

AN ANALYSIS OF JACK PINE SITES IN MINNESOTA
WITH SPECIAL REFERENCE TO SITE INDEX, PLANT
INDICATORS, AND CERTAIN SOIL FEATURES

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INTRODUCTION

THE PROBLEM

As long as man has grown crops for his own use, he has been interested in classifying areas with respect to their ability to grow such crops. Foresters have been concerned with the relative ability of different localities to produce forests. The need for systems of forest classification grew with the intensification of forestry practices which to some extent followed the greater demands made on the forests of Europe by an ever increasing population.

The most obvious system of classification of the forest lands of a region is one based on the species of trees actually present. This is the cover type system which, from the standpoint of number of types and degree of subdivision, attained its highest development in the system recommended by the Committee on Forest Types of the Society of American Foresters (98). This system gives primary consideration to the practical and immediate problems of the forester in managing the forest.

Although the cover type system of classification fulfills the need for simple descriptive information concerning forests, it does not give any qualitative information concerning either the forest or the environment in which it grows. From an economic point of view, a forester is concerned with the production of wood in maximum quantities. Different areas having similar cover types often vary greatly in their

ability to grow crops of trees. For this reason, numerous systems have been devised by which areas could be classified on the basis of their relative volume production ability into what are commonly called site classes. Most site classification systems could be grouped under one of three general classes: mensurational, including those systems using such characteristics as height growth as a basis of classification; soils systems, using soil features as a criterion of site quality, and vegetation systems, in which plants are used as site indicators.

The primary purpose of the present study is to determine whether plant indicators are reliable in predicting site quality of jack pine as computed by the commonly used site-index method which is based on height-age relationships of the dominant trees of the stand. The use of plant indicators, if found reliable, would have certain definite advantages. The system would be a natural rather than an arbitrary and mechanical one and would indicate successional tendencies of the existing forest. In addition, a forester with a practical knowledge of the plants of his region would be able to identify site classes readily without the use of special tree measuring devices and without digging into the ground to examine soil conditions.

In connection with the primary objective, special attention was given to the development and testing of new techniques in the systematic analysis of forest vegetation. This is a field of investigation almost untouched by American foresters. Forest descriptions have usually been limited to lists of species observed, sometimes with frequency ratings of the species. On the other hand, most of the intensive methods used by the European plant sociologists have been developed for describing

subsidiary vegetation and are unsuited to the needs of forest ecologists. In addition, little has been done in describing vegetation in standardized quantitative terms to enable comparisons and analysis by biometric methods.

One of the limitations of a plant indicator system is the fact that its use is impractical on non-forested areas where the absence of an over-story alters the composition of the ground vegetation. For this reason, a secondary objective of this study was to examine soil profiles with a view to the possible use of soil characteristics as site indicators. In view of the necessity of limiting the scope of this phase of the work, the decision was made to study the texture and nitrogen content of the subsoil horizons. No attempt was made, however, to examine intensively the entire soil complex.

THE AREA

The Vegetation

The stands of jack pine examined in this study occur entirely within the coniferous forest region of the northeastern one-third of Minnesota. A map showing the broad vegetational regions of the state is given in Fig. 1. The map in Fig. 2 shows the distribution of the pine types in more detail.

Weaver and Clements (129) consider this area to have a white pine-red pine climax. However, they point out the close proximity of the boreal spruce-fir-larch climax to the north and the deciduous forest climax to the south and the interspersed nature of all three climax formations in the general area of this study. Typical sugar maple-basswood forest occurs in isolated spots on heavy soils well within the coniferous area.

Figure 1. Distribution of vegetational formations.
 After map by Upham in Minnesota Geological and
 Natural History Survey Annual Report 12.

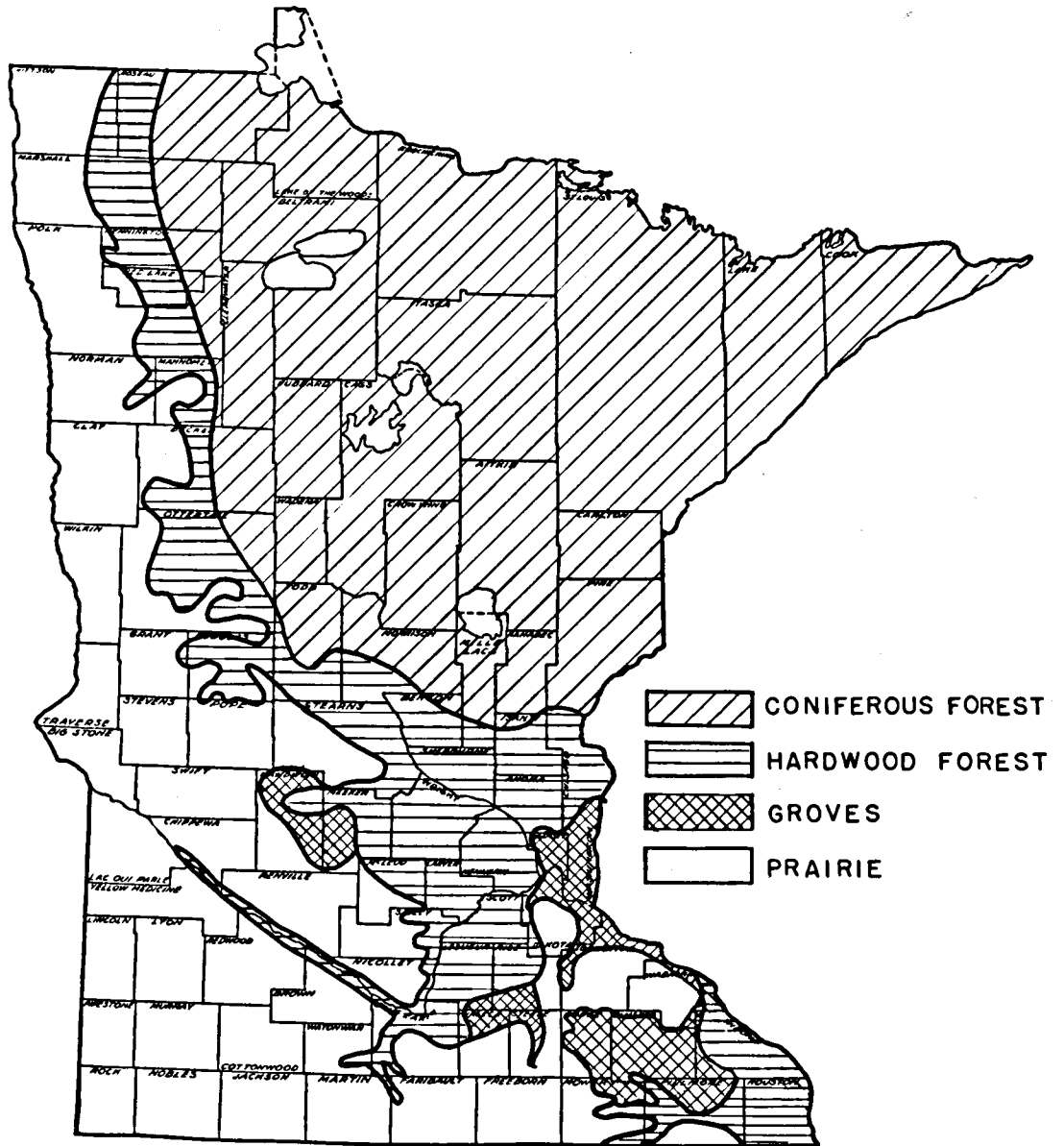
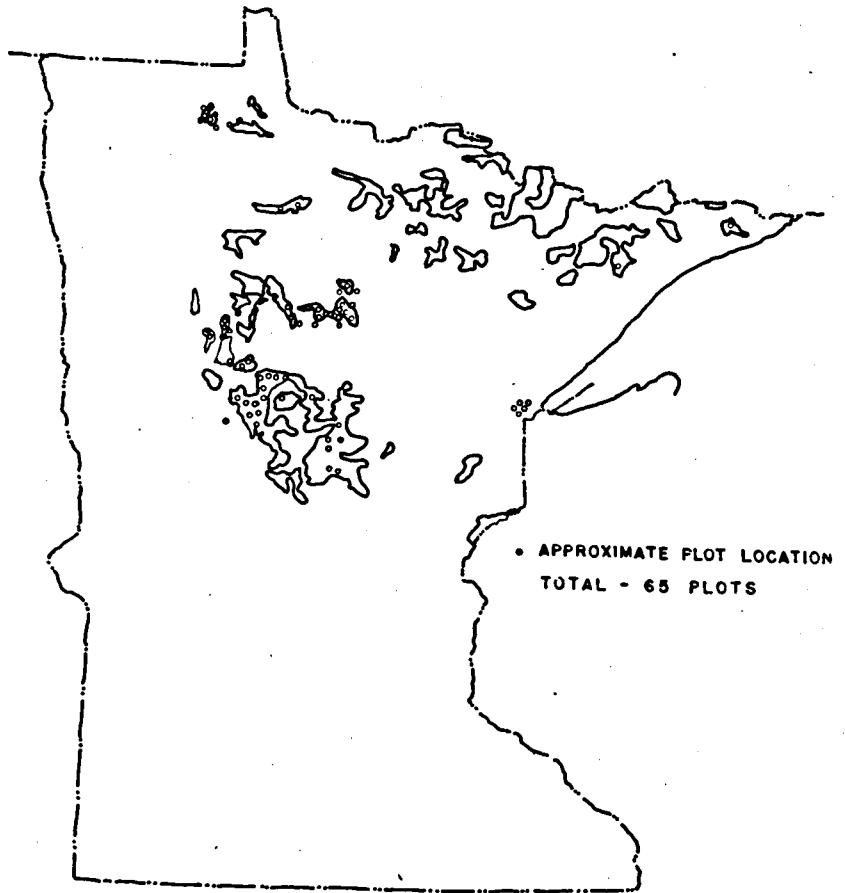


Figure 12. Plot locations and distribution of the pine types including jack pine, red pine, and eastern white pine in Minnesota. Type distributions from Lake States Forest Experiment Station data.



Buhler (19) and Grant (41) describe the occurrence of this type in Itasca County. Buell and Gordon (18) found a maple-basswood stand unable to advance into an adjacent spruce-fir stand at Itasca Park and attributed this inability to the low light intensity under the conifers. This hardwood type also occurs on some of the high ridge tops paralleling the north shore of Lake Superior, on Isle Royal in Lake Superior, and in a large area around Mille Lacs Lake.

Conversely, some coniferous types are found in isolated stands in southeastern Minnesota, far south of their usual location and well within the deciduous forest area. White pine is quite common on north facing hillsides and bluffs in that area. A stand of typical jack pine occurs in the Root River Valley. Rosendahl and Butters (77) reported the occurrence of *Arctostaphylos Uva-ursi*, *Chimaphila umbellata*, *Pyrola secunda*, and *Cornus canadensis*, all typical of the coniferous vegetation, in southeastern Minnesota. A small remnant of northern white cedar grows on the top of Gwin's Bluff along the Mississippi south of Winona.

These inclusions of deciduous climax within the present coniferous area and of coniferous types within the present deciduous area are difficult to explain. Undoubtedly the various retreats and advances of the glaciers have played a major part in bringing about this interspersion of vegetation. It is also probable that fires in prehistoric times favored the restriction of the coniferous area and the extension of the sprouting deciduous vegetation northward. The possibility that some time after the last glaciation the region had a warmer climate than it does at present can also not be ignored. Some evidence for this would be implied by the fact that borings in peat bogs in Itasca Park reveal a higher proportion of oak pollen at the lower levels than is found in more recent peat formations.

Within very recent times, fire and lumbering have greatly affected the coniferous area. The white and red pine types because of the desirability of these species as lumber were logged first, and to a great degree these types were converted to jack pine and aspen fire types. On some areas fire has apparently arrested successional development to a point where a fire subclimax has been established.

Jack pine occurs characteristically as a fire type throughout the coniferous area. The present area of the type, over a million and a quarter acres in Minnesota, is probably considerably greater than its former area. Because jack pine is a fire type, it has taken over large areas during the period of extensive logging and burning where other species were formerly predominant. Jack pine probably occurred in pure stands only on the poorest soils in pre-settlement days. It was undoubtedly also mixed in other types in openings where competition for light was not a factor.

This species is most commonly found on the lighter soils of a definitely sandy nature, and it is usually associated with large areas of glacial outwash sands and gravels. On the Superior National Forest it is also common on shallow soils covering the extensive rock formations of that area. Stands are usually pure or nearly pure jack pine; but red pine, quaking aspen and balsam fir are frequent associates, the latter usually as a definite under-story. Red pine and quaking aspen, when present, are usually of the same age as the jack pine. Species less frequently associated include paper birch, eastern white pine, bigtooth aspen, red maple, northern red oak, northern pin oak, black spruce, white spruce, and balsam poplar. Other common forest types of the area

as recognized by the Committee on Forest Types of the Society of American Foresters (98) include aspen-birch, red pine, white pine-northern hardwood, spruce-fir, black spruce swamp, northern white cedar swamp, tamarack swamp, and black ash-American elm-red maple swamp.

Physiography and Glacial History

By far the most important single factor affecting the soil has been the glacial history of the region. The activities of the glacial sheets have largely determined the chemical make up of the parent soil material, the juxtaposition of drift materials from several sources, the physiognomy of the area and its drainage, the selective segregation or the intermixing of soil particles as to size and the depth of the soil mass.

Visible evidence of three glaciations may be found in the surface formations of the area concerned in this study. The first of these three glacial advances was the Patrician. This ice sheet advanced from the north of Lake Superior across the Iron Range in Minnesota and south beyond Minneapolis. The drift carried by this glacier has been overridden by the two subsequent glacial advances. The top of this drift, where it has been exposed, has a yellow-red color, and the fresh drift is red. No limestone occurs in these deposits.

Following the partial retreat of the Patrician ice, the Labradorian glacier pushed through the Lake Superior basin and westward in Minnesota to McGrath and McGregor in Aitkin County. This was also a bright red drift without limestone. The top has since weathered to a darker rusty color. Surface formations left by this advance cover most

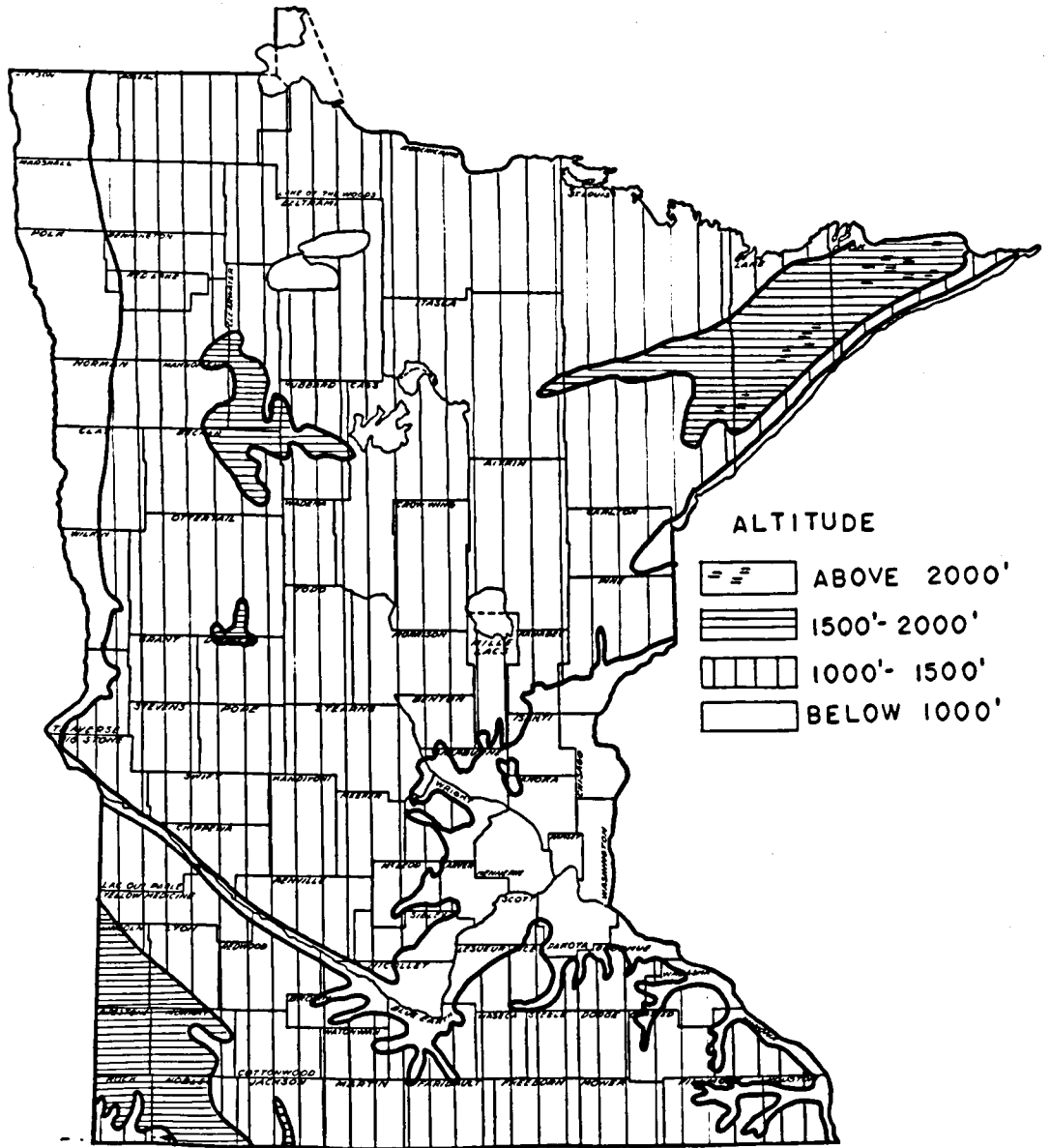
of the Superior National Forest and also the area north of Brainerd in which several plots are located.

The final glacial advance came from the Keewatin center and extended up the valley of the Red River of the North and down the valley of the Minnesota River into Iowa. To the east it advanced over the deposits left by the retreating Labrador ice. The edges of the overlap can be found near McGregor in Aitkin County and in numerous places in Hubbard and Cass counties. The material deposited was a gray limestone carrying drift the top of which weathered to a reddish color. As a complicating factor in the edaphic environment of this region, the gray deposit occurs in varying thicknesses over the red drift. However, the three glaciations followed too closely after each other to permit of any soil building in the intervals except after the last advance.

The region is drained by three major drainage systems: the Mississippi drainage to the Gulf of Mexico, Lake Superior drainage to the St. Lawrence Bay, and northward drainage into Hudson Bay. Altitudes range from 602 feet, the level of Lake Superior, to 2230 feet in western Cook County. Two rather prominent highland areas indicated in Fig. 3 occur within the coniferous region; the extensive range of rock ridges west of Lake Superior, and the hilly country west of Lake Itasca.

Much of the area is flat or undulating, but glacial activities have usually made for considerable diversity. The hills are of several types. Some, like the hills of northern Hubbard County, are the result of glacial deposit. Some in the northeastern area have been affected by the abrasive action of the glaciers on bed rock. An area of windblown sand hills occurs near Brainerd. The hills of the Mesabi, Cuyuna, and Vermillion Iron Ranges have resulted from uplifts of the earth's crust, and the sawtooth range of hills along the north shore of Lake Superior

Figure 3. Altitude map. After Leverett and Sardeson in University of Minnesota Geological Survey Bulletin 13.



is a result of volcanic activity. These form the most conspicuous relief feature of the state. The hills along the shore rise 500 to 900 feet above the lake and those farther inland rise an additional 200 feet to 400 feet.

An important topographic element is the large area of deposition in the Red Lake area which was the bottom of the glacial Lake Agassiz. Several sandy and gravelly beach lines or water-washed sand deposits have stands of jack pine which were sampled in this study.

PREVIOUS WORK

JACK PINE

Occurrence and Distribution

The extent of literature covering investigation and research on jack pine (*Pinus banksiana* Lamb.) is considerably greater than would be expected of a tree which is only of regional commercial importance. The range of the species according to Sargent (53) covers the area from Nova Scotia to the valley of the Athabasca River and down the Mackenzie to about latitude 65° north, ranging southward to the coast of Maine, northern New Hampshire and Vermont, the Island of Nantucket, Northern New York, the shores of Saginaw Bay, Michigan, the southern shores of Lake Michigan in Illinois, the valley of the Wisconsin River, Wisconsin, and central and southeastern Minnesota with isolated groves in Root River valley, near Rushford, Fillmore County. This author further explains that it is common and of large size in the region north of Lake Superior and reaches its greatest size west of Lake Winnipeg and north of the Saskatchewan, where it occurs over great areas of sandy sterile soil.

The species thus has the most northerly range of any native pine, extending to within a degree and a half of the Arctic Circle. It is also within 300 miles of being transeontinental since it reaches the waters of the Mackenzie River. Rosendahl and Butters (77) consider the previous pine distribution to have extended considerably farther south in the state from its present limits. Stands such as the one near Rushford in southeastern Minnesota are felt to be relics of the former wider distribution.

In the United States it is of greatest importance in the Lake States where it occurs extensively throughout northern Minnesota and northern and north central Wisconsin and Michigan. Data collected by the Forest Service (115) in connection with the nationwide forest survey indicate that jack pine is the predominant species on 2,706,000 acres in the Lake States. It is of greatest relative importance in the State of Minnesota where it occupies 1,266,000 acres and ranks next to the aspen-birch and spruce-swamp forest types from an area standpoint. On a volume wise basis it is also a species of importance in Minnesota where stands total 1,034,430 thousand cubic feet, including 2,262,790 thousand board feet in sawtimber sizes (largely in the 9 inch to 13 inch diameter classes). Thus, it ranks second only to aspen on a total volume basis. Excessive war time cutting has undoubtedly altered these volume figures considerably. It is of economic significance that jack pine and aspen were the only Minnesota species which had a rate of sawtimber growth exceeding the depletion rate in pre-war days (111).

It is of interest to note the increasing relative importance of Minnesota jack pine in recent years as evidenced by a tabulation of softwood stumpage and log prices in Tables 1 and 2.

TABLE I

Minnesota Stumpage Prices per Thousand Feet Board Measure *

	1923	1929	1937	1940
Balsam fir	\$ 1.56	\$2.00	\$1.86	\$1.48
Jack pine	2.62	2.23	2.42	4.35
Red pine	12.00	5.99	2.00	4.77
Eastern white pine	12.23	6.29	2.25	4.37
Spruce	6.13	2.52	2.00	2.83
Tamarack	4.96	2.62	—	—

*Summarized from data compiled by the U. S. Department of Agriculture (104) and the U. S. Forest Service (123).

TABLE II

Minnesota Lumber-Log Prices per Thousand Feet Board Measure at Mill*

	1923	1929	1937	1940
Balsam fir	\$19.40	\$14.80	\$12.92	\$12.00
Jack pine	18.55	18.47	13.15	12.68
Red pine	30.12	24.84	17.79	14.98
Eastern white pine	30.59	27.27	20.36	14.83
Spruce	22.51	17.48	13.86	15.33
Tamarack	21.32	19.08	—	—

*Summarized from data compiled by the U. S. Department of Agriculture (104) and the U. S. Forest Service (123).

From the above it may be noted that recent jack pine stumpage and log prices are only slightly lower than prices for red pine and eastern white pine, whereas only a short fifteen or twenty years ago jack pine was marketed as a decidedly inferior species.

Silvical Characteristics

The earliest silvical descriptions of this species were published by the Forest Service (105) (106). Notation is made of the more obvious characteristics of the tree, its intolerance, its scraggly form and its occurrence as a fire type on sandy soils. These publications refer to average mature heights of 30 feet to 50 feet, which would suggest that

this species was observed on the poorer sites in Michigan since average mature heights in Minnesota are definitely in excess of 50 feet.

Ellis (31) gives early information on jack pine in the Lake Winnipeg region where the species reaches maximum development. Heights of 90 feet and diameters breast high of 20 inches are said to be common. North of Lake Winnipeg jack pine rapidly becomes a tree of small size and inferior form. This author refers to excessive taper as an indication of poor site and gives a taper of 1 inch in 1 foot along the merchantable stem as average. A rough correlation of the occurrence of jack pine with the lighter sand soils is mentioned and a listing is given of the commonly associated ground cover species. The mechanical properties of the wood of jack pine are given by Markwardt and Wilson (61). Kribs (55) found that tracheid length increased from the base of the tree upward to a maximum length and then decreased to the top.

The root systems of jack pine have been studied by several investigators. Cheyney (22) (24) found the proportion of vertical to lateral roots very small and the short finger-like vertical roots not well adapted to food intake. A total of 33,529 inches of roots of all species in the upper 18 inches of a square yard plot in a jack pine forest was also reported, indicating the possibility of severe root competition for moisture. Adams (1) in a study of spacing in a jack pine plantation points out that root competition for soil moisture is the effective factor rather than competition for light. Adams and Chapman (2) emphasized the concentration of roots in the A soil horizon and found that vertical roots went deeper in soils having a low moisture equivalent and a sand content above 90 per cent. MacAloney (59) investigated the root systems in connection with insect damage to jack pine in northern Minnesota and reported a

definite relation between decadence of the crown and root condition.

He also found a correlation between total weight of the foliage and branch tips and total weight of the root tips of large trees.

Shirley (90) found that jack pine in mixed pine stands in northern Minnesota attained maximum rate of height growth under conditions of 75 per cent of full light intensity as contrasted to 63 per cent full light intensity for maximum rate of growth for red pine, and 36 per cent full light intensity for eastern white pine.

Numerous studies of the seeding habits of jack pine have been made by the Lake States Forest Experiment Station and by other investigators. Seed release from the serotinous cones was found to be greatest under the conditions of low moisture and high temperature prevailing in July and August in northern Minnesota (57) (121) (117) (32) (114) (110). Seed was found to be dispersed to a maximum of about two tree heights (116). Little dissemination occurred from standing trees not subjected to fire. Seeds falling to the ground in August, September, and October have little chance of survival (122), while seeds falling in November, April, May, and June result in reproduction best able to survive. Schantz-Mansen (87) found a statistically significant drop in quality of seed from three year or older cones, but reported that from a practical viewpoint even the oldest seed is valuable.

Silvicultural Management

The importance of soil scarification or removal of the duff in order to obtain reproduction has been emphasized (112) (120). Byre (33) and LeBarron (56) emphasize the necessity of lopping and scattering the slash during cutting operations in order to get the cones near the ground

exposed to maximum heat, and also the need for some method of removing the duff to expose a mineral seed bed. Zahngraff (132) reported successful large scale use of an Athens type disc plow pulled by a 40 horsepower tractor in mechanically scarifying the surface area so as to get good jack pine reproduction. Fall and winter logging give best results because the seed can germinate during the following summer and the seedlings have sufficient time to harden off before freezing weather. Best reproduction is obtained from logging fully stocked, 70-80 year stands before brush gets abundant on the area. Eyre (33) and Eyre and LeBarron (34) have summarized the investigations by the Lake States Forest Experiment Station on all phases of the silvicultural management of jack pine in the Lake States.

A comprehensive study was made by Schantz-Hansen (86) of the effect of thinning jack pine on the various environmental factors such as soil and air temperatures, relative humidity, soil moisture, precipitation, rate of evaporation, light, and humus condition. The most significant changes were found to occur in soil temperatures. Growth increases were roughly in proportion to the increased light but probably not caused by it. Earlier studies by Schantz-Hansen and Brown (88) and Schantz-Hansen (85) on thinning jack pine at the Cloquet Forest Experiment Station were confined to measurements of growth response. Remasurements of thinning plots in jack pine plantations on the Nebraska sand hills by Kocser (76) show growth increases on individual trees varying with the intensity of thinning.

Growth rate of jack pine in plantations has been reported by Allison (5) (6) in Minnesota, Herbert (49) in Michigan, Adams (1) in

Vermont, and Brasble (15) in Pennsylvania. Studies of plantation survival by the Lake States Forest Experiment Station (113) point out the importance of heat injury as contrasted to drought damage in plantations under conditions of extended summer heat. Partial shade was indicated as having definite beneficial effect.

The problems connected with the restoration of deforested pine lands by planting jack pine have received considerable attention from various investigators. Riata (73) (74) tested resistance of the seed to heat and recommended extraction temperatures of about 170 degrees Fahrenheit, with a relative humidity of 30 per cent. Rudolf (81) (82) analyzed the successes and failures of past plantings in the Lake States. Steckeler and Sump (100) and Shirley (91) have reported on the use of direct seeding methods of obtaining stands of conifers. The importance of a low top-root ratio in preventing excessive desiccation of the tops during winter has been demonstrated (119). LeBarron, Fox, and Blyth (58) found that spring planting gave significantly higher survivals than did fall planting.

Maliszewski (60) recommends the planting of jack pine in mixed stands, with eastern white pine being planted on spots with most overhead cover and jack pine on the open areas. The use of niacin has been recommended by some as a source of thiamin to stimulate seedling growth. Benschel (12) using cultural solutions of various concentrations of thiamin and niacin found no significant effect on root or stem growth.

Natural Enemies

Jack pine, like other tree species, is subject to the vicissitudes of weather, insect damage, damage by animal life, fire, and disease. Allison and Orr (7) reported a severe infestation of tortoise-scale insects (jack pine Lecanium) on plantations near St. Paul. MacAloney (59) investigated stands defoliated by the budworm (*Archips fumiferana*) and the jack pine sawfly (*Neodiprion banksiana*) and came to the conclusion that although the budworm was important in the final stage of decadence, drought and severe heat were the primary causes of lack of vigor and death of many trees. Hodson and Zehngraff (50) studied the food habits of the budworm and found that the staminate flowers of the jack pine are an essential part of the diet. Orchard type trees, suppressed trees, and trees of low vigor were found to have abnormally high crops of staminate flowers and consequently were latent centers of attacks of this insect. The removal of these trees in the silvicultural management of the stand was suggested as a control measure against the building up of epidemic populations.

Chayne (23) noted the nipping off of jack and red pine branch tips in great quantities by the red squirrels. White-footed mice and chipping sparrows were found (124) to be a factor in reducing jack pine reproduction because of their fondness for the seed. The role of the white-tailed deer in the jack pine environment has been studied by Aldous (4) who found that the deer prefer jack pine to other pine in the fall of the year and that pine browse makes up an important item in the diet of this animal. On certain areas deer damage to plantations and also to

natural reproduction may approach 100 per cent. Aldous and Aldous (3) reported that the snowshoe hare prefers jack pine to all other conifers and suggested planting during lows in the snowshoe hare cycle as one measure against excessive damage.

The destructive effects of fire have been noted (107) particularly on reproduction and small trees. The susceptibility of jack pine to sleet breakage was reported by Kienholz (53) who found the order of susceptibility to breakage to be jack pine (most susceptible), Scotch pine, white pine and red pine (least susceptible).

Utilization

With the rapid diminution in acreage and volume of the more valuable eastern white pine and red pine, jack pine has assumed greater importance in the wood products market in Minnesota. In more recent years it has been used as lumber, pulp, poles, posts, ties, fuel, and cabin logs. Its preeminence in volume and area over the other conifers of the state assures it of an increasingly important place commercially. As early as 1912 (102), it was predicted on the basis of the suitability of jack pine fiber and the increasing price of spruce, that jack pine would be a popular pulping species. That this popularity has materialized is borne out by the 300,000 cords of jack pine pulpwood used in 1937 (34). Chidester, Bray, and Curran (25) investigated the influence of various growth factors and found that trees of intermediate size yielded more pulp per cubic foot than either the very rapid or the very slow growth types. Bell and Jefferson (12) recommended suitable methods of sawing, seasoning, and treating wood of jack pine and aspen for home use.

Mensurational Data

A considerable amount of mensurational data have been collected for the species. Brown and Gevorkiantz (17) have compiled volume tables in terms of board foot measure, cords, cubic feet and piece products, as well as yield tables and a site index graph for the species. Volume tables using the frustum form-factor method have been prepared by Schantz-Hansen (34). The Lake States Forest Experiment Station (108) has computed normal stand tables giving the average distribution by diameters at breast height for stands of different sizes. Yield tables have also been published (109) giving volume and stand data above 1 inch, 4 inches, 6 inches, and 10 inch diameter breast high classes. Other yield tables have been prepared by Wackerman, Zon, and Wilson (126). Diameters inside the bark at various heights can be obtained from taper tables (113) based on diameter breast high and total height. In connection with the analysis of stands of jack pine it is possible to use a tree classification system devised by Gevorkiantz, Rudolf, and Zehmgraft (39). This system is based primarily on tree vigor, soundness of bole, form, and utility in terms of possible products.

FOREST CLASSIFICATION

Excellent reviews of the extensive literature in the fields related to forest site and type have been presented by Cajander (20), Kittredge (54), and Heimbürger (46). Because of the great extent of this previous work and the preponderance of foreign studies, particularly Russian and Finnish, a complete review is not possible. The following is presented as an adequate background to the analysis of the data accumu-

lated in this study. Additional references to literature pertinent to the problems discussed are incorporated in subsequent sections.

TERMS

The use of the basic terms site and type and various modified combinations of them is not well standardized in the forestry literature. Forest types of many kinds are recognized. These are considered to be vegetational units of a certain degree of uniformity which are selected by various criteria depending on the purpose of the classification. Following are some of the kinds of types used by foresters:

- a. Cover types based on the existing stand composition.
- b. Management types including the natural or artificial type desired to manage as a crop.
- c. Climax types expressing the most mesophytic type possible within the climatic region.
- d. Temporary types are those occupying only a stage in the ecological succession of the vegetation.
- e. Physical types based on soil factors as they denote the ability of the area to produce forests.
- f. Indicator types using species of plants as the basis of classification.

Site as used in this country differs basically from type in that the emphasis is on the area rather than the forest. Site classifications consider the area with respect to its ability to grow stands of trees. In view of this, the physical type previously listed is really a site classification system rather than a type designation. Forest site was originally used by systematists to denote the place on which the vegetation grew. It has since become a rather definite term used chiefly by

foresters. The Committee on Forest Terminology of the Society of American Foresters (99) defines site as:

"An area considered as to its ecological factors with reference to capacity to produce forests or other vegetation; the combination of biotic, climatic, and soil conditions of an area."

This corresponds to the term habitat commonly applied by ecologists to an area on which the environment is essentially uniform. In Europe, silviculturists use the term locality in a similar manner. Current usage restricts the term site to use in an abstract sense. Site quality is used where a classification on the basis of relative productivity is implied. Site indicators are standards by which site quality is determined. However, this term is usually used only in connection with plants as indicators.

1/ EUROPEAN SYSTEMS

In Central Europe all early efforts at site classification used growth characteristics of the trees as criteria of site quality. Five site classes were usually recognized, although Hartig advised the use of three classes and Cotta recommended a system of one hundred sites to cover all the range of site quality from barren to the most productive. Recognition of site quality was usually by long experience in repeated measurements of sample plots. Because of this, it was often difficult to compare estimates by different foresters. Of the numerous methods tried, several were widely used. De Perthuis (1788) developed a volume-age method in which volume was plotted over age for trees from numerous sample plots. Curves dividing the plots into five site classes were

1/ Much of the information concerning early European systems has been obtained from Cajander's (20) classic study of forest types, for which an English translation is available.

drawn using the extreme plots to determine the shape of the curves. A similar procedure using the mean height of the stand was used by Baur (1877) in Germany. An ingenious, directed curve method was used by C. Hayer (1846) and E. Hayer (1857). This required the use of permanent sample plots with height measurements at five year intervals. Short curve segments were then plotted instead of points and the index curve trend was more apparent. This system is now extensively used in Central Europe. Even earlier, Huber (1824) used a stem analysis system to obtain height measurements from dominant trees for their entire life. Many points could be obtained from one tree and good height growth curves could be obtained. After the work of Liebig on plant nutrients and soil chemistry, a great many attempts were made to correlate certain soil factors such as nitrogen or lime content with site quality. These proved to be of purely local value. Cajanus (1914) used a unique method based on the fact that on good sites greater dispersion of stem sizes occurs.

The use of natural systems of classification developed in Finland, Russia, and Sweden. In 1872 Blomquist divided Finland into three growth zones and described three quality sites in each. These were distinguished by a combination of soil and vegetational features. Cajander (20) has been the foremost proponent of the use of vegetation as an index to site quality. He used the mature vegetation as a site criterion and incorporated a few soil features.

AMERICAN SYSTEMS

In the United States the early classifications were largely based on stand volumes. Bates (11) recommended a system based on the periodic

annual growth for the past ten year period. Site classes separated by thirty cubic foot intervals were suggested, growth to be determined on the species present. Hanzlik (43) presented a formula method of site classification which was a modification of a Russian system. The factor used was height times basal area divided by age. Essentially, however, this is the equivalent of a volume based system, because height times basal area is the equivalent of volume.

Roth (79) (80) criticized the use of increment because it varies too much both with age and stocking. He also noted that volume is affected too much by density and that the normality of actual stands is uncertain. Therefore he recommended the use of height at a standard age. His plan was to classify all important species of trees into tall, medium or short "standards", depending on their relative height growth at a certain standard age such as one hundred years. There would also be four site classes within each standard based on the deviation from the greatest height.

Frothingham (36) (37) (38) reviews the height growth system, the climax type system, and the volume system and concludes that height growth of the dominant trees is the best index of site. However, he points out that the most fundamental system is a classification of climax forest types involving a determination of the physical factors involved. Dominant height was considered to be a better index than volume per acre because it is less apt to vary with density of the stand and other factors not inherent in the quality of the site.

Watson (128) advocates a system patterned after Roth's, except that six standards would be used instead of three and that dominant height be curved over diameter breast high instead of over age. He rejects the volume systems as being unsuited to our wild stands of varying conditions of normality.

The Committee on Site Standardization of the Society of American Foresters (97) recommended that site classes be separated on the basis of mean annual growth at the period of culmination. Site indicators would be used merely to indicate the yield and not to classify the site. The Committee suggested height growth as the most practical indicator, but pointed out the future possibilities of vegetative indicators. Other site indicators of possible value were said to be soil and climatic factors, composition of the original or existing forest, actual measurements of volume growth, form factors, and foliage characteristics.

Kittredge (54) found site index as measured by height growth better than volume growth for evaluating the differences and relative productivity of aspen habitats. Gavorkiantz and Scholz (40) determined site quality in understocked oak forests in the Lake States by means of an individual tree volume site index. This was computed by multiplying average basal area of the trees of the dominant stand by average height. This index seemed unaffected by density for a range of 50 to 120 per cent of normal stocking.

PLANT INDICATORS

Considerable use has been made of plant indicators in the classification of the forests of North America. Some of the classifications, Mayr (62), Clements (26), Shantz and Zon (39), have been concerned with broad extensive relationships. Climatic and geographic considerations are combined with plant indicators in these classifications. In addition, some investigators have used plant indicators in detailed classifications of forest areas in sections of North America as well as in Europe as previously mentioned. Intensive forest site indicator studies

have been made by Heimburger (43), Sisman (94) (95), and Ray (71) in the Laurentides Park section of eastern Canada. Six "site - types" have been recognized:

- Kalmia ----- Ledum (black spruce swamp or muskeg)
- Sphagnum --- Oxalis (swamp with some hardwoods, balsam fir, spruce, cedar, and alder)
- Cornus ----- (Softwood - red spruce, balsam fir, cedar, and paper birch)
- Oxalis ----- Cornus (softwood, hardwood with balsam, fir, and red spruce with yellow birch and mountain maple)
- Viburnum --- Oxalis (hardwood-softwood, with mountain maple, striped maple, some sugar maple and beech).
- Viburnum --- (Hardwood with striped maple, sugar maple, beech, yellow birch and a few red spruce)

These site-types were found to have equivalents of tree volume, increment, reproduction, species composition, and extent of decay varying consistently with them.

On the west coast, Rigg (75) suggests the joint study by botanists and foresters of twelve plant species considered to have indicator significance for the study of site on logged-off areas.

Hazard (45) analyzed indicator plants of the old-field white pine type in New Hampshire. She listed five main types including the Cladonia type, the Vaccinium type, the Maianthemum-Vaccinium type, the Maianthemum type, and the rich herbaceous type. The successional tendencies of these types were analyzed with particular respect to the reproduction of white pine.

Taylor (101) points out the necessity for knowing the developmental activities of forest areas. Mature spruce-hemlock forests in southeastern

Alaska consist of approximately three-fourths hemlock and one-fourth spruce. However, young stands are usually over fifty per cent spruce. This he says is due to the fact that decomposition of the litter takes place when the mature forest is cut permitting spruce to reproduce. However, the development of the new stand brings about heavy litter and humus formation to the detriment of the spruce and the favoring of the hemlock again in the mature stand.

In this country the most extensive forest type classification system based on ground cover vegetation was described by Heimbürger (46). Using essentially the same system used by Cajander, he divided the Adirondack region into three major phytogeographic regions and described 22 types within those regions. His *Vaccinium-Gaultheria* type is said to be similar to a *Vaccinium-Gaultheria* sub type tentatively described by Ilvessalo (51) from his visits in Quebec, Ontario, and Minnesota. Heimbürger says that his own *Vaccinium-Gaultheria* type has fewer species than Ilvessalo's and indicates a poorer site and a more moist climate.

Using biometric methods, Kittredge (54) analyzed the interrelations of habitat, growth rate, and associated vegetation in the aspen community of Minnesota and Wisconsin. He found that individual plant species did not indicate with sufficient reliability differences in the habitats or the growth rates of aspen. However, natural groups of plant indicators were demonstrated to be very closely associated with the productivity of the different aspen habitats. The plant groups chosen were those characteristic of forest types other than aspen and in various stages of successional development.

SOIL SYSTEMS

In the field of forest soils investigations numerous attempts have been made to correlate various soil characteristics with site quality. In general, most investigators, Coile (29), Luten (3) (9), Haig (42), report little association between chemical soil factors and site quality. However, factors affecting soil moisture have proved to be a fertile field of study in connection with the relative productivity of forest soils.

Coile (28) found that a texture-depth index obtained by dividing the per cent of silt and clay of the B horizon by the average depth of this horizon below the soil surface was a good measure of site quality of shortleaf pine.

Haig (42) considered surface soil texture a good measure of site class for red pine plantations in New England. Scholz (92) found a significant correlation between soil texture classes and the growth rates of red and chestnut oak. Coile (27) criticizes Cajander's fundamental hypothesis that ground vegetation reflects site quality. He refers to the effect of stand composition on the nature of the humus and says that certain hardwoods having humus high in calcium and low in resins would favor calciphylous ground cover, although this may not be representative of true site conditions. However, it is quite definite that such tree species prefer soil with available calcium, and the calciphylous ground cover would indirectly reflect this condition. His second criticism of Cajander's hypothesis, that ground cover vegetation is highly independent of the age and density of the forest stand, is undoubtedly correct for forest conditions in the United States. Even casual investi-

gations of various forest communities reveal definite changes in floristic composition associated with extremes of density.

Auten (10) found a highly significant correlation between depth of the A₁ horizon and site index of yellow poplar and attributed 60 per cent of the variation in height growth to that factor.

In an intensive study of the physical and chemical properties of the soil, Coile (29) found no soil factors to be definitely related in a causal manner to succession in loblolly pine. He attributed the decline in dominance of the pine and the invasion of oaks and hickories to the greater ability of the hardwood seedling roots in competition for soil moisture.

The general distribution of forest types in Arkansas was related by Turner (103) to topographic and soil factors. He considered those features related to drainage, and the duration and probability of submergence as of primary consideration, and soil profile as next in importance.

In the Lake States, Westveld (130) found site index of the northern hardwoods to be closely associated with soil groups based on the texture of the top soil and the degree of compactness of the substratum. Kittredge (54) found a similar correlation between soil groups and site index of aspen. Analyzing soil texture classes, surface formations, a combination of texture classes and surface formations, and soil profile groups each with respect to their individual association with site index, he obtained definite correlations in all cases. However, correlations were reported as being successively stronger as the soil classification represented larger proportions of the growth factors of the habitats. The closest correlation was between soil profile (the broadest soil group) and site

index, while the least close correlation was between soil texture (the smallest soil group) and site index.

MISCELLANEOUS SYSTEMS

Several site indicators which have never received general attention have been proposed from time to time. Moore (64) suggested that osmotic pressure of the plant cell sap be used to measure soil moisture conditions and consequently site quality. Helli (63) attempted to relate quality of site to the fiber length of the wood from the trees. However, variations in fiber length within each of the three sites considered was far too great to give this method any degree of reliability. Shaw (93) suggested a plan whereby the per cent of lumber going into the upper grades is correlated with the total height of the tree and hence its site class. Paul (66) (67) (68) (69) investigated the interrelations of growing conditions and silvicultural management with the specific gravity of various species of trees. He concluded that specific gravity was not always associated with soil quality or rain fall. He also found that this property was affected more by silvicultural treatment of the stand than by the soil type.

PRELIMINARY INVESTIGATIONS

GENERAL

During the summer of 1937, the writer spent considerable time at the Cloquet Forest Experiment Station collecting data as a guide in preparing a working plan for the study. In addition, some of the laboratory analyses of the soils, and some of the plot data collected later on the Superior National Forest suggested desirable limitations to the

study. These are presented as a part of the preliminary investigations, although chronologically they followed the work at the Cloquet Station. The techniques planned were in some respects new, and it was considered desirable to test them in a preliminary check. Jack pine had never been systematically investigated with respect to its associated vegetation. It was therefore necessary to apply vegetation sampling methods to determine their suitability in that forest type. It was hoped that a standard procedure could be evolved so that later changes in the working plan would be reduced to a minimum.

Inasmuch as the scope of the project did not include a complete soil study, it was felt that a preliminary study of some typical jack pine soil profiles might reveal one or two possible lines of investigation that could be followed.

The procedures to be followed in laying out the plots and in collecting stand data for use in determining site index, stand composition, age of trees, and normality of stocking were tried so as to determine the most efficient methods and instruments feasible. A seedling growth study was made in connection with the determination of total age of the dominant trees.

JACK PINE SEEDLING ANALYSIS

In the determination of site quality by the site index method, it is necessary to determine the total age of the trees in the stand. Since increment borings were all to be made at a standard height of one foot above the average ground level, it was necessary to study the growth of jack pine seedlings to determine their average age at that height. By adding this age to the age revealed by ring counts on a core removed from the tree by a Swedish increment borer, the total age of the

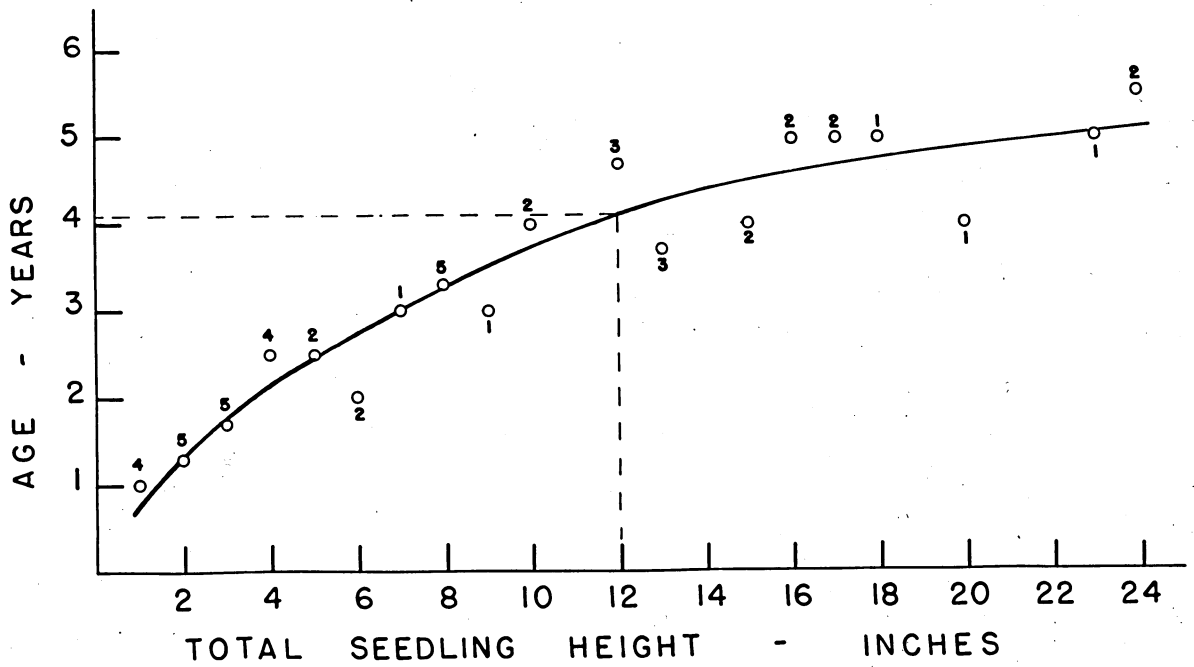
tree could be determined. Several points were considered in selecting the seedlings to be measured. Those showing effects of suppression from overhead shade, from rabbit or deer browse damage, or from disease or insects were rejected since the probability is great that they would not develop into the dominant trees upon which the site index determinations are based. Only seedlings growing in relatively open areas were selected since jack pine stands seldom come in naturally under an over-story of older trees. Finally, seedlings were collected from as wide a range of soil conditions as possible.

The procedure used in determining the height-age relationship was to determine the age of the seedling at each annual whorl of branches by counting back from the terminal leader and by ring counts of the cross section of the stem at that point. The height was measured in inches above the ground line to each annual branch whorl, and a curve of height over age was drawn for each seedling. The age for each inch of height was read from the individual seedling curves and plotted as the basis for the curve shown in Fig. 4. It was apparent that for the range of site conditions found at the Cloquet Experiment Station the average age at one foot above the ground would not vary more than a half a year above or below four years. It was therefore considered unnecessary to use separate seedling age figures for different qualities of site, and an age of four years was considered as the age at one foot on all plots.

GROUND COVER DATA

In order to sample the secondary vegetation associated with the jack pine, it was planned that a number of list quadrats covering one

Figure 4. Age - height relationships of jack pine seedlings.
 Preliminary test to determine average age at one foot of height.

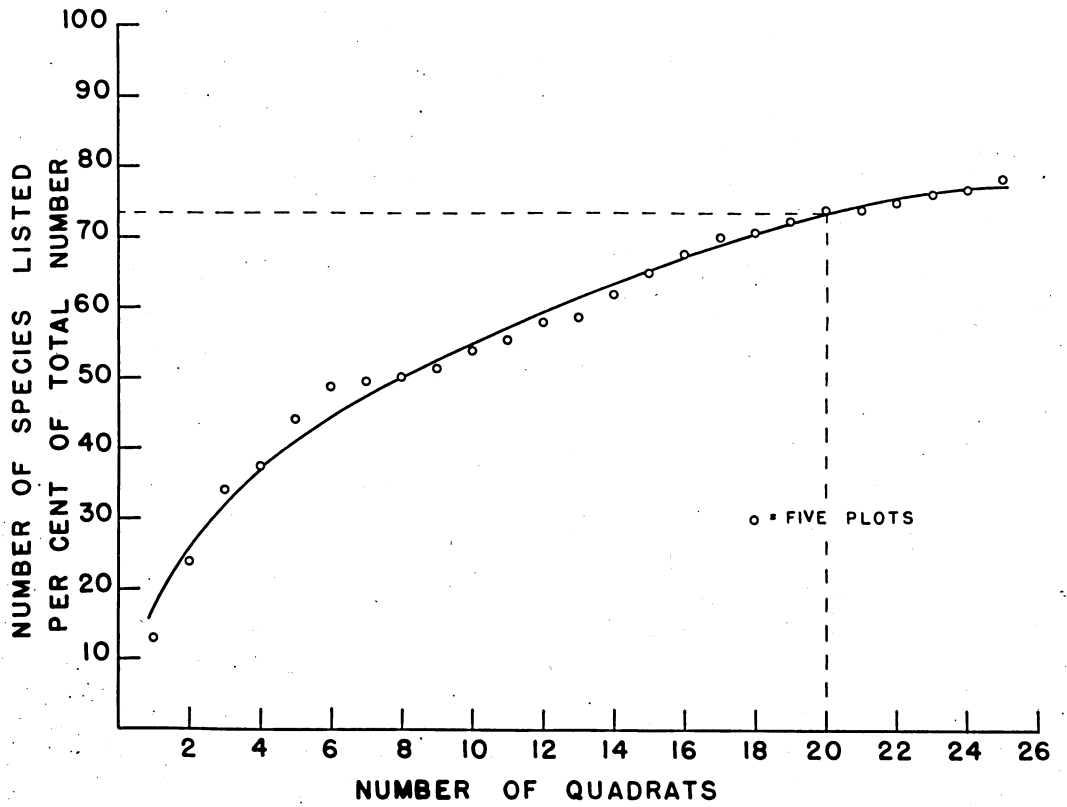


square foot each would be located within the tenth acre plot used in the collection of the tree data. It was necessary to make a preliminary check to determine the number of such quadrats necessary to adequately sample the ground cover and to give a reasonably accurate picture of the relative abundance and distribution of the constituent species of the plant community.

With this in mind, twenty-five quadrats were examined in each of five jack pine plots on the Cloquet Forest Experiment Station. The quadrats were examined intensively and all species present recorded as to their abundance. The entire plot was then examined very closely for any species present but not recorded as occurring on any of the twenty-five quadrats. The total number of species was then equal to the number present on all the quadrats plus those found in the overall examination. An accumulative tabulation was made on each plot of the number of species revealed by each successive addition of a quadrat. From these figures, it was possible to determine what percentage of the total number of species on the plot had been located by any given number of quadrats up to twenty-five. For example, the first five quadrat ^{lists} tests on plot number one had a total of eleven different species recorded, or fifty-two per cent of the true total of twenty-one species actually present. The first ten quadrat lists on the same plot had a total of twelve species or fifty-seven per cent. Data from all five plots have been averaged and plotted and are presented in Fig. 5.

An inspection of the curve of number of species over number of quadrats indicates several things. First, even the entire twenty-five quadrats do not contain all of the species present on the plots. This is to be expected, because a few species occur in such small numbers that

Figure 5. Preliminary test curve showing number of quadrats needed to adequately sample the ground cover vegetation on tenth acre plots.



only one or two individuals would be present on a tenth-acre plot. It would be quite possible to sample a tenth-acre plot with as many as a hundred quadrats and still not have such infrequent species listed. It is obvious that some compromise must be made between perfection and feasibility. It is also noted that from about the eighteenth quadrat and upward the composite curve seems to flatten somewhat and that with twenty quadrats an average of approximately seventy-five per cent of the total number of species had been listed. It was decided that twenty-five quadrats would be taken as a standard practice on later plots and that unless data accumulated later indicated otherwise, this number could be reduced to twenty without much sacrifice in completeness. It is a common practice for plant investigators to sample an area as small as a tenth acre by means of one square meter quadrat. Twenty quadrats of one square foot each cover approximately the same area as two standard meter quadrats, and in addition give a far better picture of the distribution of the vegetation by virtue of their scattered disposition over the entire tenth acre plot. It is also to be noted that a complete census of the identifiable species present would always be made on each plot, as the species not recorded on the list quadrats would be discovered by the subsequent inspection of the entire plot. However, species not found on the quadrats would be recorded simply as present, and no frequency of occurrence computations could be made of them.

TREE DATA

Methods used in collecting data on the stand density, distribution of age and crown classes, diameters breast high, total height,

reproduction, and stand composition were those of general acceptance in forest research. Site index data were collected and computed by the methods described in detail by Brown and Gowerkiants (17). Since none of this involved preliminary investigation of an original nature, the methods used will simply be described in a later section.

SOIL DATA

The preliminary soils work at the Cloquet Station consisted essentially of the examination of jack pine soil profiles and the roots therein, and the testing of texture at various depths by means of the Wilde Soil Tester. Numerous checks were made at six, twelve, eighteen, and twenty-four inches, as well as at distinct horizon levels, with the idea of getting relative comparisons of the amount of fine soil at these various depths by use of this field testing apparatus. It was decided that two horizons would be sampled systematically, and that observational data would be collected on the entire profile. Because it was not possible for practical considerations to sample and test all soil horizons, it was decided to limit sampling to the B and C horizons. The B horizon with its greater concentration of fine soil material, organic matter, and presumably of plant nutrients, and with its abundance of tree roots, was thought to offer the best possibility of a simple association with site quality. The texture of the C horizon and its effect on the soil moisture relationships of the profile was also thought to be closely associated with site quality. Although the A horizon may have as great a concentration of roots as the B horizon, its general leached condition and deficiency of fine soil material was thought to make it less promising as an index of site quality.

A mechanical analysis was made of the soil samples from nine plots using the hydrometer method proposed by Bouyoucos (14). The percentages of sand, silt, clay, and colloids for all plots have been plotted over site index in Fig. 6. An inspection of these data indicates no apparent association between soil texture as determined by this method and site quality. Because of this lack of association in the preliminary tests by the hydrometer method, the decision was made to substitute moisture equivalent determinations. This measure is generally accepted as a good indicator of texture in soils low in organic content. No further texture determinations were made by the hydrometer method, and moisture equivalent percentages were obtained on all soils samples by means of the standard centrifuge method.

JACK PINE ON THE SUPERIOR NATIONAL FOREST

During the course of the study several plots were examined in Lake and Cook counties in the extreme northeastern part of the state. It was obvious that ecological relationships of jack pine in that area are distinctly different from those on the sandy soils of the rest of northern Minnesota. Two factors, the shallowness of the soil over underlying rock formations, and the greater amount of precipitation as indicated by Fig. 7 probably account for this difference of environments. Other climatic differences are indicated in Fig. 8, Fig. 9, Fig. 10, and Fig. 11. General observations of jack pine growing throughout much of the Superior National Forest confirmed the plot data. As a result of this observed difference between the jack pine in the area referred to and that growing on the deeper sandy soils of the rest of the state, it

Figure 6. Preliminary data on texture of soil in the B and C horizons as determined by the Bouyoucos Hydrometer Method.

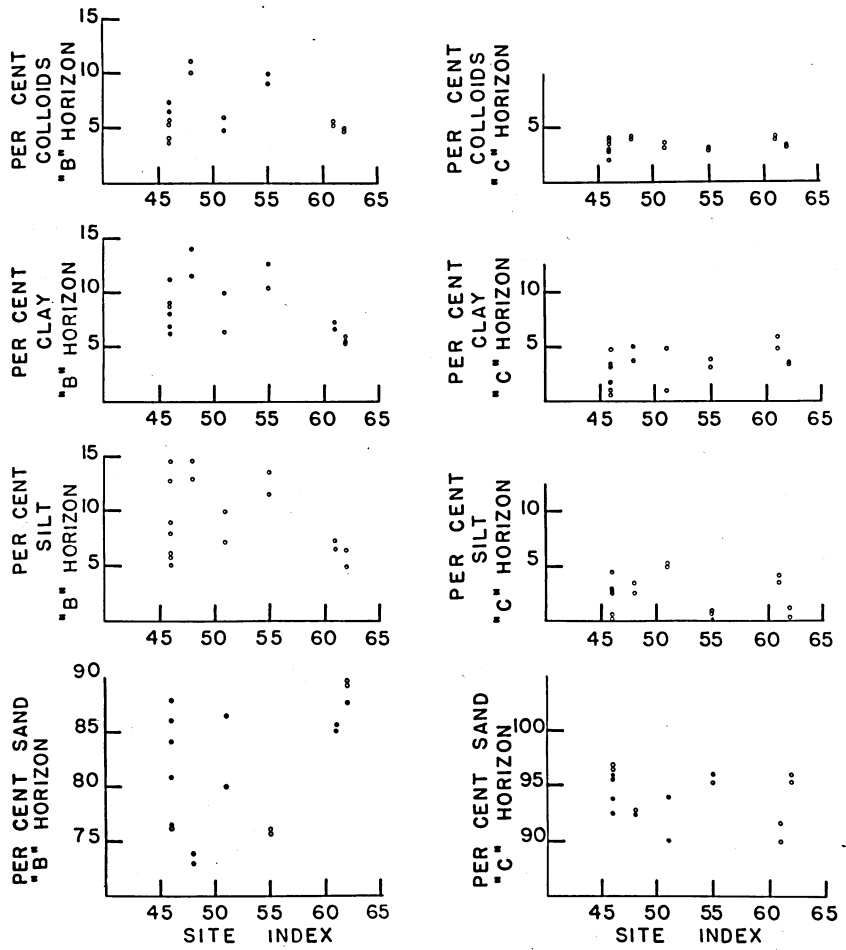


Figure 7. Average annual precipitation.
 After Purssell in the University of Minnesota
 Geological Survey Bulletin 12.

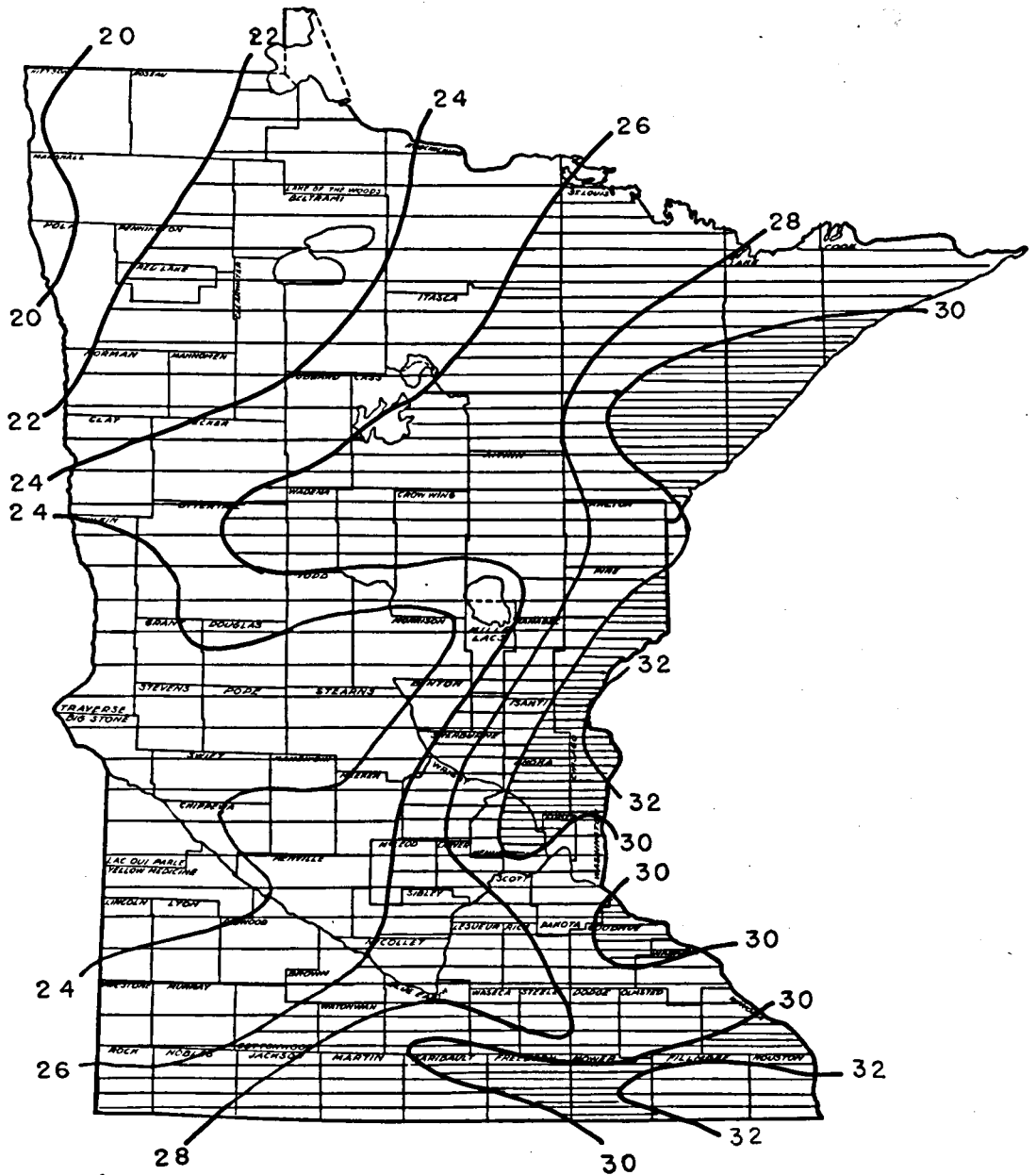


Figure 8. Mean annual temperature.
 After Purssell in the University of
 Minnesota Geological Survey Bulletin 12.

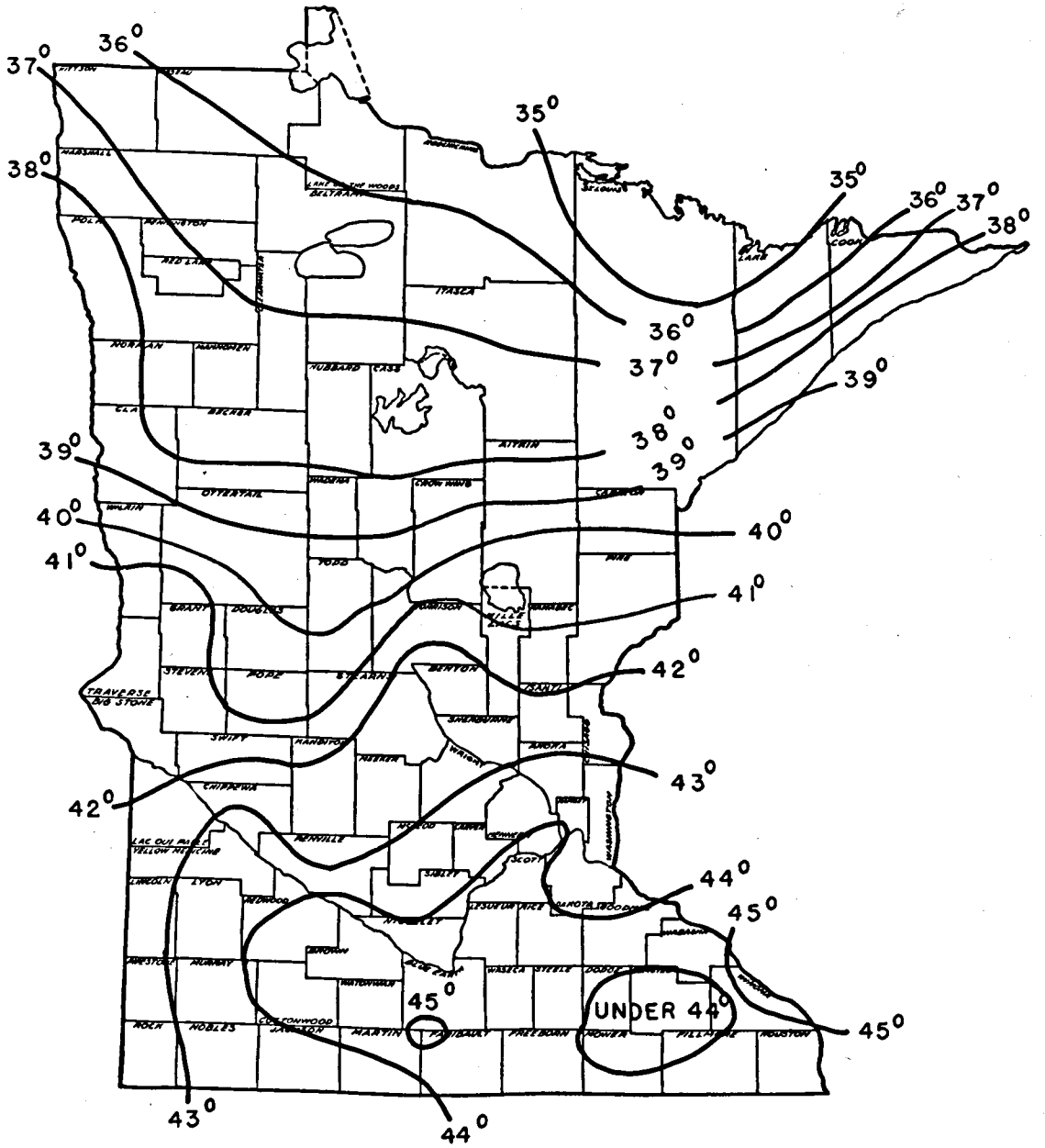


Figure 9. Average date of first killing frost.
After Pursell in the University of Minnesota Geological Survey Bulletin 12.

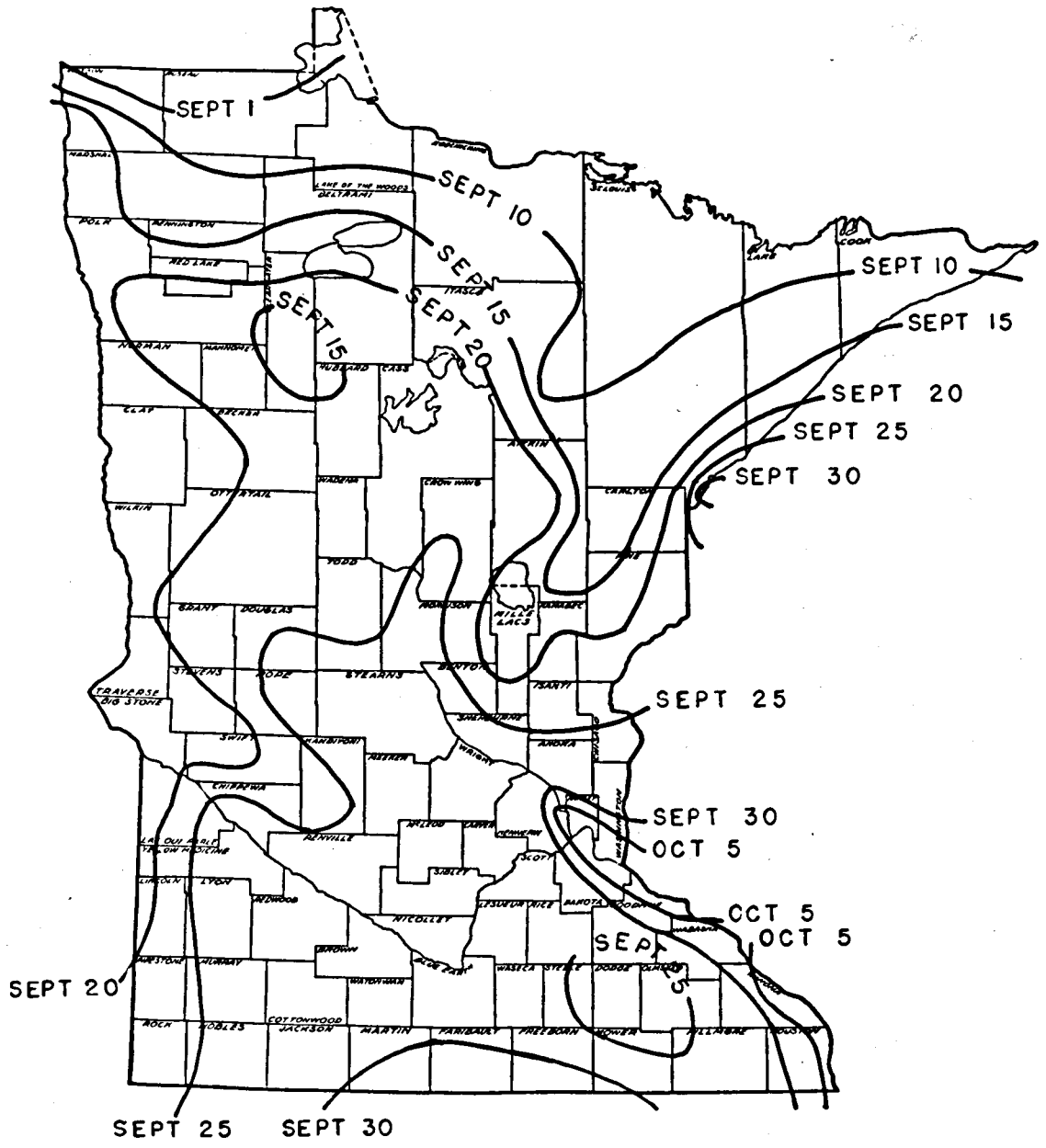


Figure 10. Average date of last killing frost.
 After Purssell in the University of Minnesota
 Geological Survey Bulletin 12.

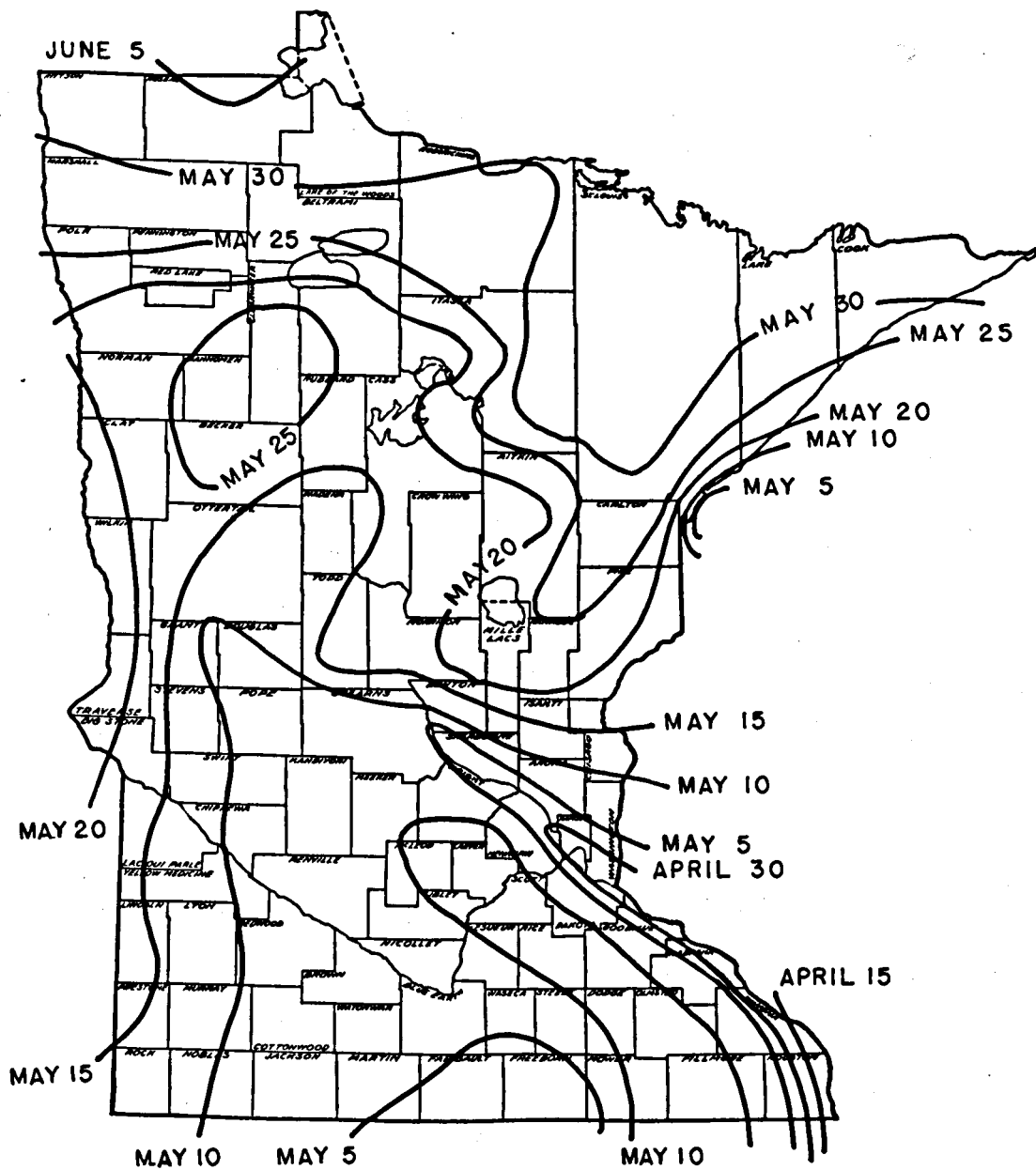
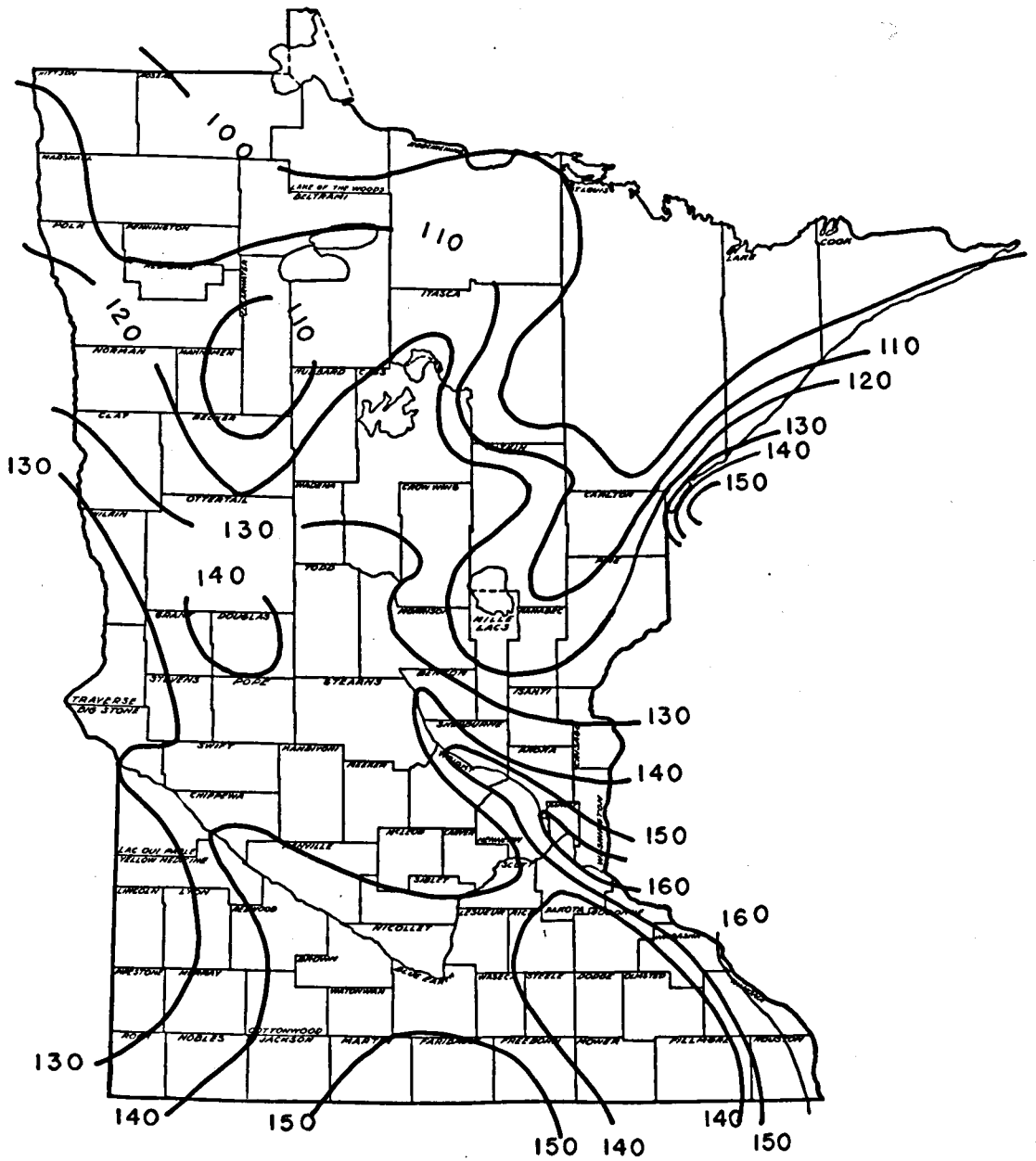


Figure 11. Average length of crop-growing season.
After Pursell in the University of Minnesota
Geological Survey Bulletin 12.



was decided to exclude the extreme northeastern part of the state from the study. In this manner, greater homogeneity of environment was obtained, and the results of the study although applicable to a smaller geographic region are felt to be more reliable.

METHODS AND PROCEDURES

GENERAL

Several methods of approach are possible in any problem dealing with a study of the environmental relationships in plant communities. The experimental method, by which one characteristic of the environment is altered in various degrees and the results with respect to the factor under consideration are noted and evaluated, is distinctly unsuited to the present study. The great complexity of the environment, the length of time during which controlled conditions would have to be maintained over relatively large areas, and the impracticability of attempting to create controlled soil conditions for growth of mature trees are readily understood.

A second approach commonly used involves the analysis of contiguous areas upon which the plant community differs in certain pertinent respects; i.e., species composition, size of individuals, or any other characteristic of interest to the investigator. Such studies often show striking contrasts by reason of the physical nearness of dissimilar conditions. However, unless such an approach is used on numbers of similar contrasting environments, there is no assurance that repetition of the alleged causative factors will bring about repetition of the apparently resultant vegetational differences. The degree to which such information can be applied to other areas is therefore questionable.

A third approach, and that used in the present study, requires the sampling of the complete range of variation of the characteristic under observation, in this case the site index of jack pine stands, and the analysis of the environmental factors found to be associated. Ideally, the sampling should cover all variations in growing conditions associated with this forest type. For practical consideration, however, it was necessary to limit the study in certain respects. As previously mentioned in connection with the preliminary investigations, it was decided to exclude jack pine growing on the shallow rock outcrop soils of much of the Superior National Forest. The data presented cannot therefore be properly applied to such areas. It was also considered desirable to limit the study to reasonably well-stocked stands. It is quite apparent to anyone who has even a casual knowledge of plant relationships that as one proceeds from an area bare of any forest cover to one which is overstocked, a great many changes in ground vegetation are encountered. By adequately sampling all such variations in degree of stocking, it would be possible to measure the associated changes in ground cover vegetation. However, the number of plots required to completely sample this range of stocking, in combination with all other variations such as site index and age, would be far in excess of that possible. In addition, site index determinations by accepted standard mensurational procedures require a reasonable normality of stocking. For similar reasons, the study was also limited somewhat with respect to the ages of the stands studied.

The data obtained have been grouped quantitatively and qualitatively and analyzed statistically insofar as possible. Uniformity of procedure was assured since all plot data were collected personally by the writer.

A conservative attitude has been maintained in the analysis and it is felt that the data presented are reliable within the limits set forth.

SELECTION OF STANDS AND LOCATION OF PLOTS

All the major jack pine areas in the state except the rock country jack pine stands on the Superior National Forest were sampled, and in addition some plots were located on smaller outlying areas of jack pine somewhat removed from the more extensive forests covering the large glacial outwash areas. A map showing locations of the sixty-five plots with respect to the occurrence of the pine forests of the state is given in Fig. 2. Because a definite effort was made to sample the entire range of site quality of jack pine, the plots taken cannot be considered a random sample of the proportionate distribution of site quality of the jack pine stands in the state. For this reason, the relative numbers of plots taken on the three site classes are not necessarily indicative of the proportion of acreage in the three site classes in the entire state.

Since jack pine almost invariably occurs in even-aged stands, no special criterion of selection was set up in this respect. In one or two stands studied a few individuals of a definitely older age class were present. Young stands under 25-30 years were eliminated since site index determinations would not be completely reliable.

Stands were selected in which jack pine was the predominant species. No attempt was made arbitrarily to select pure stands of jack pine since most of the better sites were gradually being taken over by other species, and various mixtures were present. The current dominance of jack pine on all stands studied, however, was unquestionable.

Stands were not selected unless their stocking by basal area was at least 50 per cent of normal as based on normal yield table data by Brown and Gevorkiants (17). Most of the plot data collected are based on a stocking of from 60 to 110^{per}/cent of normal.

Isolated stands of less than five acres were avoided. Proximity to cultivated land, fields or openings was considered undesirable. If the forest was continuous, stands as small as one or two acres could be sampled, provided identical conditions of stocking, growth rate, and topography existed for at least a half a chain all around the plot. In addition, a border at least two chains wide was required on which occurred jack pine of essentially the same character as that on the plot itself, but some variation in density and size was permitted. Burns, cuttings, and grazed areas were avoided.

Plots were a tenth acre in size, one chain square, and were laid out with the aid of a staff compass and steel tape. Sixty-five such plots were taken and were distributed as shown on the map in Fig. 2. As previously noted, an identical border strip at least one half chain wide, and a similar border strip at least two chains wide were required around all plots.

DATA ON TREE SPECIES

A complete census was taken of all trees on the stand. Diameters breast high were measured on all trees using a steel diameter tape. All trees less than a half inch in diameter at breast height were counted and tallied as reproduction. Trees were tallied separately by crown classes: dominant, intermediate, suppressed, and dead. Heights of dominant trees

were measured by Abney level, and enough heights were taken so that a well defined curve of height over diameter was obtained on each plot. This usually involved the measurement of from ten to twenty tree heights. Age was determined by boring five trees with the Swedish increment borer at one foot above the average ground level. Total age was obtained by averaging these five readings and adding the seedling age as determined in a special study.

Stocking was determined both on the basis of number of stems and on basal area, and the normality of stocking was computed by comparison with normal yield tables (17).

The procedure used in determining site index was as follows: The total basal area of all dominant trees was computed using basal area tables (21). The average basal area was then computed, and the diameter breast high corresponding to it was found. After curving the measured dominant heights over the diameters, the dominant height corresponding to the average diameter just computed was found. This height was plotted with the proper age in the site index graph for jack pine (17). A line was drawn from the origin through this plotted point. The intersection of this line with the fifty year age line gave the height at fifty years, which is considered the site index.

An attempt was also made to determine how the present stand on each plot had originated. Fire scars and occasional remnants of the previous stand were examined in this connection.

GROUND COVER VEGETATION

Ground cover was sampled by means of one square foot quadrats. On the first nineteen plots twenty-five quadrats per plot were used. On the remaining plots twenty quadrats per plot were taken. Quadrat locations were determined by an entirely randomized method whereby the random selection of one numbered card determined the location of the quadrat on a vertical column and the selection of another card placed the quadrat on a horizontal row. The intersection of the column and the row determined the exact quadrat location within the plot. Sides of the quadrats as well as of the plots were always run in the cardinal directions. All species found on the quadrats were listed by species and abundance. Abundance was determined by a count of individual stems for most species. In the case of several mosses, the twin flower (Linnaea borealis), and one of the grass species (Oryzopsis asperifolia), abundance was rated as sparse, common, or abundant. This was done by visualizing a circle superimposed upon the quadrat and by estimating what fractional segment of the circle would be covered by the species in question. The scale used was one-eighth, sparse; one-quarter, common; and one half or more of the circle, abundant. Every effort was made to identify dead plants on the quadrats so as to minimize the discrepancies unavoidably resulting from seasonal changes in the aspect of the vegetation. After all quadrats were listed, a careful check was made over the entire plot to find any species not listed on the quadrats. These were tallied separately as "also present".

SOIL DATA

Two soil pits were dug on each of fifty plots. These pits were located within the plots by random sampling similar to the method used

for locating the ground cover quadrats. The pits were large enough to facilitate an inspection of the individual horizons and deep enough to reach the top of the parent material. Although in most cases horizons were very indistinctly developed, an attempt was made to record thickness, texture, color, consistency, structure, and any special features of individual horizons. The occurrence of roots and stones was also noted. Texture was noted by "feel" after the writer had familiarized himself with test samples of the range of soil textures to be encountered. The A_0 horizon was considered to include all organic accumulation above the mineral soil. The A_1 horizon was the dark colored surface layer of mineral soil in which considerable organic matter was mixed. This layer was usually only a fraction of an inch thick. The A_2 horizon was considered to be the zone of maximum leaching and particularly toward the top had the grayish color characteristic of silicious, highly leached podsollic soils. No distinct A_3 horizon was evident. The B horizon was identified by its generally darker color, especially toward the top, and by the somewhat finer texture and greater concentration of fine soil particles. In most cases a very gradual transition was noted down to the C horizon.

Two soil samples were taken from opposite sides of each pit at both the B horizon and C horizon, making a total of eight soil samples per plot. The sample from the B horizon was taken from the upper zone where the fine soil material and the organic material were concentrated. Exposure, slope, and drainage were also noted for each plot.

SOIL TESTING

Standard soil testing procedures of general acceptance were used in all laboratory analyses. As previously explained, the Bouyoucos (14)

hydrometer method was used in the preliminary analysis of soil texture. A standard soil centrifuge was used in connection with the moisture equivalent determinations. Soil nitrogen tests were made by the Division of Soils of the University of Minnesota. All other testing was done by the writer.

STATISTICAL ANALYSIS

Wherever possible, standard statistical procedures have been used to express relationships and differences quantitatively. Statistical methods have also been used to test whether relationships or differences can safely be attributed to factors other than chance. It has often been desirable to compare the means from two series of data with unequal numbers of observations. In such cases, the standard error of the difference method, using a pooled standard deviation (96), has been followed. In analyzing the possible association between soil values and site index, "r" was computed by correlational analysis (127) as a numerical index of the association between the two variables being considered. In case the r value was large enough to warrant the assumption that the degree of association between the two variables was not a mere chance association, the regression equation expressing the trend of the relationship between the variables was computed.

FREQUENCY AND CONSTANCY

The frequency and constancy concepts of Braun-Blanquet (16) have been used throughout in the study of the vegetation. In general form, these are the figures obtained by dividing the number of occurrences of

a species by the number of possible occurrences and multiplying by one hundred. When this is computed for a species within a single plot, the resultant figure is termed the frequency per cent. When this same computation is applied to the occurrence of a species considered over a number of different plots, the resultant figure is a constancy per cent. A further discussion of plant distributional concepts appears in a later section.

ANALYSIS OF THE VEGETATION

TREE SPECIES ASSOCIATED WITH JACK PINE

A complete list of the nineteen tree species found associated with jack pine on the plots taken follows. Common and scientific names used are those listed by Harlow and Harvar (44) and by the latest Forest Service Check List (125). Because these references do not list a common name for *Quercus macrocarpa* var. *olivaeformis* (Michx. f.) A. Gray, the name northern bur oak as used by Rosendahl and Butters (78) is listed.

<u>Scientific name</u>	<u>Common name</u>
<i>Abies balsamea</i> (L.) Mill.	Balsam Fir
<i>Acer negundo</i> L.	Boxelder
<i>Acer rubrum</i> L.	Red Maple
<i>Betula papyrifera</i> Marsh.	Paper Birch
<i>Larix laricina</i> (Du Roi) K. Koch	Tamarack
<i>Ostrya virginiana</i> (Mill.) K. Koch	Eastern Hophornbeam
<i>Picea glauca</i> (Mill.) B.S.P.	White spruce
<i>Picea mariana</i> (Mill.) B.S.P.	Black Spruce
<i>Pinus banksiana</i> Lamb.	Jack Pine

<u>Scientific name</u>	<u>Common name</u>
<i>Pinus resinosa</i> Ait.	Red Pine
<i>Pinus strobus</i> L.	Eastern White Pine
<i>Populus balsamifera</i> Mill.	Balsam Poplar
<i>Populus grandidentata</i> Michx.	Bigtooth Aspen
<i>Populus tremuloides</i> Michx.	Quaking Aspen
<i>Prunus pennsylvanica</i> L.	Pin Cherry
<i>Prunus virginiana</i> L.	Choke Cherry
<i>Quercus borealis</i> Michx.	Northern Red Oak
<i>Quercus ellipsoidalis</i> E. J. Hill	Northern Pin Oak
<i>Quercus macrocarpa</i> var. <i>olivaeformis</i> (Michx. f.) A. Gray	Northern Bur Oak

MIXED STANDS AS INDICATORS OF SITE QUALITY

All plots were classified either as pure jack pine or as mixed stands. Mixed stands were considered to be those on which more than two hundred individuals per acre of species other than jack pine were found. All trees and seedlings were counted regardless of size. The mean site index values were then determined for both the pure and the mixed stands. The standard error of the difference method as described by Snedecor (36) for unequal numbers of observations in the groups was applied in the analysis. The essential data are listed below.

Mean site index of all mixed stand plots (\bar{x})	59.1 feet
Mean site index of all pure jack pine plots (\bar{y})	53.2 feet
Standard deviation \bar{s}	± 6.9 feet
Standard deviation \bar{y}	± 6.6 feet
t value	3.16

Fisher's (35) table of values of t gives a figure of 2.66 for the 1 per cent level of significance. This indicates that the probability of a t value larger than 2.66 occurring by chance is less than one out of a

hundred. The t value of 3.18 as actually determined in the analysis is thus considerably greater than could reasonably be expected to occur by chance. Therefore one can safely say that in the areas examined, the quality tends to be better where mixed rather than pure jack pine stands occur.

However, the standard deviation values are rather large. It is obvious that a great amount of overlapping of site index occurs between the two kinds of stands. The presence of a mixed stand on an individual plot would therefore not have predictive value in terms of a narrow range of site index. However, there is a definite tendency for mixed stands to occur on the better sites. This is in accord with the generally accepted assumption that the site requirements of jack pine are lower than those of most of the other species in the region. The relative proportions of pure and mixed stands on each of the three site classes have been presented in the form of a bar diagram in Fig. 12. The absence of mixed stands on the poor site class and their concentration on the medium and good site classes is strikingly apparent.

After it had been demonstrated that a relationship existed between site index and the presence of associated species, a further analysis was made to test whether the site index varied with the degree of stand mixture. The percentage of total stand excluding reproduction composed of tree species other than jack pine was computed for each plot. These percentages were plotted together with corresponding site index values in Fig. 13. An inspection of the scatter diagram indicated that a reasonably rectilinear relationship existed between the two variables. A correlational analysis of the data gave a coefficient of correlation of 0.469.

Figure 12. Relative percentages of pure and mixed stands on all site quality classes.

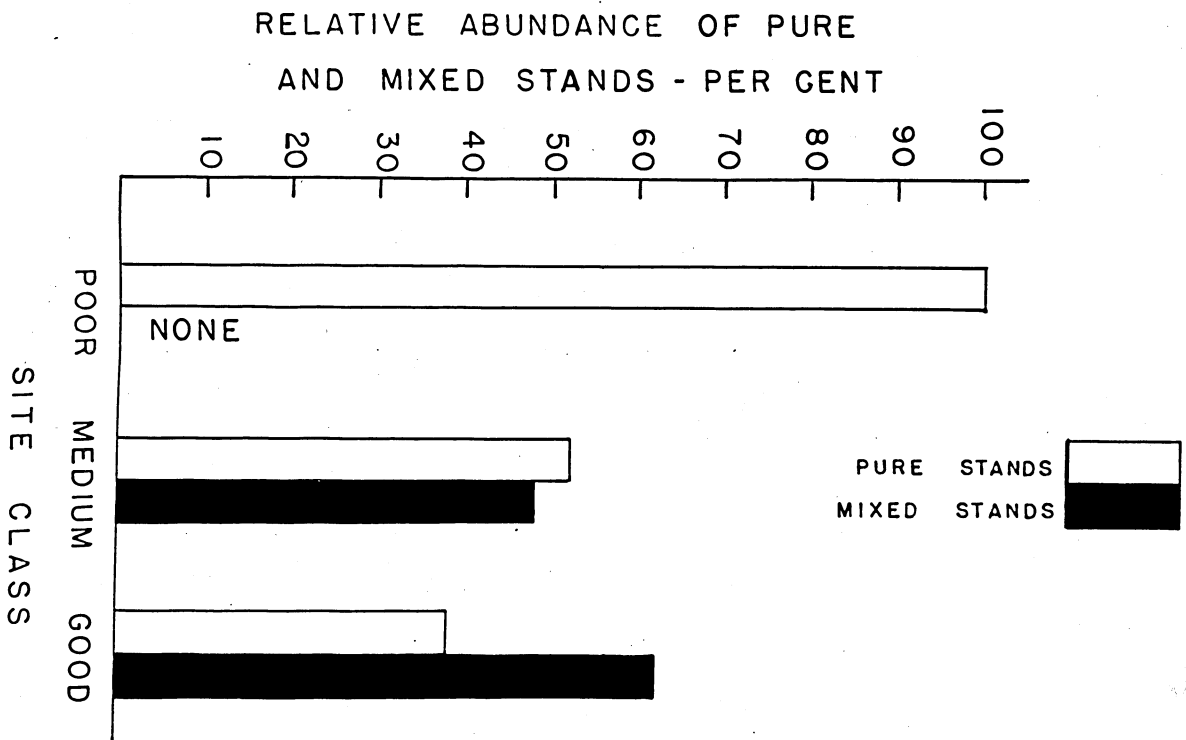
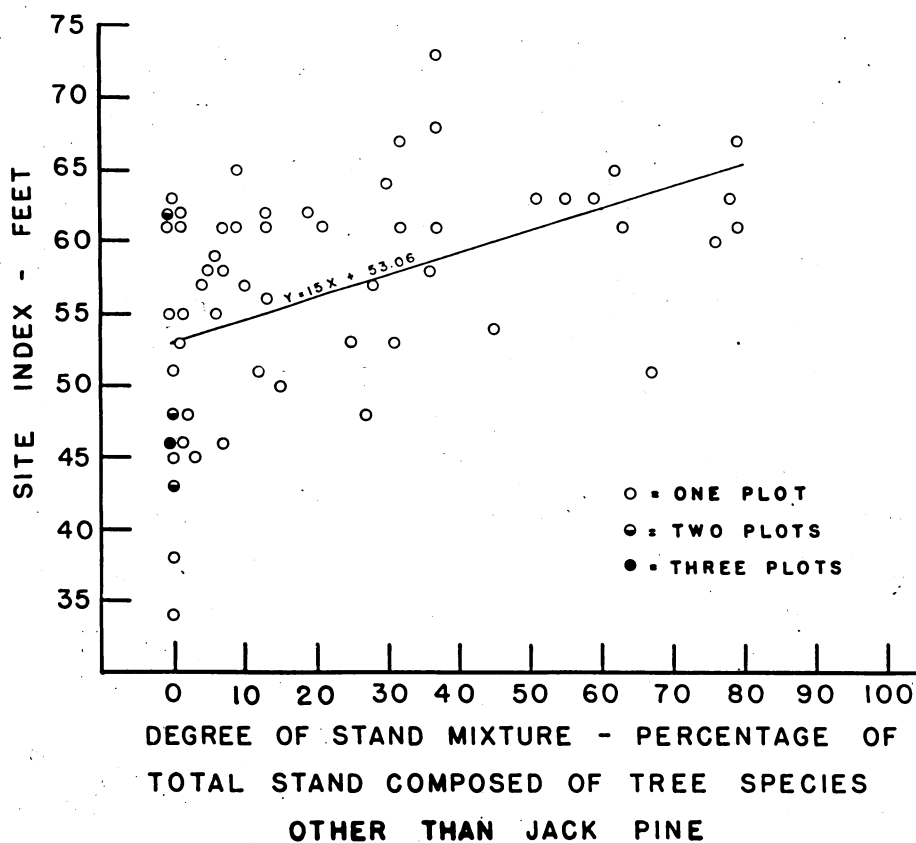


Figure 13. Correlation of site index with degree of stand mixture.



This value is highly significant and indicates that for the data collected, the site index tends to be associated with the degree of stand mixture. The regression line expressing this relationship has also been computed and appears in Fig. 13.

INDIVIDUAL TREE SPECIES AS INDICATORS OF SITE QUALITY

Association of the different tree species with site index was tested by the standard error of the difference method. Eleven species were analysed and the essential data are given in Table 8. A measure of the range of variation in the site index values is given by the standard deviations.

The t values for six species; quaking aspen, northern red oak, paper birch, bigtooth aspen, red pine, and eastern white pine are all above that required at the one per cent level of significance. Therefore, plots containing these species in mixture with jack pine have definite associations with site quality. The presence of any of the six species listed indicates better than average site quality. Inasmuch as the individual species mentioned are definitely associated with high site quality, it would logically follow that the presence of combinations of these species would increase the degree of association. This is supported by the data presented in the table for the combination of quaking aspen and northern red oak. The t value for this combination is higher than the t value for either of the individual species considered. This should be interpreted as meaning that the presence of both species increases the probability that the site index value of the plot will be high. However, it does not necessarily imply that the site index value

TABLE 8

VALUE OF INDIVIDUAL TREES AS SITE INDICATORS AS EXPRESSED BY *t* VALUES

SPECIES	Average Site Index		Standard Deviation		Standard Error of the Mean		Number of Plots	<i>t</i>
	X	Y	X	Y	X	Y		
Quaking aspen or Northern red oak or both	61.3	52.2	4.8	7.5	0.6	0.9	64	5.53 *
Quaking aspen	61.8	53.1	4.9	7.6	0.6	0.9	64	4.92 *
Northern red oak	61.7	53.9	8.1	3.7	1.0	0.5	63	3.93 *
Paper birch	61.1	53.8	5.3	7.4	0.7	0.9	63	3.63 *
Bigtooth aspen	61.1	55.3	5.5	8.0	0.7	1.0	63	3.17 *
Red pine	58.4	52.8	5.5	10.1	0.7	1.3	64	2.88 *
Eastern white pine	59.7	54.3	5.8	8.3	0.7	1.1	63	2.67 *
Balsam fir	59.0	54.9	6.2	8.4	0.8	1.1	63	1.94
Red maple	60.2	55.2	3.7	11.4	0.5	1.4	63	1.45
Northern bur oak	56.2	56.3	7.4	5.3	0.9	0.7	62	0.03
White spruce	55.4	56.2	5.9	2.8	0.7	0.4	63	0.64
Northern pin oak	52.8	56.6	7.0	8.0	0.9	1.0	63	1.29

* Exceeds the one per cent level of significance.

X - Plots containing the individual species being tested as listed in the first column.

Y - Plots not containing the species listed in the first column.

of a plot with a combination of northern red oak and quaking aspen is higher than the site index value of a plot having only one of these species.

Foresters can easily use the occurrence of such trees as indicators of the better site quality conditions, since their presence can be detected in even a casual survey. When used in conjunction with site index determinations made by measuring dominant tree heights and age in the standard manner, tree indicators not only supplement site index determinations but also give information relative to stand composition. This information has special value in indicating successional trends, and will be discussed in a subsequent section.

Figures 14 and 15 give the constancy per cent of each of the six tree indicator species on good, medium and poor jack pine site classes. In each case the constancy was found by dividing the number of plots on which the species occurred by the total number of plots in the site class considered. These charts supplement graphically the data obtained by statistical analysis. The pronounced affinity of quaking aspen (Fig. 14A) for good sites is indicated by its constancy of about 65 per cent for that class, as compared with approximately 20 per cent for medium sites and none for the poor site class. Northern red oak (Fig. 14B), although not occurring on as many plots, exhibits the same preference for the good sites. Paper birch (Fig. 14C) and eastern white pine (Fig. 15B) are somewhat less exclusively on the good sites and occur on a slightly greater proportion of medium sites. Neither, however, occurs on poor sites. Bigtooth aspen (Fig. 15A) occurs too infrequently with jack pine to be of much practical value as a site indicator. When present, it is usually associated with good site quality. The pattern of red pine constancy

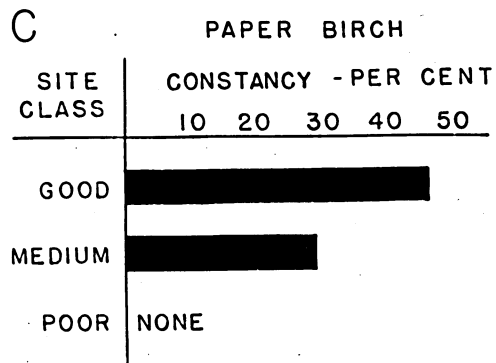
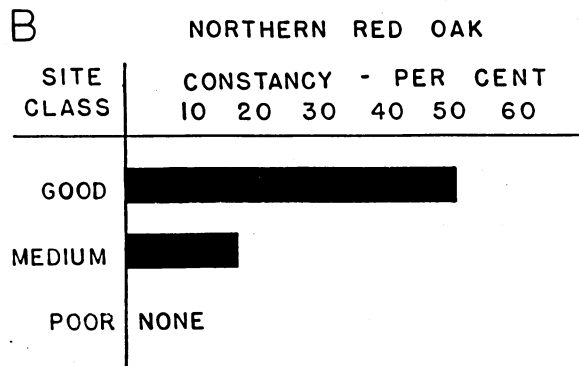
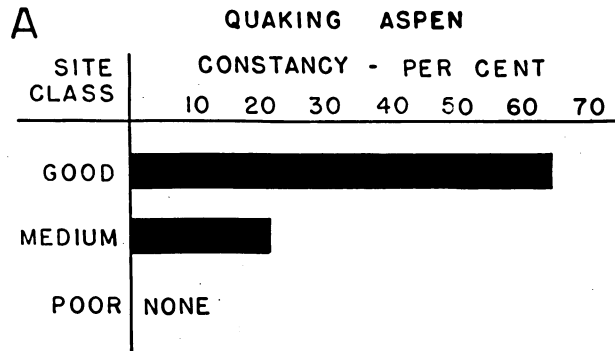


Figure 14. Constancy values for tree indicator species.

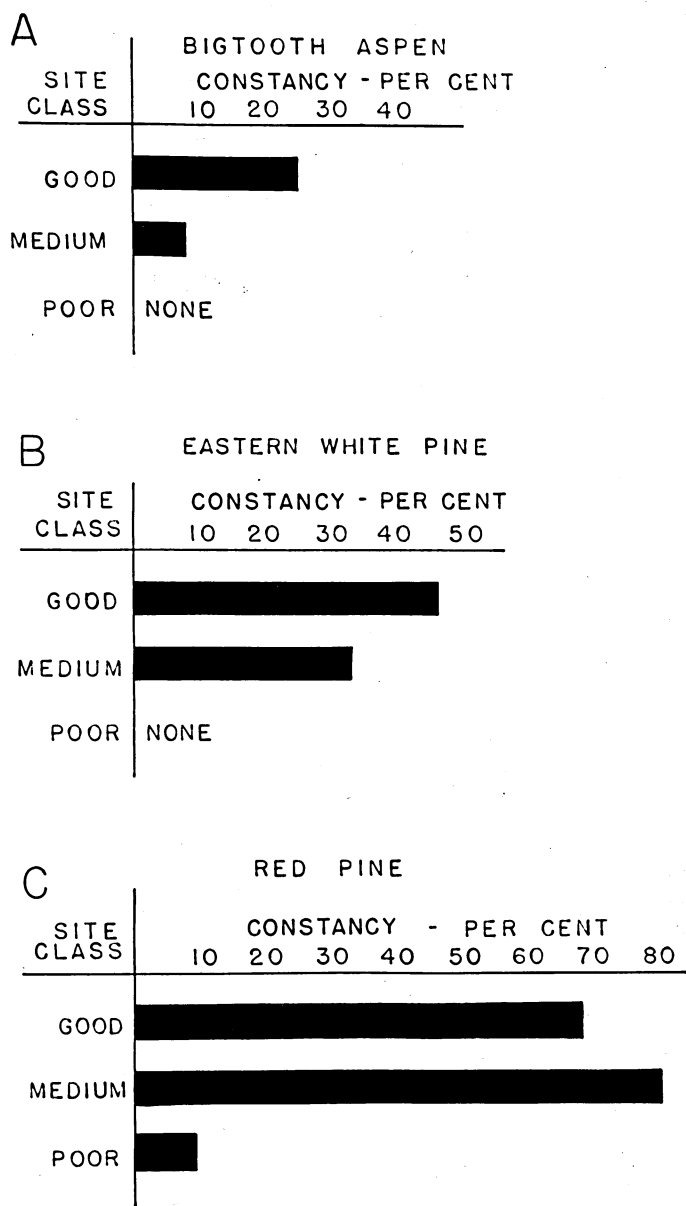


Figure 15. Constancy values for tree indicator species.

(Fig.15C) differs from that of the other species. It was found on approximately 10 per cent of the poor site plots and on a somewhat greater proportion of the medium than the good plots. It occurs on about three fourths of all the good and medium plots and is by far the most frequent of the species listed.

USE OF INDICATOR VALUE AS AN INDEX

General Concepts

The general lack of understanding of the basic concepts of plant sociological relationships by investigators of forest communities in this country has retarded the accumulation of knowledge of such communities as natural, biological entities. In connection with the selection of plant species as indicators of site quality it is necessary to decide what distributional characteristics of the species make it a good indicator. Within a single stand a species can be characterized quantitatively in respect to its presence or absence, its relative abundance or density, and its distribution.

It is obvious that a species must be present in order for it to have positive indicator value. However, indicator value of a negative nature may be implied by the absence of certain species. In the data at hand, *Vaccinium angustifolium* occurs on all jack pine plots. The absence of this species from a given area could be said to be indicative of site conditions inimical in some respect to jack pine. However, few species occur with sufficient constancy to enable their use in this negative manner. Table 3 lists the aforementioned species as the only one occurring on all sixty-five plots.

TABLE 3

SPECIES CHARACTERISTICALLY PRESENT IN JACK PINE STANDS

Including all species with a constancy of at least fifty per cent on all sites.

SPECIES	SITE CLASS		
	POOR	MEDIUM	GOOD
	(constancy per cent)*		
<i>Vaccinium angustifolium</i>	100	100	100
<i>Maianthemum canadense</i> var. <i>interius</i>	73	100	100
<i>Oryzopsis asperifolia</i>	100	77	85
<i>Antennaria</i> (all species)	91	73	63
<i>Gaultheria procumbens</i>	91	63	67
<i>Lathyrus</i> (all species)	73	55	85
<i>Carex pennsylvanica</i>	55	64	70
<i>Rosa</i> (all species)	73	50	67
<i>Linnaea borealis</i>	55	73	52

$$* \text{ Constancy per cent} = \frac{\left(\begin{array}{l} \text{Number of plots in site class} \\ \text{on which the species occurs} \end{array} \right)}{\left(\begin{array}{l} \text{Total number of plots in the} \\ \text{site class} \end{array} \right)} \cdot 100$$

The density or relative abundance of a species might be expected to have some indicator value. Presumably, the more nearly optimum a given site is for the species in question, the greater the relative number of individuals of the species that will be present. In a complex forest community, however, too many other factors are present, and clear cut correlations between numbers of individuals and site quality are not apparent. The growth habits and genetic inheritance of the species have much greater determinative effect on numbers of individuals than does the habitat. *Arctostaphylos Uva-ursi* will, when present at all, always occur in greater numbers than will a species like *Cypripedium acaule*, regardless of how favorable the site may be to the latter.

The distribution or dispersion of the species over the stand is of little value in indicating site conditions other than perhaps homogeneity of the area. This is the "sociability" factor of Braun-Blanquet (16). It is measured by the frequency method widely used by Raunkiaer (70) and explained in a previous section. Frequency determinations were made and tabulated for all species on all plots on which the vegetation was sampled. However, since this is not a factor of particular significance in connection with indicator value, the voluminous tabulations involving nearly two hundred species on over sixty different stands have not been included in this presentation.

In addition to the characteristics of the individual stands already discussed, certain relationships appear when numbers of different stands are analyzed. Two such relationships, "constancy" and "fidelity", are of special significance in connection with indicator value. These terms are applied in the same manner as defined by Braun-Blanquet (16).

The term constancy is used to indicate degrees of presence on groups of individual stands. The constancy of an individual species on the group of stands being considered; for example, all jack pine plots or all good site jack pine plots, is found by dividing the number of individual plots on which the species occurs by the total number of plots in the group and converting to a per cent figure. Constancy is often confused with frequency, which term should be applied only to individual stands.

In this study the vegetation has been analyzed separately within each site class as determined by the site index method. Constancy percentages are given for all species in Tables 4, 5, and 6. Species having their greatest constancy in the same site class have been listed together in the same table. In addition, the species having a constancy above 50 per cent in all site classes have been listed in Table 3 as species characteristic of the jack pine type.

Indicator Value

In deciding on the usefulness of a plant species as an indicator of site, the constancy of that species on the site condition it represents does not give a complete analysis of its indicator value. For example, one of the common jack pine grasses, *Oryzopsis asperifolia*, has a constancy value of 100 per cent on poor sites. However, it also has a constancy of over 75 per cent on both medium and good sites, so that it cannot be said to indicate poor site with any degree of reliability. Some measure of exclusiveness to the site conditions it should indicate must exist. This exclusiveness is the "fidelity" concept referred to by Braun-Blanquet (16). The degree of fidelity or exclusiveness expressed the rigidity of the limi-

TABLE IV

INDICATOR VALUE OF SPECIES HAVING GREATEST CONSTANCY OF OCCURRENCE ON
GOOD SITES^{1/}

Arranged in descending order of their Indicator Value

SPECIES	CONSTANCY PERCENT			INDICATOR VALUE for Good Sites
	Poor Site	Medium Site	Good Site	
<i>Rubus</i> spp. (Raspberry only)	0	32	78	57
<i>Populus tremuloides</i> Michx.	0	23	63	48
<i>Quercus borealis</i> Michx.	0	18	52	40
<i>Aster macrophyllus</i> L.	18	59	81	36
<i>Pyrola retundifolia</i> L. var. <i>americana</i> (Sweet) Fern	9	32	56	32
<i>Lathyrus venosus</i> Muhl. var. <i>intensus</i> Butters and St. John	55	45	78	30
<i>Betula papyrifera</i> Marsh.	0	32	48	27
<i>Steridium aquilinum</i> (L.) Kuhn var. <i>latiusculum</i> (Desv.) Underw. ex Heller	9	45	59	26
<i>Apocynum androsaemifolium</i> L.	9	14	37	25
<i>Diervilla lonicera</i> Mill.	27	55	70	25
<i>Acer rubrum</i> L.	0	14	33	24
<i>Pinus strobus</i> L.	0	36	48	24
<i>Pyrola</i> spp.	27	68	78	23
<i>Agastache anethiodora</i> (Nutt.) Britton	0	0	23	23
<i>Cornus canadensis</i> L.	9	36	48	21
<i>Oakesia sessilifolia</i> (L.) Kats. 0		18	33	21
<i>Rhus radicans</i> L. var. <i>Rydbergii</i> A.S. (Small ex Rydb.) Rehder		5	30	21

^{1/} Names of tree species are those listed in the latest U.S. Forest Service Check List (125). Names of other plant species are those listed in a preliminary check list by Moore and Tryon (65).

SPECIES	CONSTANCY PERCENT			INDICATOR VALUE for Good Sites
	Poor Site	Medium Site	Good Site	
<i>Populus grandidentata</i> Michx.	0	0	26	20
<i>Rubus idaeus</i> L. var. <i>strigosus</i> (Michx.) Maxim.	0	9	26	20
<i>Pyrola secunda</i> L.	9	45	52	19
<i>Lycopodium obscurum</i> L.	9	9	26	17
<i>Aralia nudicaulis</i> L.	0	32	37	16
<i>Clintonia borealis</i> (Ait.) Raf.	0	23	30	15
<i>Rosa</i> spp.	36	32	48	15
<i>Solidago hispida</i> Muhl.	36	32	48	15
<i>Vaccinium canadense</i> Kalm ex Richards.	9	18	30	15
<i>Equisetum</i> spp.	0	9	19	13
<i>Fragaria</i> spp.	36	73	74	13
<i>Hepatica americana</i> (DC.) Ker.	0	5	15	12
<i>Campanula rotundifolia</i> L.	9	23	30	12
<i>Rubus</i> spp.	0	5	15	12
<i>Corylus americana</i> (Walt.)	26	32	44	11
<i>Polygala paucifolia</i> Willd.	0	18	26	11
* <i>Streptopus longipes</i> Fern.	0	0	11	11
<i>Spigaea repens</i> L.	9	36	37	10
<i>Maianthemum canadense</i> Desf. var. <i>interius</i> Fern	73	100	100	10
<i>Rubus pubescens</i> Raf.	0	14	19	10
<i>Rubus setosus</i> Bigel.	0	9	15	9
<i>Prunus virginiana</i> L.	18	18	26	8
<i>Coptis groenlandica</i> (Oeder) Fern.	0	0	7	7

SPECIES	CONSTANCE PERCENT			INDICATOR VALUE for Good Sites
	Poor Site	Medium Site	Good Site	
* <i>Cornus rugosa</i> Lam.	0	0	7	7
<i>Equisetum pratense</i> Ehrh.	0	0	7	7
* <i>Osmunda Claytoniana</i> L.	0	0	7	7
<i>Liatris</i> spp.	0	0	7	7
* <i>Lonidera canadensis</i> Marsh.	0	0	7	7
<i>Lycopodium clavatum</i> L.	0	0	7	7
<i>Prenanthes alba</i> L.	0	14	15	7
<i>Agropyron trachycaulum</i> (Link) Steud.	0	0	7	7
* <i>Amphicarpa bracteata</i> (L.) Fern.	0	0	7	7
<i>Convolvulus spithameus</i> L.	0	10	11	5
<i>Rosa acicularis</i> Lindl.	0	9	11	5
<i>Trifolium</i> spp.	0	9	11	5
<i>Vicia americana</i> Muhl. ex Willd.	13	23	26	5
<i>Anemone canadensis</i> L.	0	0	4	4
<i>Hieracium canadense</i> Michx. var. <i>fasciculatum</i> (Pursh.) Fern.	0	0	4	4
<i>Anemone virginiana</i> L.	0	0	4	4
<i>Antennaria</i> sp.	0	0	4	4
<i>Bromus ciliatus</i> L.	0	0	4	4
<i>Glenatis verticillaris</i> DC.	0	0	4	4
<i>Comandra Richardsiana</i> Fern.	0	5	7	4
* <i>Cornus alternifolia</i> L.f.	0	0	4	4
<i>Cynoglossum boreale</i> Fern.	0	0	4	4

SPECIES	CONSTANCY PERCENT			INDICATOR VALUE for Good Sites
	Poor Site	Medium Site	Good Site	
<i>Equisetum hyemale</i> L. var. affine (Engelm.) A.A.Eaton	0	0	4	4
<i>Equisetum arvense</i> L.	0	0	4	4
<i>Equisetum sylvaticum</i> L.	0	0	4	4
<i>Galium trifidum</i> L.	0	5	7	4
<i>Galium triflorum</i> Michx.	0	0	4	4
<i>Goodyera repens</i> (L.) R. Br. var. <i>ophioides</i> Fern.	0	0	4	4
<i>Helioopsis</i> spp.	0	0	4	4
<i>Krigia biflora</i> (Walt.) Blake	0	0	4	4
<i>Liatris spheroides</i> Michx.	0	0	4	4
<i>Lonicera hirsuta</i> Eaton	0	5	7	4
<i>Lobelia</i> spp.	0	5	7	4
<i>Mitella nuda</i> L.	0	0	4	4
* <i>Monotropa uniflora</i> L.	0	0	4	4
<i>Panicum Lindheimeri</i> Nash.	0	0	4	4
* <i>Pterotis pennsylvanica</i> (Willd.) Fern.	0	0	4	4
<i>Rhus glabra</i> L.	0	5	7	4
<i>Rubus flagellaris</i>	0	0	4	4
<i>Rubus occidentalis</i> L.	0	0	4	4
* <i>Smilax herbacea</i> L.	0	0	4	4
<i>Stachys palustris</i> L.	0	0	4	4
<i>Uvularia grandiflora</i> Smith	0	0	4	4
<i>Viburnum Rafinesquianum</i> Schult. var. <i>affine</i> (Schneid.) House	0	0	4	4

SPECIES	CONSTANCY PERCENT			INDICATOR VALUE for Good Sites
	Poor Site	Medium Site	Good Site	
<i>Steironema ciliatum</i> (L.) Raf.	0	0	4	4
<i>Viola novae-angliae</i> House	0	5	7	4
<i>Lithospermum canescens</i> (Michx.) Lehm.	0	0	4	4
* <i>Dryopteris</i> spp.	0	0	4	4
<i>Aster ericoides</i> L.	0	0	4	4
<i>Pinus banksiana</i> Lamb.	100	100	100	0
<i>Vaccinium angustifolium</i> Ait.	100	100	100	0

* Considered to be excellent site indicators when present, in spite of the low indicator values computed because of their infrequency of occurrence.

** Same indicator value for good and medium sites.

TABLE V

INDICATOR VALUE OF SPECIES HAVING GREATEST CONSTANCY OF OCCURRENCE ON
MEDIUM SITES

Arranged in descending order of their Indicator Value.

SPECIES	CONSTANCY PERCENT			INDICATOR VALUE for Med. Sites
	Poor Site	Medium Site	Good Site	
<i>Muhlenbergia racemosa</i> (Michx.) B.S.P.	9	55	15	42
<i>Pinus resinosa</i> Ait.	0	91	70	38
<i>Hypnum Schreberi</i> Willd.	54	63	52	34
<i>Corylus cornuta</i> Marsh.	0	55	37	29
<i>Melanopyrum lineare</i> Lam.	18	45	19	27
<i>Linnaea borealis</i> L. var. <i>americana</i> (Forbes) Rehder	55	73	52	21
<i>Picea glauca</i> (Mill.) Voss.	0	27	11	19
<i>Chimaphila umbellata</i> (L.) Nutt. var. <i>cisatlantica</i> Blake	27	55	41	18
<i>Carex pennsylvanica</i> Lam.	55	82	70	16
<i>Salix humilis</i> Marsh.	36	55	41	16
<i>Abies balsamea</i> (L.) Mill.	0	41	37	15
<i>Lycopodium complanatum</i> L.	0	23	11	15
<i>Aster ciliolatus</i> Lindl. ex Hooker	18	45	41	15
<i>Lycopodium</i> sp.	0	14	0	14
<i>Viola adunca</i> Sa.	55	59	41	14
<i>Alnus rugosa</i> (Du Roi) Spreng.	0	18	7	13
<i>Lactuca</i> spp.	0	14	4	11

SPECIES	CONSTANT PERCENT		INDICATOR	
	Poor Site	Medium Site	Good Site	VALUE For Med. Sites
<i>Ledum groenlandicum</i> Oeder	0	14	4	11
<i>Amelanchier laevis</i> Wiegand	0	18	11	10
<i>Maianthemum canadense</i> Desf. var. <i>interius</i> Fern.	73	100	100	10
<i>Trientalis borealis</i> Raf.	0	18	11	10
<i>Solidago juncea</i> Ait.	0	14	7	9
<i>Anemone quinquefolia</i> L. var. <i>interior</i> Fern.	36	64	63	9
<i>Senecio pauperculus</i> Michx.	27	27	15	9
<i>Hieracium scabrum</i> Michx.	0	9	0	9
<i>Andropogon scoparius</i> Michx.	9	18	11	7
<i>Cypripedium acaule</i> Ait.	0	9	4	6
<i>Cornus stolonifera</i> Michx.	0	9	4	6
<i>Lonicera dioica</i> L.	9	9	0	6
<i>Panicum Leibergii</i> (Vasey) Scrib.	0	9	4	6
<i>Andropogon Gerardii</i> Vitman	0	5	0	5
<i>Amelanchier sanguinea</i> (Pursh) DC.	0	5	0	5
<i>Anaphalis margaritacea</i> (L.) B. & H. var. <i>intercedens</i> Hara	0	5	0	5
<i>Artemisia ludoviciana</i> Nutt.	0	5	0	5
<i>Comptonia peregrina</i> (L.) Cult.	0	5	0	5
<i>Epilobium angustifolium</i> L.	0	5	0	5
<i>Galium</i> spp.	0	5	0	5
<i>Cerastium arvense</i> L.	0	5	0	5

SPECIES	Poor Site	Medium Site	Good Site	INDICATOR
				VALUE for Medium Sites
<i>Juniperus communis</i> L. var. <i>depressa</i> Pursh.	9	5	0	5
<i>Menarda mollis</i> L.	0	5	0	5
<i>Petasites palmatus</i> (Ait.) A. Gray	0	5	0	5
<i>Pyrola elliptica</i> Nutt.	0	5	0	5
<i>Viola</i> sp.	0	5	0	5
<i>Poa palustris</i> L.	0	9	7	4
<i>Equisetum</i> sp.	0	9	7	4
<i>Lathyrus ochroleucus</i> Hooker	9	14	11	3
<i>Anemone nemorosa</i> L.	18	18	15	2
<i>Helleborus viridis</i> (Cass) Desf.	0	5	4	2
<i>Lathyrus palustris</i> L.	0	5	4	2
<i>Lobelia spicata</i> Lam.	0	5	4	2
<i>Pedicularis canadensis</i> L.	0	5	4	2
<i>Viola conspersa</i> Reichenb.	0	5	4	2
<i>Stachys ciliata</i> (L.) Raf.	0	5	4	2
<i>Taraxacum</i> sp.	0	5	5	2
<i>Pinus banksiana</i> Lamb.	100	100	100	0
<i>Vaccinium angustifolium</i> Ait.	100	100	100	0

TABLE VI

INDICATOR VALUE OF SPECIES HAVING GREATEST CONSTANCY OF OCCURRENCE ON
POOR SITES

Arranged in descending order of their Indicator Value.

SPECIES	CONSTANCY PER CENT			INDICATOR VALUE for Poor Sites
	Poor Site	Medium Site	Good Site	
<i>Arctostaphylos Uva-ursi</i> (L.) Spreng.	100	59	22	61
<i>Polytrichum</i> spp.	75	9	14	61
<i>Gaultheria procumbens</i> L.	91	68	67	44
<i>Aster laevis</i> L.	64	27	19	42
<i>Danthonia spicata</i> (L.) Beauv.	73	32	30	42
<i>Galium boreale</i> L.	82	36	48	40
<i>Solidago nemoralis</i> Ait.	45	9	4	39
<i>Symphoricarpos albus</i> (L.) Blake	55	14	26	35
<i>Antennaria canadensis</i> Greene	82	55	48	31
<i>Antennaria plantaginifolia</i> (L.) Richards	36	5	7	30
<i>Calliergon Schreveri</i> (Willd.) Grout	45	18	19	27
<i>Rosa blanda</i> Ait.	36	9	11	26
<i>Hieracium scabriusculum</i> Michx.	36	18	4	26
<i>Oryzopsis pungens</i> (Torr.) Hitchc.	64	45	37	23
<i>Dicranum</i> spp.	36	18	11	22
<i>Prunus pumila</i> L.	27	5	7	21
<i>Prunus pennsylvanica</i> L.f.	36	9	22	20
<i>Cladonia</i> spp.	36	23	15	18

SPECIES	CONSTANCY PERCENT			INDICATOR VALUE For Poor Sites
	Poor Site	Medium Site	Good Site	
<i>Dryopsis asperifolia</i> Michx.	100	77	85	18
<i>Potentilla tridentata</i> Ait.	18	0	0	18
<i>Aster</i> sp.	18	0	0	18
<i>Quercus ellipsoidalis</i> E. J. Hill	27	14	7	17
<i>Ceanothus ovatus</i> Desf.	18	0	4	16
<i>Moucheira Richardsonii</i> R. Br. var. <i>hispidior</i> R.B.L.	18	0	8	12
<i>Antennaria nudiflora</i> Greene	64	55	44	15
<i>Lathyrus</i> spp.	18	5	4	14
<i>Quercus macrocarpa</i> Michx. var. <i>olivaceiformis</i> (Michx.f.) A. Gray	36	14	33	12
<i>Schizachne purpurascens</i> (Torr.) Swallen	27	23	11	11
<i>Panicum xanthophysum</i> A. Gray	18	14	4	10
<i>Acerates virigiflora</i> (Raf.) Mill.	9	0	0	9
<i>Agropyrum</i> sp.	9	0	0	9
<i>Amelanchier alnifolia</i> Nutt.	9	0	0	9
<i>Thalictrum dioicum</i> L.	27	9	26	9
<i>Anemone</i> spp.	18	9	11	8
<i>Cornus racemosa</i> Lam.	9	5	0	7
<i>Zizia aptera</i> (A. Gray) Fern.	9	0	7	5
<i>Trifolium</i> spp.	0	9	7	4
<i>Aquilegia canadensis</i> L.	9	5	7	3
<i>Sanicula narilandica</i> L.	9	5	7	3

SPECIES	CONSTANCY PERCENT			INDICATOR VALUE for Poor Sites
	Poor Site	Medium Site	Good Site	
<i>Amelanchier humilis</i> Wiegand	18	18	15	2
<i>Pinus banksiana</i> Lamb.	100	100	100	0
<i>Vaccinium angustifolium</i> Ait.	100	100	100	0

tation of the species to a particular community or habitat. Several classifications of the degree of fidelity have been used, but none is well suited to quantitative determination and evaluation.

It must also be noted that fidelity alone is no better as a criterion of value as an indicator species than is constancy. In Table 4 there are approximately 60 species restricted entirely to good sites as indicated by a 0 constancy in the other site classes. Such species have high fidelity to the good site habitat, but are so infrequent of occurrence as to be of no practical value as indicators of good site. The ideal indicator is thus one which is always found on a given habitat or in a certain community and is never found elsewhere. Such a species is perhaps nonexistent in nature, and we must be content with a reasonable approach to this ideal. In connection with the present study it was considered desirable to devise some numerical index by which an evaluation could be made of the various species in terms of both constancy and fidelity. This index has been called "Indicator Value" and is very easily computed:

$$\text{Indicator value} = \frac{X}{N_1} - \frac{Y}{N_2} \cdot 100$$

X = number of plots of the site being considered on which the species occurs.

N_1 = total number of plots examined in the site in question.

Y = number of plots on all other sites examined on which the species occurs.

N_2 = total number of plots on all sites examined except those in N_1 .

The $\frac{X}{N_1}$ factor is an expression of constancy while the $\frac{Y}{N_2}$ factor expresses lack of fidelity. If a species were a theoretically perfect

indicator species, occurring on one site only and on all stands of that particular site, it would have an $\frac{Y}{N_1}$ factor of 1 and a $\frac{Y}{N_2}$ factor of 0. The indicator value would thus be 100 per cent by the above formula. Conversely, if a species were not present on the sites in question, it would have a constancy factor of 0 and the Indicator Value would also be 0. Thus it is possible to express indicator value numerically on a scale in which 0 represents no practical value and 100 represents the perfect indicator.

The number of stands examined must be sufficient to give reliability to the two factors of the formula. In the case of the number of stands examined for the second factor (sites other than the one being considered), all the communities or sites which are to be distinguished from the site or community in question should be adequately sampled.

Indicator values of all species encountered in the study have been computed and are listed in Tables 4, 5, and 6.

Indicator Value and the t Ratio

As mentioned in a previous section, frequent statistical comparisons have been made between the means of two groups of data, using the standard error of the difference method with pooled standard deviations. The t value obtained by this method can be used to determine the probability of a chance difference between means larger than that actually occurring between the two groups tested.

In Table 7, t values and indicator values are listed for a series of ground cover and tree species covering a range of Indicator Values from 12 to 61. Because the t value under certain conditions may be considered to give statistical evidence of the indicator value of a species,

TABLE VII

INDICATOR VALUES AND t VALUES OF SPECIES FROM A WIDE

RANGE OF INDICATOR VALUE

Arranged in descending order of Indicator Value.

SPECIES	Mean Site Index		Standard Deviation		t Value **	Indica- tor Value	Site Indicated
	X	Y	X	Y			
<i>Arctostaphylos Uva-ursi</i>	52.1	59.7	8.3	5.9	4.02	61	Poor
<i>Rubus</i> (all raspberries)	59.9	53.8	5.8	8.3	3.03	57	Good
<i>Populus tremuloides</i>	61.8	53.1	4.9	7.6	4.92	43	Good
<i>Quercus borealis</i>	61.7	53.9	8.1	3.7	3.93	40	Good
<i>Pinus resinosa</i>	58.4	52.8	5.5	10.1	2.88	38	Medium
<i>Antennaria canadensis</i>	53.9	58.4	8.1	7.3	2.27	31	Poor
<i>Betula papyrifera</i>	61.1	53.8	5.3	7.4	3.53	27	Good
<i>Pinus strobus</i>	59.7	54.3	5.8	8.3	2.67	24	Good
<i>Acer rubrum</i>	60.2	55.2	3.7	11.4	1.45	24	Good
<i>Caultheria procumbens</i>	54.9	57.3	8.5	7.5	0.90	24	Poor
<i>Oryzopsis pungens</i>	53.6	58.0	8.5	7.2	2.21	23	Poor
<i>Populus grandidentata</i>	61.1	55.3	5.5	8.0	3.17	20	Good
<i>Picea glauca</i>	55.4	56.2	5.9	2.8	0.64	19*	Medium
<i>Quercus ellipsoidalis</i>	52.8	56.6	7.0	8.0	1.29	17*	Poor
<i>Abies balsamea</i>	59.0	54.9	6.2	8.4	1.94	15*	Medium
<i>Clintonia borealis</i>	59.2	55.4	7.5	8.4	1.56	15*	Good
<i>Quercus macrocarpa</i> var. <i>olivaefornis</i>	56.2	56.3	7.4	5.3	0.03	12*	Poor

* Species with Indicator Values below 20 are not considered reliable

** Values of t above 2.00 considered significant at the 5 per cent level, while those above 2.66 are significant at the 1 per cent level (highly significant)

X - Plots containing the individual species being tested in column one.

YY - Plots not containing the species being tested.

the comparison has been made between it and Indicator Value as computed previously.

For each of the species listed, an analysis has been made of the difference between the mean site index of the plots containing the species considered and the mean site index of the plots not containing the species. The t value is a reflection of two factors. The first is the difference between the mean site indices of the two groups. The larger this difference, the greater the t value. The second factor is the standard error of the difference of the means. This factor reflects the range of site index for the plots involved. The smaller this range of site variation, the larger the t value. This second factor is in a sense an expression of both constancy and fidelity. An increase in either constancy or fidelity will decrease the standard error of the difference of the means. The first factor, the actual difference between the mean site index values of the two groups, is an additional factor which is not considered in Indicator Value computations. It measures the degree of dissimilarity found to exist between the two groups being compared. As such it is a somewhat extraneous factor which has no particular bearing on the indicator value of a species. In fact, this factor tends to hide indicator relationships which actually exist for indicators of medium site conditions. This is true because the average site index for the plots containing the species considered will approximate the average for all the plots taken and only a small difference will be used in the t value computation.

This condition is demonstrated in Table 7. Red pine, which is a good indicator of medium and good site and which has an Indicator

Value of 36 for medium site, has a value lower than those of bigtooth aspen and paper birch, both of which have lower indicator values. In general, however, on good and poor sites, t values tend to express the same concept as does Indicator Value, and its analysis supplements the computation of Indicator Value. However, in view of the inapplicability of the t value computation to medium site conditions, considerable judgment must be used in applying it in connection with plant indicators.

The Indicator Value, because it is based on pertinent sociological concepts, because it represents on a logical scale of 1 to 100 the relative ability of a species to indicate site conditions, and because it can be applied to a complete range of site conditions including medium site quality, is felt to be a suitable index for quantitative expression of the value of a species as an indicator of site quality.

Minimum Indicator Values

For each species listed it is necessary to decide whether or not its Indicator Value is high enough to justify its use as a practical indicator to site conditions. In this study a more or less arbitrary minimum Indicator Value of 20 has been used. Species having values lower than 20 are not considered to be sufficiently reliable or abundant to be of practical value. The decision was based on several considerations. The writer's own judgment after an intensive study of 65 plots distributed over the complete range of site quality was considered. This was supplemented by the judgment of several individuals considered to have a close working knowledge of jack pine vegetation. Finally, the statistically determined t values were used as a definite guide, with the limitations connected with the use of that ratio considered.

Indicator Values of Individual Ground Cover and Tree Species

Applying a minimum Indicator Value of 20, for reasons as previously discussed, to the species in Tables 4, 5, and 6, those species of apparent reliability can be selected. Of the 19 species selected as reliable indicators of good site conditions, 6 are trees and 13 secondary vegetation. Only 6 species qualify as indicators of medium site. Of these red pine is the only tree. It should be noted, in view of the constancy of red pine on both good and medium sites, that it is really an indicator of site conditions other than poor. Seventeen species including pin cherry as the lone tree species, indicate poor site. The abundance of mosses in this class (*Polytrichum*, *Dicranum*, *Calliergen*) is very pronounced and is indicative of the pioneer aspect of these areas with respect to ecological succession.

STAND COMPOSITION AND SUCCESSIONAL TRENDS

Several points pertaining to the composition of the jack pine stands studied have already been discussed. The pronounced tendency for pure stands to occur on poor sites and for mixed stands to occur on good sites has been analyzed statistically and the data presented in a previous section.

In order to show possible natural combinations of species of trees on this type the chart in Fig. 16 was prepared. This chart shows the constancy with which every possible combination of two or three species was found. In these computations only trees of one inch diameter breast high or larger were considered. In addition, Table 9 lists the more commonly found associates of jack pine in order of their constancy of occurrence.

Figure 16. Constancy of occurrence of species combinations. Figures indicate the percentage of plots on which jack pine is associated with all other individual species and combinations of two species.

	RED PINE	EASTERN WHITE PINE	BALSAM FIR	QUAKING ASPEN	BIGTOOTH ASPEN	PAPER BIRCH	NORTHERN RED OAK	RED MAPLE	NORTHERN BUR OAK	NORTHERN PIN OAK	WHITE SPRUCE	BLACK SPRUCE
JACK PINE	60	32	31	35	15	31	28	15	25	12	12	5
RED PINE		32	26	28	14	28	23	14	15	8	12	5
EASTERN WHITE PINE			20	17	9	20	15	11	15	2	11	5
BALSAM FIR				12	6	15	6	6	0	2	8	5
QUAKING ASPEN					12	18	18	9	12	5	3	3
BIGTOOTH ASPEN						8	12	5	8	3	3	0
PAPER BIRCH							15	11	8	3	6	5
NORTHERN RED OAK								11	9	0	5	0
RED MAPLE									5	0	0	0
NORTHERN BUR OAK										11	3	0
NORTHERN PIN OAK											0	0
WHITE SPRUCE												0

TABLE 9

RELATIVE CONSTANCY OF OCCURRENCE OF TREE
SPECIES COMMONLY FOUND ASSOCIATED WITH
JACK PINE

Species	Constancy Per cent *
Red pine	60
Cucking aspen	35
Eastern white pine	32
Balsam fir	31
Paper birch	31
Northern red oak	28
Northern bur oak	25
Bigtooth aspen	15
Red maple	15
Northern pin oak	12
White spruce	12
Black spruce	5

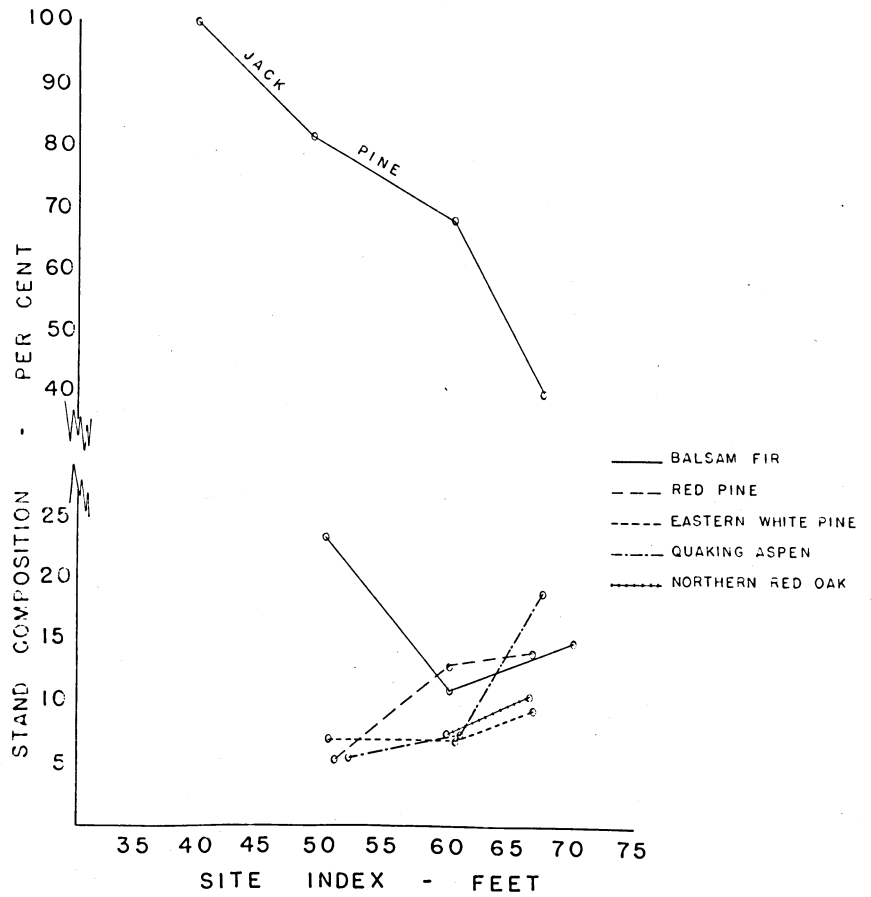
* Constancy
per cent = $\frac{\text{number of plots on which species is found}}{\text{total number of plots examined}} \cdot 100$

The combination of jack pine with balsam fir and paper birch occurs on 20 per cent of the plots while the combination of jack pine with balsam fir and quaking aspen occurs on only 17 per cent of the plots. Although the difference between these two figures is small, it assumes some significance because the total number of plots on which aspen occurs is considerably greater than the total number of plots on which birch occurs. This comparison indicates a tendency for balsam and birch to be somewhat associated with the same site conditions. This is in agreement with the inclusion of paper birch as a characteristic associate of balsam fir and spruce in the coniferous climax as noted by Cooper (20) and Weaver and Clements (129).

Fig. 17 portrays stand composition graphically by means of percentage of total stand curves for all the chief associated species found. These curves are based on the total number of individuals including reproduction one foot high or larger.

The jack pine curve in this figure shows the previously mentioned trend toward mixed stands on good sites. This trend is a result of two main factors; the inability of many of the associated tree species to live on the poor sites, and the inability of jack pine to compete with the more tolerant species on the better sites. Examinations of fire scars and relic trees on many plots indicate that the previous forest type on many of the better sites was a mixture containing red pine, white pine and aspen. In fact, the present species found on the plots is a fairly good indication of what species were present before the fire which in most cases established the jack pine. This is true because of all the common associates of the jack pine, the aspen is the only tree which has

Figure 17. Variations in stand composition with changes in site quality as determined by site index. Curves based on percentage of stand of the important jack pine associates.



seed light enough to be carried long distances and thus a fairly close seed source must have been present for all species. The relative ages of the jack pine and the other tree species can often be used to determine the stand history.

The trend of the curve for balsam fir is distinctly different from that of all other associated species. This curve indicates that balsam is the most important species associated with jack pine on the sites of moderate site quality. On the better sites aspen and the other pines become increasingly abundant. This is further evidence that a balsam-spruce-birch line of succession develops on jack pine sites of only fair quality if moisture relationships are good. Another line of succession represented by red pine, white pine, aspen, and miscellaneous hardwoods develops on the better jack pine sites only.

THE AGGRESSIVENESS INDEX AND SUCCESSIONAL TRENDS

Intelligent silvicultural management of forests requires a knowledge of the natural successional tendencies of the composite stands. For practical management purposes this involves a knowledge of the tree species which are in the process of invading each existing type or which will do so upon maturity of the present type. This is essentially the measurement of the aggressiveness of the various species under conditions of the present stage of succession.

Aggressiveness, by concept, refers to the relative ability of a species to invade an area and to reproduce itself thereupon. Since no numerical measure of aggressiveness could be found in the literature which could be applied to forest tree species, an Aggressiveness Index

was devised which it is felt is superior to the commonly used "ocular estimate". The fundamental factors affecting aggressiveness include characteristics related to seed production, distribution and germination, seedling growth and development, vigor and competitive ability, and the ability of the species to reproduce itself in the new habitat.

These factors, however important they undoubtedly are, are difficult to measure and evaluate in connection with their total effect on aggressiveness. A better approach lies in measurements of the actual aggression rate of a species under the conditions of habitat being studied. Two measurements are of paramount importance in this connection; the percentage of the total number of plots which the species has invaded (constancy), and the relative abundance of the species on the invaded plots. The constancy and abundance factors were considered to be of equal weight. Since both perfect constancy and complete abundance as found in pure stands are expressed as 1 or 100 per cent, a gradation of values from 0 to 100 percent can be obtained by the following computation:

$$\text{Aggressiveness Index} = \frac{\frac{X}{N_1} + \frac{Y}{N_2}}{2} \cdot 100$$

where X = total number of plots on which the species occurs.

N_1 = total number of plots taken.

Y = total number of individuals of the species in question on all plots.

N_2 = total number of individuals of all species on all plots.

Since numbers of individuals enter into this index, species to be compared must be of the same life form. In fact, the Index has been

devised primarily for comparing tree species, and has not been applied to secondary vegetation in this study. Index values have been computed for each site class for the seven most frequent associates of jack pine. These have been summarized in Table 10. The most aggressive species by this measure on both medium and good sites is red pine with Index values of 42 per cent and 35 per cent respectively. On poor sites, no species exhibits any appreciable aggressiveness except northern pin oak which has a 14 per cent Index. On medium sites red pine is followed by balsam fir, paper birch, eastern white pine, quaking aspen, northern red oak and northern pin oak in order of decreasing aggressiveness. On good sites red pine is followed by quaking aspen, eastern white pine, northern red oak, paper birch, balsam fir, and northern pin oak.

The data presented in the foregoing section on aggressiveness and in Table 10 furnish a guide to the discovery of any successional tendencies on the areas studied. In general, it may be said that few if any successional changes are evident on poor sites. The presence of a small amount of northern pin oak does not necessarily indicate a forward successional step. The northern pin oak occupies the same relatively low place in the ecological succession in the deciduous area as the jack pine does in the coniferous area. It is probable that the aggressiveness of the northern pin oak on poor sites is a measure of the invasion by that species of the jack pine in its southern limits where it merges with the deciduous vegetation. On such stands, repeated fires tend to favor the oak because of its sprouting ability at the expense of the jack pine. All evidence points to the continuation of jack pine in pure stands or mixed with northern pin oak on the poorest sites as an edaphic subclinax.

TABLE 10

AGGRESSIVENESS INDEX VALUES FOR THE TREE
 SPECIES COMMONLY ASSOCIATED
 WITH JACK PINE

Species	Site Class		
	Poor	Medium	Good
	Aggressiveness Index -Per Cent		
Red pine	4.5	42.2	35.3
Eastern white pine	0.0	17.4	26.5
Balsam fir	0.0	22.8	16.8
Quaking aspen	0.0	13.2	34.4
Paper birch	0.0	17.7	23.9
Northern red oak	0.0	12.0	26.1
Northern pin oak	14.3	6.0	3.7

On medium sites strong successional forces appear to be in operation. A great many areas of this site are being invaded successfully by red pine and balsam fir. White pine and paper birch are also coming in on such sites in fair numbers. All mixtures of these species have been noted, and have also been reported by Kell (52) in Itasca Park. However, some tendency for balsam fir and birch to be associated together and to be on wetter sites was noticed in the field, and that combination is also suggested by the chart in Fig. 16. It is possible that two different but not entirely distinct lines of succession begin here, one leading to a pine-hardwood mixture, and the other going to balsam fir, spruce, and paper birch.

On the good sites balsam drops from second place to sixth in aggressiveness. This would indicate one of two things. Either the balsam could not compete with the added aggressiveness of the hardwoods on the good sites or else there was some factor in the medium sites which favored it particularly. It is difficult to believe the first alternative in view of the tolerance of the balsam and its demonstrated ability to come in as an understory to any of the species listed. The writer has felt in the field examinations of the plots that balsam is most aggressive on soils of rather coarse texture but with better than average availability of water. On such sites it is probable that balsam with its usual paper birch and spruce mixture is at least an edaphic subclimax. A second line of succession definitely goes to a pine-hardwood mixture with white pine more abundant than red pine on the heavier soils. No evidence concerning a possible climatic climax was collected.

Successional trends which have been discussed refer to natural processes. Artificial management, of course, introduces factors not considered within the scope of this study. No data were collected upon

which to base conclusions as to succession in seriously understocked stands. The role of brush species, particularly hazel, is an important one in this connection, and should be subjected to intensive study. The effects of cutting practices and the use of scarification methods in obtaining reproduction have been reported by Eyre and LeBaron (24).

ANALYSIS OF THE SOILS

Results of the preliminary tests of soil texture in relation to site index using the Bouyoucos hydrometer method have been reported in the preliminary section. The following data are based on soil samples from forty nine different plots representing the complete range of jack pine site quality. Every figure given is an average of two laboratory analyses on each of four samples on a given plot. Each point plotted on the diagrams in Figures 18, 19, 20, and 21 thus represents an average of eight laboratory tests and four soil samples.

MOISTURE EQUIVALENT AND SITE INDEX

Determinations of moisture equivalents by the standard centrifuge method were made by the writer on samples from the B and C soil horizons. Results are plotted in Figures 18 and 19 together with site index values for the respective plots. In addition, correlational analyses have been run on the two sets of data to determine whether moisture equivalent values for the B and C horizons are correlated with site index. The results of these analyses are summarized in Table 11. The coefficient of correlation, or r value, between the moisture equivalent of the B horizon and the site index, is not large enough to be considered significant.

Figure 18. Correlation of site index with moisture equivalent of the B horizon.

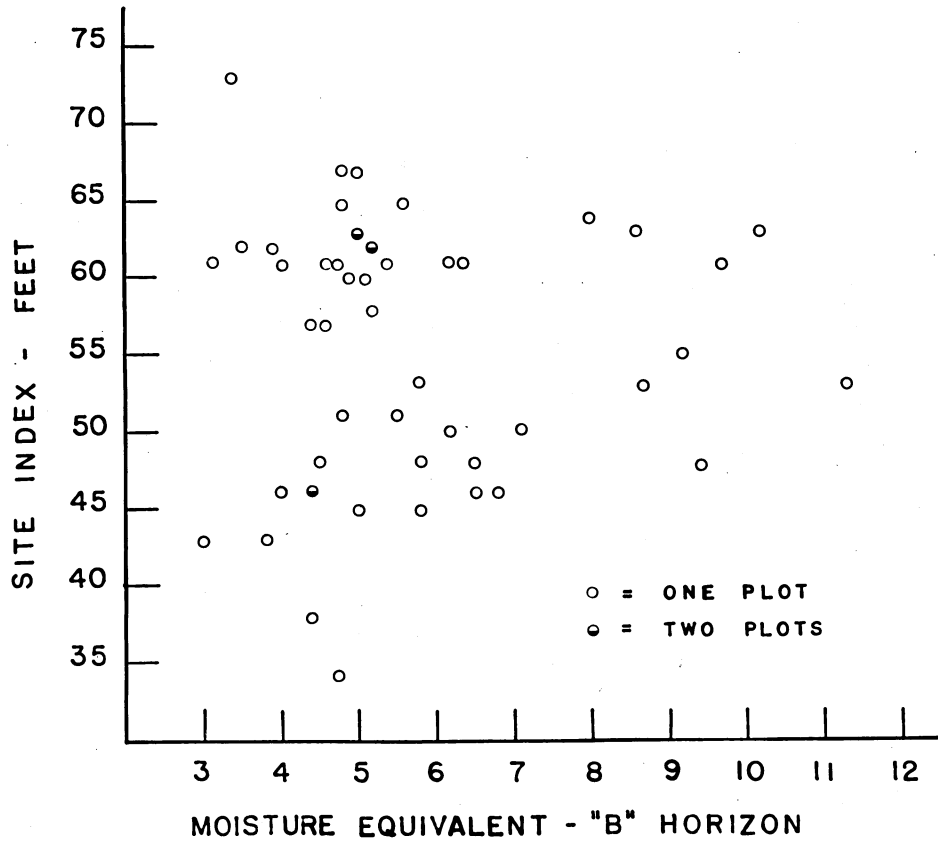


Figure 19. Scatter diagram showing correlation between site index (vertical axis) and moisture equivalent of the C horizon. See Table 11 for r values.

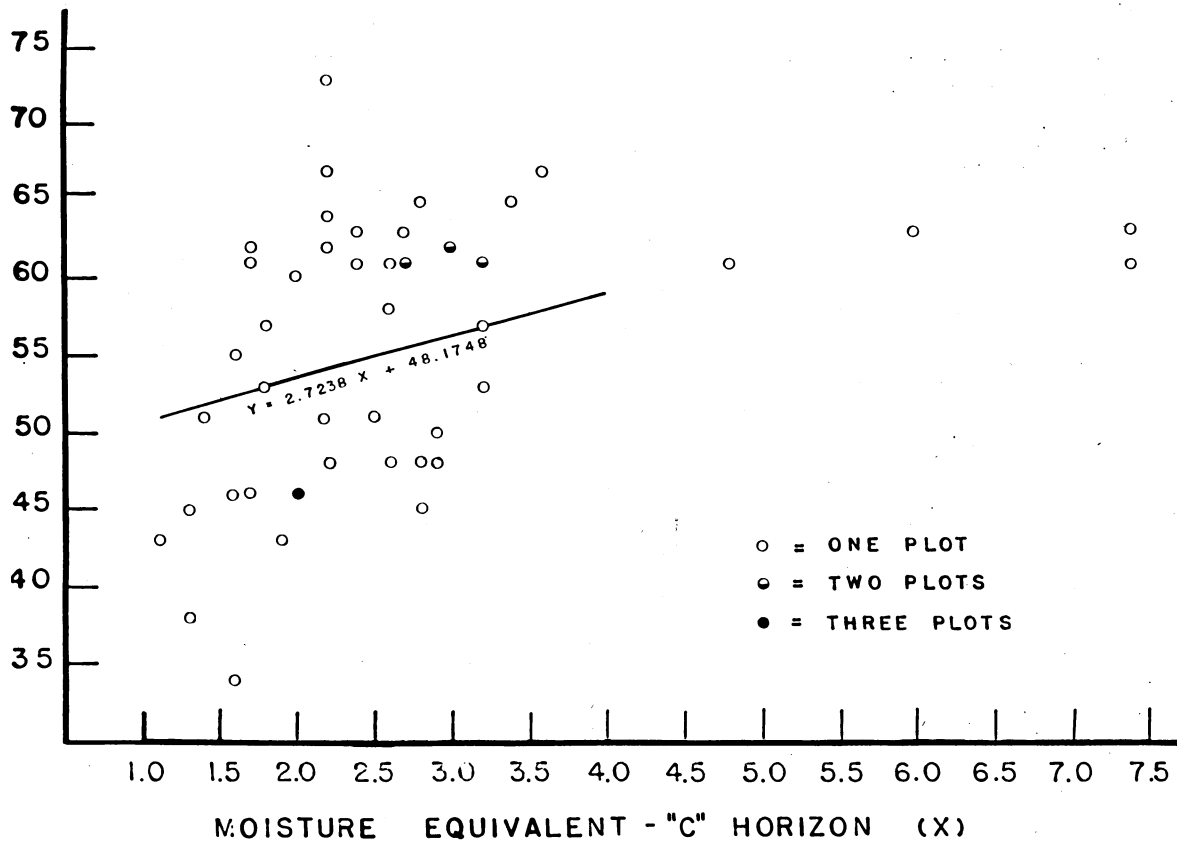


Figure 20. Scatter diagram showing lack of correlation between site index and total nitrogen content of the B horizon. See Table 11 for r values.

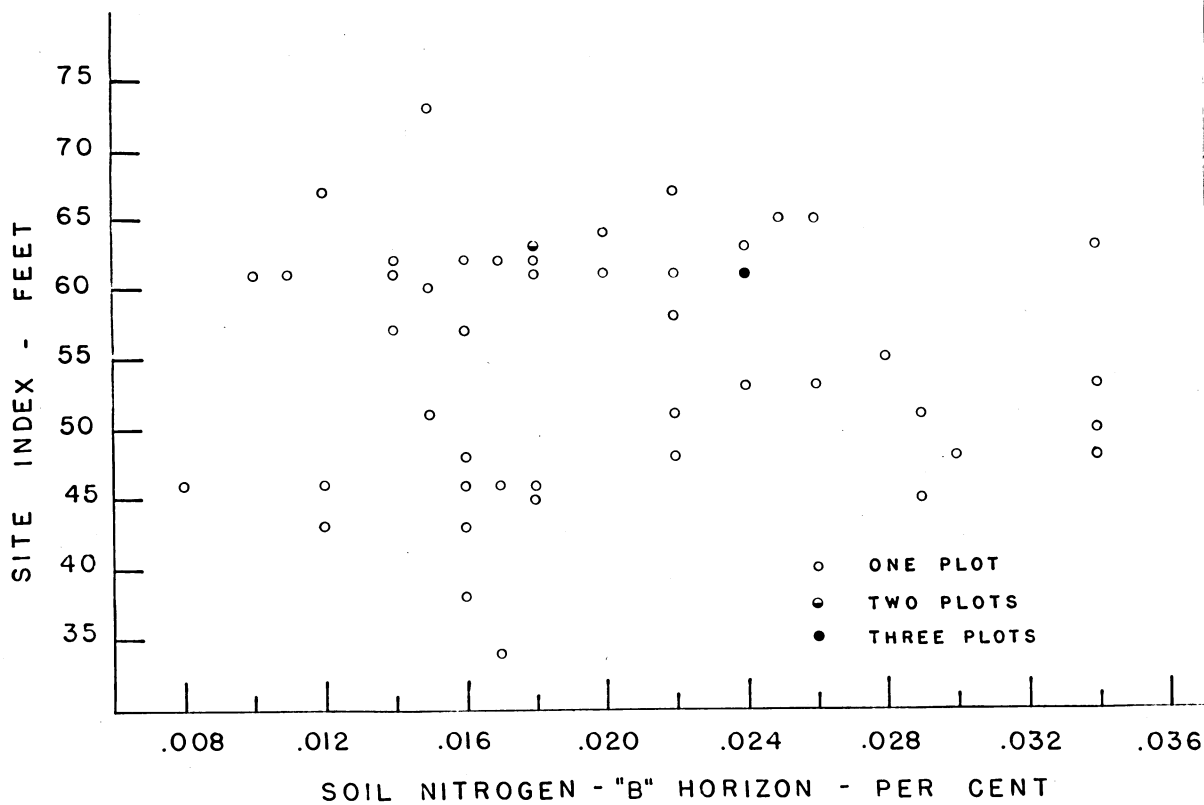
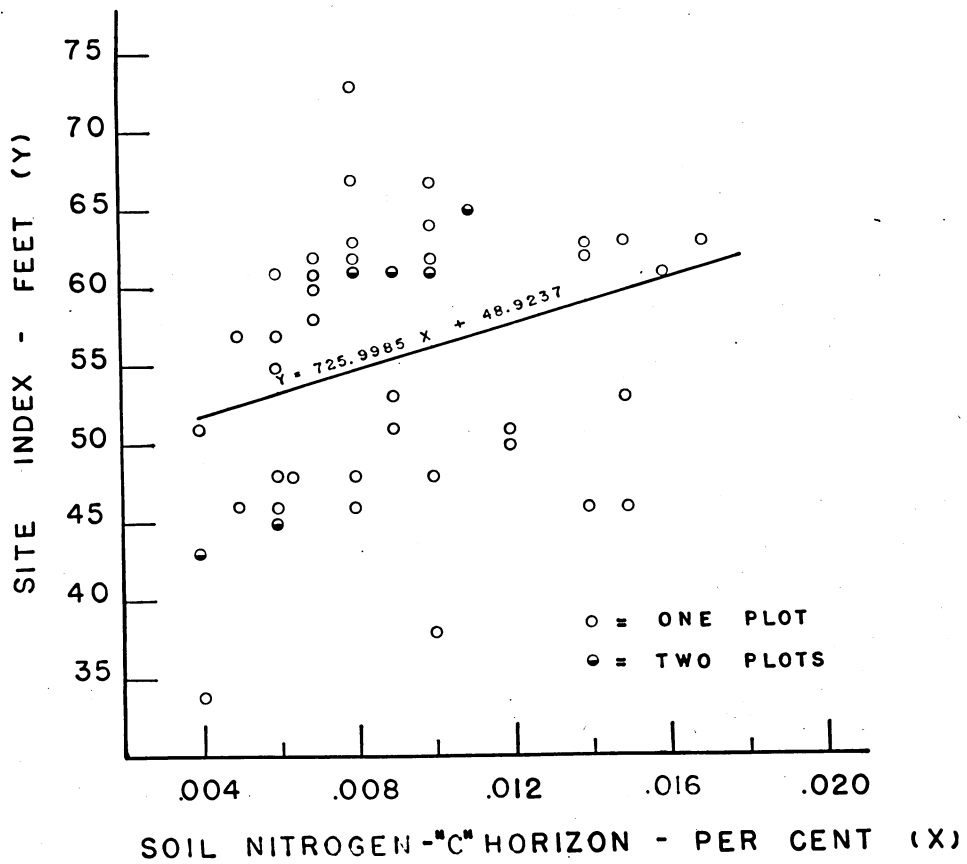


Figure 21. Correlation of site index with total nitrogen content of the C horizon.



On the other hand, the coefficient of correlation between the moisture equivalent of the C horizon and the site index is significant at the one per cent level (highly significant). The regression line expressing the relationship between the two factors has also been computed and is drawn on the appropriate diagram.

SOIL NITROGEN AND SITE INDEX

Determinations of total soil nitrogen were made by the Soils Division of the University of Minnesota. The values obtained have been plotted together with site index values for the corresponding plots and appear in Figures 20 and 21. Correlational analyses have also been made and the essential data listed in Table 11. It is evident that the coefficient of correlation between total soil nitrogen of the E horizon and site index is too small to be considered significant. The coefficient of correlation between total soil nitrogen of the C horizon and site index is significant at the five per cent level (significant). The regression line expressing this relationship has been drawn in Fig. 21.

SOIL NITROGEN AND MOISTURE EQUIVALENT RELATIONSHIPS

The moisture equivalent is generally accepted as a good index of soil texture. This is particularly true in sandy soils of the type encountered in this study where the organic content is very low. The high coefficient of correlation between moisture equivalent of the C horizon and site index indicates that the soil texture of that horizon has considerable effect on the growth rate of jack pine.

TABLE 11

SUMMARY OF DATA OBTAINED FROM CORRELATIONAL ANALYSES
OF THE SOIL FACTORS

Correlations tested	Number of plots	Coefficient of correlation
Total nitrogen and moisture equivalent of C horizon	49	0.479 *
Moisture equivalent and site index of C horizon	49	0.413 *
Total nitrogen and site index of C horizon	49	0.296 **
Moisture equivalent and site index of B horizon	49	0.026 ***
Total nitrogen and site index of B horizon	49	0.002 ***

* highly significant ($r = 0.354$ at the 1 per cent level of significance)

** significant ($r = 0.273$ at the 5 per cent level of significance)

*** not significant

Texture is the most important soil factor affecting soil moisture and its availability for plant growth. On sandy upland soils, an increase in the proportion of fine material is generally associated with better soil moisture conditions. It is felt that the data presented indicate the primary importance of soil moisture to site quality of jack pine on the range of sandy soils encountered in northern Minnesota.

It should be noted, however, that soils of fine texture generally are higher in chemical nutrients than are soils of coarse texture. In the absence of a complete analysis of the physical and chemical properties of the soil, it is difficult to determine whether the increase in site quality accompanying an increased proportion of fine material in the soil is the result of improved moisture relations or of the increased nutrient content. The data indicate quite definitely, however, that moisture relationships are of greater relative importance to site than is the total nitrogen content of the soil. This is evident from the definitely higher coefficient of correlation ($r = 0.413$) for the texture characteristic as compared to a coefficient of correlation ($r = 0.296$) for the nitrogen characteristic which is barely significant.

It is also possible that the apparent association of soil nitrogen content with site quality is a result of the fact that nitrogen content is somewhat of a measure of soil texture and thus of soil moisture relationships. High soil nitrogen content is generally associated with fineness of soil texture. In order to test this possibility, an analysis was made of the correlation between total nitrogen and moisture equivalent. As indicated in Table 11, a highly significant coefficient of correlation ($r = 0.479$) was found between total soil nitrogen and moisture equivalent.

The high coefficient of correlation between moisture equivalent and site index and the rather low coefficient of correlation between total nitrogen and site index, coupled with the high coefficient of correlation between total nitrogen and moisture equivalent would seem to indicate:

1. That moisture relationships are of relatively greater importance to site quality of jack pine than are nitrogen contents.
2. That nitrogen content is important primarily because it is an indirect indicator of fineness of texture and therefore of moisture relationships.

The relatively greater importance of the texture of the C horizon than that of the B horizon as indicated in the correlational analysis supports field observations as to the character of droughty soils. It is generally recognized by farmers and foresters that areas which have coarse subsoil horizons are definitely droughty in this region unless the ground water level is very high. On the other hand, areas with finer textured subsoils have better moisture relationships even though the surface soil may be of a sandy nature. Thus the texture of the C horizon is of greater importance than that of the B horizon although most of the feeding roots of jack pine are found in the upper foot of soil. (22) (21)

SUMMARY AND CONCLUSIONS

During the summers of 1937, 1938, and 1939, sixty five plots covering the complete range of site quality of jack pine in Minnesota were located and examined.

Data collected on these plots are representative of conditions prevailing in the jack pine type in northern Minnesota except for the extreme northeastern part of the state. In this area a generally shallow surface soil over underlying rock formations and somewhat different climatic conditions exist, which make general ecological relationships a problem distinct from that in the area studied.

Data were collected relative to site factors on the plots with special attention to site index, stand composition, plant indicators, and texture and nitrogen content of the B and C soil horizons.

All data, including the vegetational, were described quantitatively and evaluated by standard statistical procedures wherever possible.

Two new index values designed for the quantitative description of the vegetation in forest communities were developed and tested by application to the plot data.

The major conclusions reached apply within the limits of the data to stocking conditions of at least fifty per cent of normality. Stands seriously under stocked or considerably over one hundred per cent of normal stocking may have characteristics somewhat different from those studied.

The following major conclusions have been reached:

- (1) Various characteristics of the jack pine vegetation are

reliable indicators of site quality as measured by dominant height and age relationships according to the standard site index method.

(2) The presence of certain tree species is the most reliable as well as the most practical of all the indicators tested in predicting site index classes. Six species; quaking aspen, northern red oak, paper birch, bigtooth aspen, red pine, and eastern white pine have t values above that required at the one per cent level of significance. The individual t values were obtained by testing the significance of the difference between the mean site index value of the plots containing the species in question and the mean site index value of the plots not containing the species.

(3) Five of the tree species are indicators of the good site class, while red pine is considered an indicator of medium or good site quality.

(4) The presence of combinations of indicator species increases the reliability with which site quality may be predicted.

(5) Pure stands of jack pine are associated with poor site quality and mixed stands with better site quality. However, in areas where coniferous and deciduous forests merge, the northern pin oak is often associated with jack pine on poor sites.

(6) There is a statistically significant association between the degree of stand mixture and the site quality. As the degree of stand mixture increases, the site quality indicated also increases.

(7) An Indicator Value Index was devised by which a numerical evaluation could be made of the value of individual species in predicting site quality. The index is computed by subtracting a lack of fidelity

factor from a constancy factor and expressing the result as a per cent on a scale from 0, representing no indicator value, to 100, representing a theoretically perfect indicator.

(8) Considering an Indicator Value of 20 as the minimum necessary for reliability, a total of 42 species of trees and secondary vegetation have practical value in predicting site quality. Of these, 19 are indicators of good site, 6 indicate medium, and 17 are indicators of poor site.

(9) An Aggressiveness Index was devised for comparing tree species in respect to their ability to invade and establish themselves on an area. This index is an average of the constancy and abundance factors expressed as a per cent over a scale of from 0 to 100.

(10) The most aggressive species on both medium and good jack pine sites is red pine with an Aggressiveness Index of 42 per cent and 35 per cent respectively. On medium sites red pine is followed by balsam fir, paper birch, eastern white pine, quaking aspen, northern red oak, and northern pin oak in order of decreasing aggressiveness. On good sites red pine is followed by quaking aspen, eastern white pine, northern red oak, paper birch, balsam fir, and northern pin oak. On poor sites no species exhibits any aggressiveness except northern pin oak which has a low index value.

(11) Using the Aggressiveness Index and stand composition curves as guides, no evidence of successional development is evident on the poor sites.

(12) On medium sites strong successional forces are in operation. One line of succession tends toward a pine-hardwood mixture and another

toward a balsam fir-spruce-paper birch mixture.

(13) On good sites the pine-hardwood line of succession is much more evident than is the balsam fir-spruce-birch.

(14) Texture of the C horizon as measured by the moisture equivalent is significantly correlated with site index.

(15) Texture and total nitrogen content of the B horizon, considered separately, are not reliable indicators of site quality of jack pine.

(16) Within the range of sandy soils examined, total nitrogen content of the soil varies directly with soil texture as measured by moisture equivalent.

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