Spruce	w					P 20					P	.1 20	P 25	.1 100	P 25	.01	14	36	0.6
Dicranum majus Smith	h											1.2 20		1.7 40	P 25	.21	6	21	0.6
Hypnum crista-castrensis Hedw.	h			P	P	.2 20		.7 40				P 20		.2 80		.08	11	29	0.6
Rhytidiadelphus triquetrus (Hedw.) Warnst.	h			.6 50				.4 80				P 20		P 20		.07	12	29	0.6
Hypnum cupressiforme (typical) Hedw.	t				P 25	P		.1 20		P	P 22		P 25	P 20		.01	8	36	0.5
Plagiothecium striatellum (Brid.) Lindb.	t,h	.1 67		P 50		P 20			P 33					P	P 25	.01	14	29	0.5
Plagiothecium elegans (Hook.) Sull.	h,w			P 50		P	P 60		P 17			.1 20				.01	10	29	0.5
Odontoschisma Dumort sp.						P 20				P 17		.1 20		P 60		.01	8	29	0.4
Calypogeia Raddi spp.				P 25		P				P			P 25	P 40	P 25	-	8	29	0.4

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Table 22. continued

SPECIES	Sub-stratum	GI	CE	CH	HI	WM	BH	BHH	PM	BW	OP	II	TL	RI	C	%c	%F	%C	%IV
Odontoschisma prostratum (Sw.) Trevis.	w			P 25					P 17		P		P 50	P 20		-	8	29	0.4
Heterophyllium haldanianum (Grev.) Kindb.	h,w		P 20	.6 50	P 25			P								.04	7	21	0.4
Mnium hornum Hedw.	h,w			P		P 20				P 17	P 11	P	P 25	P	P 50	-	9	21	0.4
Cephaloziella (Spruce) Schiffn. sp.				P 25						P		.1 60			P 25	.01	8	21	0.4
Brachythecium starkei (Brid.) Bry. Eur.	h,w		P 20		P 25						P 11	.5 20				.04	5	21	0.4
Blepharostoma trichophyllum (L.) Dumort.						P 40							P 25		P 50	-	8	21	0.3
Aulacomnium androgynum Schwaegr.				P 25	P 50						P 22			P		-	7	21	0.3
Lophozia Dumort sp.									P 33				P 25	P 20		-	6	21	0.3
Scapania nemorosa (L.) Dumort.						P 20	P		.1	P 17			P	P	P 25	.01	4	21	0.3
Dicranum drummondii C. Mull.				P 25			P 20						P 25			-	5	21	0.3
Dicranum fulvum Hook.					P 25						P 11				P 25	-	4	21	0.3

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Table 22. continued

SPECIES	Sub-stratum	GI	CE	CH	HI	WM	BH	BHH	PM	BW	OP	II	TL	RI	C	%c	%F	%C	%IV
Frullania asagrayana Mont.	t							P		P 17	P 11	P		P 20		-	3	21	0.3
Sphagnum capillaceum (Weiss) Schrank	h		P 60			P							P 25	P		-	6	14	0.2
Odontoschisma denudatum (Mart.) Dumort.	w	P 33								P 17				P 40		-	6	14	0.2
Pohlia nutans (Hedw.) Lindb.				P 25			P 20								P 25	-	5	14	0.2
Lophozia gracilis (Schleich) Steph.						P 40							P 25			-	5	14	0.2
Onchophorus wahlenbergii Brid.													P 25		P 50	-	5	14	0.2
* Dimerella diluta (Pers.) Trev.			P	P 50							P 22					-	5	14	0.2
Tetraphis geniculata Girgens.	w									P 17	P			P 40		-	4	14	0.2
Sphagnum palustr. L.	h	P 33			P 25									P		-	4	14	0.2
Lophocolea Dumort sp.									P 33		P 22					-	4	14	0.2
* Lecidea (Ach.) Zahl. sp.						P 20	P 40									-	4	14	0.2

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Table 22. continued

SPECIES	Sub-stratum	GI	CE	CH	HI	WM	BH	BHH	PM	BW	OP	II	TL	RI	C	%c	%F	%C	%IV
Frullania Raddi sp.									P 17	P			P 25			-	3	14	0.2
Radula complanata (L.) Dumort.	w,h								P 17	P				P 20		-	3	14	0.2
Eurhynchium strigosum (Hoff.) Bry. Eur.									P 17					P 20		-	3	14	0.2
Mnium cuspidatum Hedw.									P 17			P 20				-	3	14	0.2
* Cladonia caroliniana (Schwein.) Tuck.						P 20	P 20									-	3	14	0.2
* Bacidia DNot.em.Zahl.sp.					.8 50											.06	4	7	0.2
Platygyrium repens (Brid.) Bry. Eur.											P 11			P 20		-	2	14	0.2
Sphagnum squarrosum Crome.														.9 20		.06	1	7	0.2
Andreaea rupestris Hedw.									.5 33							.04	2	7	0.2
Sphagnum magellanicum Brid.		P 67												P		-	5	7	0.1
Riccardia palmata (Hedw.) Carruth.	w													P 60		-	4	7	0.1

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Table 22. continued.

SPECIES	Sub-stratum	GI	CE	CH	HI	WM	BH	BHH	PM	BW	OP	II	TL	RI	C	%c	%F	%C	%IV
Cephalozia bicuspidata (L.) Dumort.															P 50	-	4	7	0.1
* Cladonia turgida (Ehrh.) Hoffm.									P 50							-	4	7	0.1
Lophocolea cuspidata (Nees) Limpr.						P						P 40				-	3	7	0.1
Lophozia ventricosa (Dicks.) Dumort.						P 40	P									-	3	7	0.1
* Peltigera polydactyla (Neck.) Hoffm.										P				P 40		-	3	7	0.1
Polytrichum juniperinum Hedw.	h		P		P		P	P 20			P 11			P	P	-	2	7	0.1
Hypnum pallescens (Hedw.) Bry. Eur.	t				P 25			P			P					-	2	7	0.1
Hypnum curvifolium Hedw.														.1 20		.01	1	7	0.1
Lophocolea bidentata (L.) Dumort.														.1 20		.01	1	7	0.1
Brachythecium Bry. Eur. sp.					P 25											-	2	7	0.1
Plagiothecium sylvaticum (Brid.) Bry. Eur.					P 25											-	2	7	0.1

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Table 22. continued

SPECIES	GI	CE	CH	HI	WM	BH	BHH	PM	BW	OP	II	TL	RI	C	%c	%F	%C	%IV
* Cladonia furcata (Huds.) Schrad.												P 25			-	2	7	0.1
* Parmelia physodes (L.) Ach.						.1 20									.01	1	7	0.1
Mnium punctatum Hedw.									P				P 20		-	1	7	0.1
Anastrophyllum michauxii (Web.) Buch								P 17							-	1	7	0.1
Brachythecium velutinum (Hedw.) Bry. Eur.								P 17							-	1	7	0.1
Eurhynchium serrulatum (Hedw.) Kindb.													P 20		-	1	7	0.1
Sphagnum recurvum var. tenue H. Klinggr.													P 20		-	1	7	0.1
* Cladonia coniocraea (Flk.) Sandst.							P	cfP. 17		P			P		-	1	7	0.1
* Cladonia uncialis (L.) Web.			P			P 20			P	P					-	1	7	0.1
* Cladonia cf. sylvatica (L.) Hoffm.										P 11					-	1	7	0.1
Thuidium delicatulum (Hedw.) Mitt.							P		P	P 11	P	P			-	1	-	-

Table 22. continued

SPECIES	GI	CE	CH	HI	WM	BH	BHH	PM	BW	OP	II	TL	RI	C	%c	%F	%C	%IV
Polytrichum ohioense Ren. & Card.					P 20								P		-	1	-	-
Sphagnum L. sp.	P	P					P								-	-	-	-
Dicranella heteromalla (Hedw.) Schimp.					P								P		-	-	-	-
Geocalyx graveolens (Schrad.) Nees							P		P						-	-	-	-
Aulacomnium palustre (Web. & Mohr) Schwaegr.			P												-	-	-	-
Brachythecium salebrosum (Web. & Mohr) Bry. Eur.					P										-	-	-	-
Bryhnia novae-angliae (Sull. & Lesq.) Grout							P								-	-	-	-
Cephalozia media Lindb.										P					-	-	-	-
Dicranum spurium Hedw.							P								-	-	-	-
Frullania eboracensis Gottsche									P						-	-	-	-
Lophozia longidens (Limdb.) Macoun					P										-	-	-	-
Paraleucobryum longifolium (Hedw.) Loeske					P										-	-	-	-

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Table 22. continued

SPECIES	GI	CE	CH	HI	WM	BH	BHH	PM	BW	OP	II	TL	RI	C	%c	%F	%C	%IV
Ulota Mohr sp.						P									-	-	-	-
* Cladonia caespiticia (Pers.) Flk.							P			P					-	-	-	-
* Cladonia (Hill.)Vain. sp.			P									P			-	-	-	-
* Lecidea vernalis (L.) Ach.			P		P										-	-	-	-
* Cladonia alpestris (L.) Rabh.									P						-	-	-	-
* Cladonia grayi Merr.							P								-	-	-	-
* Leptogium cyanescens (Ach.) Kbr.									P						-	-	-	-
* Lopadium pezizoideum (Ach.) Kbr.					P										-	-	-	-
* Parmelia enteromorpha Ach.						P									-	-	-	-
* Peltigera aphthosa (L.) Willd.													P		-	-	-	-

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Hylocomium splendens, and Dicranum rugosum. The overall mean ground cover was 33.2 ± 6.3%. The remainder of the ground was covered by tree bases and litter. Underneath the ground cover mat was a variety of substrata such as humus, rotten wood, and rocks. Certain species were found regularly only on certain of these, and this characteristic is also included in Table 22.

Corticolous Lichens and Bryophytes:

Table 23 lists corticolous lichens and bryophytes in terms of stand presence and tree species surfaces. No special effort was made to collect the species on trees other than red and white spruce. Thus, these results can only be considered complete for the regularly occurring epiphytes on that genus. Distributional comments in the table were contributed by Mason E. Hale. These comments will be discussed later.

Other Plant Records:

Certain species which I did not record were found to be present in the coastal spruce-fir forests by Hill (1923) and Moore and Taylor (1927). These were Cladonia fimbriata, Cladonia pyxidata, Peltigera canina, Crocynia lanuginosa, Dryopteris disjuncta, Viola blanda, Solidago macrophylla, and Ribes glandulosum.

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Table 23. Corticolous Lichens and Bryophytes (*). Collected on trunks and dead branches at 3-8 feet above the ground. Red spruce - r; white spruce - w; balsam-fir - f; red maple - m; paper birch - p; arbor vitae - a. Distributional comments, relative to North America are by Mason E. Hale, Jr.

Species	GI	CE	CH	HI	WM	BH	BHH	BW	OP	RI	C	Distribution
Haematomma ochrophaeum (Tuck.) Mass.	r	r	r	r	r f	r	w	r	r	r	r	N conifer forests, S to N&S C. in mts.
Lopadium pezizoideum (Ach.) Kbr.		r	r	r	r	r a			r	r	r	N, S in the mts.
Parmelia enteromorpha Ach.		r	r		r		w	r	r	r	r	Boreal, S to W. Va. & N& S C. in high mts.; spruce-fir
Parmelia physodes (L.) Ach.	r	r	r	r	r		w		r	r		N, to Ga. in mts.; conifers & maple
Usnea dasypoga (Ach.) Rohl		r	r	r			w	r	r	r	r	N, S to Pa. in mts.; spruce-fir
Parmelia saxatilis (L.) Ach.			r	r	r		w		r	r	r	Cosmo. N temperate; conifers & hardwoods
Alectoria nidulifera Norrl.	r	r	r				w		r	r		N conifers & hardwoods; S to Ga. in mts.
*Frullania asagrayana Mont.				r	r		w	p		r	r	
Cetraria glauca (L.) Ach.					r		w	r	r	r	r	High N, S to Me.; spruce-fir
Crocynia membranacea (Dicks.) Zahl.	r	r	r	r			w				r	Cosmopolitan

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Table 23. continued

Species	GI	CE	CH	HI	WM	BH	BHH	BW	OP	RI	C	Distribution
Cetraria ciliaris Ach.		r			r		w			r	r	N conifers & hardwoods; S to Ga. in mts.
Cladonia (Hill.) Vain. sp.	r				r	r	w	r				
Evernia mesomorpha Nyl.		r	r	r			w		r			N, S to Va. in high mts.
Alectoria americana Mot. (A. jubata (L.) Ach.)							w		r	r	r	N, S to N&S C. in high mts.; spruce-fir
Pertusaria amara (Ach.) Nyl.				r	r		w			r		Cosmopolitan
Usnea comosa (Ach.) Rohl					r		w		r	r		N, S to Pa. in mts.; spruce-fir
Usnea Wigg. sp.			r	r	r		w					
Cetraria tuckermanii Oakes			r			r		r			r	N conifers, S to Ga. in mts.
Chaenotheca chrysocephala (Turn.) Th. Fr.		r	r			r			r			N forests
Mycoblastus sanguinarius (L.) Norm.					r	r			r	r		N, S to Pa. in mts.
Lobaria pulmonaria (L.) Hoffm.							w	m	w			N, S to Ga. in mts.; common on hardwoods

Table 23. continued

Species	GI	CE	CH	HI	WM	BH	BHH	BW	OP	RI	C	Distribution
Parmelia caperata (L.) Ach.			r	r			w					Cosmopolitan temperate & N hardwoods
*Frullania Raddi sp.	r	r	r									
Parmelia sulcata Tayl.				r		r	w					N, to Ga. in mts.
Usnea rubicunda Stirt.			r				w		r			Cosmopolitan
Usnea trichodea Ach.				r				r	r			Cosmopolitan, but commoner N
*Ulota crispa intermedia (Schimp) Grout							mp	mp				
Parmelia crinita Ach.							w				r	Cosmopolitan
Parmelia rudecta Ach.				r			w					Cosmopolitan eastern U.S.
Cladonia chlorophaea (Flk.) Sprong.							r		r			Cosmopolitan
Lecanora Ach. (subfusca group)					f	f						
Lecidea (Ach.) Zahl sp.				r				r				
*Ulota ludwigii Brid								p				
Alectoria nadvornikiana Gyel.										r		N boreal, S to Tenn. in high mts.; spruce-fir

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Table 23. continued

Species	GI	CE	CH	HI	WM	BH	BHH	BW	OP	RI	C	Distribution
Alectoria sarmentosa Ach.										r		N boreal, S to Carolinas in high mts.; spruce-fir
Catillaria (Ach.) Th. Fr. sp.						f						
Cladonia cristatella Tuck.									r			Cosmopolitan
Cladonia squamosa (Scop.) Hoffm.					r							N; S to Ga. in mts.; soil-humus lichen common in conifer forest
Dimerella diluta (Pers.) Trev.							w					Northern
Lecidea cf. vernalis (L.) Ach.						a						Cosmopolitan; northern
Cf. Ochrolechia pallescens (L.) Mass.						r						
Parmelia cladonia (Tuck.) DR.					r							Strictly Appalachians, Ga. to Me.
Parmelia furfuracea (L.) Ach.	r											Northern; to Ga. in mts.
Pertusaria laevigata (Nyl.) Arn.											r	?
Ramalina roesleri (Hochst.) Hue										r		Boreal; S to New England and Great Lakes

Table 23. continued

Species	GI	CE	CH	HI	WM	BH	BHH	BW	OP	RI	C	Distribution
Usnea mutabilis Stirt.		r										Cosmopolitan
Usnea strigosa (Ach.) Eaton		r										Cosmopolitan
*Platygyrium repens (Brid.) Bry. Eur.								r				
*Neckera pennata Hedw.								r				
*Frullania eboracensis Gottsche								p				

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Tree Rings and Height Studies:

In Figures 7-20 the results of tree ring studies are presented. As the borings were taken at breast height, ring counts from them underestimate tree ages. Most of the stands were second growth, having been initiated by lumbering, fire, or the abandonment of agricultural land. Thus, the trees were usually decidedly even-aged. However, where blow-down or deaths in the upper story had taken place during the history of the present stand, secondary age classes had begun. Such age-class diversification was most advanced in the oldest stands. At Western Mountain, the only virgin stand studied, diversification was greatest. In Table 24 the mean ages and age ranges of spruces over eight inches DBH are listed for each stand. Also, the table lists tree heights.

Stand Descriptions and Analyses

There is a considerable amount of information which could not be included in the tabulations, extensive as they are. Much of this information is considered pertinent and important for an understanding of the structure, composition, and dynamics of the coastal forests. The following descriptions may be considered as syntheses of the tabular data plus observations of a more qualitative nature.

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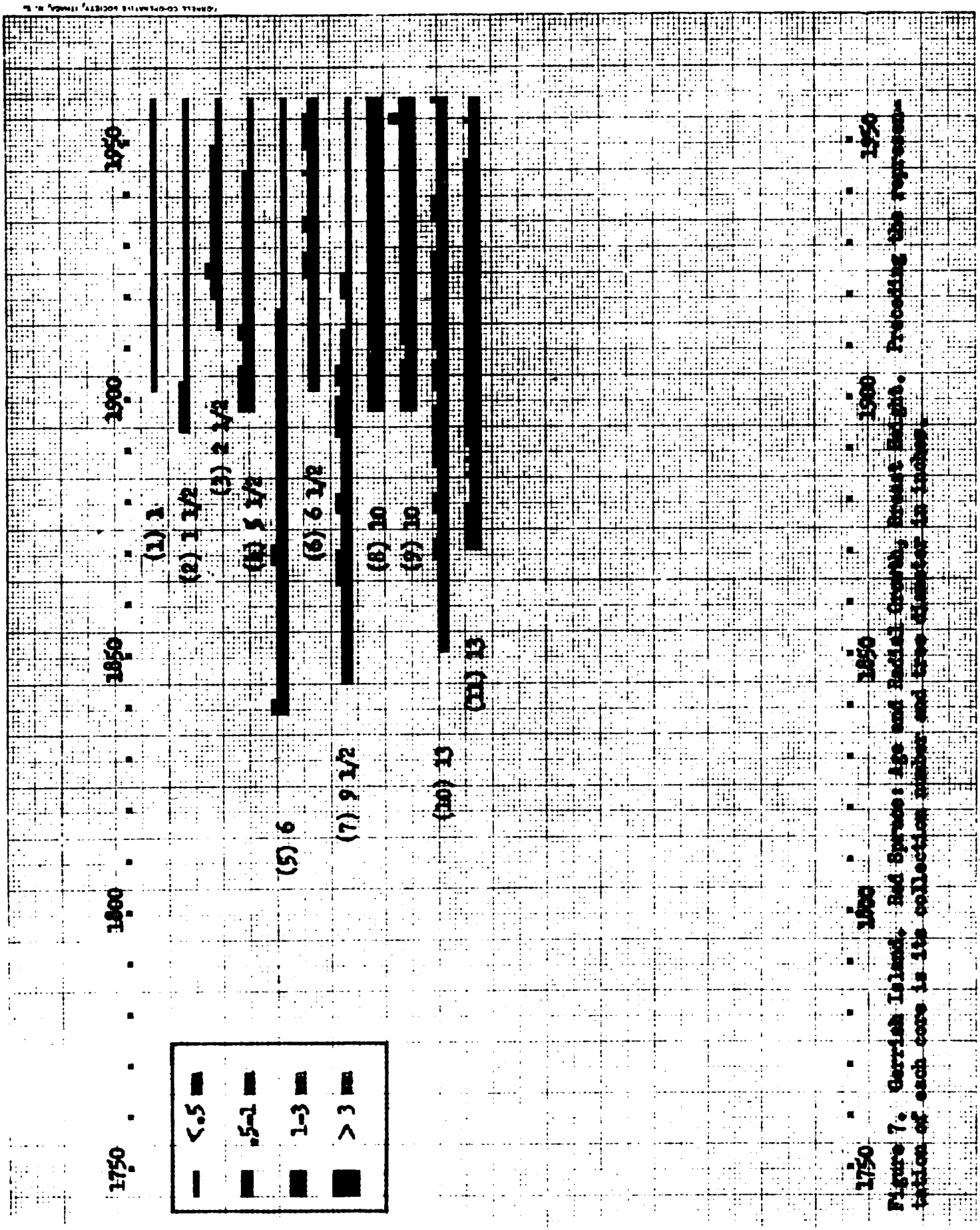


Figure 7. Carrick Island, Bid Stream: Age and Radial Growth Rates Bright. Preceding the reversal-bias of each core is the collection number and the number in brackets

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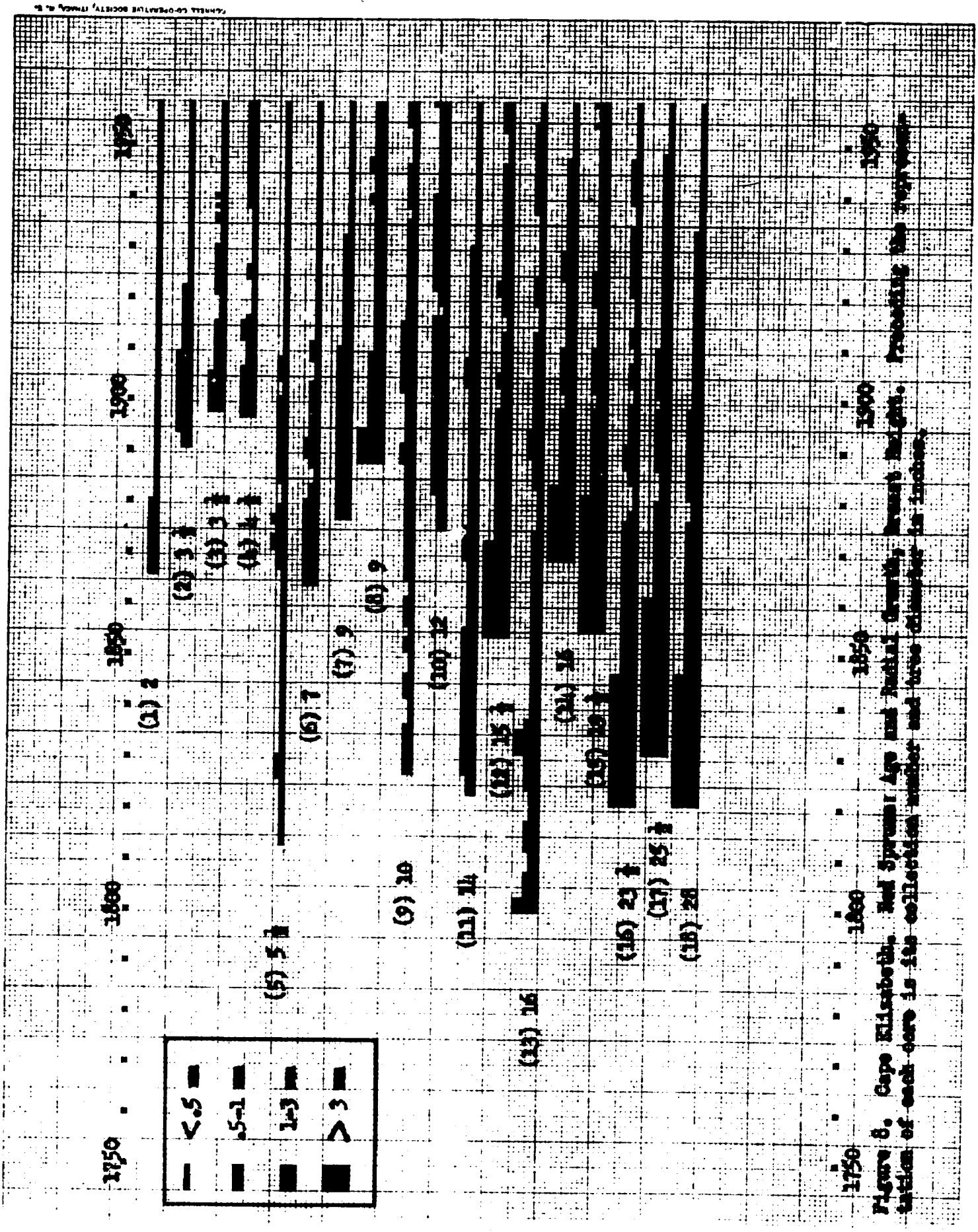
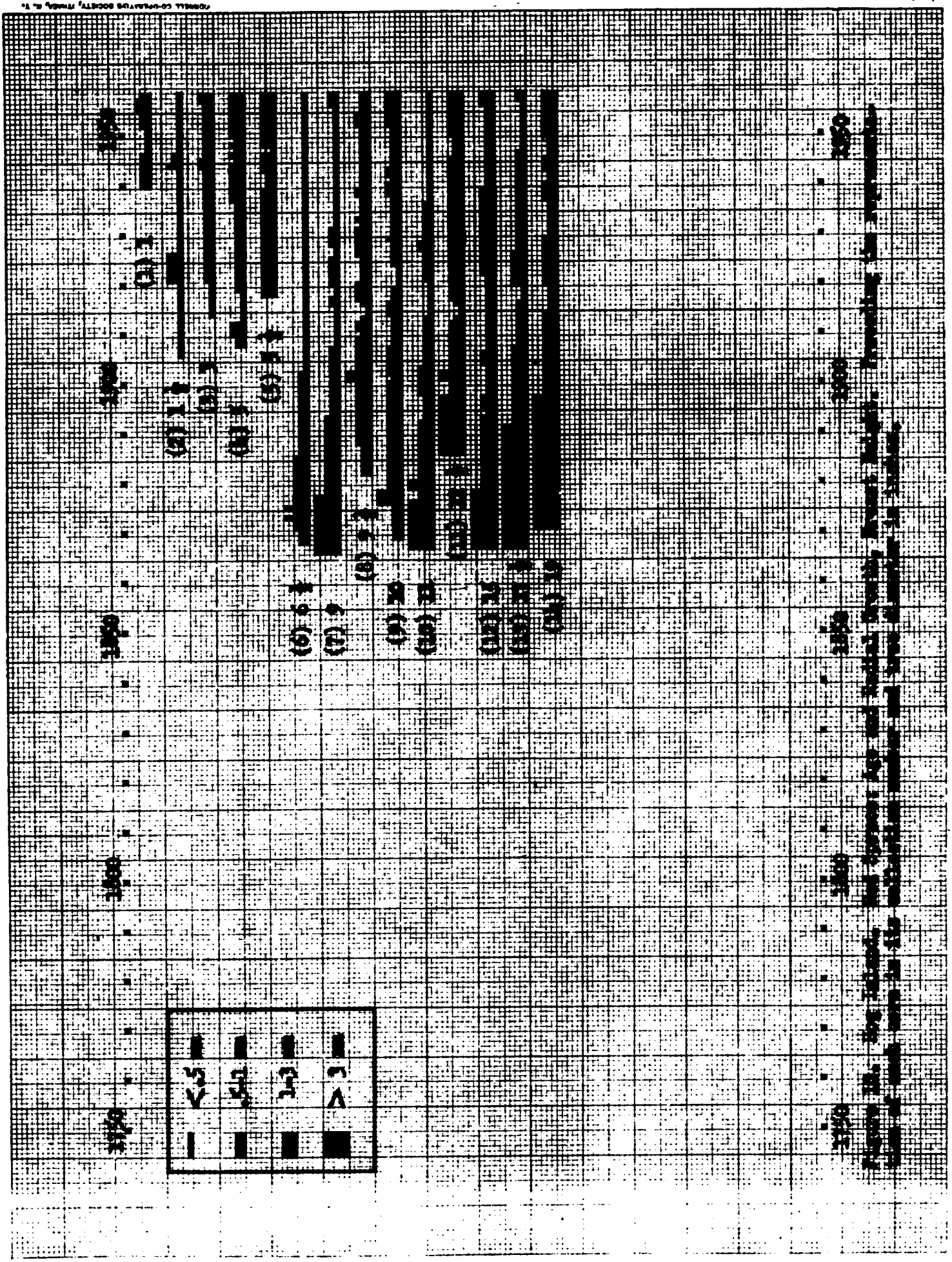


Figure 8. Cape Elizabeth, Red Spruce Age and Depth Chart. Numbers and depth of each core is the collection number and core depth. Presence and extent of each core is the collection number and core depth.

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Figure 9. Cundys Harbor. Red Spruce: Age and Radial Growth, Breast Height. Preceding the representation of each core is its collection number and tree diameter in inches.

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Figure 11. Western Hemlock, Page 1 (cont'd next page). Leaf Survey Data Sheet. See text for explanation of each item. Preceding the representation of each item is the estimated [illegible] in grams.

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Figure 11. Western Mountain, Page 2 (cont'd next page). Red Spruce: Age and Radial Growth, Breast Height. Preceding the representation of each core is its collection number and tree diameter in inches.

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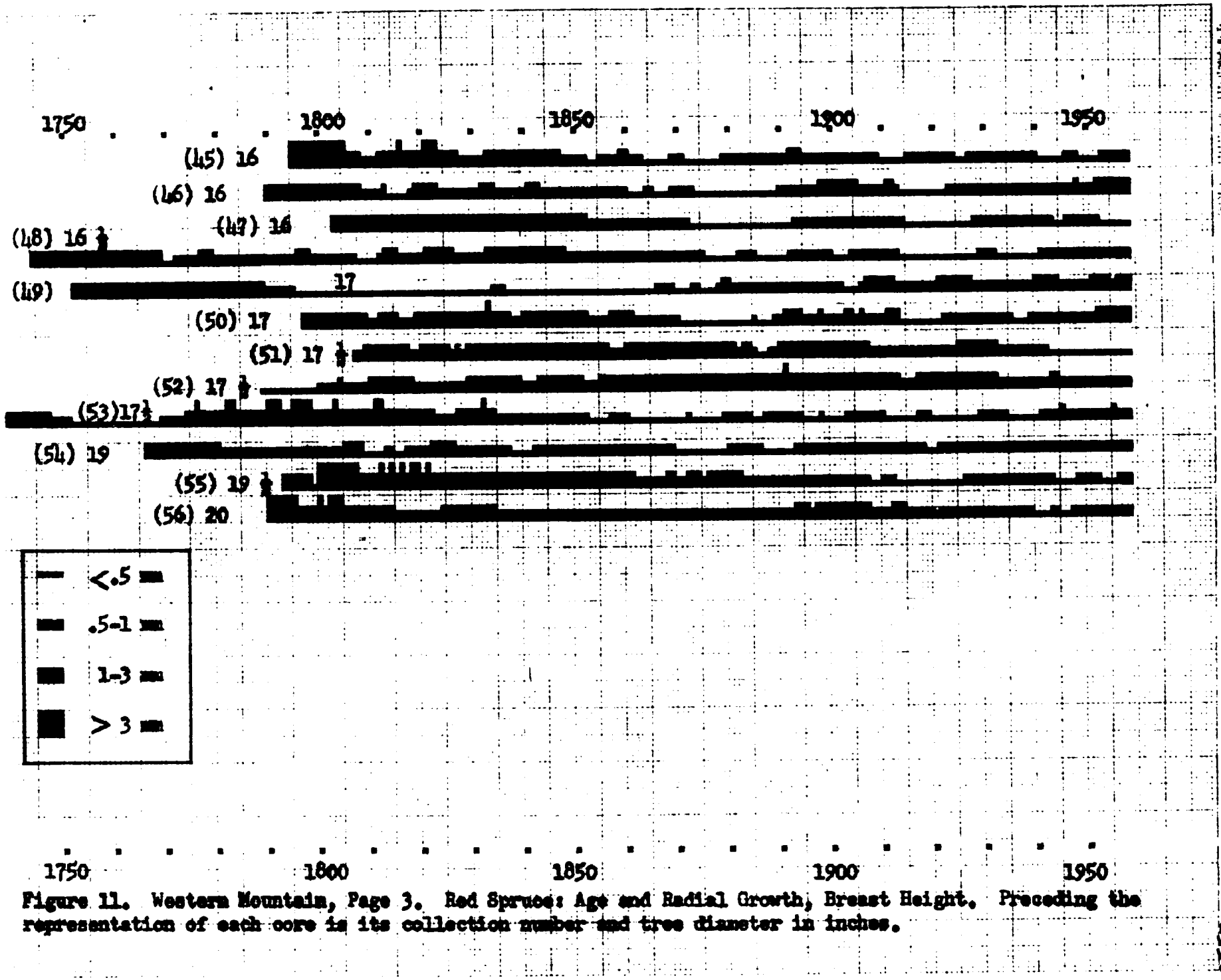


Figure 11. Western Mountain, Page 3. Red Spruce: Age and Radial Growth, Breast Height. Preceding the representation of each core is its collection number and tree diameter in inches.

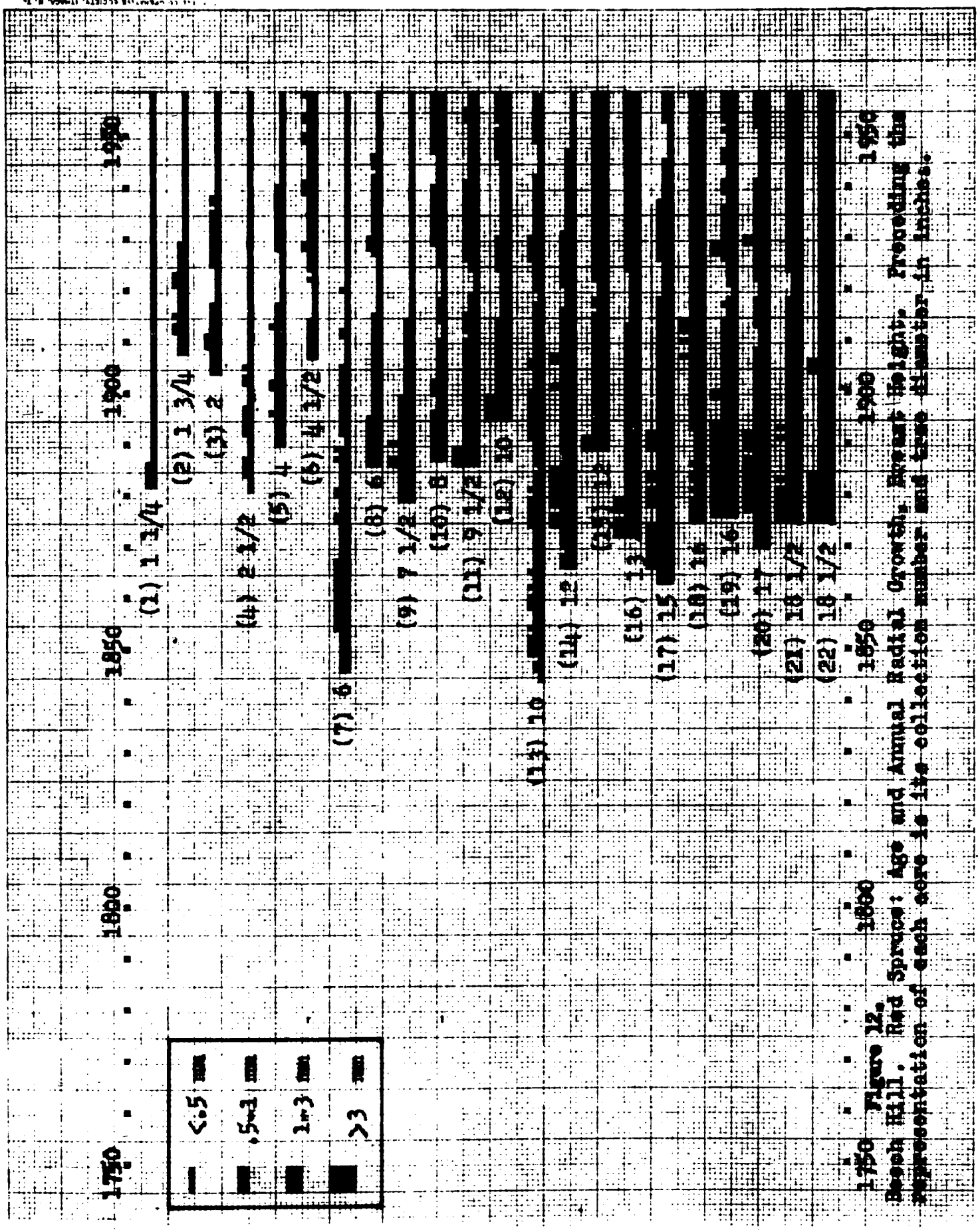


Figure 12. Red Spruce: Age and Annual Radial Growth, Breast Height, Preceding the Presentation of each core to the collection number and the diameter in inches.

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Figure 13. Bass Harbor Head, White Spruce: Age and Radial Growth, Breast Height. Preceding the representation of each core is its collection number and tree diameter in inches.

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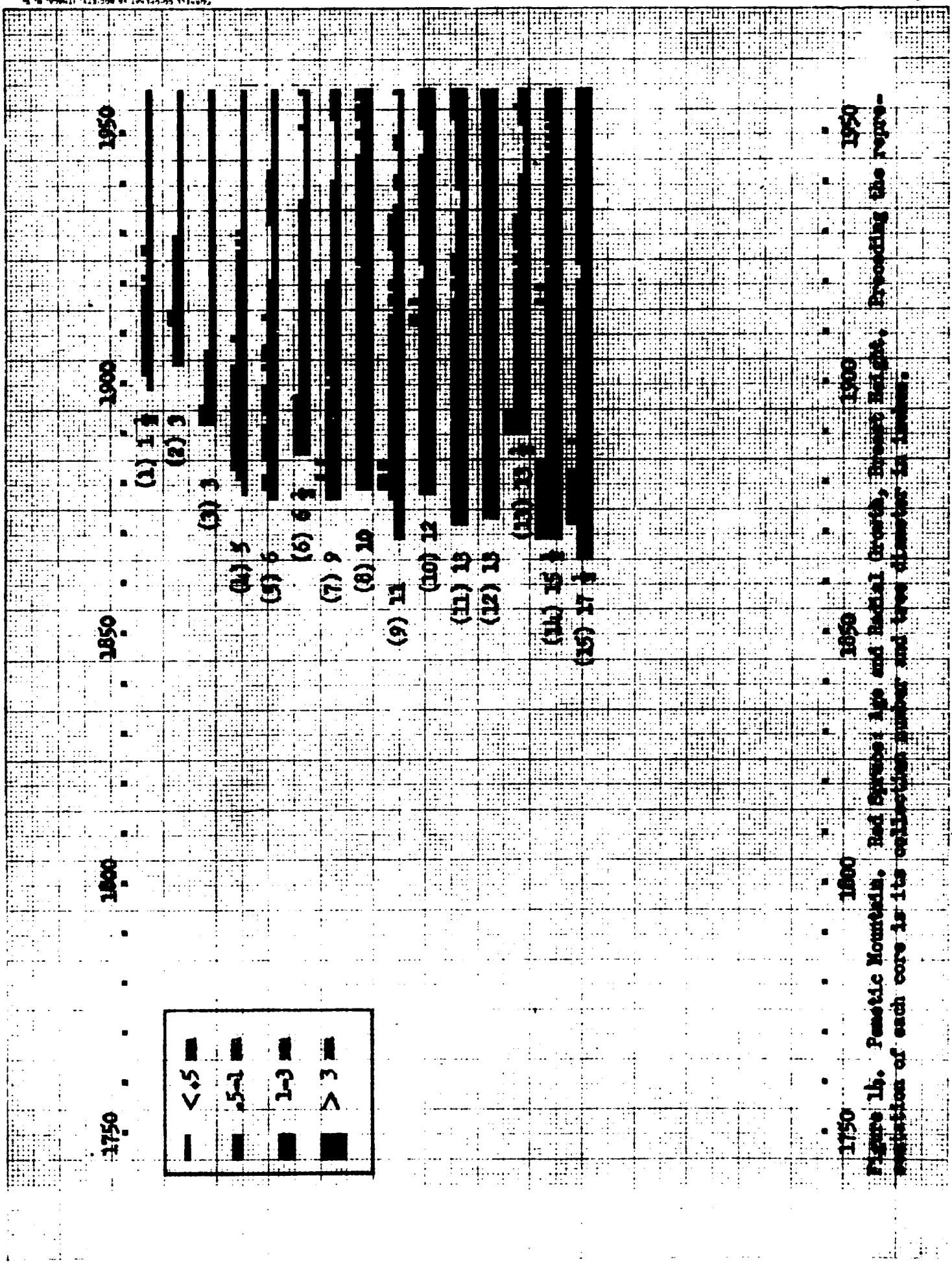


Figure 14. Pemetic Mountain, Red Spruce 1ge and Radial Growth, Burnt Height. Preceding the reproduction of each core is its collection number and tree diameter in inches.

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Figure 15. Black Woods. Red Spruce: Age and Radial Growth, Breast Height. Preceding the representation of each core is its collection number and tree diameter in inches.

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Figure 16. Otter Point, Page 1 (cont'd next page). White Spruce: Age and Radial Growth, Breast Height. Preceding the representation of each core is its collection number and tree diameter in inches.

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Figure 16. Otter Point, Page 2. Red Spruce: Age and Radial Growth, Breast Height. Preceding the representation of each core is its collection number and tree diameter in inches.

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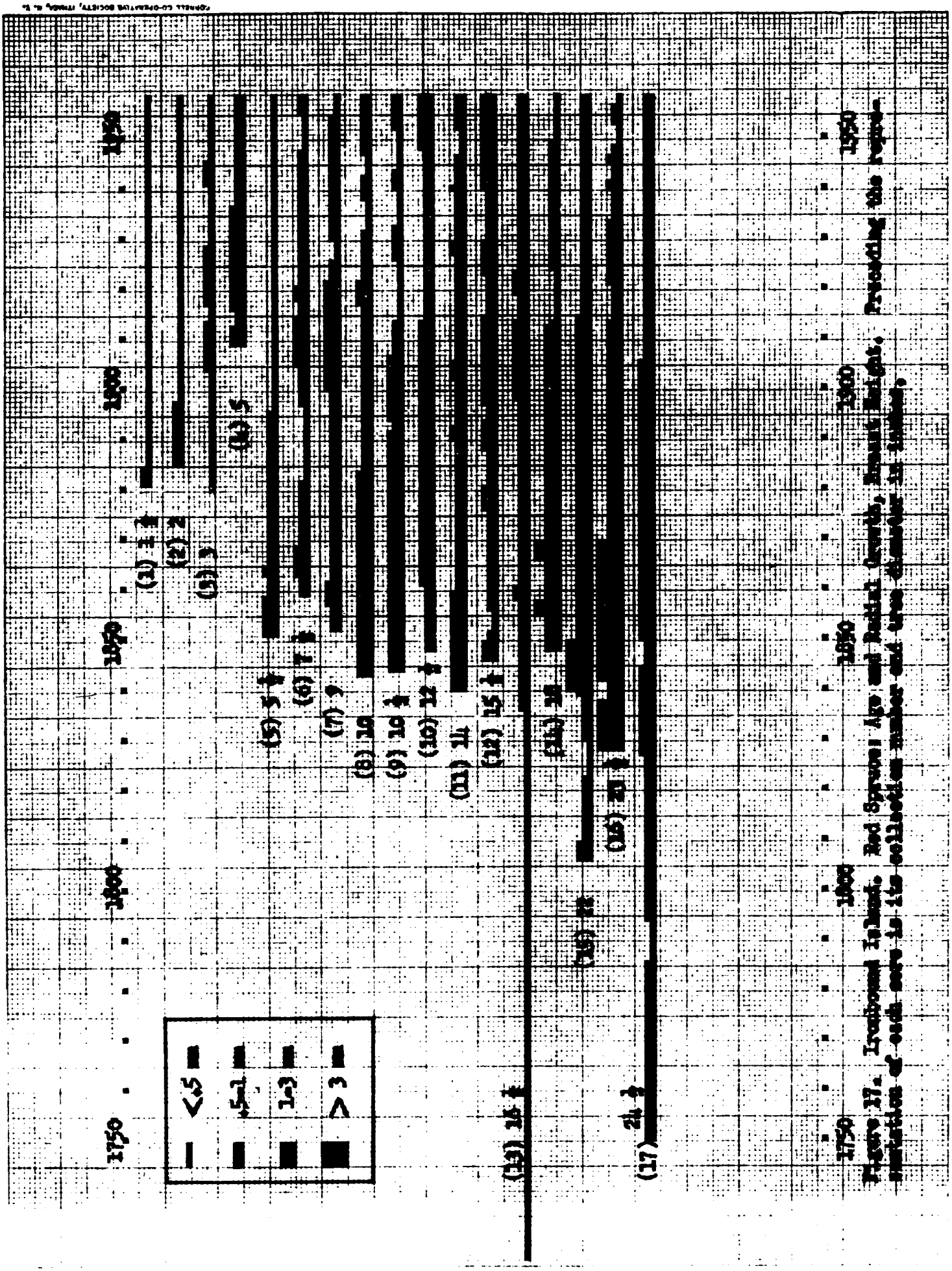


Figure 17. Irrational kibbutz. Red Spread Age and Death (Death, Birth Rate) etc. Presenting the duration of each case in the collective as a percentage of the total duration of the kibbutz in that case.

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Figure 18. Funk Lake. Red Spruce: Age and Radial Growth, Breast Height. Preceding the representation of each core is its collection number and tree diameter in inches.

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Figure 19. Roque Island, Red Spruce Age and Radial Growth, Breast Height. Preceding the representation of each core is its collection number and tree diameter in inches.

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Figure 20. Cutler. Red Spruce; Age and Radial Growth, Breast Height. Preceding the representation of each core is its collection number and tree diameter in inches.

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Table 24. Stand Development. Developmental stage numbers (see text description of Western Mountain stand for explanation); number of annual rings at breast height of spruces over eight inches DBH; and heights (ft.) of spruces. Data are from red spruces, except at Bass Harbor Head where they are from white spruces and at Otter Point from both species.

Stand	Dev't Stage	Annual Rings Mean	Annual Rings Range	Heights Max.	Heights Common Range
Gerrish Island	5	87	60-113	60	40-50
Cape Elizabeth	6	115	70-158	80	55-65
Cundys Harbor	5	78	64-95	80	55-65
Hog Island	6	85	76-92	70	50-60
Western Mountain	7	162	77-219	70	40-50
Beech Hill	5	84	63-114	60	40-50
Bass Harbor Head	6	63	53-85	70	55-65
Pemetic Mountain	5	86	68-93	65	40-50
Black Woods	5	74	71-75	60	40-50
Otter Point	6	99	61-137	80	60-70
Ironbound Island	6	138	106-232	90	65-80
Tunk Lake	6	106	78-123	70	50-60
Roque Island	6	125	102-166	85	65-75
Cutler	6	66	48-81	70	45-55

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Gerrish Island:

This was a small spruce stand on an imperfectly drained low area. Red maple assumed an important position in stand composition. Balsam fir was notably absent. The stand was a sheltered remnant of nearby better drained spruce areas which had been blown down by storms in recent years. It was under the borderline in meeting size requirements, but was included because of its important geographic position. It may represent the southernmost non-montane red spruce stand in eastern North America.

Slow initial growth by the oldest trees suggests that they were saplings under an earlier canopy. Growth began accelerating about 1870 at which time the previous stand may have been cut. When sampled, trees six inches diameter and under were becoming suppressed and larger individuals were dominating the canopy. Sapling-sized trees represented aged suppressed individuals, and not reproduction. Abundant red maple seedlings and moderate numbers of red spruce seedlings were present. However, under the uniform canopy these were not able to survive beyond the seedling stage.

A striking feature was the relative abundance of herbs, including an exceptionally high quantity of goldthread. The abundance of this species was no doubt correlated with high soil moisture. Although not encountered in such great

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numbers in any of the other stands sampled, it has elsewhere been observed abounding in coastal spruce stands on imperfectly drained sites. Certain other more typically well-represented herb species also reached higher densities here than in any of the other stands. A sparsely developed and contagiously distributed shrub stratum was present in which highbush blueberry (Vaccinium corymbosum) was represented. A bryophytic ground-cover was not developed. The absence of Calliergonella schreberi was striking. The tree-surface lichen flora was poorly developed. Notably absent were Usnea spp.

Thus, this outlier stand displayed a number of important differences from stands further to the northeast. These differences reflect both imperfect drainage and southern affinities. Future changes which take place here, and the redevelopment of the nearby blow-down areas should be followed.

Cape Elizabeth:

Like Gerrish Island this stand was an important southern outlier. Another similarity was the widespread blow-down that had occurred in recent years. Quadrats had to be distributed among intact one to four acre patches which survived the storms. As at Gerrish Island, this forest type presented a striking contrast to the vegetation just inland.

Here red spruce strongly dominated. Groups of small

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balsam firs were found concentrated here and there. Scattered white pines were seen, sometimes towering above adjacent young red spruce thickets.

Analysis of tree ring data and field observations suggest that much of the stand originated in open growth, during the early to mid 1800's. Subsequent denser reproduction was initiated from place to place. Most of the open growth matriarchs are dead and fallen, but a few of these large spruces still remained at time of sampling. A moderate scattering of spruce seedlings was present under the canopy, and spruce and fir saplings were thriving in small openings.

A poorly developed low shrub stratum was present, and included mostly scattered low sweet blueberry. Highbush blueberry was scarce but still present. Herbs were typically sparse. Starflower was notably absent, while the more southern teaberry (Gaultheria procumbens) and trailing arbutus (Epigaea repens) were present in moderate amounts.

About 90% of the forest floor was covered with spruce litter, but where the bryophytic carpet was developed it did not differ appreciably from stands to the northeast. Tree surface lichens were well represented and also similar to the more northeastern stands. Thus, while in most respects similar to the bulk of coastal spruce-fir forests, a few essentially non-spruce-fir associates were still found in

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this southern outlier stand.

Cundys Harbor:

This was essentially a mixed conifer stand in which about 50% of the trees were red spruces. White pine, second in basal area to red spruce, was represented mainly by large individuals which towered above the remainder of the canopy. Nearby stands more heavily dominated by spruce were either too young or too small for sampling.

Ring counts of spruces revealed an essentially even-aged population. Small diameter individuals were often almost as old as the largest trees. Individuals below nine inches in diameter were being suppressed by larger trees. A moderate number of spruce seedlings were present. Reproduction by other species was less abundant. Young saplings were absent under the uniform canopy.

Few shrubs were present and herbs were sparsely distributed. Bryophytes and lichens covered about 10% of the ground and were floristically typical. Tree-surface lichens were abundant and also floristically typical.

Hog Island:

This was the southwestern-most stand sampled which included white spruce. Unfortunately, the stand on Hog Island which had been used for so many years by Cruickshank and Cadbury for bird censusing (1936, ff.) had been so severely

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damaged by blow-down in recent years that it did not meet sampling requirements. Instead, a stand near the junction of the mid-and-southern thirds of the island on the eastern shore was used.

The spruces were exceptionally even-aged. Evidence indicates that much of this stand began as an old field type. The growth form of the large trees, their rapid early growth, and the absence of substantial paper birch all suggest this.

Red spruce was the dominant tree. Considerable numbers of small red spruces and firs appeared to be making rapid growth where blow-down had thinned parts of the canopy during the 1930's. On the other hand, white spruce was represented only in the large size classes. White spruce seedlings were scarce, except for the most open portions of the stand, while red spruce seedlings were present in moderate amounts and were well distributed. Firs larger than four inches DBH appeared sickly. Many had died and were broken off at the butt by winds before reaching eight inches DBH.

Thus the trends in this stand were clear, and barring extreme and widespread blow-down, fire or cutting, promised to continue during the subsequent few decades at any rate. Red spruce was becoming more dominant, fir was maintaining itself as a small tree in a subordinate role, and white spruce was rapidly declining in numbers.

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At the time of sampling, shrubs and herbs were both scarce. Scattered huckleberry (Gaylussacia baccata), fireweed (Erechtites hieracifolia), and hay-scented fern (Dennstaedtia punctilobula) were probably remnants of earlier open stages. About 40% of the ground had become covered with a mat of bryophytes and lichens, among which Calliergonella schreberi and Ptilidium pulcherrimum were foremost. Much of the bark, and many of the dead branches were covered with lichens. Near the shore, dead branches were luxuriantly festooned with Usnea spp.

Western Mountain:

This was the only virgin spruce-fir stand found within the entire coastal area. It was pointed out as such by Moore and Taylor (1927). It covered portions of the top and uppermost southeast-facing slopes of Western Peak (Bernard Mountain) of Western Mountain. Although somewhat inland on MDI, its elevated position exposed it to the force of sea winds. Fortunately, this area is now protected within the bounds of Acadia National Park.

The forest was as heterogeneous as the topography of the irregular mountain ridges and notches on which it stood. On thin soils in areas exposed to the wind, various stages of recovery from early blow-downs were seen. Some areas had succumbed to the winds during the preceding few years.

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The two oldest groves were found in small protected notches. Whether this forest was best classified as a single stand is a matter for debate. Certainly a large number of sampling units would have been required for an accurate quantitative description.

The forest was dominated by red spruce. The trees were not large, being forty to fifty feet in height, though in some areas individuals occasionally reached seventy feet without being blown over. Balsam fir, here as elsewhere in the coastal area, was a small tree, comprising only a small percentage of the total basal area. It was mostly distributed in small groups where the canopy was least dense. However, it was second in importance only to spruce, and in density made a greater contribution than it did in basal area. Unless conditions had changed markedly since Moore and Taylor made their observations here in the 1920's, their statement that the forest was composed of 100% red spruce must have been based on a quick glance indeed.

As in most other stands, only a sparse development of shrubs and herbs was found. Most of the major species were the same as elsewhere, except for higher numbers here of creeping snowberry (Gaultheria hispidula), mountain cranberry (Vaccinium vitis-idaea), and mountain wood-fern (Dryopteris spinulosa americana). The tree-surface lichen

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flora was well-developed, and in species composition was not strikingly different from other stands. A mat of bryophytes and lichens covered most of the ground, except under dense thickets. In the oldest groves, a plush carpet dominated by Calliergonella, Bazzania, and Ptilidium formed an almost perfect cover (see Figures 21 and 22).

Spruce reproduction was higher here than in any of the second growth stands. Abundant seedlings were well distributed except where dense thickets had overgrown earlier created openings. Old suppressed spruce saplings were widely scattered, while flourishing clumps of young spruce and fir saplings were concentrated where the canopy was most open. The size class distribution (Table 10) differed markedly from the even-aged second growth stands. Here, the greatest number of individuals were in the smallest size classes, and numbers gradually tapered off in the larger size classes.

Because of the virgin character of this forest, and its value for comparative purposes, a more thorough study of increment borings was made here than elsewhere. Fifty-six cores were taken. As was expected, the forest was extremely uneven-aged. Spruces over eight inches DBH had from seventy-eight to 220 rings, and averaged 162. Spruces four to eight inches DBH had from sixty to 167 rings, averaging 108. Two

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Figure 21. Litter strewn bryophytic mat in Western Mountain stand. Large tree was 14 inches DBH and ca. 200 years old.

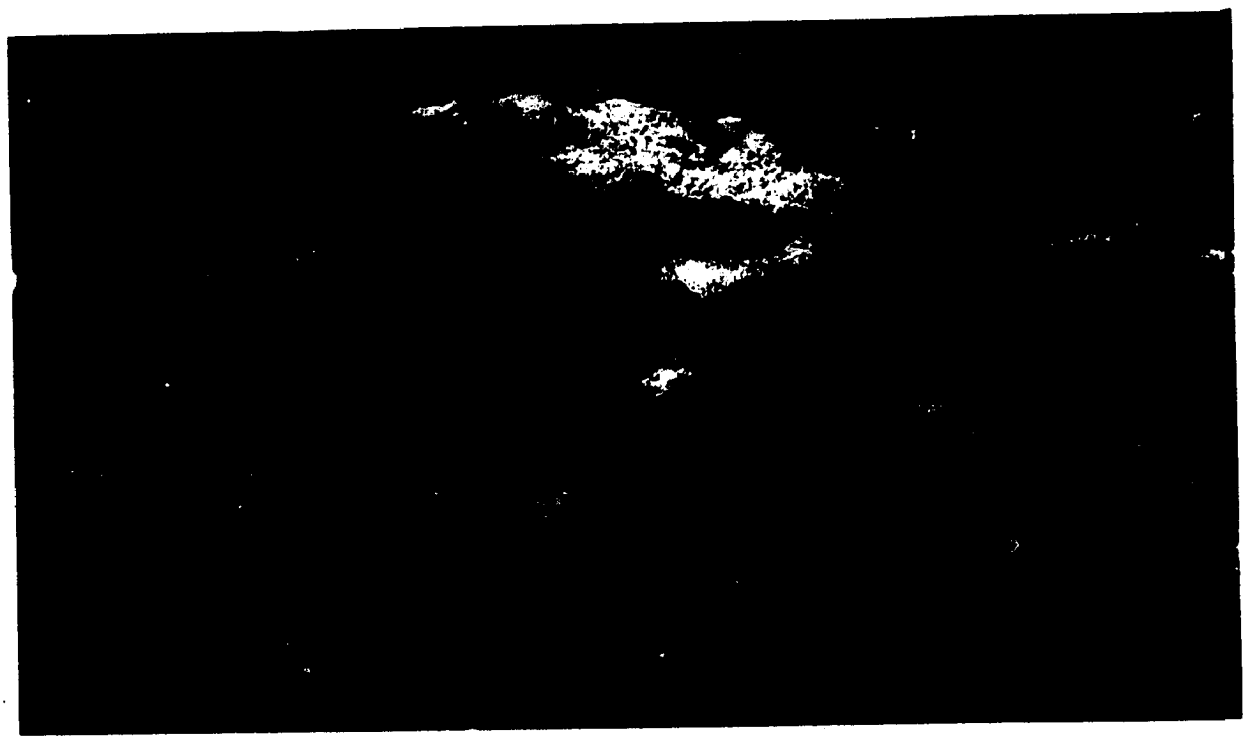


Figure 22. Six inch DBH spruce recently blown over. As it decays it will gradually be overgrown by the bryophyte mat.

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to four inch DBH spruces ranged from forty-six to ninety rings, and averaged sixty-six. One to two inch spruces were rare except in recent blow-down areas, and no borings were taken from these. Three smaller "saplings" were cut just above the base and counts were made under strong magnification. One individual, half an inch in diameter, had thirty-six rings; another, one-quarter inch in diameter, had thirty-nine rings; and the third, one-sixth of an inch in diameter and only eight inches high, had at least sixteen rings (some were obscure).

On the average, growth was slow, averaging less than one millimeter radial increment per year. A number of cores showed rapid growth during the years 1775-1830, suggesting a series of openings during that period. However, sudden and complete destruction of the canopy was not indicated, and a few cores showed no release from suppressed growth. The oldest cores did not generally indicate strong suppression in their most central rings. Thus it appears that (with one exception) these individuals were neither making rapid growth in the open nor were they at that time under a dense canopy.

A few old dead and dying paper birches were encountered in various places. Birch logs, long rotten within, mere empty sheaths of decay-resistant birch bark, were found here and there. Birch bark remnants were found in the upper layers of the soil at a number of widely spaced locations.

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Thus, it appeared that paper birch was once abundant throughout the stand. Many authors recognize that in northern New England and in the boreal forests in general, stands containing high proportions of paper birch are practically restricted to former burns (Dana, 1909, and Harlow and Harrar, 1958, for the species in general; Hosmer, 1902, and Oosting and Reed, 1942, for Maine; and Hill, 1923, and Moore and Taylor, 1927, for coastal Maine). Traces of charcoal were found just above the inorganic soil layers at widely spaced locations in the stand.

It thus appears likely that an extensive fire, or series of smaller ones, occurred on the mountain during the early 1700's, and this was followed by a stand including high proportions of paper birch (stage 1). Spruce came up under the birches and many reached breast height by the mid-1700's (see Figure 11) (stage 2). The birches were gradually replaced during the remainder of the century, and rapid spurts of growth (1775-1830) suggest the dying off and/or overtopping of the birches by the spruces (stage 3).

The remainder of the story indicates crowding by the spruces, slowing of growth, coupled with the dying off of great numbers of suppressed saplings (as occurs today under similar circumstances, the "thicket stage") (stage 4); a slowing down of stand-thinning processes and the attainment

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of appreciable height by the trees (ca. thirty-five feet +), the beginnings and gradual development of a bryophytic ground cover, and the establishment of red spruce seedlings (unable to survive beyond seedling stage) (stage 5); continued tree growth and repeated establishment of fresh seedlings, openings in the canopy caused by death or blow-down of large trees, development of spruce and fir saplings (entrance of secondary age classes) (stage 6); subsequent deaths, blow-downs, and replacement by young trees, increase in quantity of small firs, increase in overall diversification of stand age and size structure (stage 7) (see Figure 23).

All these stages (1-7) may be seen in the coastal region today. The interpretation presented above is supported by analyses of succession following fire by Hill (1923) and Moore and Taylor (1927). Stages 4 through 7 need not be prefaced by fire and birch. The first four stands exhibited certain of the latter stages. Cape Elizabeth and Hog Island appeared to have entered upon stage 6. Gerrish Island may have been a special case of stage 5, while Cundys Harbor was more typical of this stage. This sequence will be referred to during the discussions which follow.

Beech Hill:

This was a small spruce dominated stand located at mid-altitude amid the mountains of southwestern MDI. It grew on

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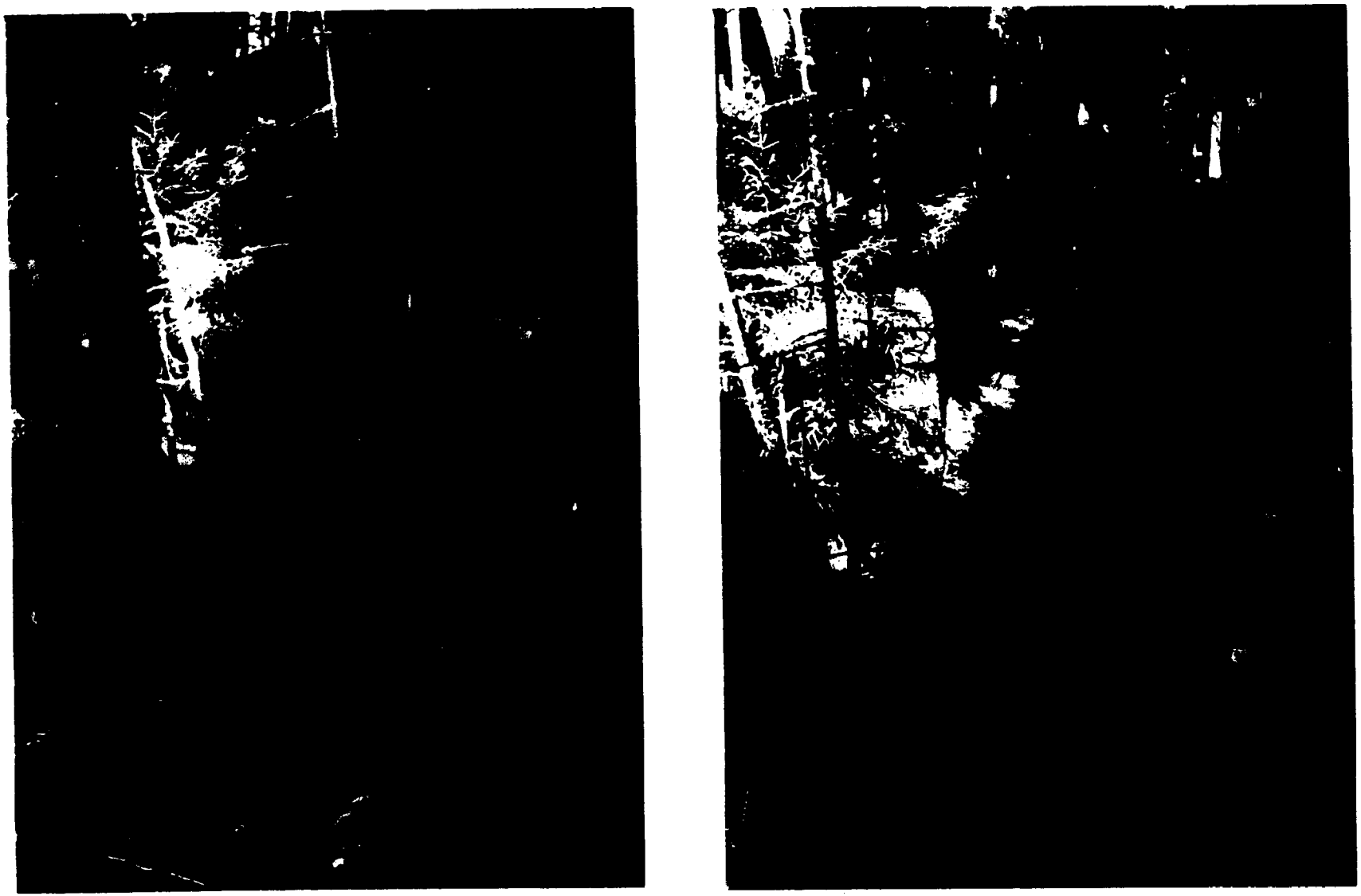


Figure 23. Heterogeneous stand structure on edge of small blow-down which occurred several score years earlier. Suppressed spruces and firs remain dead or slowly dying where they were overtopped by faster growing individuals. Western Mountain, MDI.

a thin soiled west-facing slope.

The average number of annual rings of cores taken from trees over eight inches DBH was eighty-four. All but one of these fell in the range of sixty-five to ninety-seven, revealing an essentially even aged stand. Two exceptional cores, one from a six inch and the other a ten inch DBH tree, had 114 and 116 rings respectively. Here and there, paper birch logs lay decaying on the forest floor. A few old birches still survived. Birch bark remnants were found throughout the humus layer of the soil. Charcoal lay just above the leached gray layer.

This stand, like the one on Western Mountain, presented a readily interpretable history. At the time of sampling it was in stage 5. About 100 to 125 years ago, a stand which then included red spruce was either lumbered, blown over, or destroyed by fire. If one or both of the first two occurred, a fire probably followed afterwards. The organic layer of the soil was destroyed and charcoal deposited upon the mineral layer below. A few spruces were able to survive this destruction. The slow initial growth of the two old trees indicated that they may have been suppressed saplings in an earlier stand. Numerous birches overgrew the area (stage 1). Nearby unburned spruces supplied the seed which enabled spruce to get started under the birches. By about 1862,

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these had begun to reach breast height (stage 2). Rapid spruce growth during the latter quarter of the century (stage 3) resulted in a number of thriving spruces already over four inches DBH. The intolerant birches were then probably being rapidly eliminated. Intraspecific competition was beginning to set in and spruce growth had slowed down somewhat (stage 4). By about 1915, spruces under two inches DBH were being suppressed. By 1958 trees under eight inches DBH were being suppressed, while most larger spruces still appeared to be growing at a moderate rate, at the expense of the few remaining birches. A sample of eight suppressed red spruces, varying from three to forty-eight inches in height and one-twelfth to one inch in diameter, averaged twenty-one rings at the base and ranged from eight to fifty-five rings.

Reproduction at the time of sampling indicated that the stand was going over even more strongly to spruce. Shrubs and herbs were sparse under the canopy. Those species that were present were typical. Bryophytes and lichens covered only about 12% of the ground, with thin mats of Ptilidium making up a large proportion. The tree surface lichen flora was poorly developed.

Bass Harbor Head:

This was the only stand sampled which was dominated by

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white spruce. It was one of the major areas used by MacArthur in his study of population phenomena (1958). Figure 24 shows the appearance of the stand from the air.

No evidence was found which suggested that a forest was present on this site immediately prior to the beginnings of the present stand. All factors indicated that an old field had been overgrown by rapidly growing white spruce, with lesser numbers of red spruce and balsam fir. An elder forester, B. C. Worcester, long resident of this area, attested to this. He also reported that after the stand had outgrown a thicket stage, many dead spindles remained standing. These were removed by CCC crews in the latter 1930's, shortly after the land was obtained by Acadia National Park. Such disturbance was probably of little or no significance, so far as stand composition and structure is concerned. Thus, although the small stumps may still be seen here and there, the stand was judged to meet sampling requirements.

In Figure 13 ages and annual growth of the white spruces are illustrated. Four red spruces, 1 3/4, 14, 15, and 15 1/2 inches DBH, had 67, 63, 62, and 70 rings respectively. Two balsam firs, ten and eleven inches DBH, and a white pine, sixteen and a half inches DBH, had 71, 76, and 66 rings respectively. This stand was even aged.

White spruces smaller than five inches DBH had become

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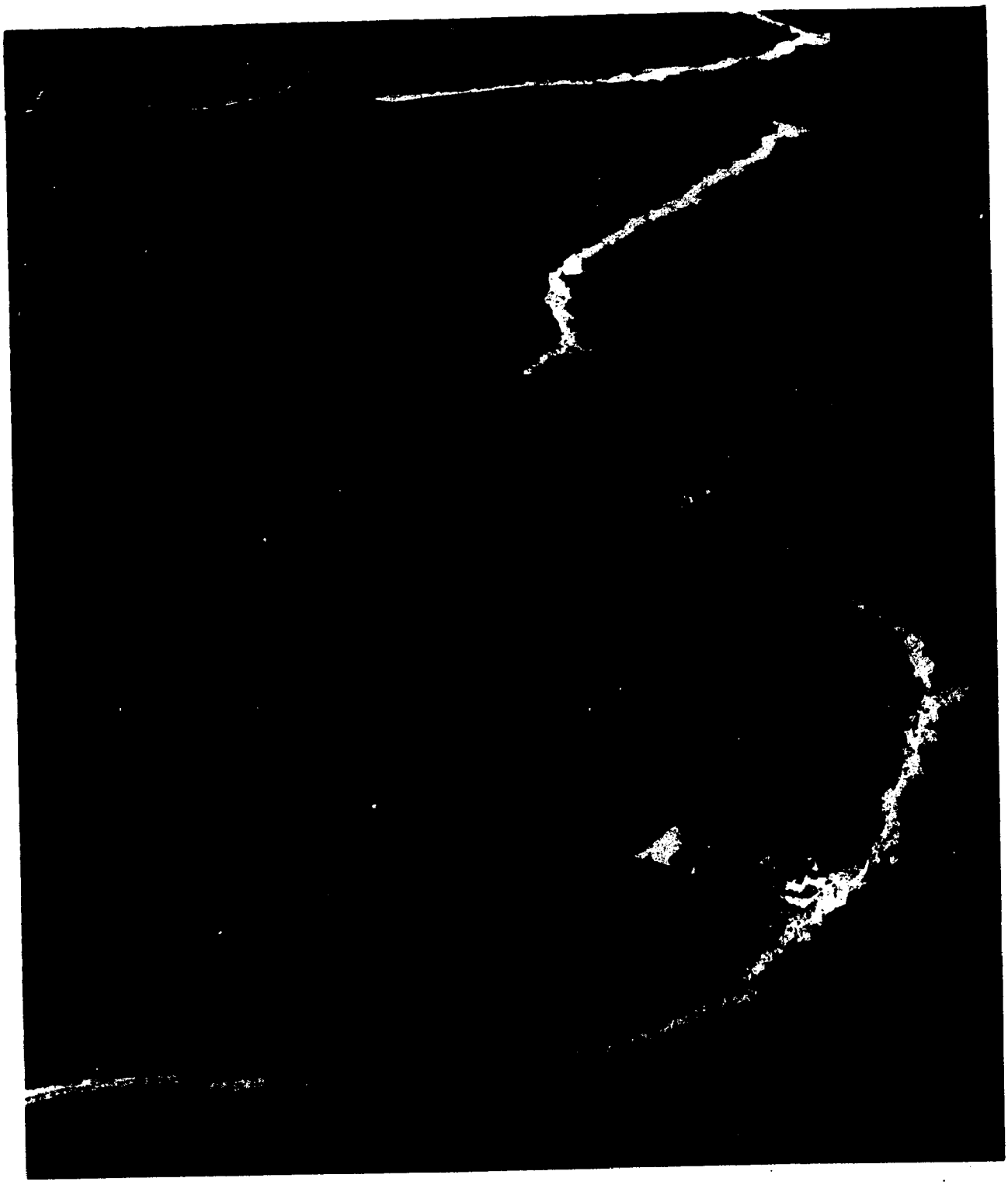


Figure 24. A heavy stand of white spruce in the foreground on Bass Harbor Head, MDI. The lighthouse is seen at the lower right. Ship Harbor appears in the distance.

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strongly suppressed. Reproduction was mostly by red spruce. Sapling-sized white spruces were absent except for the edges and least dense portions of the stand. Suppressed sapling-sized red spruces were scattered about under the canopy. The stand had apparently been very uniform up to about fifteen years ago. Since then, small blow-downs have been diversifying it. Therefore, it was entering upon stage 6. This process promised to continue in future years. Such small openings were accelerating replacement by red spruce, but relatively short-lived firs also thrived there. On the other hand, if blow-down takes place too rapidly and extensively, white spruce may again seed in and maintain its dominance.

Shrubs were characteristically sparse here. In addition to typical spruce-fir associates, remnants of more open conditions remained scattered about. These latter included green alder (Alnus crispa) and meadow sweet (Spiraea latifolia). Herb density was second only to Gerrish Island, but eighteen stems per square meter of these small herbs did not constitute a dense herb cover. Repeated observations during earlier surveys of the coastal region revealed that herb densities were almost invariably greater in white spruce stands than in similarly structured red spruce stands. Also, here as elsewhere under seaside white spruce stands, a num-

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ber of herbs reminiscent of more open conditions survived in low quantities. These include certain graminoids and composites indicated in Table 21.

About half the forest floor was covered by a bryophyte-lichen mat, dominated by Calliergonella. Tree surface lichen growth was particularly well developed. Dead branches were draped with Usnea and Alectoria, most luxuriantly on trees along edges closest to the sea.

Pemetic Mountain:

This was a uniform red spruce dominated stand, still in stage 5. In location, age, history, and composition it bore certain similarities to the Beech Hill stand. It was located at mid-altitude on the north slope of Pemetic Mountain, near the center of the mountains of southeastern MDI.

The soil was extremely thin, in many places consisting merely of a humus mat directly over granite bedrock. In other places, modified granite fragments contributed by the weathered bedrock formed a thin mineral layer. Paper birch bark fragments were found in the organic layer, and decayed birches lay on the ground in some places. A few large birches still lived. Charcoal was strewn about under the duff, atop the mineral layers or bedrock.

According to Moore and Taylor (1927), a major fire swept this portion of MDI in 1864. The history of the pres-

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ent stand seems clear. The organic soil was destroyed, and much of whatever mineral soil was present probably eroded down the mountain-side. The birch remnants, the growth form of the spruces, and moderate increment of the central rings suggest that the spruces originally came up together with and under a thin birch canopy. Many of the spruces had reached breast height as early as ten years after the fire, while others either grew more slowly or started a few years late. By the early 1900's considerable competition between spruces had set in. Litter was being deposited atop charcoal remnants.

By 1958, individuals less than six inches DBH were being markedly suppressed. Reproduction by spruce was still low, but was much greater than by other species. The hemlocks in the stand were not establishing seedlings in measurable quantities. Sapling-sized spruces and hemlocks represented suppressed individuals. Shrubs and herbs were very scarce, but those present in low quantities were typical species. About 17% of the ground was covered by a mat of bryophytes and lichens. Hypnum imponens made up an unusually large percentage of this cover.

Black Woods:

Here was another stand for which fire origins are proposed. It was strongly dominated by red spruce, but a few

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paper birches still lingered. The ground was heavily strewn with dead and decaying birches, and remnants of birch bark were found throughout the soil humus layer. Charcoal lay above the leached gray layer.

The dendrochronological chart (Figure 15) is very similar to the one for Pemetic Mountain. These two stands, plus the one at Beech Hill, showed rapid growth most consistently eight to twenty years after the trees had reached breast height. This may be interpreted as corresponding to the period when the spruces had already largely overtaken the birches, but had not yet begun to suppress one another appreciably. Stage 3 appeared to have been attained more rapidly in these three stands than atop Western Mountain.

Black Woods was an extremely dense stand, as Table 14 indicates. All but the largest trees were being suppressed, probably a result of intense competition for space in an overcrowded canopy (probably also root competition). The stand appeared to represent a stage 5 which was not preceded by adequate thinning in stage 4. Blow-down was not yet in evidence. A few isolated ledgy hillocks were still quite open, and were only slowly being overgrown by the forest.

Reproduction was already present. However, shrubs and herbs were as scarce as at Pemetic Mountain. A bryophyte-

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lichen mat had attained fair development, and covered about one-third of the ground. Tree-surface lichens were poorly developed, except at the seaward edge of the stand. Aerial reconnaissance revealed that just to the south of this stand white spruces formed a border distinctly limited to a narrow band along the shore.

Otter Point:

This was one of the most impressive spruce-fir stands on the entire Maine coast (see frontispiece). Red spruce was the most important tree in the central portion of the peninsula, where the stand was sampled. But even here red and white spruce were about equally numerous among the larger size classes. White spruce was most important near the sea and, from the air, a nearly pure grayish-blue-green border was seen interposed between the rocky shore and the more yellowish-green forests of the center of the peninsula. The observations made at Otter Point by Johnson and Skutch (1928) are in agreement. They referred to a seaside border of white spruce "several trees deep" along a portion of the eastern shore of the peninsula.

The seaward portions of the stand could not be sampled because roadside clearing had taken place in recent years, in some places causing appreciable disturbance over 200 feet landward of the road which skirts the peninsula. Moore and

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Taylor's (1927) major spruce station at Otter Point had thus been disqualified from sampling, and important successional data lost. The area studied by Johnson and Skutch (1928) had also been severely disturbed. Many acres of forests in other portions of Acadia National Park were disqualified because of this unfortunate policy.

This stand appeared to have had a complex history. Suppressed growth, shown by the earliest rings of the two oldest trees bored (red spruce), suggested that a forest canopy existed in certain portions of the tract 125 to 150 years ago. On the other hand, a few old large-diameter open-field-form red spruces were present (Figure 16, cores 25, 30, 31). These indicated that other portions of the tract were open perhaps as old fields or pastures, over 120 years ago. The picture was further complicated by the fact that charcoal was present above the mineral soil layers, and birch bark remnants were found in the humus where no birches stand today. Moore and Taylor claimed that the portion of the stand they observed in the 1920's was then about forty years old, and the photograph they present in their paper shows a dense grove, just outgrowing a thicket stage (stage 4.)

Extensive enough open conditions had to be present for the initiation of the essentially even-aged class of white spruces 100 to 120 years ago. New openings were apparently

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created in the 1890's when a new class of red and white spruces began. Throughout its complex history, the canopy never became consistently dense, as suppressed growth is at a minimum. Today the stand is being diversified and thinned by deaths in the upper story and occasional blow-downs (late stage 6).

Reproduction was mainly in the form of red spruce. Saplings of this species and balsam fir were flourishing in small blow-downs removed from the seaward edge of the stand. In large blow-downs, especially near the shore, white spruce was rapidly seeding in. In the undisturbed central part of the stand, a number of large old white spruces appeared sickly (e.g. cores 10 and 13) and a few had recently died off. No individual white spruces smaller than four inches DBH were found there. Thus, red spruce was increasing in dominance and promised to continue to do so unless widespread opening takes place. There is good reason to believe that, in large part, the Otter Point stand represented a stage in succession roughly fifty years subsequent to that represented by the Bass Harbor Head stand.

As in most other mature spruce-fir stands, neither shrubs nor herbs formed a significant cover. At Otter Point, low sweet blueberry was widely scattered about. Herbs were somewhat more numerous than in most other stands sampled.

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About half the ground surface was well covered by a bryophyte-lichen mat dominated by Calliergonella and Ptilidium. Tree-surface lichens were well developed.

Ironbound Island:

This red spruce dominated stand was located in the small protected valley which divides the southern portion of Ironbound Island. The site was rather moist. The spruces were the tallest seen anywhere in the coastal region, several individuals being almost ninety feet tall. Their boles were long, straight, and free of lower branches.

The ground was everywhere strewn with paper birch remnants, though only a few living individuals of this species remained. The dendrochronological chart (Figure 17) indicates that a major disturbance occurred about 120 to 135 years ago. The abundant birch remnants and generally only moderate and slow early spruce growth suggest that large numbers of paper birch originally reforested the area, accompanied and followed by spruces under their canopy. Cores 13 and 17 were from trees that had survived destruction of the earlier stand. It appeared likely that fire, or lumbering followed by fire was the agent of destruction.

Some diversification had begun to take place (stage 6), and where small openings had occurred they had been populated by thickets of young balsam fir. Sapling-sized spruces

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still, for the most part, represented old suppressed individuals. Seedlings of both red spruce and red maple were present in moderate numbers, though the former were more abundant.

Shrubs were scarce, and the moderate numbers of herbs did not amount to significant cover. About 50% of the ground was well covered by a bryophyte-lichen mat dominated by Bazzania, Calliergonella, and Hylocomium. The remainder of the ground was litter covered.

Tunk Lake:

This was an example of a more inland stand, composed of about half red spruce plus a mixture of mostly coniferous associates. In composition it was quite similar to the more coastally located Cundys Harbor stand.

The dendrochronology chart (Figure 18) reveals that the spruces were composed of two age classes. Trees represented by cores 3, 6, 9, 11, and 12 had apparently been saplings in an earlier stand which may have been cut, burned, or both a little over 100 years ago. Reforestation followed, and the second group of spruces reached breast height about twenty years later. Reproduction was low, though present for most species including spruce. The successional prospects for this stand were not clear from this sample. It appeared to be entering upon stage 6.

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Shrubs reached moderate numbers and contributed low but significant cover. Herb density was typically low. A few species not characteristic of spruce-fir forests were present. Only about 10% of the ground was covered by a bryophyte-lichen mat.

Roque Island:

This small red spruce stand occupied the low-lying shore area near the southwest corner of Paradise Cove, a small inlet at the southwestern corner of larger Shorey Cove. In several respects it was similar to the Ironbound Island stand. In height, the trees were second only to Ironbound. In tree form, age, stand composition, and kinds and quantities of non-arborescent species, the two stands were markedly similar. Both occupied moist sites. Perhaps the major difference was the lesser numbers of red maple at Roque Island.

Figure 19 shows that moderate growth was the rule in the most central rings of the spruces. One core (18) was from a tree that had survived destruction of a former stand. Birch remnants were common. Temporary spurts of growth, about five to thirty years after some spruces had reached breast height, suggested they were then overtaking early competitors, perhaps the birches (stage 3).

Spruce reproduction was second in abundance only to Western Mountain. Diversification had begun (stage 6) and

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spruce and fir saplings were thriving where the canopy had been opened. Over half the ground was covered by a lush growth of bryophytes and lichens, dominated by Calliergonella, Bazzania, and Hylocomium. Tree-surface lichen growth was well developed.

Cutler:

This was the easternmost stand sampled. It was located immediately east of the town of Cutler, on the south side of the road just before crossing the bridge over Money Cove. Portions of the stand nearest the road had recently been lumbered. It was a dense stand dominated by red spruce, but also contained substantial quantities of white spruce, balsam fir, and paper birch.

The largest firs, and many of the birches were dying out, and a number of dead specimens of both species were still standing. Reproduction of both red spruce and fir was moderately abundant, with the latter more so. The stand was in stage 6.

Shrubs and herbs were typically sparse. About 60% of the ground was covered with a bryophyte-lichen mat, dominated by Calliergonella and Hylocomium. Tree-surface lichen growth was moderately developed.

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Concluding Remarks

Preliminary surveys revealed that the coastal forests have been subject to frequent disturbances by man. In recent times stands are usually cut as soon as the trees reach about eight inches DBH. Fires have been frequent. Under such circumstances it has been the difficult objective of this portion of the thesis to describe these forests in their "natural state".

Spruce-fir forests were judged to constitute the climax on most sites in the black areas on the forest distribution map (in rear pocket). However, few stands had attained ages and structures fully characteristic of a climax type. A single virgin stand, atop Western Mountain in Acadia National Park, MDI, was used as a reference for analyzing trends within the other stands. The second growth stands could be classified according to their stage of development toward the climax structure exemplified on Western Mountain.

The uniformity in size and age of the trees in the so-called "mature" second growth stands begins to break down at about seventy-five to a hundred years of age. Small blowdowns and deaths in the upper story initiate secondary age classes and introduce heterogeneity into the size class structure. Such diversification, if continued for several score years gradually results in the climax structure found

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on Western Mountain. This stand structure is characterized by an abundance of small sized trees and a gradual lessening of numbers with increased size. Oosting and Billings (1951) found this type of stand structure in virgin spruce-fir stands in the Appalachians.

Although deficient in climax structure, most second growth stands had already acquired a typical complement of associated climax species. The climax is characterized by a dominance of red spruce, with balsam fir as a small tree populating openings together with small red spruces. Balsam fir is less tolerant and shorter-lived than red spruce (Hawley and Hawes, 1912; Spaulding and Hansbrough, 1944; Harlow and Harrar, 1958), and gradually dies out with the maturing of the canopy. However, it is maintained by repeatedly created openings. Paper birch and red maple may be present, but trends in stands where they are now abundant indicate they will gradually diminish in number unless a major disturbance takes place there. The place of hemlock, a highly tolerant species (Baker, 1949) is difficult to evaluate. In those stands where it now occupies an important position, it does not appear to be reproducing itself.

In these forests shrubs are characteristically sparse. Herbs may be present in moderate numbers, but the small size of the most common species results in an overall contribu-

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tion of negligible cover. A bryophyte-lichen mat, covering considerable portions of the forest floor, is characteristic.

White spruce plays a distinctive role in the spruce-fir forests of the coast of Maine. It is not as tolerant as red spruce nor as long-lived in this region, but is probably faster growing--as my observations and those of others indicate (Nichols, 1918; Recknagel, 1923; Baker, 1949; Harlow and Harrar, 1958). Whenever the two species were found together in "mature" forests, red spruce appears to be in the process of replacing white. The Hog Island, Bass Harbor Head, Otter Point, and Cutler stands are cases in point.

There can be little doubt that the present abundance of white spruce in the coastal region is a direct result of the decline of agriculture and abandonment of old fields which began in the 1800's. East of Casco Bay near the coast, but also further inland east of Penobscot Bay, old fields and pastures becoming overgrown by white spruce are a common sight (red is usually also present). If agriculture remains at low ebb in this area, as seems likely, white spruce will eventually reach a peak. Then, on sites where spruce-fir forests are the climax, red spruce will gradually replace white.

However along the immediate shore, white spruce may maintain itself as a special type of climax. Observations

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suggest that, at the "white spruce border" on the exposed edge of the sea, the periods may be so short between extensive blow-downs that red spruce is not given a chance to replace white. Where adequate seed sources for white spruce are present, the rapid growing species populates the blow-down areas each time the trees go down. During long periods between blow-downs the white spruces may be squeezed into a strip just a few trees wide along the open edge (as can now be observed along certain shores).

On some offshore islands, growth may be so slow that open conditions are virtually permanent. In some cases red spruce seed sources may be few or absent. Where white spruces occupy the tips of elongate peninsulas, as they often do, they possess a certain protection from the red spruce seed sources nearer the peninsula base. The winds which come mostly from the open sea are unlikely to spread seeds toward the tip of the peninsula.

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Forest Soils

Soils were studied in detail at five spruce-fir stands on MDI.

Methods

Four widely and evenly spaced pits were dug in each stand. Profile measurements and descriptions were obtained for each pit, and samples were taken from each horizon. The four profiles were usually similar, and equal quantities from corresponding horizons were combined to make a composite sample for each horizon from each stand. Depth measurements were likewise averaged, and descriptions combined. At Western Mountain, however, it was necessary to make two separate descriptions, each on the basis of two pits.

Each horizon was tested for pH, using a glass electrode meter, following the method described by the United States Bureau of Plant Industry (...etc.) (1951). The samples were taken to Orono, Maine, where K. V. Goodman (U.S.S.C.S.) described the texture, structure, and consistence of each horizon, and colors were determined with a Munsell Color Chart. Samples were then shipped to the Agronomy Department at Cornell University where chemical analyses were made. That laboratory determined organic matter by loss on ignition, using the method of Walkley (1935), as modified by Peech, et al. (1947).

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Potassium, magnesium, manganese, iron, and aluminum were determined using the method of Peech and English (1944); Calcium and potassium were analyzed with a flame photometer.

Results

The results are presented in Tables 25 and 26. Table 25 consists of profile descriptions for the five stands. The soils were all shallow and rested on granite bedrock overlain by thin mostly-granitic till. They were well drained to somewhat excessively drained, except for Western Mountain where seepage was indicated by the profile. The soils were iron podsols, with a well-developed fibrous mor layer and a gray layer of variable depth, except for Western Mountain where the soil might be classified as a variant of an iron humus podsol (as in Tamm, p. 129 ff., 1950). The soils were all extremely acidic.

Mycelia were abundant in the mor layer. Earthworms were never found in any layers. Collembola and soil mites were abundant in the mor layer, while other arthropods appeared to be scarce. Plant roots were strongly concentrated above the gray layer but a few extended below. Charcoal was always found just above the A_2 layer, and the remains of birch bark in the mor.

The results of chemical analyses are presented in Table 26. Organic matter was strongly concentrated in the mor,

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Table 25. Soils, Bass Harbor Head. Canaan stony loam. Composite profile from four pits.

Horizon	Inch Depth	Color when Moist (Munsell C. Chart)	Texture	Structure	Consistence Moist	Lower Boundary	pH
A_{oo} & A_o	2-0	black 5Yr 2/1	finely fibrous	loamy	loose	distinguishable	3.9
A_1	0-4	very dark gray 5Yr 3/1	loam	strong medium granular	friable	distinguishable	4.2
A_2	4-5	pinkish gray 5Yr 6/2	sandy loam	weak coarse granular	very friable	distinguishable	4.3
B_{21}	5-7	reddish brown 5Yr 4/4	sandy loam	weak fine subangular blocky	slightly firm	gradual	4.6
B_3	7-16	reddish brown 5Yr 4/4	gravely loam	moderately strong medium subangular blocky	firm		4.8
water	16						

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Table 25. Soils, Black Woods. Canaan stony loamy coarse sand. Podzol. Composite profile from four pits.

Horizon	Inch Depth	Color when Moist (Munsell C. Chart)	Texture	Structure	Consistence Moist	Lower Boundary	pH
A_{oo} &A_o	7-0	black 5Yr 2/1	loamy	finely fibrous	loose	abrupt	3.5
No A_1							
A_2	0-7	gray 5Yr 5/1	gravely loam coarse sand	weak moderately granular	loose	distinguishable	4.2
B	7-21	dark reddish brown 5Yr 3/3	gravely coarse sandy loam	strong moderately coarse granular	friable		4.4
Additional notes: No apparent subdivision or color change in the portion of the B horizon sampled.							

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Table 25. Soils, Beech Hill. Canaan loam. Composite profile from four pits.

Horizon	Inch Depth	Color when Moist (Munsell C. Chart)	Texture	Structure	Consistence Moist	Lower Boundary	pH
A_{oo} & A_o No A_1	4-0	black 5Yr 2/1	fibrous	loamy organic matter	loose	abrupt	3.8
A_2	0-1	gray 5Yr 5/1	gritty fine sandy loam	weak fine granular	friable	distinguishable	4.0
B_{21}	1-2	reddish brown 5Yr 5/3	loam	weak fine granular	friable	gradual	4.3
B_{22}	2-7	reddish brown 5Yr 4/4	loam	weak fine granular	very friable	gradual	4.5
B_3	7-11	dark reddish brown 5Yr 3/4	fine sandy loam	very weak fine granular	very friable	distinguishable	4.7
C	11-21	brown 10Yr 5/3	sandy loam	weak moderate granular	friable	granite ledge	4.9
Water seepage at top of C. Granite ledge at 21".							

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Table 25. Soils, Otter Point. Canaan extremely stony coarse sand. Podzol. Composite profile from four pits.

Horizon	Inch Depth	Color when Moist (Munsell C. Chart)	Texture	Structure	Consistence Moist	Lower Boundary	pH
A_{oo} & A_o	4-0	dark reddish brown 5Yr 3/2	finely fibrous	matted organic duff		abrupt	3.8
A_2	0-5	light gray to pinkish gray 5Yr 6/1 - 6/2	coarse loamy sand	weak coarse granular	loose	distinguishable	4.3
B_{21}	5-8	reddish brown 5Yr 4/4	sandy loam	moderately strong medium granular	friable	gradual	4.6
B_{22}	8-16	strong brown 7.5Yr 5/6	sandy loam	moderately strong medium granular	very friable	gradual	4.7
B_3	16-24	strong brown 7.5Yr 5/8	gravely sandy loam	weak coarse granular	loose		4.8
C	24-		coarse granitic till				

Additional notes: Some brown soil between large pebbles, cobbles, small boulders below 3 feet from surface. Lower gray (C) not reached. Apparently moderately deep Canaan.

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Table 25. Soils, Western Mountain. I. Leicester silt loam (shallow phase). Low humic gley. Composite profile from two pits.

Horizon	Inch Depth	Color when Moist (Munsell C. Chart)	Texture	Structure	Consistence Moist	Lower Boundary	pH
A_{oo} & A_o	7-0	black 5Yr 2/1	medium fibrous	loamy organic matter	loose	abrupt	3.3
A_1	0-4	very dark gray 5Yr 3/1	silt loam	strong fine granular	firm	distinguishable	4.0
A_{3g}	4-5	dark reddish brown 5Yr 3/2	silt loam	strong fine granular	slightly firm	distinguishable	4.0
B_{2gm}	5-10	reddish brown 5Yr 4/3	gravely sandy loam	weak fine sub-angular. blocky	friable	gradual	4.5
B_{3gm}	10-18	reddish brown 5Yr 5/4. slightly mottled with light reddish brown 6/3	sandy loam	medium coarse granular	very friable	distinguishable	4.5
C_{1gm}	18-	yellowish brown 10Yr 5/4	gritty sandy loam	weak moderate sub-angular. blocky	firm	on granite	4.7
water at 24 (November 12, 1959)							

II. Leicester loam (shallow phase). Low humic gley. A_{oo} & A_o, B_{3gm} (Depth: 6-18), and C_{1gm} the same as above. No A_1 or A_{3g}. Composite profile from two pits.

A_{2g}	0-4	dark gray & gray 5Yr 4/1 - 5/1	sandy loam	weak medium granular	very friable	irregular	4.0
B_{2gm}	4-6	dark reddish brown 5Yr 3/3 slightly mottled (C_{1gm} & water seepage on granite bedrock at 20")	loam	weak medium granular	friable	irregular	4.5

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Table 26. Soils. Chemical Analysis

Area	Horizon	pH	Organic Matter %	Pounds per Acre (2,000,000 pounds of soil) P	Ca	Mg	K	Mn	Fe	Al
Black Woods	A_{oo}-A_o	3.5	78.5	22	1000	1600	810	80	6	35
Otter Point	"	3.8	78	34	1400	1400	600	100	8	20
Bass Harbor Head	"	3.9	47	6	1000	640	470	180	28	130
Western Mountain	"	3.3	86	20	400	1500	720	4	4	20
Beech Hill	"	3.8	77.5	2	400	500	700	60	35	400
Average	"	3.66	73.4	16.8	840	1128	660	84.8	16.2	121
Bass Harbor Head	A_1	4.2	17.5	1	50	100	115	24	600	500
Western Mountain	"	4.0	24.5	1	<50	75	150	3	180	950
Black Woods	A_2	4.2	3.8	1	50	25	85	7	36	150
Otter Point	"	4.3	2.5	1	<50	15	45	2	44	200
Bass Harbor Head	"	4.3	2.1	<1	<50	5	25	3	65	525
Beech Hill	"	4.0	4.8	<1	50	5	55	5	170	525
Average	"	4.2	3.3	<1	<50	12.5	52.5	4.2	78.8	350
Western Mountain	A_{2g}	4.0	2.2	<1	<50	5	40	2	105	110
	A_{3g}	4.0	12.3	<1	<50	50	65	2	185	525
Otter Point	B_{21}	4.6	12.2	ci 3	<50	35	70	3	460	2000
Bass Harbor Head	"	4.6	6.9	1	<50	25	40	24	190	1100
Beech Hill	"	4.3	8.7	1	50	35	80	3	750	1200
Average	"	4.5	9.3	1.7	<50	31.7	63.3	10	466.6	1433

Table 26. continued

Area	Horizon	pH	Organic Matter %	Pounds per Acre (2,000,000 pounds of soil) P	Ca	Mg	K	Mn	Fe	Al
Black Woods	B_2	4.4	8.9	1	50	60	95	108	420	1400
Otter Point	B_{22}	4.7	6.2	1	<50	5	40	4	85	1800
Beech Hill	"	4.5	4.5	<1	50	15	35	2	40	1150
Average	"	4.5	6.5	<1	<50	26.7	56.7	38	181.7	1450
Western Mountain	B_{2gm}	4.5	22.3	<1	<50	15	45	1	80	1500
	B_{3gm}	4.5	6.0	<1	<50	5	20	2	35	2200
Otter Point	B_3	4.8	4.1	1	<50	5	25	4	30	1000
Bass Harbor Head	"	4.8	8.7	1	<50	20	40	5	180	2500
Western Mountain	C_{gm}	4.7	3.5	<1	50	10	20	2	30	1000
Beech Hill	C	4.9	2.3	<1	50	8	20	1	60	1000

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except for Bass Harbor Head and Western Mountain, where an intermediate concentration was found in the A_1 layer. Phosphorus was quite low in the mor and extremely low under it. Calcium, magnesium, potassium, and manganese concentrations generally paralleled organic matter, and apparently the vegetation rapidly pumped and recycled these minerals as soon as they became available in the organic layers. On the other hand, as is typical in podsols, iron and aluminum were leached from the mor layer and reached high values below the A_2.

Other Study Areas

Systematic observations of soil characteristics were not made in study areas off MDI. However, in other areas casual examination of the upper soil horizons always revealed a well developed mor layer, and almost always a gray layer of variable development.

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Forest Climate

In Part I United States Weather Bureau data were used to describe the macroclimate of the coastal region. Differences between stations in spruce-fir areas and elsewhere on the coast were illustrated. Also, comparisons were drawn between the coastal section and regions further inland. Those comparisons encompassed areas many score miles in extent.

The object of the study to be presented in this section was to ascertain whether spruce-fir stands at the seaside had a different climate under their canopy than spruce-fir stands just a few miles inland. In addition, comparisons of climatic conditions under the canopy to those in the open were made.

Data here are from MDI only. Two "inland" stands, Beech Hill and Pemetic Mountain; two seaside stands, Bass Harbor Head and Otter Point; and one open field station, Whitney Farm, were used for comparison. The four stands were described on earlier pages. Location data for all five sites were listed in Table 5.

Temperatures

The weekly temperature ranges at the five locations were measured with maximum-minimum thermometers. As such readings

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were not considered to be frequent enough to justify the derivation of mean temperatures, soil readings were used instead. Shanks (1956), in his studies in the Great Smoky Mountains, pointed out the practicality of this procedure when sites cannot be visited frequently and automatic recording equipment is not available. He stated:

> Soil temperature data from 6-inch depth at weekly intervals provide a useful index to altitudinal and microclimatic temperature differences in the closed forest vegetation of the Great Smoky Mountains, correlating more closely than the means of weekly maximum and minimum air temperatures with standard weather record means. The lag in heat transfer is such that the soil temperatures constitute a useful integration of radiation and air temperature conditions during the preceding week.

The complete argument behind this approach may be obtained from the article itself. It should be understood that soil readings are merely an "...index...correlating...with standard weather record means." and not necessarily equal to such means. In other words, this is a method for <u>comparison</u> between sites--to determine how their means may differ--and not a measure of the absolute mean temperature (though it might be possible to adapt the method to such purposes).

Methods:

Five Taylor Sixes (brand) maximum-minimum thermometers and one Weston (brand) dial-reading eight inch stem thermometer were used. These were calibrated to read to the nearest half degree Fahrenheit. Shanks (1956) established

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the reliability of the latter instrument for the purposes used here.

In the four forest locations, the maximum-minimum thermometers were attached to the north sides of the trunks of large spruces. These trees were located near the center of the rectangles indicated on the maps in Figure 5. They were chosen to represent locations where the canopy was of average closure. At the open location (Whitney Farm) the thermometer was placed in a well ventilated shelter in a grassy field. This particular location was on a mild (ca. 2%) slope in an area of moderate air drainage. In every case the thermometer bulbs were sixty inches above the ground.

Readings were taken at weekly intervals through most of the period from February 1959 through January 1960. Each time the maximum-minimum thermometers were read, a soil reading was taken nearby. The soil was first probed with a piece of stiff wire to find a spot devoid of rocks. The thermometer was inserted its full length. As the instrument was sensitive at its terminal two inches, the reading may be considered as having been taken at a depth of seven inches. The extra inch (compared to a depth of six inches, by Shanks) was deemed advisable because of the porous, relatively well-aerated upper soil layers here.

During preliminary trials it was ascertained that a single reading (compared to several), and variation in the

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time of day when the reading was taken, introduced error rarely amounting to more than one-half degree Fahrenheit. This was re-checked and found to be true at various times of the year.

Results, Forest Air Temperature Extremes:

The weekly maximum and minimum readings were each averaged by months. The readings at the two seaside stands were averaged, and the same was done for the two inland stands. The monthly minimum and maximum means were then graphed in combination with sea surface temperatures from Bigelow (1924).

Figure 25 shows that with the exception of June, July, and August the monthly minima are lowest at the open field and highest in the seaside stands, with the inland stands intermediate. Where the curves approach and rise above the sea water temperature during June, July, and August the minima at the seaside stands become lower than the inland stands. In July the seaside minima average lower than the open field.

Weekly inland forest minima were subtracted from sea surface temperatures and the differences (y) were plotted against those for coastal forest minima minus inland forest minima (x) (Figure 26). A correlation ($r=.79$) was demonstrated at the 1% level of significance. This suggests that the degree to which minima at the seaside are modified may be directly proportional to the departure of sea surface

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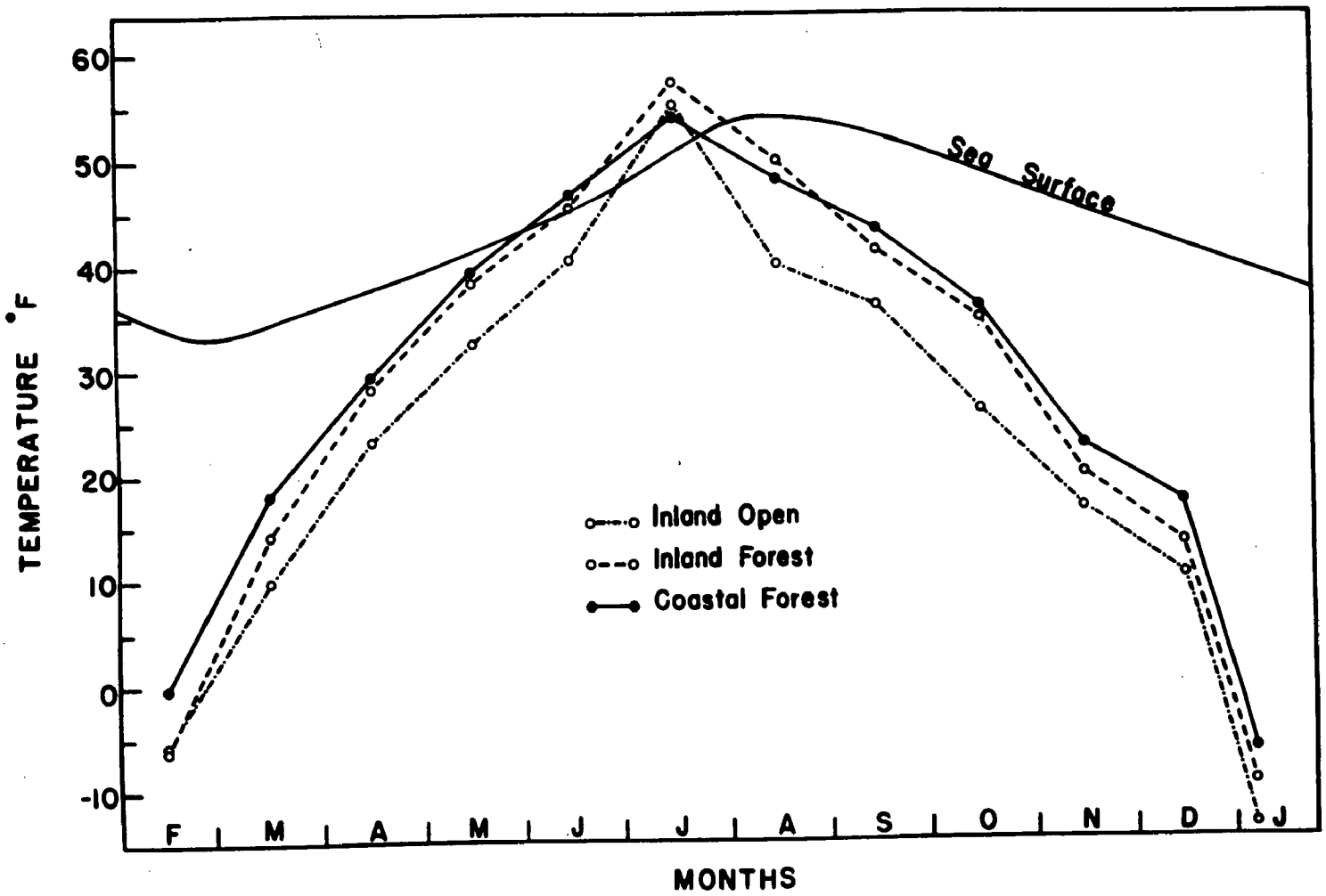


Figure 25. Monthly Means of Weekly Minimum Temperatures. Forest and open stations are compared to sea surface temperatures (after Bigelow, 1924).

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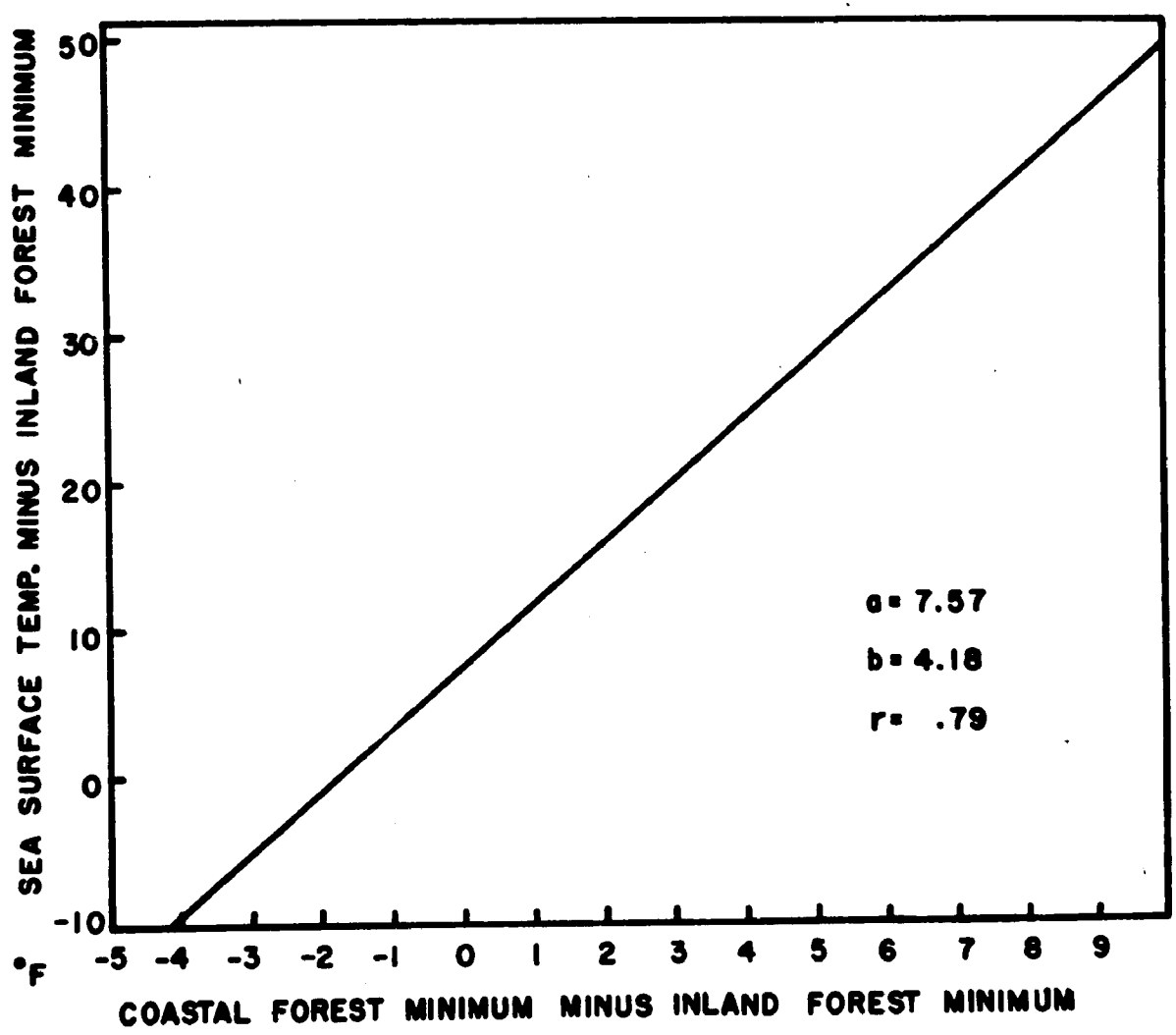


Figure 26. The Modification of Coastal Forest Minimum Temperatures by the Sea. Sea surface temperatures are from Bigelow (1924).

temperatures from those inland.

Figure 27 shows that an inverse form of the same relationship holds for the maxima. However, the air temperature lines do not cross one another in this case, as they do not cross the sea temperature line. In Figure 28 weekly readings of inland forest maxima were subtracted from sea surface temperatures (deduced from Bigelow's curve) and the differences (y) were plotted against seaside forest maxima minus inland forest maxima (x). A correlation (r=.76) was found at the 1% level of significance again suggesting a buffering of forest temperature extremes by the sea.

Results, Soil Temperatures:

Soil readings were not begun until the soil had thawed sufficiently to insert the thermometer. While awaiting that time, the progress of soil thawing was followed at the five thermometer stations, plus three additional locations, Black Woods, Western Mountain, and the lawn in front of the Ranger Station at Seawall. This latter station was located on MDI along the shore south of Southwest Harbor. All stations started thawing the first week of April. Within two weeks the two open sites had completely thawed. It was not until the last week of April that portions of the forest floors became completely unfrozen. At that time soil temperature readings began. The forest soils were frozen in small patches at all sites until mid-May, and at Western

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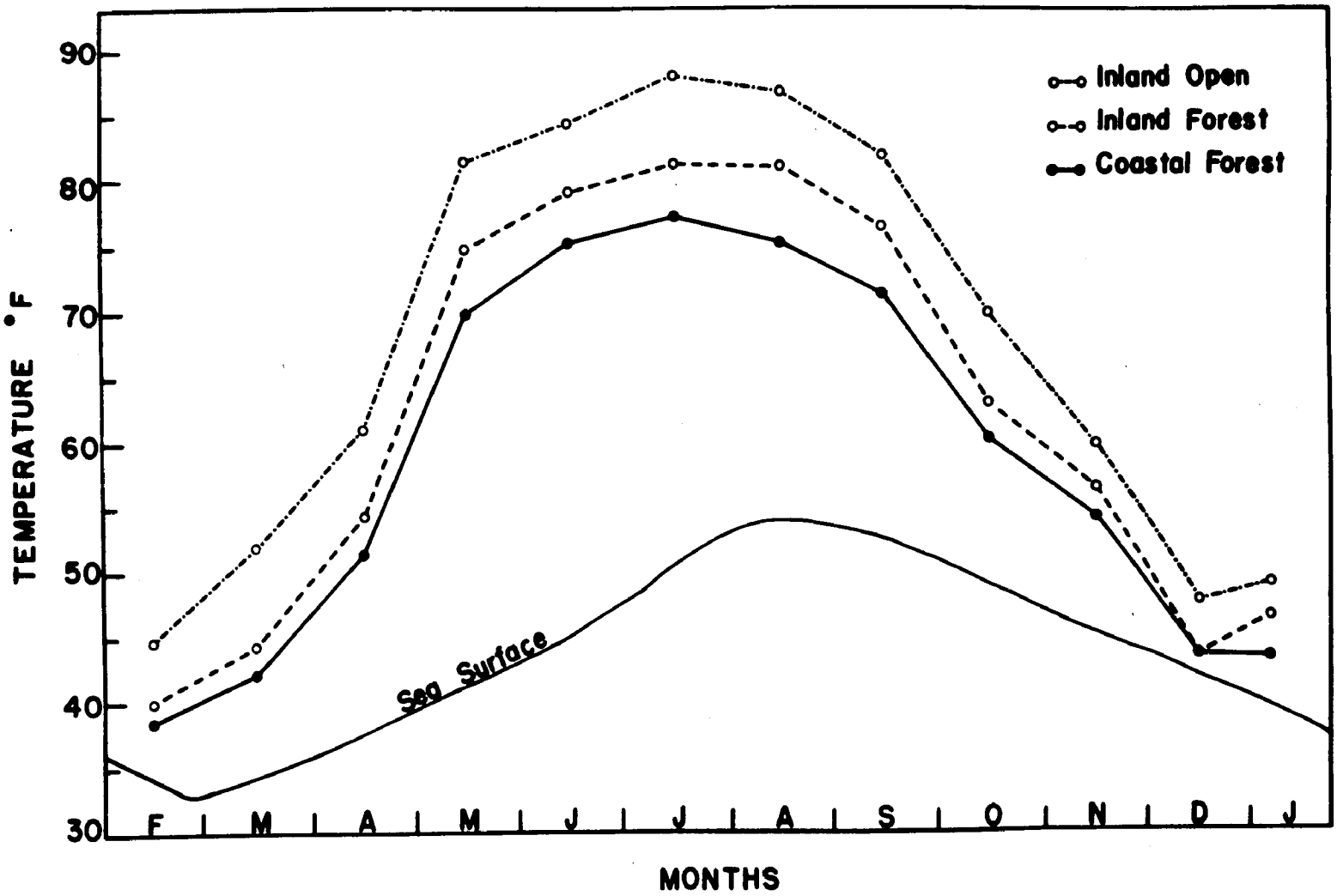


Figure 27. Monthly Means of Weekly Maximum Temperatures. Forest and open stations are compared to sea surface temperatures (after Bigelow, 1924).

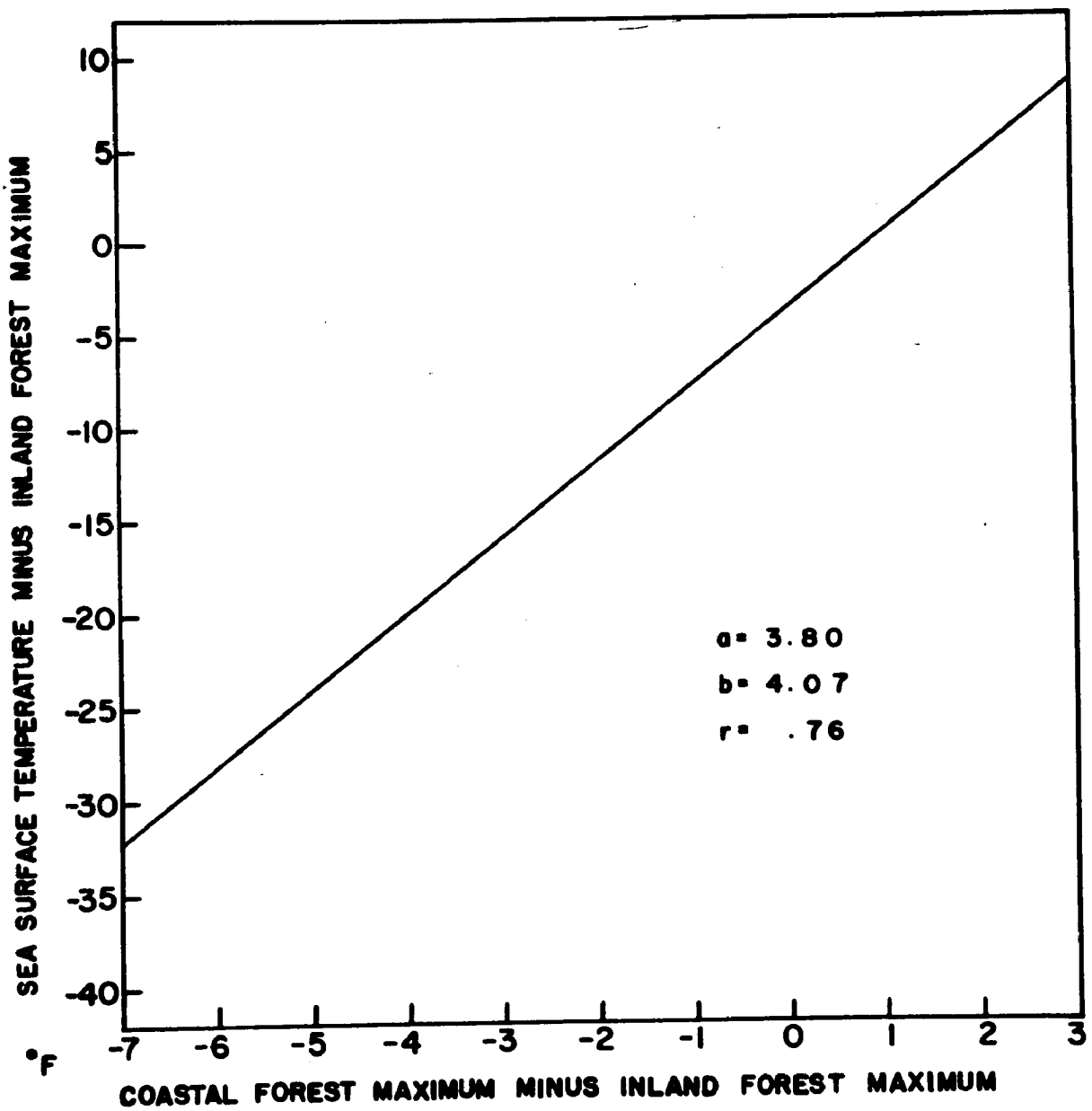


Figure 28. The Modification of Coastal Forest Maximum Temperatures by the Sea. Sea surface temperatures are from Bigelow (1924).

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Mountain until the first of June.

In Figure 29 the graph of mean monthly soil readings for inland and seaside stands is presented. It appears that summer mean temperatures in both forests were similar, even though temperature extremes differed markedly. In the spring and fall, the inland forests may have been a degree or two cooler, on the average.

Precipitation

It is known that only a certain percentage of precipitation which falls upon a forest canopy reaches the forest floor (Horton, 1919; Geiger, 1957). The humus layers on the floor of the spruce-fir forests have a tendency to dry out, and moisture conditions there may be critical so far as the success of lesser vegetation and tree reproduction is concerned. A number of authors (e.g. Moore, 1917-1926; Place, 1955, see his bibliography) have stressed the importance of moisture in the establishment of spruce and fir seedlings. In the drier spruce-fir areas of the northern Great Lakes region this factor may be more important than in the moist northeast.

I mentioned earlier that spruce seedlings usually do not appear in the development of the coastal forests until they have reached a certain degree of maturity (stage 5). In stage 4 the dense uniform canopy may prevent reproduction,

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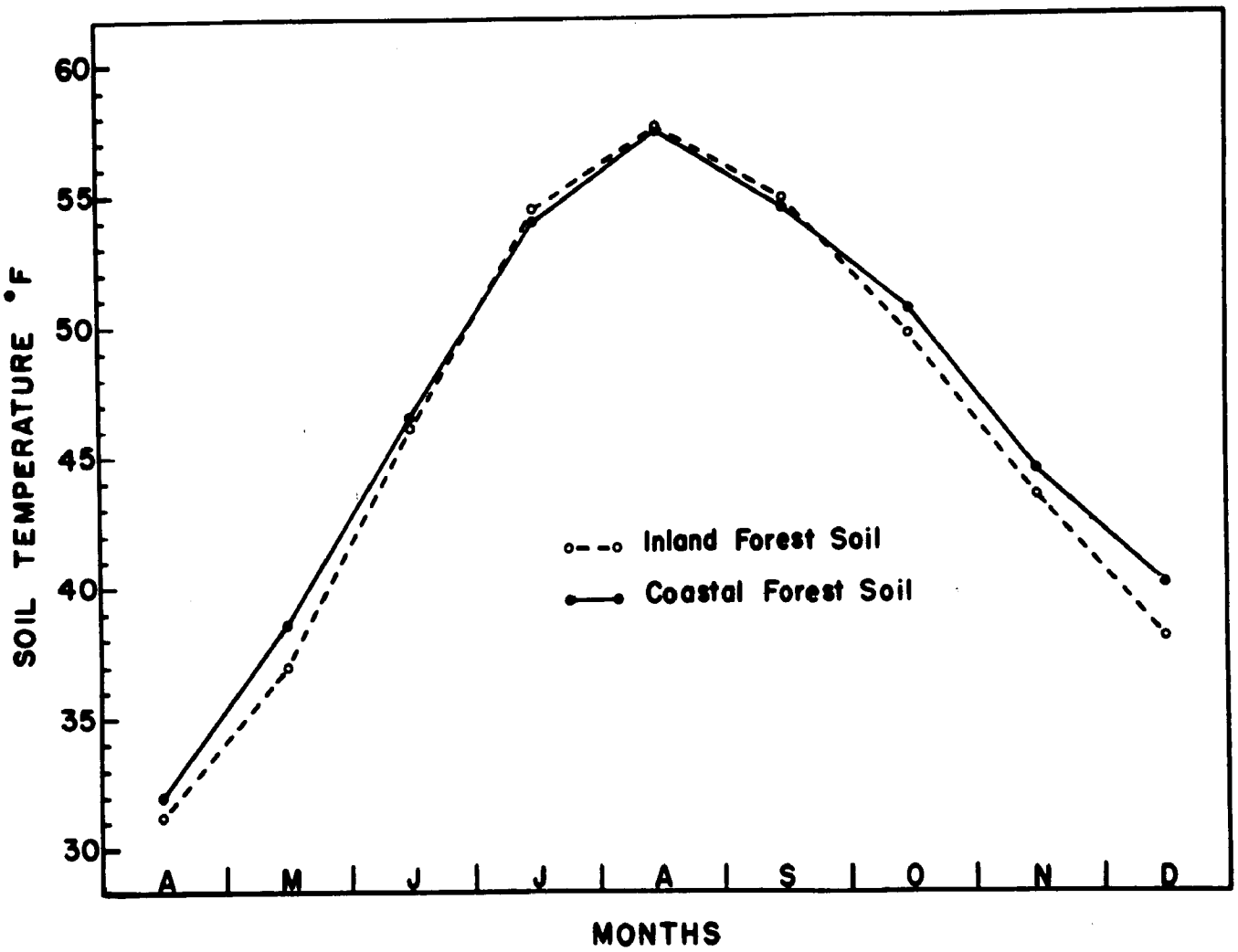


Figure 29. Soil Temperatures at Seven Inch Depth. Monthly means at inland stations contrasted to monthly means at coastal stations.

not only by shading and the rapid deposition of litter, but also because of its interception of precipitation (Moore, 1922).

It was the purpose of this portion of the study to sample the precipitation on the floor of a stage 5 stand. The Beech Hill study area was used for this purpose.

Methods:

Twenty rain gauges were constructed out of beer cans (12 ounce size) and sheet-metal funnels. The funnels were sealed to the beer can tops; and the hole conveying water into the can was of minimum size so as to prevent evaporation from the reservoir below. The standard diameters of the funnel tops, and of the beer cans themselves, made it a simple matter to read precipitation by means of a calibrated dip stick. Simple wooden bases were constructed so that the gauges could be leveled on the forest floor.

Nineteen of the gauges were placed ten meters apart in an L-shaped line, nine - one - nine. Between storms, the arms of the L were shifted in orientation 90° by pivoting around the apex. This assured more adequate sampling of canopy variability. One gauge was placed in the middle of a forest opening approximately 100 meters distant. This opening was at similar slope and altitude. It was large enough so that all but the windiest storms would not cause error

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due to interception by the bordering trees (no especially windy storms were sampled). This gauge was used as a standard and was considered to catch 100% of the precipitation falling upon the stand.

Results:

Seven storms were sampled during the summer and fall of 1959. These were of variable duration and intensity. In Figure 30 the mean percentage precipitation is plotted against the total precipitation in each. In the figure, each mean is bracketed by a range corresponding to its standard error. The results show that the lighter the storm, the smaller the percentage which reaches the forest floor. The average storm was .38 inches, of which 60% reached the forest floor.

Discussion:

Geiger (1957) discussed the paper by Hoppe (1896) and presented a graph of his results. Hoppe sampled the precipitation in a "60 year old spruce stand", using techniques similar to mine. The curve he plotted resembles mine, though it was not quite as steep. At a precipitation of .38 inches (9.3 mm) outside the forest, 47% was found to reach the forest floor. His stand was younger than mine and may have been denser. Horton (1919) found that about 25% of the precipitation falling in heavy rains of long duration was lost be-

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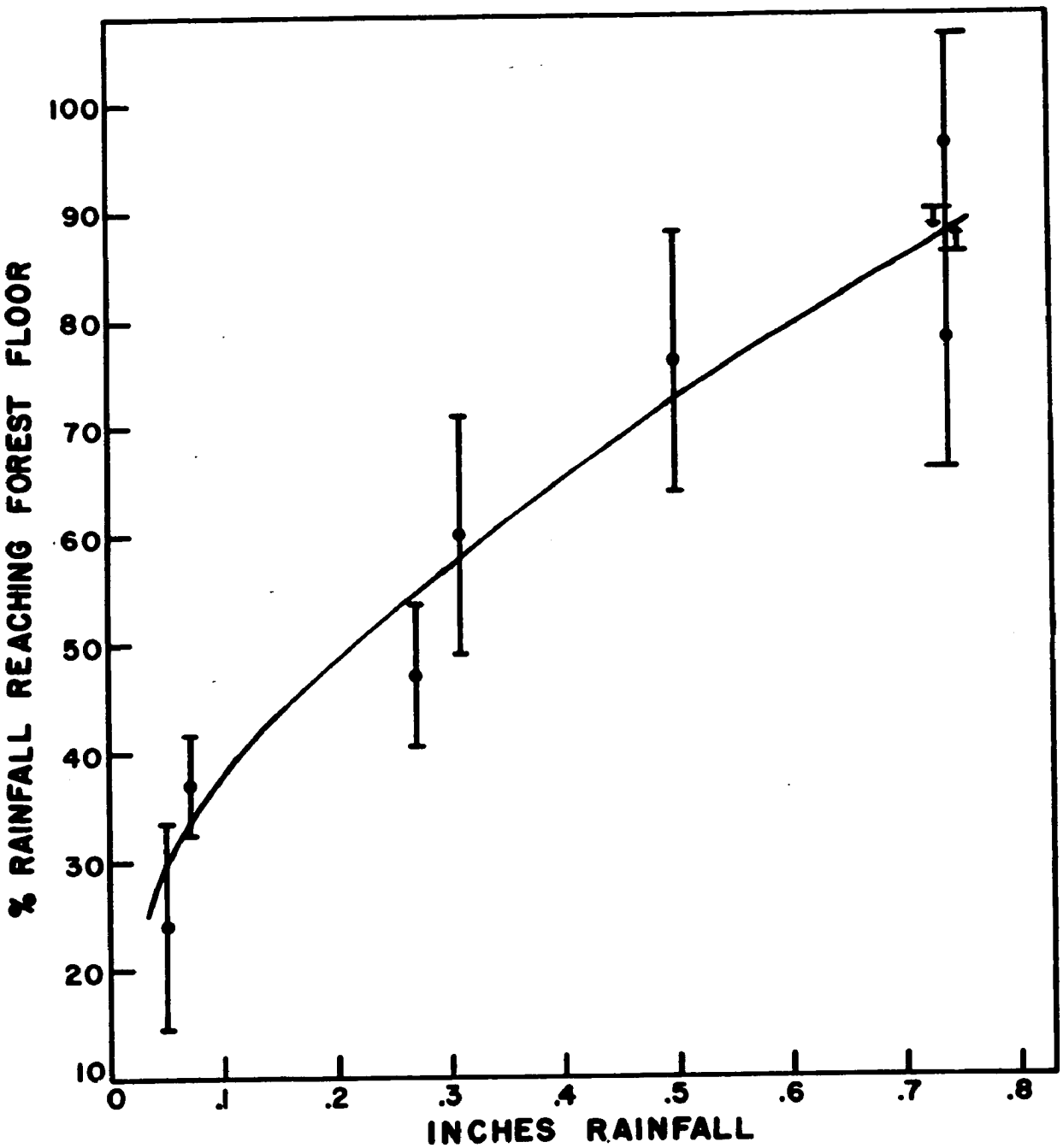


Figure 30. Percentages of Precipitation Reaching Forest Floor. Each mean percentage is bracketed by its standard error.

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fore reaching the forest floor in the deciduous stands he sampled. However, he added that "...loss from needle-leaved trees,...is greater..." In general, his results were similar to mine and Hoppe's.

Thus it is clear that a considerable percentage of the precipitation falling on the forest is lost before reaching the ground. If the average rainstorm were .25 inches (of average duration), about 50% of the precipitation would be lost at a stand such as Beech Hill. This loss cannot be evaluated regarding the net moisture relationship on the forest floor unless the evaporation there is known.

First hand data were not obtained on evaporation from the forest floor. However, Moore and Taylor (1927) obtained a series of measurements at Otter Point. The portion of the stand where they placed their instruments was then in the late thicket stage 4. Using Livingston atmometers, they found that evaporation under the canopy was about 47% of that in the open. They stated that evaporation was somewhat higher in the less foggy stands further inland on MDI. A definitive study of evaporation and precipitation under the same canopy would be of great value in understanding these relationships.

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Fauna

Breeding-birds

The purpose of this section is to describe the bird populations in the coastal spruce-fir forests. These populations were studied during the breeding season of 1959.

During June and early July, sample counts of territorial males were obtained in twelve spruce-fir stands from Cape Elizabeth to Cutler.

Sample Areas:

The following stands were sampled: Cape Elizabeth, Cundys Harbor, Gay Island, Beech Hill, Bass Harbor Head, Pemetic Mountain, Black Woods, Otter Point, Dyer Neck, South Addison, Roque Bluffs, and Cutler. Location data for these are listed in Table 5. The positions of the stands are indicated on the forest distribution map in the rear pocket. Eight of the twelve have been described in sections on vegetation. Brief descriptions for the other four are as follows:

Gay Island was a dense young stand of almost pure red spruce, in early stage 5. Most of the ground was covered by litter and there were very few herbs or shrubs. The trees were mostly between forty and fifty feet high.

Dyer Neck was an old field stand of mostly red spruce, but with white spruce more abundant near the shore. Dense

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portions were interspersed with ledgy poorly overgrown areas. Trees were between forty and fifty feet high. The stand was in stage 5. Portions of the ground were covered with bryophytes, but there were few herbs and shrubs.

South Addison was a dense stand of about half balsam fir and 30% red and white spruce. Paper birch and other hardwoods made up the remainder. The trees were mostly thirty to forty feet high, and the stand was judged to be in late stage 4. The ground was almost completely covered with litter. Herbs and shrubs were virtually absent.

The stand at Roque Bluffs was composed almost entirely of red spruce and balsam fir in approximately equal numbers. These were about thirty-five to forty-five feet high. Although only in early stage 5 a high percentage of the ground was covered with bryophytes (especially Hylocomium splendens). The site was moist.

Methods:

In methodology I largely followed Bond (1957). The sample count method which was used includes many of the same assumptions inherent in the more exacting spot-map methods. Both approaches are based upon the territoriality of breeding pairs. These are assumed to be fixed entities and are counted as if one were counting trees. In the spot-map method, an area is staked out and the number of singing males

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(presumably representative of territorial pairs) is mapped by recording their positions on spot-maps during a number of visits to the stand. In the sample count method, no area is staked out, but a transect is run over a number of territories. This yields relative numbers of various species, and not absolute density. However, this shortcoming is compensated by the lesser time required to sample one stand. Thus many stands may be compared in a single breeding season by one worker. A more detailed discussion of the method may be found in Bond's paper, and in the publication by Kendeigh (1944). Bond found good correspondence between data from both methods.

It had been my original intention to visit each stand twice during the breeding season, as did Bond, but twenty rainy days during June and the distance between stands made this impossible. All counts were made between June 25 and July 5. In some mornings two stands were visited. Counts were conducted between daylight and 9 a.m. No counts were made during high wind or rain, though at Gay Island a light drizzle set in during the count.

In order to make a count the approximate size and shape of the stand had to be known. The shape of the transect was planned to cover as much of the stand as possible without overlapping the same territories twice. This was sometimes

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a straight line, sometimes a U-shape, or an L-shape.

A series of "sample units" were employed along the transect. Each sample unit consisted of a five minute standing and a five minute walking period. The forest was entered to a distance of 100 feet and the first standing period started. During that time all birds heard or seen ahead and to my sides were counted. Then I slowly walked along the transect and recorded all birds ahead and to my sides that were not counted during the standing period. The sampling unit ended after 100-150 yards of walking, and there a new sampling unit was begun.

A constant effort was made not to count the same bird twice. This source of error is not believed to have affected the results appreciably. The total number of sampling units per stand depended on its size and shape. The average number was 4.4, and the range 3 to 7. Birds were not counted within 100 feet of the edge.

Common names are used here to conform to the American Ornithological Union Check List (1957), where corresponding Latin names may be found.

Results:

In Table 27 the species are tabulated by area. The relative density (RD%) indicates the percentage which each species contributed to the total number counted in the stand.

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Table 27. Breeding-birds. Relative Density (RD%), followed by Density (D)-mean number per sampling unit.

Species		CE	CH	GayI	BHH	BH	PM	BW	OP	DN	SA	RB	C	Means
Black-throated Green Warbler	RD%	16	30	19	18	16	42	9	19	18	21	24	26	21.5
	D	2.5	4.5	1.5	3.2	1.5	3.2	0.9	3.0	2.0	2.7	1.6	2.5	2.42
Myrtle Warbler	RD%	8	4	12	14	14	5	11	11	6	5	9	10	9.0
	D	1.2	0.5	1.0	2.4	1.2	0.4	1.1	1.7	0.7	0.7	0.6	0.9	1.04
Golden-crowned Kinglet	RD%	5	5	9	4	11	21	15	2	14	10	12	3	9.5
	D	0.8	0.8	0.8	0.8	1.0	1.6	1.4	0.3	1.6	1.3	0.8	0.3	0.96
Magnolia Warbler	RD%	6	4	9	4	8	5	4	8	16	13	6	10	7.8
	D	1.0	0.5	0.8	0.8	0.8	0.4	0.4	1.3	1.8	1.7	0.4	0.9	0.89
White-throated Sparrow	RD%	8	10	6	7	5	-	2	11	6	10	6	5	6.3
	D	1.2	1.5	0.5	1.2	0.5	-	0.2	1.7	0.7	1.3	0.4	0.5	0.80
Swainson's Thrush	RD%	-	2	12	4	8	10	11	2	8	10	6	5	6.6
	D	-	0.3	1.0	0.8	0.8	0.8	1.1	0.3	0.9	1.3	0.4	0.5	0.68
Blackburnian Warbler	RD%	18	16	-	2	-	-	-	4	2	5	3	5	4.6
	D	2.8	2.4	-	0.4	-	-	-	0.7	0.2	0.7	0.2	0.5	0.65
Red-breasted Nuthatch	RD%	2	8	-	4	-	5	9	8	-	5	3	8	4.5
	D	0.2	1.2	-	0.8	-	0.4	0.9	1.3	-	0.7	0.2	0.8	0.54
Slate-colored Junco	RD%	-	1	3	9	8	-	6	4	8	-	12	7	4.8
	D	-	0.1	0.2	1.6	0.8	-	0.5	0.7	0.9	-	0.8	0.6	0.52
Parula Warbler	RD%	2	8	12	9	-	-	4	6	2	-	-	3	3.9
	D	0.2	1.2	1.0	1.6	-	-	0.4	1.0	0.2	-	-	0.3	0.50
Purple Finch	RD%	2	-	6	4	3	-	13	6	2	3	-	-	3.2
	D	0.2	-	0.5	0.8	0.2	-	1.3	1.0	0.2	0.3	-	-	0.38

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Table 27. continued

Species		CE	CH	GayI	BHH	BH	PM	BW	OP	DN	SA	RB	C	Means
Winter Wren	RD%	5	3	-	4	-	5	-	P	-	3	6	-	2.1
	D	0.8	0.4	-	0.8	-	0.4	-	P	-	0.3	0.4	-	0.26
Robin	RD%	2	1	3	-	8	-	-	2	4	5	-	2	2.2
	D	0.2	0.1	0.2	-	0.8	-	-	0.3	0.4	0.7	-	0.2	0.25
Bay-breasted Warbler	RD%	-	1	-	9	-	-	2	2	6	-	-	-	1.6
	D	-	0.1	-	1.6	-	-	0.2	0.3	0.7	-	-	-	0.24
Black-capped Chickadee	RD%	3	2	3	-	11	P	4	-	-	-	3	3	2.4
	D	0.5	0.3	0.2	-	1.0	P	0.4	-	-	-	0.2	0.3	0.24
Hermit Thrush	RD%	6	4	-	2	3	-	-	2	-	-	-	3	1.7
	D	1.0	0.5	-	0.4	0.2	-	-	0.3	-	-	-	0.3	0.24
Solitary Vireo	RD%	-	1	-	-	-	5	-	4	-	3	3	-	1.3
	D	-	0.1	-	-	-	0.4	-	0.7	-	0.3	0.2	-	0.14
Yellow-shafted Flicker	RD%	2	-	3	-	-	-	2	-	2	-	3	2	1.1
	D	0.2	-	0.2	-	-	-	0.2	-	0.2	-	0.2	0.2	0.10
Brown Creeper	RD%	3	1	-	-	-	-	4	-	-	-	3	-	0.9
	D	0.5	0.1	-	-	-	-	0.4	-	-	-	0.2	-	0.10
Olive-sided Flycatcher	RD%	3	-	-	2	-	-	2	P	-	-	-	-	0.6
	D	0.5	-	-	0.4	-	-	0.2	P	-	-	-	-	0.09
Ovenbird	RD%	2	1	-	-	3	-	-	-	-	3	-	-	0.6
	D	0.2	0.1	-	-	0.2	-	-	-	-	0.3	-	-	0.08
Downy Woodpecker	RD%	2	-	-	-	-	-	2	-	2	-	3	-	0.7
	D	0.2	-	-	-	-	-	0.2	-	0.2	-	0.2	-	0.07

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Table 27. continued

Species		CE	CH	GayI	BHH	BH	PM	BW	OP	DN	SA	RB	C	Means
Catbird	RD%	3	-	-	-	-	-	-	-	-	-	-	2	0.4
	D	0.5	-	-	-	-	-	-	-	-	-	-	0.2	0.05
Eastern Wood Pewee	RD%	2	-	-	-	-	-	-	2	-	-	-	-	0.3
	D	0.2	-	-	-	-	-	-	0.3	-	-	-	-	0.05
Brown-headed Cowbird	RD%	2	-	-	-	-	-	-	P	2	-	-	-	0.3
	D	0.2	-	-	-	-	-	-	P	0.2	-	-	-	0.04
American Redstart	RD%	-	-	-	-	-	-	-	-	4	-	-	-	0.3
	D	-	-	-	-	-	-	-	-	0.4	-	-	-	0.04
Blue Jay	RD%	-	1	-	-	3	-	-	-	-	-	-	-	0.3
	D	-	0.1	-	-	0.2	-	-	-	-	-	-	-	0.03
Black-and-white Warbler	RD%	-	-	-	-	-	-	-	-	-	3	-	-	0.2
	D	-	-	-	-	-	-	-	-	-	0.3	-	-	0.03
Ruby-crowned Kinglet	RD%	-	-	-	-	-	-	-	2	-	-	-	-	0.2
	D	-	-	-	-	-	-	-	0.3	-	-	-	-	0.03
Yellowthroat	RD%	-	-	-	-	-	-	-	2	-	-	-	-	0.2
	D	-	-	-	-	-	-	-	0.3	-	-	-	-	0.03
Boreal Chickadee	RD%	-	-	-	-	-	-	-	-	-	-	-	3	0.3
	D	-	-	-	-	-	-	-	-	-	-	-	0.3	0.03
Yellow-bellied Fly-catcher	RD%	-	-	-	-	-	-	-	-	-	-	-	3	0.3
	D	-	-	-	-	-	-	-	-	-	-	-	0.3	0.03
Canada Warbler	RD%	2	-	-	-	-	-	-	-	-	-	-	-	0.1
	D	0.2	-	-	-	-	-	-	-	-	-	-	-	0.02

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Table 27. continued

Species		CE	CH	GayI	BHH	BH	PM	BW	OP	DN	SA	RB	C	Means
Hairy Woodpecker	RD%	-	-	-	-	-	-	2	-	-	-	--	-	0.2
	D	-	-	-	-	-	-	0.2	-	-	-	-	-	0.02
Song Sparrow	RD%	-	1	-	-	-	-	-	-	-	-	-	-	0.1
	D	-	0.1	-	-	-	-	-	-	-	-	-	-	0.01
Cape May Warbler		-	-	-	?	-	-	-	-	-	-	-	-	
Common Crow		P	P	P	P	P	-	-	P	P	P	-	P	
Herring Gull		-	P	-	P	-	-	P	P	P	-	-	P	
Common Raven		-	-	-	-	P	P	-	P	-	-	-	-	
Osprey		-	-	-	-	-	-	-	P	P	-	-	-	
Red Crossbill		-	P	-	-	-	-	-	P	-	-	-	-	
American Goldfinch		-	-	-	-	-	-	-	P	-	-	-	-	
Great Black-backed Gull		-	-	-	-	-	-	-	P	-	-	-	-	
Great Crested Flycatcher		-	-	-	-	-	-	-	P	-	-	-	-	
Ruby-throated Hummingbird		-	-	-	-	-	-	-	P	-	-	-	-	
Tree Swallow		-	-	-	-	-	-	-	P	-	-	-	-	
Great Horned Owl		-	-	-	-	-	-	-	P	-	-	-	-	
Mean # birds (all species) per sample unit		16	15	8	18	9	8	10	16	11	13	7	9	

The density (D) indicates the mean number of individuals counted per sampling unit. Species which were observed during the breeding season in a particular stand, but which were not counted during a sample count are indicated by a P.

The species were tabulated in order of their greatest overall mean densities. On this basis, the six most common species are as follows:

black-throated green warbler	2.42 ± .29
myrtle warbler	1.04 ± .16
golden-crowned kinglet	0.96 ± .13
magnolia warbler	0.89 ± .14
white-throated sparrow	0.80 ± .16
Swainson's thrush	0.68 ± .11

Standard errors are based on the twelve group means.

Discussion:

A number of errors are inherent in the method used. The assumption that total populations of each species are proportional to the number of singing males is the source of one of these (see Bond, 1957). Some males may be members of a floating unmated population.

Some species are more conspicuous than others, either by greater activity, more striking coloration, or louder voices. The last factor is most important here as almost all birds were recorded by song. An "index of conspicuous-

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ness" was proposed by Kendeigh (1944) (and other authors) to remedy this situation. But each worker must determine conspicuousness on the basis of the bird species involved, their habitat, and his own powers of sight and hearing.

In this study, I would propose the following: If the black-throated green warbler is given a conspicuousness value of 1.0, the golden-crowned kinglets should be multiplied by 1.5, the magnolia warblers and purple finches by 0.8, and Swainson's thrushes and white-throated sparrows by 0.5. The others on the first page of Table 27 are judged to be about as conspicuous as the black-throated green warbler. This procedure would result in the reordering of the table as follows: black-throated green warbler, golden-crowned kinglet, myrtle warbler, magnolia warbler, blackburnian warbler, red-breasted nuthatch, slate-colored junco, parula warbler, white-throated sparrow, Swainson's thrush, and purple finch.

One of the most striking aspects of the bird populations of these forests is the abundance of wood warblers (Parulidae). The family constituted about 50% of the total bird population. If this percentage is combined with the percentages of other tree inhabiting and tree feeding species, the total is raised above 75%. It is not surprising that birds characteristic of shrubs and herb strata are present only in low numbers. Ground feeding species are present in moderate numbers.

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Golden-crowned kinglets appeared to be most characteristic of dense stands, and the most dense portions of diversified stands; blackburnian warblers where the trees were tallest; magnolia and myrtle warblers where the stand was most diversified and at least a few openings present; parula warblers nearest the sea (especially where Usnea spp. was most abundant--as Knight, 1908, and Bond, 1947, also observed); and Swainson's thrush throughout, except at Cape Elizabeth where it was replaced by the hermit thrush.

These data have the strong limitation of being from only one year. Observations during a series of earlier summers spent along the Maine coast suggest that, in their gross aspects, the results obtained in 1959 were not atypical. A number of other workers obtained results in essential agreement with mine. However, population fluctuations are known to occur here. For example, MacArthur (1958) mentioned that Cape May and bay breasted warbler populations may vary strongly with the abundance of spruce budworm (Choristoneura fumiferana). A number of studies in the spruce-fir forests of Northern Maine and adjacent Maritime Provinces of Canada have recently elucidated the relationships between the warblers and spruce-budworm. The populations of most of the warbler species which I found to be common are known to respond to budworm population fluctuations (e.g. see Morris,

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et al., 1958, and their bibliography).

Earlier observations in the coastal spruce-fir forests include those of Knight (1908), who considered Cape Elizabeth to be the southwestern limit of the forest type and the bird species that go with it. The species he considered typical were the same as those I found. He mentioned that white-winged and red crossbill populations were erratic from year to year. Of the birds typical of spruce-fir areas in northern Maine, Knight noted that the Canada jay and spruce grouse were absent from the coast.

Montgomery (1890) studied the birds of the coast between Bath (2C) and MDI. He stated that the parula, myrtle, magnolia, bay-breasted, and black-throated green warblers were all typical of coastal spruce-fir forests, with the last-mentioned the most abundant. Mendall (1937) wrote that abundant breeding birds of the spruce-fir areas to the south of South Thomaston (3D) were the magnolia and black-throated green warblers, Swainson's thrush, white-throated sparrow, and slate-colored junco. Gross and Norton (1926) considered the following species to be typical of coastal spruce areas: olive-sided flycatcher, red crossbill, slate-colored junco, white-throated sparrow, myrtle and magnolia warblers and golden-crowned kinglet.

To the east, on Grand Manon (4H+), Pettingill (1939)

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found that the following species were typical of spruce-fir forests: yellow-bellied flycatcher, boreal chickadee (I found that species breeding only at Cutler, my easternmost area), red-breasted nuthatch, winter wren, hermit and Swainson's thrush, golden-crowned kinglet, bay-breasted warbler, blackpoll warbler (only in scrub spruce areas), magnolia and myrtle warblers, red and white-winged crossbills, slate-colored junco, and white-throated sparrow. Black-throated green warblers and American redstarts were common species throughout the forests there. The goshawk, black-backed three-toed woodpecker, and Tennessee warbler were scarce. Like Knight, he noted that the Canada jay and spruce grouse were absent.

Cruickshank and Cadbury (et al., 1936-42, 46, 47, 49-58) have run breeding bird censuses (spot-map) at a mature red and white spruce stand on Hog Island in Muscongus Bay. The thirty acre tract included five acres of partially cleared land with buildings and a few hardwoods. In latter years, the habitat was strongly modified by blow-down. During the 1936-42 period, averages of their results yield a list of species, in order of abundance, as follows:
1. parula warbler, 2. black-throated green warbler, 3. magnolia warbler, 4. golden-crowned kinglet, 5. myrtle warbler, 6. slate-colored junco, 7. song sparrow,

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8. blackburnian warbler, 9. Swainson's thrush, 10. chipping sparrow, 11. American redstart, 12. black-capped chickadee, 13. robin, 14. Cape May warbler, 15. crow, 16. bay-breasted warbler, and small numbers of other species.

Of their sixteen most common species, twelve were among my top sixteen. Their numbers 7, 10, and 11 probably reflect the marginal character of portions of their stand. Notably absent from the list is the white-throated sparrow, though it did appear in 1953 and became abundant with increased blow-down in ensuing years. The great abundance of parula warblers (the black-throated green was only slightly less abundant), may have resulted from the seaside nature of the stand and the abundant Usnea spp.

Winter Birds

On twenty-five occasions during the winters of 1958-59 and 1959-60, counts of birds in spruce-fir stands on MDI were taken. Of the twenty-five, fifteen were of an informal nature, bird data merely being included in general field notes on the stands. Ten counts were taken by a one hour early morning observation period, during which time the stands were completely covered. The methods were not aimed at exactitude, but merely at determining which species were most abundant. Even this may be questionable in the light of the wide and erratic movements of many wintering bird species. Never-

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theless, the results are presented in Table 28. Black-capped chickadees constituted about 50% of all birds counted. Red crossbills, red-breasted nuthatches, pine grosbeaks, and crows followed in that order.

Amphibia and Reptiles

Formal sampling procedures were not undertaken for these animals. However, during many days of work in the spruce-fir forests, a good idea of what species were present and their relative abundance was obtained. Amphibia are uncommon in mature coastal spruce-fir forests. Reptiles are rare.

Red-backed salamanders (Plethodon c. cinereus) were found on three occasions at Otter Point and Beech Hill by turning rocks. A total of eight individuals were seen, of which three were the lead-backed phase. Two wood frogs (Rana s. sylvatica) were observed, one at the Gerrish Island stand, and the other at Cape Elizabeth. An American toad (Bufo terrestris americanus) was found at the Cundys Harbor stand. Two spring peepers (Hyla c. crucifer), one at Otter Point and the other at Bass Harbor Head, were located in low conifers in the fall of 1958. In May of 1959 two dead milk snakes (Lampropeltis doliata triangulum) were found, one at Otter Point and the other at Beech Hill.

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Table 28. Winter Bird Censuses and Counts ( ).

	Black Woods	Otter Point	Beech Hill	Pemetic Mt.	Bass Harbor Head	Total	Census Total	Census %
# censuses (# counts)=	4 (2)	2 (5)	2 (3)	1 (2)	1 (3)			
Black-capped Chickadee	28 (1)	15(23)	12 (5)	0 (2)	24 (4)	114	79	45.7
Red Crossbill	45 (3)	0 (1)	0	0 (1)	0	50	45	26.0
Red-breasted Nuthatch	8 (2)	2 (2)	4 (2)	0	1	21	15	8.7
Pine Grosbeak	10 (1)	3	0(22)	0	0 (1)	37	13	7.5
Common Crow	1	4	0	0	0	5	5	2.9
Herring Gull	1	0	4	0	0	5	5	2.9
Common Raven	0	1 (1)	2	0	0	4	3	1.7
Hairy Woodpecker	2	0	1	0	0	3	3	1.7
Slate-colored Junco	0	0	1	0	1	2	2	1.2
Downy Woodpecker	1 (1)	0 (1)	0	0	0	3	1	0.6
Ruffed Grouse	0	0 (1)	1	0	0	2	1	0.6
Brown Creeper	0	1	0	0	0	1	1	0.6
Evening Grosbeak	0	0 (1)	0	0	0	1	0	0.0
Black-backed Three-toed Woodpecker	0	0 (1)	0	0	0	1	0	0.0

Small Mammals

Methods:

Several trap lines were run to compare relative numbers of small mammals in spruce-fir stands and adjacent habitats. These lines totalled 7,570 trap nights, of which 4,267 were in spruce-fir stands and 3,303 in other habitats. Most of the trapping locations have already been described. Brief descriptions of new locations are included with the tabulation of results.

On MDI, where the bulk of the trapping was done, trap lines of a type described by Calhoun, et al. (1948 ff.) were used. A trap line consisted of twenty stations, fifty feet apart, with three small-sized snap traps at each. These were run for variable periods of time, as tabulations of the results will indicate. A mixture of peanut butter and oats was used for bait.

At stands off MDI trapping was done in conjunction with visits for vegetational sampling. I was sometimes able to arrive the evening before vegetation was to be studied. One hundred traps were placed in a line of twenty-five stations, each fifty feet apart. Four traps were placed within eight feet of each station. Only one night of trapping was possible at each of these stands.

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Results:

The results are listed in Table 29. Three species are tabulated, Red-backed voles (Clethrionomys gapperi ochraceous), deer mice (Peromyscus maniculatus abietorum), and masked shrews (Sorex cinereus). The first was trapped more frequently in spruce-fir forests than the second, while the reverse was true for the deer mice. A reliable estimate of relative abundance of the shrews was not obtained, as only two were captured on the trap lines. However, eighteen others were captured in the insect traps, and these are tabulated. A single woodland jumping mouse (Napaeozapus insignis) was captured near the borderline of the spruce-fir and hardwood stands on Pemetic Mountain (near the small stream).

Discussion:

Manville (1942) noted that red-backed voles tended to be most abundant in the coniferous forests of MDI, while deer mice were common throughout the forests. The masked shrew was abundant in a wide variety of habitats. In a spruce stand west of the southern end of Eagle Lake, MDI (U.S.G.S. Mount Desert Quadrangle), Calhoun, et al. (1948 ff.) found deer mice to be much more abundant than red-backed voles in 1949 and 1950.

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Table 29. Small Mammals, Mount Desert Island and elsewhere.

Area	Line No.	Habitat	Date	Trap-nights	Species		
					R.b. vole	deer mouse	masked shrew
Cape Elizabeth	I	red spruce, balsam-fir, red maple	8/11/59	100	3 (2♀,1♂)	0	0
Cundys Harbor	I	red spruce, white pine, arbor vitae	8/12/59	100	0	0	0
Beech Hill	I	red spruce, hemlock, arbor vitae - edge hard.	5/8/59 to 6/14/59	2280	4 (3♂,1?)	3♂	1
Beech Hill	3 insect traps	hardwoods, mostly paper birch.	summer 1959		0	0	2
Beech Hill	II	red spruce, hemlock, arbor vitae	5/8/59 to 6/14/59	2280	1 immature	1♂	0
Beech Hill	3 insect traps	red spruce, hemlock, arbor vitae	summer 1959		0	0	2
Bass Harbor Head	3 insect traps	white spruce, red spruce, balsam-fir	Aug.&Sept.		0	0	3
Pemetic Mountain	I	red spruce, hemlock	6/3/59 to 6/14/59	720	6 (5♂,1♀)	2♂	0
Pemetic Mountain	4 insect traps	red spruce, hemlock	summer 1959		0	0	2
Pemetic Mountain	II	beech, sugar maple, yellow birch	6/3/59 to 6/14/59	720	3 (2♂,1?)	0	0
Pemetic Mountain	4 insect traps	beech, sugar maple, yellow birch	summer 1959		0	0	1

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Table 29. continued

Area	Line No.	Habitat	Date	Trap-nights	Species R.b. vole	deer mouse	masked shrew
Black Woods	I	edge of woods near road where blow down & clearing has taken place	10/5/58 to 10/7/58	63	0	1	0
Black Woods	II	red spruce, paper birch, balsam-fir	10/16/59to 10/21/59	252	13 (6♂, 7?)	1	0
Otter Point	I	spruce near ledges; 100 yds. to burn; 100 ft. to road	8/12/58	15	0	2♂	0
Otter Point	II	spruce - fir	5/23-30/59 6/7-8/59	600	6 (5♂, 1♀)	0	1
Otter Point	insect trap		summer 1959		0	0	8
Otter Point, "The Ledges"	III	12 yrs. since burn; shrubby veg.&bare granite.	5/30/59 to 6/2/59	240	4(1 imm. 2♂, 1♀)	10(6♂, 2♀, 2imm	0
Ironbound Island	I	spruce-fir-red maple	late Aug.59	100	0	0	0
Roque Island	I	spruce-fir	late Aug.59	100	0	0	0
Total				7570	40 (24♂, 5♀, 2imm. 9?)	20 (14♂, 2♀, 2 immature) 2?	20
Total in spruce				4267	29	6	
Percentage catch per trap night					.68	.14	
Total in non-spruce				3303	11	14	
Percentage catch per trap night					.33	.42	

Large Mammals

As was the case with amphibia and reptiles, the observation of large mammals was incidental to other undertakings in the forests. During the winters of 1958-59 and 1959-60 scores of observations of mammal tracks were made.

Among the most abundant mammals in the coastal spruce-fir forests was the red squirrel (Tamiasciurus hudsonicus). One northern flying squirrel (Glaucomys sabrinus) was captured in a trap at the Beech Hill Stand, but the abundance of this species was unknown. According to Manville (1924) it occurs in spruce forests on MDI.

Snowshoe hares (Lepus americanus) rarely entered the mature stands, though their tracks were often seen along the edges and in openings. Red fox (Vulpes fulva) tracks were common in the forests. Along the edge of the sea, mink (Mustela vison) tracks sometimes occurred.

Deer (Odocoileus virginianus) appeared to frequent the spruce-fir areas mostly in the winter. This was probably due to the high shelter value of such forests (Banasiak, 1956). During the winters deer were observed repeatedly at the Beech Hill and Otter Point stands, and deer tracks were found in all stands. Deep snow did not accumulate during either of the winters, and heavy yarding did not take place. Foods for the animals are rare in mature stands.

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It is probable that deer exert some modification on the floristics of spruce-fir stands in coastal Maine. For example, Favour (1958), in his surveys of the high deer populations on MDI, pointed out that red maple, arbor vitae (Thuja occidentalis), striped maple (Acer pensylvanicum), and witherod are favorite foods. Reproduction by these plants may be severely reduced in the spruce-fir stands by the overwintering deer. Schierbeck (1911) noted that honeysuckles (Lonicera spp.) and American yew (Taxus canadensis) were favorite foods of the deer in Nova Scotia. The latter species may have become strongly reduced by heavy repeated browsing. Hamerstrom and Blake (1939) noted that in Wisconsin winter foods included lowbush blueberry (Vaccinium spp.), teaberry, shadbush (Amelanchier spp.), mountain holly, and winterberry (Ilex verticillata). Pearce (1939) studied the effects of deer on forest types in the western Adirondacks of New York state in some detail. He noted that "Deer feed on practically every woody plant except spruce, when in yards in the western Adirondacks." Although "...deer naturally can exert little influence in a stand of dense virgin spruce with practically no undergrowth.", during early succession they "...may enable red spruce to assume dominance by selective browsing on its competitors." This possibility was said to be strongest in lowland stands where red maple and yellow

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birch might otherwise have been more important.

Carabidae

The object of this portion of the study was to determine if certain species of carabid beetles are characteristic of the spruce-fir forest type on MDI. This insect group was chosen because of the relative ease with which they may be collected.

Beetles were collected in several habitats other than spruce-fir forests in order to obtain a measure of "fidelity" to the spruce-fir habitat. Both full-winged and flightless forms were collected in most habitats. Flightless forms are good runners and capable of migrating over land from one habitat to the next.

Sample Areas:

Collections were made at fourteen stations. These included Black Woods, Western Mountain, Beech Hill, Bass Harbor Head, Pemetic Mountain, Otter Point, Whitney Farm, Haywood Garden, and the shore of Little Echo Lake. The spruce-fir stands at the first six areas have already been described, and location data for them and the Whitney Farm were presented in Table 5. At Beech Hill and Pemetic Mountain, collections were made at adjacent hardwood stands. The locations of these are indicated by an H on the maps in Figure 5. Brief descriptions are given in the following paragraphs for

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habitats not previously described:

The hardwood stand at Pemetic Mountain was sharply distinguished from the spruce-fir area by a small stream valley. The stand was sampled in 1959 by G. M. Woodwell of the Botany Department of the University of Maine (personal communication). He found it to be composed (by basal area) of 39% beech, 32% sugar maple (Acer saccharum), 22% yellow birch, and lesser quantities of other species.

The hardwood stand at Beech Hill was composed of about 90% paper birch, plus lesser quantities of red maple and arbor vitae, and other species. To the north along the Beech Hill Road, a distance of 3/4 mile, the Haywood Garden (HG) was located, surrounded by old fields and mixed woods.

Little Echo Lake (LEL) was a pond just to the north of Echo Lake (U.S.G.S., Mount Desert Quadrangle). Collections were made there along the north shore. The water level was low and aquatic vegetation lay decaying on the shore.

Four habitats at the Whitney Farm were sampled. The first (WF1) was a one acre woodlot surrounded by old fields. The woodlot contained red spruce, white pine, paper birch, and less abundant species. The second (WF2) was an apple orchard surrounded by old fields and mixed woods. A small vegetable garden constituted the third habitat (WF3). It too was surrounded by old fields and mixed woods. The fourth

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habitat (WF4) was my residence.

Methods:

Twenty-four #10 tin cans (ca..8 gallon) were used as traps. These were distributed as follows:

Area	Number of Traps
Otter Point	5
Pemetic Mountain	
spruce-fir	4
hardwoods	4
Beech Hill	
spruce-fir	3
hardwoods	3
Bass Harbor Head	3
Whitney Farm	
mixed woodlot (WF1)	1
apple orchard (WF2)	1

The cans were placed in the ground with the open tops flush with the ground surface. Boards raised on stones, served as roofs to keep the rain out of the cans. These were arranged so as to allow free access by the beetles. The shortest distance between traps was 100 feet, and none was placed nearer than 100 feet to marginal habitats.

Traps were baited with a number of different substances. These included cheeses, banana peels, melon rinds, grapes,

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pears, molasses, peanut butter, chopped beef, and fish. Baits were distributed among traps and areas so as to affect equal representation as much as possible.

Trapping began in early May, 1959, and continued until mid-October of that year. Traps were visited for collections and rebaiting at least once every two weeks. Hand collecting was done when time was available, both at the trap areas and at the other locations.

All specimens were identified by C. A. Frost.

Results:

In Table 30 the results are presented. For each species, the total number captured in each area is listed. This figure is followed by the mean number per trap. The latter figure allows comparison between areas where different numbers of traps were present. A total of 665 beetles of thirty-seven species were collected.

Only species collected in appreciable numbers can be used for reliable estimates of habitat preference. No species were collected in large numbers in the spruce-fir habitat which were not found in goodly numbers elsewhere. Those that may be more common in the spruce-fir habitat are Myas foveatus, Pterostichus adoxus, and Euferonia coracina. Spruce-fir areas were distinctive in their low overall densities and limited numbers of species. Several species

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Table 30. Carabidae. Mount Desert Island. May 5 to October 11, 1959.
Total number collected, followed by mean number per trap.

SPECIES (and Leng Cat. No.)	AREAS															
	Spruce-Fir							Deciduous			Other					
	WM	BH	BHH	PM	BW	OP	Sum	BH	PM	Sum	WF1	WF2	WF3	WF4	HG	LEL
162 Sphaeroderus lecontei Dej.								2	3	5					1	
								1	1	1						
171 Carabus serratus Say		4					4									
		1														
175 Carabus nemoralis Mull.								5	46	51	3	1	3		2	
								2	12	7	3	1				
214 Callisthenes zimmermanni (Lec.)								1		1						
246 Notiophilus aeneus Hbst.					1											
-- Bembidion (new species?)								1		1						
723 Bembidion versicolor (Lec.)																1
725 Bembidion muscicola Hayw.								1		1						
731 Bembidion fraternum Lec.													1			
737 Bembidion oppositum Say													6			
744 Bembidion cf. pedicellatum Lec.													1			

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Table 30. continued

SPECIES (and Leng Cat. No.)	AREAS																
	Spruce-Fir							Deciduous			Other						
	WM	BH	BHH	PM	BW	OP	Sum	BH	PM	Sum	WF1	WF2	WF3	WF4	HG	LEL	
929 Myas cf. cyanescens Dej.			1				1										
930 Myas foveatus Lec.			1	6		1	8	1	1	2							
				2			1										
933 Cylindrocharis rostrata (Newn.)				10			10	1	3	4	5						
				2			1		1	1	5						
1005 Pterostichus rejectus Lec.		5		1			6	9	2	11							
		2						3	1	1							
1006 Pterostichus adoxus (Say)		23	1	20		30	74	23	1	24	3						
		8		5		6	5	8		3	3						
1024 Gastrellarius honestus (Say)	1				1		2		1	1							
1089 Euferonia stygica (Say)								60		60		2					
								20		9		2					
1093 Euferonia coracina (Newn.)		9	16	22		23	70	4	12	16	1						
		3	5	6		5	5	1	3	2	1						
1097 Euferonia lachrymosa (Newn.)								3	1	4	4						
								1		1	4						
1162 Poecilus lucublandus Say								1				3	1				
												3					

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Table 30. continued

SPECIES (and Leng Cat. No.)	AREAS																
	Spruce-Fir							Deciduous			Other						
	WM	BH	BHH	PM	BW	OP	Sum	BH	PM	Sum	WF1	WF2	WF3	WF4	HG	LEL
1173+ Omaseus vulgaris = Feronia melanarius				1												
1178 Dysidius mutus (Say)								4	3	7		4				
								1	1	1		4				
1188 Bothriopterus pennsylvanicus (Lec.)			2	9			11		20	20			5			
			1	2			1		5	3						
1188complex Bothriopterus pennsylvanicus (Lec.)		6	6	14		3	29	8	26	34						
		2	2	4		1	2	3	6	5						
1471 formerly - Badister neopulchellus Lindroth																1
1482 Calathus gregarius Dej.		12		2		6	20	10	7	17						
		4		1		1	1	3	2	2						
1488 Pristodactyla advena (Lec.)		4	1	7			12	20	31	51						
		1		2			1	7	8	7						
1489 Pristodactyla impunctata (Say)	*1	2		1			4	4	6	10						
		1						1	2	1						
1513 Platynus decens Say									1	1						
1514 Platynus sinuatus (Dej.)			3			1	4	11		11						
			1					4		2						

*mixed forest

Table 30. continued

SPECIES (and Leng Cat. No.)	AREAS															
	Spruce-Fir							Deciduous			Other					
	WM	BH	BHH	PM	BW	OP	Sum	BH	PM	Sum	WF1	WF2	WF3	WF4	HG	LEL
1546 Platynus cf. affinis (Kby.)																6
1554 Platynus hardyi Chd. mss. Lec.															1	
1577 Platynus aeruginosus (Dej.)																15
1903 Harpalus viridiaeneus Beauv.														1		
1925 Harpalus cf. pennsylvanicus DeG.													1			
1926 Harpalus convivus Lec.													1			
1956 Harpalus cf. herbivagus Say								2 1		2						

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present in high numbers elsewhere were either absent or present in low numbers in the spruce-fir habitat. In mean numbers per trap, 2.7 times as many beetles were captured in non-spruce-fir habitats. Although fifteen traps were used in the spruce-fir stands, and only seven in hardwood forests, twenty-three species were captured in the latter and only fifteen in the former.

These results may reflect a lower biological activity on the ground level in spruce-fir forests, as compared to other major vegetational types in the coastal area. Data in other sections of this thesis support this contention.

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PART IV

BIOGEOGRAPHIC RELATIONS

In this section the spruce-fir forests of the coast of Maine are compared to spruce-fir forests elsewhere in eastern North America. Such comparisons are best conceived when the history of the biotic regions is understood, and when their migratory and changeable nature is appreciated. At the present time very few areas of eastern United States are covered by spruce-fir forests. However, as was discussed in Part II, at the height of glaciation spruce-fir forests probably occupied considerable portions of the east-central states. Since that time these forests have retreated northward with the ice. Southern remnants remain in areas such as the high ridges of the Appalachians, in bogs in formerly glaciated territory, and near sea level on the coast of Maine and Nova Scotia.

Spruce-fir Forest Types

Three spruce-fir types will be described here, and the coastal Maine forests compared to them. These are the boreal, Acadian, and southern Appalachian spruce-fir forests.

Boreal Spruce-fir Forests

A large area of southeastern Canada is covered by the

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eastern portion of the transcontinental boreal coniferous forest. This thesis is concerned only with the part from Lake Superior and James and Hudson Bays eastward. The distribution of this forest may be seen by reference to one of several available maps of the vegetational zones of North America (e.g. Transeau, et al., 1940; or Pitelka, 1941).

During the past few decades these forests have been described in some detail. Among the publications are those of Ilvessalo (1929), Halliday (1937), Tanner (1944), Hustich (1939, ff.), Hare (1950, ff.), and Wilton (1959). These authors agree, in broad terms, that the forests can be divided into three subtypes: lichen-woodland, muskeg, and closed forest. The categorization is primarily structural, though each type possesses distinctive floristic characteristics.

In this eastern area there is little correlation between forest type and precipitation. Hustich (1949) calls the three subtypes "dry series" (lichen woodland), "moist series" (closed forest), and "wet series" (muskeg). But these moisture "series" are related mainly to physiography and soil development rather than precipitation. According to Hare (1950), "...the northern forests are governed in their growth by temperature, and that precipitation is everywhere adequate to supply the needs of the growth pos-

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sible under such cool conditions,..." Midsummer temperatures appear to be the major control of tree growth. According to Villeneuve (1946), the mean temperature during the four warmest months in boreal conifer areas is 50-60°F, the July mean 50-66°F, and the annual mean 30-38°F. Precipitation averages about thirty-eight inches per year and ranges from about twenty to fifty-six.

It is the boreal closed forest subtype that will be used here for comparison to more southern types. The distribution of this subtype is not clearly differentiated from the other subtypes. It is best developed in southern parts of the boreal forests. The closed forest is the boreal forest of the lumberman. Here trees attain a good size and productivity is high enough to support repeated cuttings. According to Hare (1950), the closed forest extends from

> ...north of Lake Superior across southern Labrador-Ungava to Anticosti Island and Newfoundland. Large outliers cover inland Gaspe, the highlands of New Brunswick, and parts of Maine.

The definition of the Acadian region, which follows later, includes Hare's outliers, thereby excluding them from the boreal region as I define it.

Near the Great Lakes the closed forests tend to be dominated by balsam fir and white spruce, and in the east by black spruce and balsam fir. Associated with these are relatively intolerant species of a seral nature. They in-

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clude jack pine (especially western regions), balsam poplar (Populus balsamifera), quaking aspen (Populus tremuloides), and alders. Near the southern margin, species such as arbor vitae and certain maples (Acer spp.) appear.

The meaning of the word "climax", as it applies to boreal forests, is somewhat different from its meaning when applied to more southern forest types. Southward, forest climax theory holds that climax tree species must be able to reproduce and survive under their own canopy. The climax is perpetuated by continual replacement from below. Species incapable of doing this may be replaced by more tolerant forms and thus are not climax species.

On the other hand, in climax boreal forests, seedlings do not usually survive under the canopy. For replacement of the upper story the forest must be opened. However, replacement and growth terminates in the same type of forest which preceded the opening. The spruce-fir type is perpetuated because it is best adapted to the rigorous environmental conditions.

Where boreal and more southern forest types grow side-by-side, the boreal type does not usually occupy the most mesic sites available. Rather, it grows where it is free of competition from the more exacting tolerant hardwoods (Maycock, 1957). As Hutchinson (1918) pointed out, and Raup

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(1946) later agreed, the northward movement of mesophytic conditions required by hardwood forests for their optimum development has lagged behind temperature changes in post-glacial time, and awaits the slower development of soils.

Fire, blow-down, and budworm infestation are recurrent in boreal forests. Replacement may be by a temporary stage of birch and poplar or directly by spruces and firs. Hustich (1939) observed that over half the forests near the east coast of Newfoundland-Labrador had burned in the twenty-five to thirty year period prior to his study. Wilton (1959) noted that in the Grand Lake and northwestern Lake Melville areas of Labrador a high percentage of the forests had been burned at least once during the prior 250 years.

In boreal forests the upper tree stratum is usually the only one present. It is typically even-aged, even in virgin areas. Hustich (1950) found this to be the case in the eastern James and Hudson Bay areas, where successful development of seedlings under the canopies was virtually absent. In Labrador, Hustich (1949) called the closed forest (feather moss type) "climax", and yet emphasized its homogeneity and even-aged (150-200 years) character. There he found "...hardly any regeneration at all, the moss cover being too thick and too dry." Wilton (1959) stated that substantial reproduction of black spruce from seed only took place after

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fire had opened the forest. On Isle Royale, Cooper (1913) found that in the "climax forests" successful replacement of old white spruces by young ones required that the canopy be opened by blow-down or other agency. Maycock and Curtis (1960) emphasized these characteristics in the conclusion of their analysis of the forests in the northern Great Lakes region. It will be recalled that in Part III I proposed that the white spruce border on the coast of Maine is largely maintained by blow-down.

Non-boreal Spruce-fir Forests

The non-boreal spruce-fir forests in eastern North America are distinguished by an abundance of red spruce. I am in agreement with Hustich (1949) who stated that red spruce does not extend into the boreal region proper. The present distribution of this species was described by Heimburger (1949) and was mapped by Harlow and Harrar (1958). According to Halliday and Brown (1943) it survived during the height of glaciation together with boreal species in the southern Appalachians and perhaps on the continental shelf. However, unlike the boreal species, it did not follow the ice far northward.

The success of forests dominated by red spruce in maintaining themselves against encroachment by hardwood forests may be due to several factors. Among these is the ability

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of the species to grow on poor sites where other species cannot easily compete. Thus, according to Korstian (1937), spruce-fir stands in the Great Smoky Mountains are not found where physical conditions are best for their growth, but where the soil is too poor or thin for the more exacting hardwoods to compete successfully. Obviously, this factor alone cannot account for the success of red spruce-fir forests.

Another factor may be the high tolerance of red spruce. The ability of its saplings to survive under its own dense shade contributes to the perpetuation of the forest type.

The distribution of red spruce-fir forests appears to be definitely correlated with coolness and high moisture. Successful reproduction by spruce and fir in the easily dried spruce-fir duff is most likely where the climate is moist. High precipitation and coolness at high elevations in the Appalachians, or summer fog and coolness on Acadian shores, supports reproduction and helps prevent destruction by fire. In the deep moss and duff of dense humid virgin stands, red spruces may germinate and survive, but hardwoods cannot.

The high tolerance of red spruce not only contributes to its climax status, but also serves to distinguish the structure of non-boreal spruce-fir forests from those fur-

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ther north. Virgin red spruce dominated stands are characteristically uneven-aged. Examples are the virgin stands studied by Korstian (1937), by Oosting and Billings (1951), and by me on Western Mountain. This is not to say that even-aged groves do not occur in virgin red spruce areas. Brown (1941) found even-aged spruce-fir forests on Roan Mountain in the Smokies, where windfall played an important role in stand structure. I found the same to be the case in parts of the Western Mountain stand. However, sizeable openings do not appear to be necessary for reproduction and canopy replacement, in contrast to boreal forests.

The frequent fires in red spruce areas in modern times might convey a mistaken impression of the importance of fire in the perpetuation of the forest type. These fires are in large part directly or indirectly related to human activity, especially lumbering. Brown (1941) knew of no history of fires above 4000 feet on Roan Mountain in the Smokies. Korstian (1937) emphasized that the dense virgin spruce-fir forests in the Smokies maintained high humidity within and were "...nearly immune to fire except in seasons of excessive dryness..." This contrasts strongly to the lumbered areas there.

Acadian Region:

The Acadian region is here defined as the area where

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the ranges of red, white, and black spruce overlap. The southern border corresponds roughly to the southern limit of glaciation. In this region, stands containing high percentages of red spruce are found at high elevations (above ca. 3000 feet in the south to ca. 1000 feet in the north) in New York State, central and northern New England, New Brunswick, Nova Scotia, and certain portions of Quebec (Heimburger, 1941); and near sea level in coastal regions of Maine and Nova Scotia. Certain of these regions included by Hare (1950) in the boreal forest are here included in the Acadian because of the prominence of red spruce.

The Acadian region defined here does not correspond to the "Acadian Region" of Halliday (1937) who included all the Appalachian spruce-fir forests. However, I agree with Halliday's emphasis on the non-boreal character of these spruce-fir forests. Dominant tree species in various sections of the Canadian portions of the Acadian region are listed by Halliday.

In their map of spruce percentages in the forests of Canada, Halliday and Brown (1943) indicated sizeable areas of more than 30% spruce in New Brunswick and Nova Scotia. These represent striking non-montane southern outliers for so high a spruce percentage. The presence of red spruce may be the factor responsible, as it may be able to withstand

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replacement by hardwoods better than the other spruces.

Southern Appalachian Region:

In the southern Appalachian region, white and black spruce are absent. From West Virginia southward spruce-fir stands occupy high elevations in the mountains, above 3,200 feet in West Virginia (Core, 1950) to above 4,500 feet in the Great Smoky Mountains. South of Virginia, balsam fir is replaced by Fraser fir (Abies fraseri).

Comparison between northern and southern Appalachian spruce-fir forests was made by Oosting and Billings (1951). Among the most important differences are the greater height of trees in the south and the greater development of bryophyte and herb cover there. They recognized two phases of the Appalachian spruce-fir forests: the red spruce-Fraser fir forests of the south, and the red spruce-balsam fir forests of the north. I prefer to use the Pennsylvanian gap and presence of numerous boreal species to the north as the bases for my division.

The climate of the spruce-fir areas of the Great Smoky Mountains, as described by Shanks (1954), is similar to that of the Acadian region. As Shanks put it,

> "Perhaps the nearest low-altitude equivalent in terms of both climate and vegetation occurs somewhere in northeastern Maine or adjacent New Brunswick, about 1000 miles to the northeast."

Spruce-fir areas in the Appalachians have a mean tem-

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perature during the four warmest months of about 53-61°F, a July mean of about 55-65°F, and an annual mean temperature of about 33-45°F. Precipitation varies from sixty to 110 inches per year in the high southern mountains to about thirty to eighty inches in the Acadian region. Both the growing season temperatures and precipitation tend to become lower from south to north. For further discussion of these climates the reader is referred to an earlier section called "Summary and Evaluation in Terms of Thornthwaite's Methods:".

Floristic Comparisons

Two approaches were used to evaluate the geographic relationships of the flora of the Maine coastal spruce-fir forests. First, the literature was consulted in order to characterize the flora of each of the three regions discussed on preceding pages. The coastal Maine forests are compared to these. Second, the ranges of the common species of the coastal forests were ascertained in order to determine the area where the greatest number of them are concentrated.

Comparisons of Regional Spruce-fir Flora

In order to characterize the spruce-fir forests of the three regions, data were obtained from the following papers:

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Southern Appalachians: Brown, 1941, Great Smoky Mountains (GSM); Cain, 1935, GSM; Cain and Sharp, 1938, GSM; Cooley, 1954, GSM; Core, 1929, West Virginia; Crandall, 1958, GSM; Davis, 1930, GSM; Harshberger, 1903, GSM; Oosting and Billings, 1951, GSM; Sharp, 1939, GSM; and Whittaker, 1956, GSM.

Acadian Region: Adams, et al., 1920, Mt. Marcy, N. Y.; Collins, 1951, N. Cape Breton Island; Drinkwater, 1957, Nova Scotia; Harshberger, 1905a, Adirondack Mts., N. Y.; Harshberger, 1905b, Catskill Mts., N. Y.; Harvey, 1903, Mt. Katahdin, Maine; Heimburger, 1934, Adirondack Mts., N. Y.; Heimburger, 1941, Lake Edward area, Quebec; Ilvessalo, 1929, Laurentides area, Quebec; Long, 1952, New Brunswick; Nichols, 1918, N. Cape Breton Island; Oosting and Billings, 1951, White Mts., N. H. (indicated by number 2 on New England map in rear pocket); and Oosting and Reed, 1944, western Maine (number 1 on rear pocket map).

Boreal Region: Hustich, 1949, Labrador; Hustich, 1950, east coast Hudson and James Bays, Quebec; Hustich, 1955, Moose River area, Ontario; Lepage, 1945, James Bay to Lake Mistassini, Canada; Linteau, 1955, Quebec; Tanner, 1944, Newfoundland-Labrador; and Wilton, 1959, Grand Lake and northwestern Lake Melville areas, Labrador.

The species listed by each of the authors were trans-

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ferred to large master tables. There were five such tables: trees, shrubs, herbs, pteridophytes, and ground-cover lichens and bryophytes. Species were entered as common or present (in low quantity). Judgment had to be used here because authors listed their species in a variety of ways. Some authors indicated actual quantities, others relative abundance, others merely presence. In the first two instances, I considered their five most abundant species to be common, and the remainder present. For authors using only presence data I transferred their listings without modification to the master tables.

The master tables were then summarized to determine the most common species in each of the three regions. This was done by summing the entries under each species, weighting the commons twice that of the presences. In summary tables for herbs, and for lichens and bryophytes, the twenty most common species in each region were listed. However, when a species was among the twenty most common in one region and was present but not among the twenty most common in a second region, it was added to the end of the list of the latter. Thus, the final listings included more than the twenty most common in each region. In the tree and shrub tables the ten most common species were first listed, and in the pteridophyte table the six most common. Then, extras were added on

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the lists as they were for herbs.

Tables 31-35 are the summaries in final form. Three symbols were used for entries. An A (abundant) indicates that a species was among the five most common in the region. An F (frequent) indicates that it was among the sixth through fifteenth most common, and a P (present in low quantity) that it was less common. Because of the usually low quantity of pteridophytes, entries for this table were made only in terms of presence (P). From these tables the following conclusions are reached:

The trees in the Maine coastal spruce-fir forests are typical of the forests in the Acadian region. Boreal species here include paper birch and white spruce. Appalachian species include red spruce and yellow birch. Only three tree species are tabulated which are common to all three regions.

Table 32 lists seven shrub species which are found in all three regions. The spruce-fir stands in the southern Appalachians possess several shrub species not found in other spruce-fir forests. No floristic element appears in the table which is common to the southern Appalachian and Acadian regions but absent from the boreal. This is with the exception of hobblebush, Viburnum alnifolium, which is uncommon in Acadian stands. The shrubs of the coastal Maine spruce-fir forests are typical of Acadian spruce-fir forests. Among

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Table 31. Floristic Comparisons; Trees. The ten most common species in the spruce-fir forests of each region are included. A = abundant, F = frequent, P = present in low quantity.

	Southern Appalachians @	Acadia	Boreal	Coastal Maine
Abies balsamia	A	A	A	A
Pyrus americana	A	A	P	F
Acer spicatum	A	F	P	F
Picea rubens	A	A		A
Betula lutea	A	F		F
Acer pensylvanicum	F	F		F
Prunus pensylvanica	F	F		P
Fagus grandifolia	F	P		P
Abies fraseri	A			
Amelanchier laevis	F			
Aesculus octandra	F			
Acer rubrum		A		A
Betula papyrifera		A	A	A
Picea glauca		F	A	A
Picea mariana		F	A	
Populus tremuloides		F	F	**
Thuja occidentalis		F	F	F
Larix laricina		P	A	
Populus balsamifera			F	
Pinus banksiana			F	

@ Present in mountains of Virginia and West Virginia, but not recorded by authors consulted here.

** Only in Moore and Taylor, 1927.

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Table 32. Floristic Comparisons; Shrubs. The ten most common species in the spruce-fir forests of each region are included. A = abundant, F = frequent, P = present in low quantity.

	Southern Appalachians	Acadia	Boreal	Coastal Maine
Viburnum cassinoides	F	A	P	A
Sambucus pubens	A	F	P	P
Ribes glandulosum	P	A	P	***
Lonicera canadensis	P	F	P	F
Alnus crispa	P	F	F	F
Rubus canadensis	F	?	F	
Viburnum alnifolium	A	F		F
Rhododendron catawbiense	A			
Vaccinium erythrocarpum	A			
Diervilla sessilifolia	A			
Menziesia pilosa	F			
Rhododendron carolinianum	F			
Ribes rotundifolium	F			
Ilex montana	F			
Vaccinium myrtilloides		A	A	A
Vaccinium angustifolium		A	F	A
Rubus pubescens		F	A	?
Taxus canadensis		F	P	F
Kalmia angustifolia		F	A	A
Viburnum edule		F	A	
Corylus cornuta		F	P	
Rubus idaeus var. strigosus		F	P	?
Ledum groenlandicum		P	A	
Diervilla lonicera		P	F	P
Rubus chamaemorus		P	F	

*** Only in Hill, 1923.

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Table 32, cont'd.

	Southern Appalachians	Acadia	Boreal	Coastal Maine
Nemopanthus mucronata		A		A
Betula glandulosa			F	
Empetrum nigrum			F	
Vaccinium uliginosum			F	

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Table 33. Floristic Comparisons; Herbs. The twenty most common species in the spruce-fir forests of each region are included. A = abundant, F = frequent, P = present in low quantity.

	Southern Appalachians	Acadia	Boreal	Coastal Maine
Oxalis montana	A	F	F	F
Clintonia borealis	A	A	F	F
Maianthemum canadense	P	A	A	A
Aster acuminatus	A	F	P	F
Streptopus roseus	F	F	P	P
Monotropa uniflora	F	F	P	F
Trillium undulatum	F	P	P	P
Trillium erectum	F	P	P	
Epigaea repens	P	P	P	P
Actaea rubra	P	P	P	
Medeola virginiana	F	P		P
Circaea alpina	F	P		P
Tiarella cordifolia	F	P		
Veratrum viride	P	P		P
Solidago glomerata	A			
Senecia regelia	A			
Chelone lyoni	F			
Houstonia serpyllifolia	F			
Aster divaricatus	F			
Eupatorium rugosum	P			
Galax aphylla	P			

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Table 33, cont'd.

	Southern Appalachians	Acadia	Boreal	Coastal Maine
Impatiens pallida	P			
Saxifraga michauxii	P			
Dalibarda repens		F		
Cornus canadensis		A	A	A
Trientalis borealis		A	A	A
Linnaea borealis		F	A	F
Coptis groenlandica		A	F	A
Aralia nudicaulis		F	F	A
Gaultheria hispidula		F	A	F
Solidago macrophylla		F	P	***
Pyrola secunda		F	F	P
Moneses uniflora		P	F	P
Aster macrophyllus		P	P	P
Vaccinium vitis-idaea		*	F	F
Streptopus amplexifolius		P	P	
Habenaria obtusata		P	P	
Viola incognita		P	P	
Galium triflorum		P	P	
Mitella nuda		P	P	
Viola pallens			F	
Mertensia paniculata			P	

*** Only in Hill, 1923.

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Table 34. Floristic Comparisons; Pteridophytes. The six most common species in the spruce-fir forests of each region are included. P = present.

	Southern Appalachians	Acadia	Boreal	Coastal Maine
Osmunda claytoniana	P	P	P	P
Lycopodium clavatum	P	P	P	P
Lycopodium obscurum	P	P	P	P
Lycopodium lucidulum	P	P		P
Dryopteris spinulosa var. intermedia	P	P		P
D. spinulosa var. americana	P	P		P
Polypodium virginianum	P	P		P
D. spinulosa var. fructosa	P	P		
Athyrium felix-femina	P	P		
Athyrium felix-femina var. asplenoides	P			
Pteridium aquilinum		P	P	P
Dryopteris phegopteris		P	P	P
Osmunda cinnamomea		P	P	P
Lycopodium annotinum		P	P	P
Equisetum sylvaticum		P	P	P
Dryopteris disjuncta		P	P	***
Equisetum arvense			P	

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Table 35. Floristic Comparisons; Ground-cover Bryophytes and Lichens. The twenty most common species in the spruce-fir forests of each region are included. A = abundant, F = frequent, P = present in low quantity.

	Southern Appalachians	Acadia	Boreal	Coastal Maine
Hylocomium splendens	A	A	A	A
Calliergonella schreberi	P	A	A	A
Hypnum crista-castrensis	F	A	A	P
Bazzania trilobata	A	A	P	A
Dicranum scoparium	A	F	P	A
Dicranum fuscescens	A	F	P	P
Dicranum rugosum	P	A	F	F
Rhytidiadelphus triquetrus	F	P	F	P
Polytrichum commune	P	F	F	P
Thuidium delicatulum	A	P	P	P
Brotherella recurvans	F	F	P	P
Hylocomium umbratum	F	F	P	?
Lepidozia reptans	P	P	P	F
Tetraphis pellucida	P	P	P	F
Anastrophyllium michauxii	F	*	P	P
Blepharostoma trichophyllum	P	P	P	P
Dicranum montanum	P	P	P	F
Mnium punctatum	P	P	P	P
Cephalozia media	P	*	P	P
Jamesoniella autumnalis	P	*	P	P
Cladonia mitis	?		P	

* Only record for Acadian area is in this thesis.

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Table 35, cont'd.

	Southern Appalachians	Acadia	Boreal	Coastal Maine
Polytrichum ohioense	F	F		P
Hypnum imponens	P	F		F
Nowellia curvifolia	F	*		P
Paraleucobryum longifolium	F	*		P
Dicranella heteromalla	P	*		P
Frullania asagrayana	P	*		P
Dicranodontium denudatum	F			
Atrichum undulatum	F			
Bazzania denudata	P			
Herberta tenuis	P			
Plagiochila sullivantii	P			
Tritomaria exsecta	P			
Hylocomium pyrenaicum		P		
Rhytidiadelphus loreus		P		
Ptilidium pulcherrimum		F	F	A
Cladonia rangiferina		F	A	F
Brachythecium salebrosum		F	F	P
Sphagnum capillaceum		P	F	P
Cladonia alpestris		P	A	P
Plagiothecium denticulatum		P	P	P

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Table 35, cont'd.

	Southern Appalachians	Acadia	Boreal	Coastal Maine
Drepanocladus uncinatus		*	F	P
Cladonia uncialis		*	F	P
Eurynchium strigosum		*	P	P
Cladonia pyxidata			P	**
Calliergonella sarmentosum			P	
Stereocaulon tomentosum			P	
Sphagnum cuspidatum			P	

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the shrubs, the Acadian region is more closely allied to the boreal than the southern Appalachian region. The abundant mountain-holly is distinctly Acadian.

In Table 33 ten herb species are listed which are found in all three regions. Common wood-sorrel (Oxalis montana), bluebead-lily (Clintonia borealis), and false lily-of-the-valley are common throughout. Four species are shared by the southern Appalachian and Acadian regions only, and these are not common in the latter. As was the case with the shrubs, the southern Appalachian stands possess a set of species all their own. Six species which are absent from the southern Appalachians are shared and are abundant or frequent in the Acadian and boreal spruce-fir forests. On this basis it may be said that the herbs of the Acadian forests are more like the boreal. The coastal Maine forests are typically Acadian.

It is difficult to evaluate the pteridophyte element. Several of the species are widespread and not particularly characteristic of spruce-fir forests. The coastal Maine forests appear to be typical of the Acadian region and intermediate between southern Appalachian and boreal.

Perhaps the most outstanding binding feature in the flora of spruce-fir forests in eastern North America is their ground-cover bryophytes. Table 35 includes twenty species

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found in all three areas, and additional but less abundant species were tabulated in the master table. Species mostly confined to the southern Appalachian and Acadian regions include Bazzania trilobata and Polytrichum ohioense, though the first is present but uncommon further north. The Acadian-boreal element is more prominent, exemplified by Ptilidium pulcherrimum, Cladonia rangiferina, and Brachythecium salebrosum. As with the shrubs and herbs, a certain group of bryophytes is distinctively southern Appalachian. However, the distinction between the southern Appalachian and Acadian bryophyte flora is not as marked as Oosting and Billings' paper (1951) might suggest.* Of the twenty-four species which they list only for the Great Smoky Mountains stands, at least fourteen have been found by me and others in Acadian and/or boreal spruce-fir stands. Of the fourteen species they list only for the White Mountains (New Hampshire) stands, at least eight have been found by others in Great Smoky Mountains stands.

Distributional Relationships of the Coastal Maine Spruce-fir Forest Flora

Vascular Plants:

The question asked here is: What geographic areas are

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*The same is true to a lesser extent for the vascular species listed by Oosting and Billings (1951).

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best represented in the flora of the coastal Maine spruce-fir forests? To answer this question, one could merely list the species and their ranges, but this would place disproportionate emphasis on the ranges of rare species, and not enough on those of abundant forms. Hence, the ranges of each species are weighted according to their importance value in the coastal forests.

The relative importance values were obtained for trees, shrubs, and herbs from Tables 20 and 21. Each of these was tabulated under one of four geographic categories: Appalachian, boreal, Acadian, or throughout. The Acadian and boreal regions have already been defined. The Appalachian region includes the Appalachian highlands plus the Acadian region. In order for a species to be placed in one of the first three categories it need not be confined there, but must be rare or limited to adjoining portions of the other regions. To be placed in the "throughout" category the species must be well distributed in all three regions. Information on ranges was obtained from Fernald's book (1950). These procedures yielded the following results (%):

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	Appalachian	boreal	Acadian	throughout
Trees	79	20		
Shrubs	36	31	22	10
Herbs	25	39	1	35
Pteridophytes	65	16		18
Non-arborescent Tracheophytes	26	38	2	33

The last row summarizes shrubs, herbs, and pteridophytes by weighting the values of each in terms of their relative densities in the coastal spruce-fir forests. Therefore, herbs make the greatest contribution.

The relative importance value of red spruce, 65%, raises markedly the Appalachian category for the trees. Among the lesser vascular plants the boreal region is best represented. However, Appalachian and widespread species together account for over 50% of the non-arborescent forms. Thus, an overall appraisal of the geographic representation in the vascular flora of the coastal Maine spruce-fir forests reveals that it is intermediate between Appalachian and boreal regions.

In Figure 31 the distribution of the five most important trees is mapped. These distributions were adapted from Harlow and Harrar's maps (1958). In Figure 32 the five most important herbs are mapped. These maps demonstrate the intermediate character of the Acadian spruce-fir forests. They show the extensive Canadian distribution of several of the

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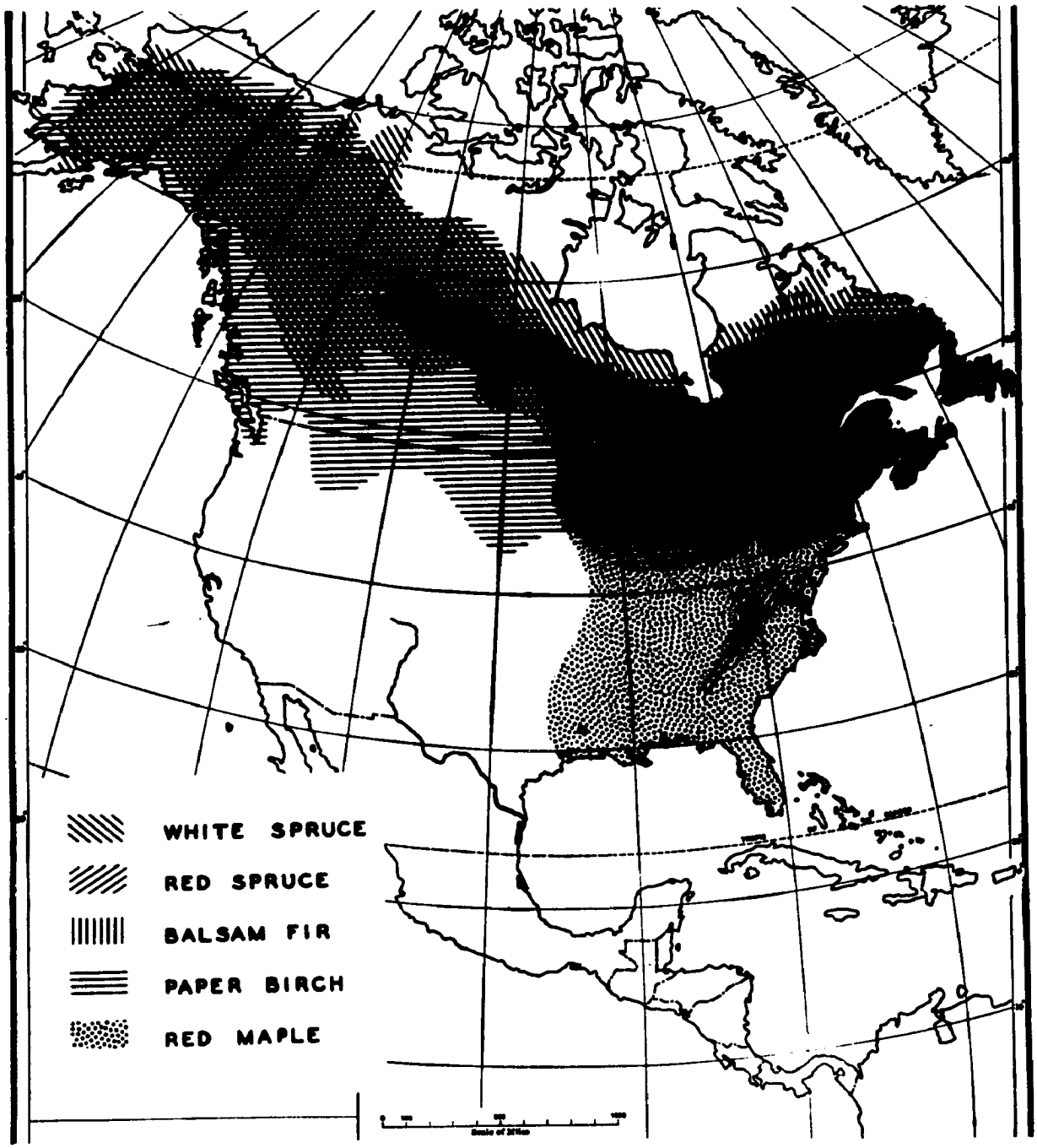


Figure 31. Tree Distributions. The distributions of the five most important species in the coastal Maine spruce-fir forests are mapped.

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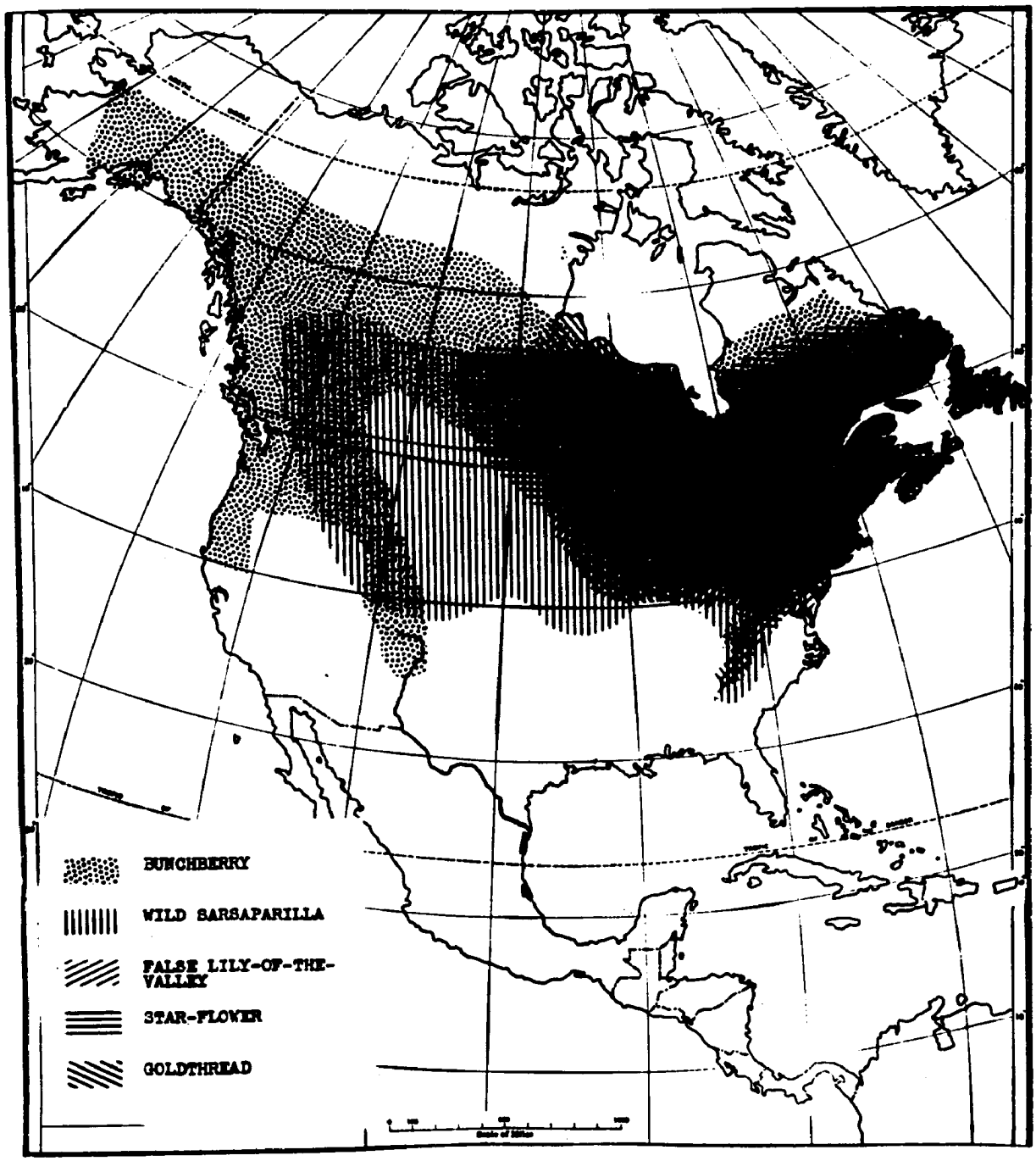


Figure 32. Herb Distributions. The distributions of the five most important species in the coastal Maine spruce-fir forests are mapped.

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species, and southward Appalachian extension of others.

Non-vascular Plants:

Ground cover bryophytes and lichens could not be used in this analysis because reliable distributional information was not readily available. Comments by Mason E. Hale, Jr. on the distribution of corticolous lichen species were tabulated earlier (Table 23). Of these, eight (22%) are boreal; fourteen (39%) occur in boreal, Acadian, and southern Appalachian regions; one (3%) is strictly Appalachian; and thirteen (36%) are cosmopolitan.

Comparisons of Regional Spruce-fir Breeding-bird Fauna

The same methods used for the flora were used for assembling and tabulating bird data. Publications on the bird populations of the boreal forests east of the Great Lakes are not numerous. However, several papers on the avian fauna of the spruce-fir forests of the northern Great Lakes area are available. Hence, this latter region is used as an additional category here.

The following papers were consulted in order to characterize each region:

Southern Appalachians: Adams, 1959, Great Smoky Mountains; Brooks Bird Club, 1953, West Virginia; De Garmo (and De Garmo, et al.), 1948 ff., West Virginia; Murray, 1939,

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Southern Appalachians; Stewart and Aldrich, 1949, West Virginia; and Stewart and Robbins, 1951, Maryland.

Acadian Region: Eaton, 1910, New York State; Kendeigh, 1946, Catskill Mts., N. Y.; Mitchell, 1952, Northern Maine; Morris, et al., 1958, New Brunswick; Palmer, 1949, Maine; Palmer and Taber, 1946, Mt. Katahdin, Maine; Stewart and Aldrich, 1952, Northern Maine; and Stewart and Webster, 1951, Northern Maine.

Northern Great Lakes Boreal Region: Kendeigh, 1947, Lake Nipigon area, Ontario; Kendeigh, 1948, Northern Lower Michigan; Martin, 1956, Algonquin Park, Ontario; and Roberts, 1932, Minnesota.

Eastern Boreal: Godfrey, 1949, Quebec; and Townsend and Allen, 1907, Labrador.

Coastal Maine: In addition to my own data I utilized those of the authors mentioned in the section on birds in Part III.

In Table 36 regional comparisons are presented. An avifauna peculiar to Appalachian spruce-fir areas is absent. A large number of species are found breeding throughout much of the spruce-fir forest of eastern North America. The most common of these include the slate-colored junco, winter wren, golden-crowned kinglet, blackburnian warbler, black-throated green warbler, magnolia warbler, Swainson's thrush, and red-

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Table 36. Breeding-birds, Comparisons. The twenty most common species in the spruce-fir forests of each region are included. A = abundant, F = frequent, P = present in low quantity, * = northern portions only.

	Southern Appalachians	Acadia	Great Lakes Boreal	Eastern Boreal	Coastal Maine
Slate-colored Junco	A	A	F	F	F
Winter Wren	A	F	A	F	F
Golden-crowned Kinglet	A	F	A	P	A
Blackburnian Warbler	A	F	A	P	A
Black-throated Green Warbler	F	F	F	F	A
Magnolia Warbler	F*	A	F	P	A
Swainson's Thrush	F*	A	F	P	F
Red-breasted Nuthatch	F	F	F	F	F
Canada Warbler	A	F	P	P	P
Solitary Vireo	F	F	P	P	P
Black-capped Chickadee	F	P	P	P	F
Robin	F	P	P	P	F
Purple Finch	P*	P	F	P	F
Northern Water Thrush	F*	P	P	P	?
Pine Siskin	P	P	P	F	P
Ruffed Grouse	P	P	P	F	P
Hermit Thrush	P*	P	P	P	P
Brown Creeper	P	P	P	P	P
Hairy Woodpecker	P	P	P	P	P
Red Crossbill	P	P	P	P	P

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Table 36, cont'd.

	Southern Appalachians	Acadia	Great Lakes Boreal	Eastern Boreal	Coastal Maine
Parula Warbler	P	F	P		F
Black-throated Blue Warbler	F	P	P		
Blue Jay	P	P	P		P
Ovenbird	P	P	P		P
Scarlet Tanager	P	P	P		
Veery	F		P		
Cedar Waxwing	P		P		
Towhee	P				
White-throated Sparrow		A	A	A	F
Myrtle Warbler		A	A	F	A
Yellow-bellied Flycatcher		F	F	F	P
Bay-breasted Warbler		F	F	P	F
Boreal Chickadee		F	P	F	P
Black-backed Three-toed Woodpecker		P	F	F	P
Canada Jay		P	F	F	
Spruce Grouse		P	F	F	
Tennessee Warbler		F	P	P	P
Ruby-crowned Kinglet		F	P	P	P
American Three-toed Woodpecker		P	P	F	
Olive-sided Flycatcher		P	P	P	P
Black-poll Warbler		P	?	F	P

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Table 36, cont'd.

	Southern Appalachians	Acadia	Great Lakes Boreal	Eastern Boreal	Coastal Maine
Pine Grossbeak		P		F	
Cape May Warbler		F	P		P
Nashville Warbler		P	F		P
Great Horned Owl	?	?	?	P	P

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breasted nuthatch. A number of species are common in spruce-fir forests only north of the southern Appalachians. These include the white-throated sparrow, myrtle warbler, yellow-bellied flycatcher, bay-breasted warbler, boreal chickadee, and black-backed three-toed woodpecker. Five species which were listed for the southern Appalachians are absent south of Virginia. These are the magnolia warbler, Swainson's thrush, purple finch, northern water thrush, and hermit thrush. In Figure 33 the distribution of the five most common species from Table 27 are mapped. This distributional pattern is shared by other species as well. Data on these distributions came from the American Ornithological Union checklist (1957).

The avifauna appears to be affected little by the differences in dominant tree species (e.g. red vs. white spruce) between forests. Indeed, the dominant trees for many of the common spruce-fir birds need not even be spruce or fir. Thus, for example, Robbins (1949) found the blackburnian, magnolia, black-throated green, parula, and Canada warblers, and the solitary vireo to be common in a virgin hemlock forest in Maryland. Kendeigh (1954), Odum (1945), and Pitelka (1941) all agree that the "life form" (e.g. coniferous vs. deciduous forest) is more important in determining breeding bird populations than the specific taxa present.

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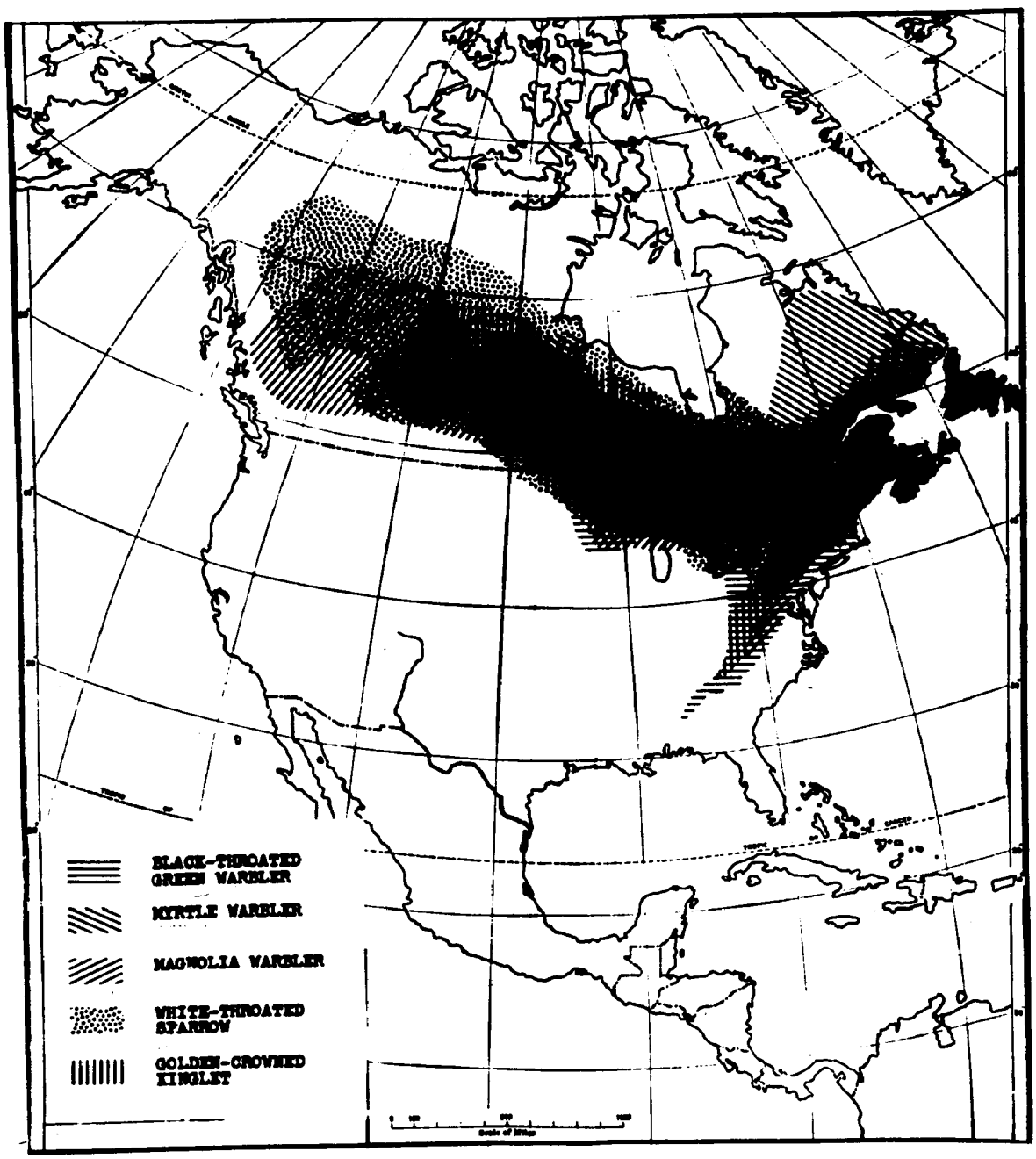


Figure 33. Breeding-bird Distributions. The distributions of the five most important species in the coastal Maine spruce-fir forests are mapped.

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According to the habitats and ranges listed in the American Ornithological Check List (1957), the species I found to be common are mostly limited in their breeding ranges to coniferous forests of the Appalachians and northward. It is perhaps best to designate this avifauna as boreal, because the bulk of the distribution is in Acadian and boreal spruce-fir forests.

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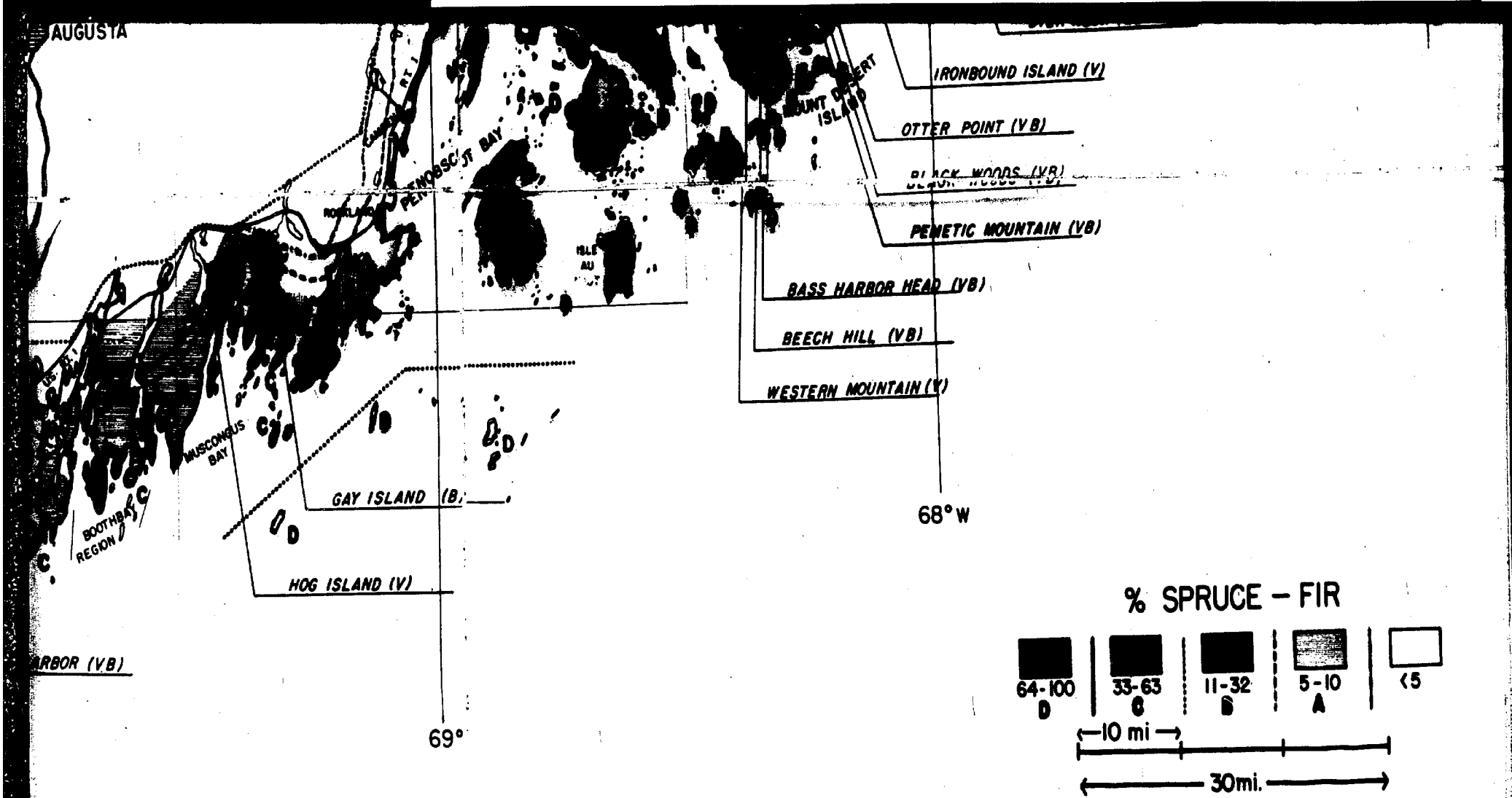
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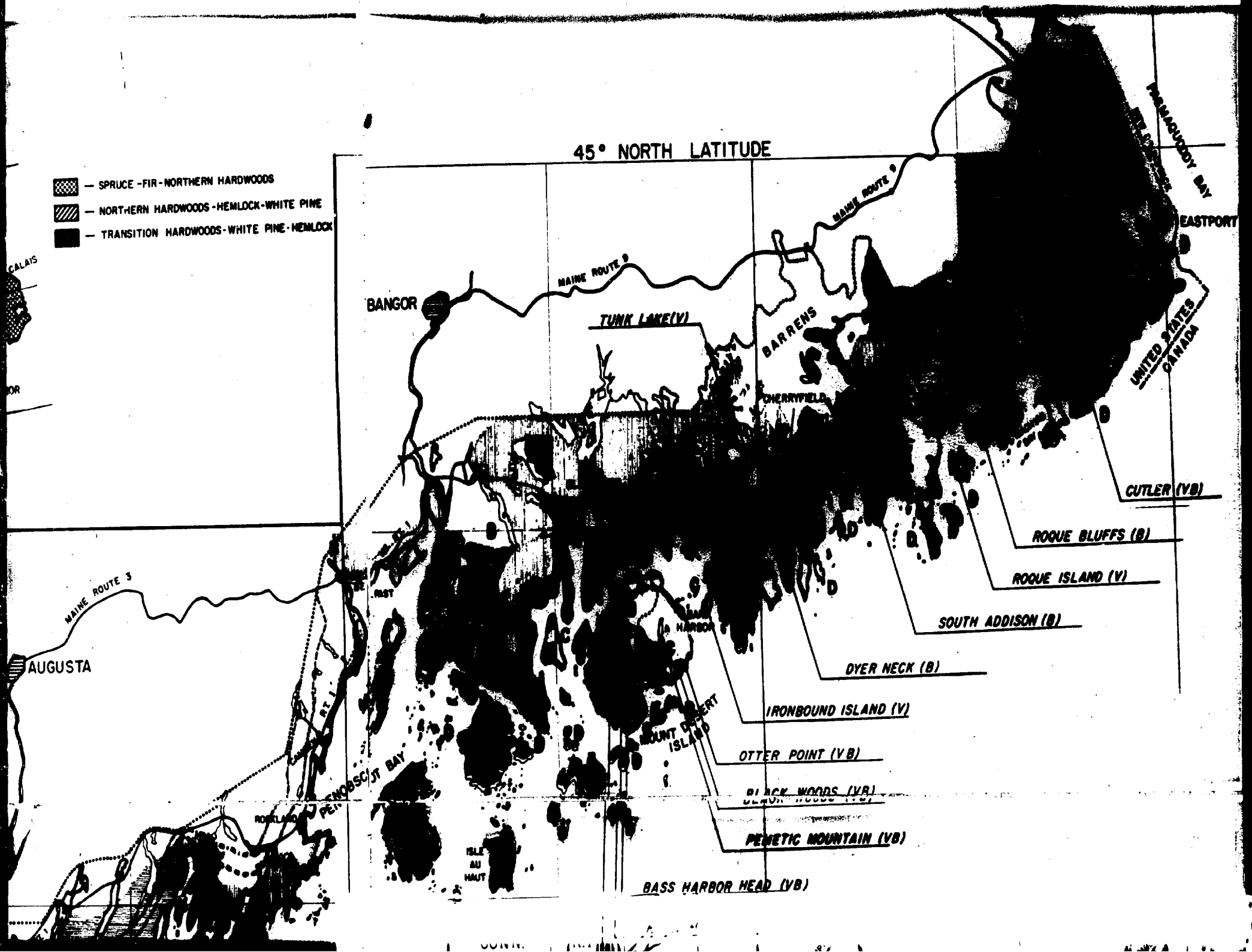
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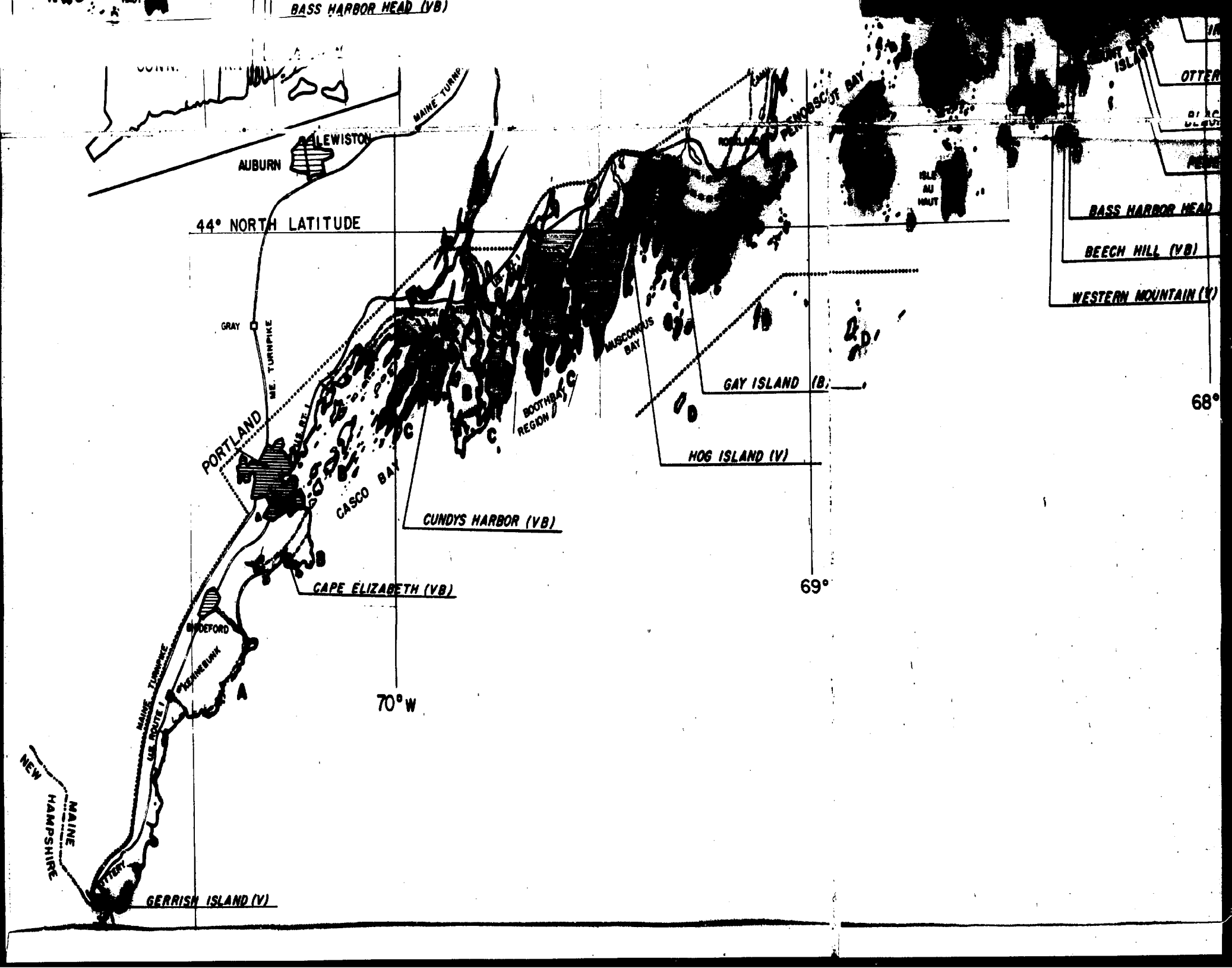
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