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FACTORS CONTROLLING FOREST SUCCESSIONS AT
LAKE ITASCA, MINNESOTA.

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FACTORS CONTROLLING FOREST SUCCESSIONS

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PART 1.

Introduction.

From the standpoint of vegetation Minnesota may be divided into two great regions by a line running from the northwestern to very nearly the southeastern corner of the state. Of these the prairie occupies the southwestern and the forest the northeastern half. The coniferous forests are the continuation of the northern coniferous forest formation and the deciduous are the extension of the central hard-woods, although the number of species of trees of the latter diminishes steadily from south-east to north-west. The distribution of these forests and prairies may be indicated by the accompanying map (figure 1).

Factors controlling the distribution of
the three great climax formations.

(a) Climatic factors.

It has been widely recognized that the main control of the distribution of the great climax formation of prairie, coniferous and deciduous forest has been determined by climate. Among the efficient climatic factors low precipitation combined with high evaporating power of the air is the limiting one in the distribution of prairies. Schimper (1) has pointed out that the prairie district of

the United States of North America is determined by the amount and the seasonal distribution of the precipitation. The dry winter, the uniformly moist early summer, and the relatively scanty precipitation are typical of grassland climates. Thus, the distribution of prairie and forest in Minnesota is, evidently, determined by the precipitation not merely because of its small amount but also by the character of its seasonal distribution. The accompanying chart (figure 2) given by Purcell (2) indicates a close correlation between the geographic distribution of the precipitation and the tension line of the prairie and forest.

Comparing figures No. 1 and 2, one can readily see that the distribution of broad-leaved and coniferous forests in Minnesota, unlike that of the prairie and forest, is not determined by precipitation but by other climatic factor or factors, among which temperature is, undoubtedly, the most important one. The geographic distribution of any plant at its zero point, depends upon its ability to reproduce itself. The survival and growth of seedlings and the consequent advance or retrogression of the particular forest type is determined by two main sets of factors. These are:

(1) external or environmental, principally temperature, which is responsible for the early and late killing frost and for determining the length of the growing season, and,

(2) the hereditary character of the different individuals, which gives special ability to withstand hard environmental conditions.

Most of the conifers, with a thick cell sap and various xeromorphic structures, usually withstand much lower temperature than do most of the broad-leaved trees. This would naturally divide the forests of the temperate zones into two great belts; a cold temperate belt, with a very cold winter, characterized by the conifers, and a warm temperate belt, with rather mild winter, characterized by the broad-leaved trees. The border line between the two belts, ~~separating the coniferous~~, corresponds to the isothermal line of approximately 43° F or 6° C ~~for the average month~~. However, this line is by no means sharp, a broad or narrow belt of transition being always found. The transitional line between these two great types of forest in Minnesota runs along about the 45th parallel of north latitude, corresponding to the isothermal line of the mean annual temperature of about 42° F, and with the line of ^{an} average number of days of the crop growing season of about 130 days. (see figure 3)

(b) Edaphic Factors.

It is commonly recognized that the distribution of the great plant communities or major divisions of vegetation is not governed by edaphic factors. This general statement is especially well demonstrated by the distribution of soil and ^{of} vegetational types in Minnesota. Broadly speaking,

in Minnesota there are only three principal types of vegetation dividing the state into three portions: the west, the prairie type; the north-east, the coniferous forest type; and the south-east, the hardwood forest type, but the soil types are extremely numerous in different part of the state. These soils are mostly glacial drifts, and consequently are extremely variable in nature and composition dependent upon the kind of rock formation over which the ice-sheet passed and the difference in localities over which the drifts are deposited. The Minnesota Geological Survey gives nine principal surface soil formations (see figure 4), each of them containing a variety of soil types. Thus, if we compare figure 1, the distribution of vegetation in Minnesota, and the figure 4, the surface soil formations, we find such a lack of agreement that we may safely conclude that edaphic factors do not determine the extent of the great formation types of its vegetation.

(c) Biotic factors.

Among the biotic factors we usually consider such plant and animal agencies as affect vegetation. The former comprise parasitic and saprophytic plants as well as some of the lower forms of vegetation, such as algae, liverworts, mosses, etc. Their relation to the major plants is either detrimental, beneficial, or symbiotic. Their effect upon plant succession and upon the distribution of the larger

plant communities is very slight. The latter group involves animals, insects, and human influences. The effect of this group on plant succession is usually very marked, and is seen in such changes as are due to grazing, insect invasions, cutting or burning forests, etc., all of which may occur in any place at an time but are generally confined to rather limited areas. Thus, in the more important changes of a vegetation type these factors are of very little significance, however, attention should be called to the fact that repeated burning along the tension line between two types of vegetation will cause a continuous retrogression in the more advanced successional type. The fact can be very well illustrated by conditions in the Western Minnesota, where the retreat of the forest and the extension of the prairie type eastward are, probably, due to repeatedly burning of the forests by fires set by Indians to kill bugs or to convert forest lands into pastures. Although this may not be able to change natural types in the main, a constant destruction of forest cover will lower the water table, increase the evaporating power of the air, and bring about more xerophytic conditions and this will be sufficient to shift the natural border line a considerable distance.

Conclusion.

To sum up the previous discussions it may be said that the distribution of the larger plant communities

is controlled by climatic factors, among which the character and the amount of precipitation determine the prairie and forest type and the temperature determines the coniferous and hardwood forest formations.

As stated previously the border line between the coniferous and hardwood forest is by no means sharp but a transitional belt of varying width is usually present. Both the conifers and hardwoods within this transitional belt are supposed to have an equal opportunity in distribution and development,^{for} this transitional belt contains the "zero point" of distribution for these two types of forest. The purpose of this study is, therefore, an attempt to discover which factors play the most important role in forest successions within this critical transitional belt.

Ecological Studies within a transitional
belt between Coniferous and Deciduous
Forest.

Location and Physiographic features.

Location- Lake Itasca is situated about 25 miles north of Park Rapids, in the southern tip of Clearwater County, Minnesota, in latitude 47° N, long. 95° W. The lake basin comprises an area of 35 square miles. Lake Itasca is known as the headwaters of the mighty Mississippi and the basin was hence created as a state park to preserve the source of the river. At ^{the} present time it is, probably, the only large tract of virgin timber left in Minnesota and in it this study was made.

Topography - The region is a glacial drift plain dissected by water. The general topographic feature is , therefore, a sandy plain with numerous moranic knolls and ridges spotted by more than ~~a thousand~~ ^{hundred} lakes and swampy basins. The highest knoll of the region is 200 feet above the lake surface and the general relief is about 120 feet. (figure 5).

Geological and soil conditions - The entire region is covered by glacial drift, probably, hundreds of feet in depth laid down at the border of an ice sheet. No rock outcrop occurs in the region, but large boulders laid down by ice are found here and there. The soils are extremely vari-

able ranging from those composed of very stony and sandy material to heavy clay with few stones. The soil types are thus arranged in such a complicated manner that small areas of heavy clay soil are often found within sterile sandy plains. This intermixing is, of course, in harmony with the general character of glacial drifts in other regions. The glacial deposits also vary with the kind of country over which the ice passed. Thus, in the northeastern part of the state the drifts are composed mostly of the volcanic and hard crystalline rocks of the region carried southward, while in the western and southern parts of the state the drifts are mostly of clay with imbedded limestone pebbles. All the calcareous materials were gathered by the ice as it passed across the shale and limestone country of southern Minnesota and these deposited in south western part of Minnesota ^{are} all known as the gray drift. Lake Itasca being situated in a position to receive both types of the drift has probably more varieties of soil than any other region.

In places where the soils are rather heavy and able to support dense growth of vegetation a layer of organic soil of five or six inches thick has been formed. In places where outwashes occurred the soil is sterile and unable to support a thrifty growth, and as a consequence very little organic soil is formed. Such areas are generally occupied by Jack ^P Pines or any other pioneer xerophilous vegetation.

The swampy basins and lake shores receive yearly deposits of vegetable matter, hence the humus accumulation on these areas is very thick and the soil is usually rich and fertile but generally very poorly drained, consequently such areas are usually occupied by black spruce, tamarack, or other xerophilous vegetation.

Climate - Minnesota has a mid-continental climate characterized by a rather warm summer and a cold winter. There is no prevailing wind and no high mountain ranges to chill the clouds and cause local convections. However, a large ^{pro-}portion of the low-presure areas which move across the United States from west to east touches Minnesota. These low-presure areas are preceded by southerly winds and higher temperature and followed by notherly winds and low temperature and are usually accompanied by cloudy weather and precipitation.

Temperature- The average ^{mean} annual temperature of Lake Itasca shown by a continuous records of seven years is 38° F. The average temperature for January is 3° F and that for July 67° F. The highest temperature is 100° F and the lowest-51° F. The average date of the last killing frost is May 25th, and that of first killing frost September 15. The number of frostless growing days of the average crop-growing season is 110 days.

Precipitation - The mean annual precipitation of

Lake Itasca ^{as} or shown by 25-year's records is 25.66 inches. Probably more than 50% on the total annual rainfall falls during the summer season, thus the winter season is usually dry. ^{of} If the mean annual snowfall of Lake Itasca there is no record but that of Park Rapids is 46.2 inches, which would probably be not far from what we might expect at the Lake Itasca region. A rather detailed summation of the climatic components at Lake Itasca for the summer season of 1922 may help us in understanding the climatic conditions during the growing season.

Month	Total Rainfall inches	Maximum Temperature	Minimum Temp.	Number of days		
				Cloudy	P. Cloudy	Clear
June.	3.19	94° F.	37° F.	21	6	3
July.	2.56	92° F.	41° F.	16	8	7
August.	3.10	101° F.	36° F.	21	5	5

Forest conditions - Probably two centuries ago the whole region was covered by white and red pine forest. The evidence of this statement is to be found in the remnants of dead stumps and logs left here and there. Upon the settlement of human beings within the region fires, the ax, and the saw began to destroy the virgin forests. This continued until 1891 when the region was created a state park and some of the virgin pines have, thus, been preserved. In areas in which the virgin pines were destroyed either by fire or by ^{the} ax a secondary growth of a mixture of Jack and red pine together

with a number of deciduous species such as white birch (*Betula alba* var. *papyrifera*), aspen (*Populus tremuloides*), sugar maple (*Acer saccharum*), red oak (*Quercus rubra*), bur oak (*Q. macrocarpa*), etc. were developed. The further development of these mixed stands depends upon the kind of soil; hardwoods usually occupy the heavier and more fertile soil and the conifers the poorer sandy soils.

Among the virgin forests the following associations may be classified:

- (a) pure red pine (*Pinus resinosa*) type, which predominates the region,
- (b) pure Jack pine (*Pinus Banksiana*) type, which abounds in sterile sandy areas,
- (c) hardwood and white pine (*Acer-Pinus Strobus*) type, which usually occupies fertile and heavy clay soil and in limited areas,
- (d) fir and spruce (*Abies-Picea*) type, which usually occupies the swampy basins or any depression where the moisture supply is abundant, and
- (e) tamarack or cedar (*Marix* or *Thuja*) type, usually found in the swamps or bogs.

Among the second growths five types may be classified, viz.

- (a) pure Jack pine type, mostly on sterile sandy soil,

- (b) pure aspen type, mostly on very fertile soil,
- (c) pure white birch type, usually succeeding the aspen stage,
- (d) hardwood mixtures, composed of maples, oaks, aspens, birches, elms, and others, which generally occupy very rich soils, and
- (e) pine-hardwood mixture composed chiefly of Jack pine, red pine, aspen and birch.

Beside these five types there is also a birch-fir-spruce type, which usually occupies lake shores or any depressions where soil moisture is abundant. On account of the region being full of lakes this type is, therefore, predominating the region. In most places where the virgin red pines are standing this type is developing as an understory. A cross section of such a forest will show three distinct stories, namely: the old pines with open canopy the first, the white birch the second, and the thicket of balsam fir and spruce the third. The age of the virgin trees is 150-200 years and that of the second growths about 30. (see figure 6)

PART II

FOREST SUCCESSIONS.

To study the forest successions of any region three periods must be considered. (a) The past successions - how the forests ^{have} been developed; (b) The present - how the forests are developing, and (c) ^{The future -} What the forests are going to be. The last one would naturally lead to a conclusion in the climax development of the region. In order to trace the past successions it is necessary to begin with initial causes from which the forests had been developed. It has been customary to classify the causes into primary and secondary series; the former designates that succession which begins from denudation of either bare rock surface, sterile soil surface, or clear water edge; and the latter indicates that successions may take place in any habitat where the existing vegetations have been disturbed by external factors such as burning, cutting, insect outbreaks, etc. For the natural classification of primary successions Cooper (3) first introduced the two terms - Xerarch for land or ^xxerophytic habitat and Hydrarch for water or hydrophytic habitat. For the sake of clearness these two terms are used in the following classification;

I. Primary successions.

(a) Hydrarch.

1. Bog succession.

2. Swamp succession.

3. Lakeshore succession.

(b) Xerarch.

1. Sterile sand or glacial drifts succession.

II. Secondary successions

(a) Lumbering succession.

(b) Burn succession.

The present paper deals with the Forest Successions, therefore, for the sake of concreteness, no discussion of the pre-forest stages of the hydrarch succession is attempted, however, a brief statement to show such successional relationships seems to be desirable.

(a) Hydrarch Succession - Hydrarch successions in northern Minnesota have been admirably studied by Bergman and Stallard (4). The sequential development of hydrophytic successions from Chara-Philetria Associes through Castalia-Nymphaea, Scirpus-Zizania, Carex, Chamaedaphne-Andromeda, as given by Bergman, leading to the Larix-Picea Associes is applicable to the situation of this region, however, that through Larix-Picea and Abies-Betula leading to Pinus Association, which Bergman called climax forest, seems hardly to apply to the conditions of the Lake Itasca region. The keynote of determining the climax forest is not merely judging the present predominance of a certain species but a spontaneous maintenance of its own race for future generations. Pines in

this region are not only unable to invade *Abies-Betula* Associates and reproduce themselves but are being invaded by the latter (see figure 6). The intolerance of shade by pines comparing with *Abies* and the thickets of growths of the latter make it impossible for pines to culminate the successions in this particular region. A more detailed explanation on this point will be given in succeeding discussions.

(b) Xerarch Succession: Classification of stages of Xerarch succession (see figure 7)

A. Past Successions.

1. Denudation stage.
2. Herbaceous stage.
3. Shrubby stage.
4. Pioneer forest tree stage.
5. a/ Mixture of conifers and hardwoods stage.
b/ Segregation of Jack pine type.
6. Segregation of *Pinus resinosa* and hardwood-
Pinus strobus.

B. Present Successions.

7. a/ Edaphic climax stage of *Pinus banksiana*.
b/ Transformation from *Pinus banksiana* to *Pinus resinosa*.
8. a/ Edaphic climax stage of *Pinus resinosa*.
b/ Simultaneous development of hardwood-
Pinus strobus type.
c/ Invasion of *Abies-Picea*.
d/ Transformation from *Pinus resinosa* to
hardwood-white pine type.

C. Future Successions.

9. a/ Edaphic climax stage of hardwood- *Pinus strobus* type.
b/ Simultaneous development of *Abies-Picea canadensis*.
10. *Abies-Picea canadensis* Climax stage.

~~CLASSIFICATION~~

A. Past Successions.

Denudation stage- During the glacial periods this region was covered with ice, probably thousands of feet deep. The pre-glacial flora, then, must have been either killed off or swept away by the ice. After the retreat of the ice the region was covered with glacial drifts, upon which the plants started their successions.

Herbaceous stage- The initial substratum in this region, unlike many others, was bare soil instead of hard rock surface, as a consequence the first stage of vegetation would be grasses and herbaceous forms. Among these bunch grass, sedges, golden rods, etc. may have been present.

Shrub stage- The availability of soil for a foothold for vegetation would shorten very decidedly the earlier stages of succession. Soon after the development of herbaceous forms Xerophytic shrubs such as willows, birches, hazels, and other northern shrubs left behind by glaciers would have developed and driven out the herbaceous forms.

Pioneer forest tree stage- By the gradually increasing density of shrubby growths the soil surface was shaded and the evaporating power of the air was reduced. This resulted in a condition favorable for the germination of some of the pioneer forest tree species notably, *Populus tremuloides*, *P. deltoides*, *Betula alba* var. *papyrifera*, *Pinus Banksiana*, and

others that would be the first members of the forest succession.

Mixture of conifers and hardwood stage- After the establishment of forest trees the successional development in this region was controlled largely by the kind of soil and the tolerance to shade of different species. At this stage two principal types of soil may be recognized. (a) The sterile sandy areas resulting from glacial outwashes, which are occupied mostly by *Pinus Banksiana*. (b) Sandy loam and clay soils, which are fertile enough to support a dense tree population, thus, a mixture of hardwoods and the three native pines would be developed.

Segregation of *Pinus resinosa* and the Hardwood-*Pinus strobus* stage- Due to the coarseness and looseness in texture and structure of the sterile sandy soils the organic materials deposited on the surface and the mineral elements set free by physical and chemical agencies in the soil are being constantly leached out by rain water and the improvement of soil conditions is very slow, as a consequence *Pinus Banksiana* will continue to occupy this sterile habitat. Meanwhile the struggle for existence among the mixtures on the heavier soils would be very keen. The degree of sensitivity to soil moisture and to the supply of mineral salts and the ability to tolerate shade would mark a step in the succession. Consequently at this stage two types of forests oc-

cupying two types of soil would, naturally, be segregated; clay soils with higher moisture holding capacity and with a higher percentage of nutritive salts would be dominated by the more shade tolerant species such as *Pinus strobus*, *Acer saccharum*, *Tilia americana*, *Quercus rubra*, etc.; and the sandy and sandy loam soils with lower moisture and salt content would be occupied by less shade tolerant and less moisture and nutrition exacting species, notably *Pinus resinosa*, the timber crop tree of the region.

B. Present Successions.

The forgoing paragraphs have briefly indicated the forest successions of the past and up to this stage three distinct forest types have been developed viz. *Pinus Banksiana* type, *Pinus resinosa* type, and Hardwood-*Pinus strobus* type. These three types constitute the principal forest formations of the region at the present stage.

Edaphic Climax of *Pinus Banksiana*- On account of the slow improvement of soil conditions in the sterile sandy soils *Pinus Banksiana* is free from competition and hence able to permanently occupy the areas where it became originally established. This permanent development may be called the Edaphic Climax of *Pinus Banksiana* type.

Transformation from *Pinus Banksiana* to *Pinus resinosa*- Although most of the sterile sandy soils make imperceptibly slow improvement, some areas, especially those upon which

Pinus Banksiana had reached its best development, would be increasing in their organic matter content, this would result in a decided increase in the moisture holding capacity of the soil, more of the rainfall would be made available and less leaching would take place. The resultant improvement of the soil would make an invasion by *Pinus resinosa* both possible and probable. Such an invasion would result at first in a mixed stand of *Pinus Banksiana* and *Pinus resinosa*, and when two species of unequal ecological rank occurs, the inferior or more Xerophytic usually gives place to the superior. *Pinus Banksiana* has shorter life cycle and is more intolerant to shade than *Pinus resinosa*, as a consequence the former is gradually dying out and being replaced by the latter. Such transformations may be illustrated by figure 8.

Edaphic Climax of *Pinus resinosa* stage- A large percentage of the soils of this region being rather fertile sand and sandy loam well suited to *Pinus resinosa* and a gradual increase in the areas of improved sterile sandy soils in the region, both make conditions favorable for the regional dominance of *Pinus resinosa*. This very situation is probably present in other parts of northern Minnesota and has led Bergman and Stallard (4) to conclude that the climax formation of northern Minnesota is one of pines. Among the pines they have included *Pinus resinosa* and *Pinus strobus* growing in mixture and they have further stated that probably the latter

would finally replace the former. Conditions of this particular region, however, appeared to the writer such that neither of these two pines seems to be able to culminate the succession of this region, simply because, as stated previously, a true climax forest should not be determined by the present quantitative predominance of a certain species but by the continuity of their reproduction in the habitat which they are occupying. As a matter of fact both *Pinus strobus* and *Pinus resinosa* in this region not only are failing to reproduce themselves but they are being replaced by either *Acer saccharum*, *Abies balsamea*, or *Picea canadensis*, (see figure 6) The present predominance of *Pinus resinosa* in the region is simply due to the amelioration and the suitability of soil conditions of the present stage, consequently the writer would call it an Edaphic Climax Stage of *Pinus resinosa*.

Simultaneous development of Hardwood-*Pinus strobus* type-
On the limited areas of clay soil at this stage there is a simultaneous development of the hardwood, *Pinus strobus* type. Among the hardwoods, *Acer saccharum*, *Tilia americana*, *Ulmus americana*, *Quercus rubra*, *Quercus macrocarpa*, *Betula alba* var. *papyrifera*, etc. are the principal tree species. Since these different individuals are growing in a mixture the competition for necessities of life between them is inevitable. The result of the struggle for existence would again result in the dominance of the superior individual species, those best suited to

the habitat, the inferior species remaining in the less suitable habitat. *Acer saccharum* and *Pinus strobus* being more tolerant to shade and more exacting in soil fertility would naturally occupy the heavy clay soils. Due to greater tolerance of shade and more prolific reproduction *Acer saccharum* may be able eventually to possess this habitat very completely, reaching its climax. *Pinus strobus*, on account of its weakness in reproducing itself under too heavy shade, may just fill up openings in the stand. It also seems that the somewhat lighter soils occupied by the other species of hardwood will be occupied, at some future time, by either *Acer saccharum*, *Pinus strobus*, *Picea canadensis*, or *Abies balsamea*.

Invasion of *Abies*-*Picea*-*Abies balsamea* and *Picea canadensis* constitute a large percentage of the forests in Minnesota, being especially abundant in northern part of the state where there are many glacial lakes. In this region, however, no extensive areas of matured forest of these two species are found, but young stands of the two occupy probably the largest percentage among all the tree species except the pioneer ones such as Jack pine, aspen, birch, etc. These last, as a rule, are abundant everywhere within their ranges. The most striking feature of these two species is that they reproduce themselves readily in any habitat that has room and an adequate moisture supply. Thus, the less heavy clay habitat oc-

cupied by hardwoods mentioned in the preceeding paragraph and having more open spaces and higher moisture content are more subject to invation by the Abies and Picea.

Transformation from Pinus resinosa to Acer-Pinus strobus type- It has been stated previously that Pinus resinosa cannot culminate the forest succession of this region. A further explanation on this point may, hitherto, be given. The northern limit of Acer saccharum extends as far as the Lake of the Woods, more than 50 miles north of the region. Although there are no large areas of matured maple forest in this region, but the prolific reproduction of this noted mesophytic climax tree appearing here and there (see figure 9) throughout the region ^{to their future development. Cooper (3), too, called attention} calls attention to the fact that Acer saccharum is dominant upon the main ridge at the southern end of Isle Royale and that southward it is probably able to supersede the conifers and birch. All these indications make it hard to overlook this species as one of the most important competitors for the supremacy in forest succession of this region. However, due to the limited area of suitable soils the present development is slow, but the rapid improvement of the sandy loam soils occupied by Pinus resinosa and the inability of pine to produce itself in its own shade enable the Acer saccharum to develop fairly rapidly. Figure 9 indicates the beginning of this transformation. Pinus strobus due to its weakness in reproduction under dense shade may hang

on with the maple and fill up the openings of the stand but cannot develop a large population.

C. Future Successions.

Edaphic Climax of *Acer-Pinus Strobus* stage- Forests being very susceptible to damage by fire, animals, insects, wind etc. are subject to external disturbance. No matter how well the region is being protected these external or accidental injuries can hardly be avoided. Should there be no external disturbance, the constant improvement of soil condition in the region would enable the *Acer-Pinus strobus* type to supersede the *Pinus resinosa* and develop a climax. This climax stage, as one can readily see, is advanced by soil conditions, therefore the writer would call it an Edaphic Climax Stage of *Acer-Pinus Strobus*.

Abies-Picea Climax Stage- Both, the development of the mesophytic *Acer-Pinus Strobus* on its optimum soil condition and the rapid development of the shade-enduring *Abies-Picea* type as outlined in preceding paragraphs, would lead one to conclude that a parallel development of these two types may culminate the succession, because as far as the tolerance to shade is concerned one type is just as shade-enduring as the other and soil conditions are probably equally favorable and available for both types. However, evidences from quadrat studies (see figure 10) on *Abies-Pi-*

cea reproduction and other reasons given in succeeding paragraphs make the writer believe that the struggle for supremacy in forest succession cannot end in the survival of both of these two types. This parallel development may last long time but eventually the Abies-Picea type would probably dominate the climax of the region.

Quadrats Studies in Abies-Picea Reproduction.

Method- The reproduction of the Abies-Picea association seems to be best near the margin of the numerous lakes and less abundant in areas remote from such bodies of water. It therefore seemed that the nearness to such water supply as was represented by the lake water determined the relative richness of reproduction. In order to test this assumption certain quantitative studies were made. Two parallel straight lines were run by compass at approximately right angles to the western shore of the big lake, for a distance of about $1/2$ ^{mile} ~~inch~~. The lines passed through virgin stands of each of the four types of forest characteristic of the region, viz. the matured red pine, (Pinus resinosa), mixed stand of red and Jack pine (Pinus resinosa and Pinus Banksiana), pure Jack pine (Pinus Banksiana) and hardwood type. Along these two lines ten quadrats of $1/4$ of an acre each (104 feet on each side) on each line were laid out with strings. The intervals between quadrats varied from over 200 feet to over 600 feet depending upon the distribution of each type of forest crossed. Within

the quadrats all the tree seedlings below 15 feet in height were tallied. Taking the total reproduction in each quadrat as 100 percent the percentage of Abies-Picea reproduction was calculated. The average percentage of the two lines or of the 20 quadrats is plotted as coordinate against the distance in feet away from the lake-shore as the abscissa and an average curve was drawn through the points (see figure 10).

Discussion--The above curve shows decidedly interesting fact that the percent of reproduction of Abies-Picea increases in almost inverse proportion to the distance from the lake-shore. This evidently indicates that moisture is the determining factor for the development of the Abies-Picea type and the effect of soil is only an indirect one, because even in the sterile sand or Jack pine soils, when sufficient available moisture is supplied by the small lakes or depressions nearby, the Abies-Picea reproductions are found abundantly. Since the region is thickly spotted with lakes and depressions (see figure 5) the writer ventures to predict that Abies-Picea probable finally be able to supersede the Hardwood-Pinus type. A further confirmation on this point may be found in the thicket growing habit of the former which crowd out the latter very readily. Then too, one should not lose the sight of the fact that, other conditions being equal, the lower temperature and the shorter growing season in this region ~~in this region~~ would naturally favor the development

of the northern *Abies-Picea* rather than that of the more southern species.

Secondary Successions.

Secondary successions begin after the destruction of the primary vegetation by external causes. Of these lumbering and burning are the principal ones. After removing the trees by either cutting or burning the forest floor is exposed to light. Then, the evaporating power of the air is increased, the water table will be lowered and the nutrient constituents may be lost by washing. All these conditions will tend to bring about a more xerophytic situation and cause retrogression in forest succession as a consequence. However, retrogression depends also upon the degree of destruction and the stage at which the destruction occurred; if a forest is cut with such care as not to cause deterioration of the soil conditions and at such a stage of a good seedling year as would assure an immediately reproduction of the same species in the habitat, there would be no retrogression in the forest succession; on the other hand, a wreckless cutting may set back the succession for two or three stages.

Burning, unlike the cutting, removes not only the forest stand but all other vegetation as well. As a consequence, in addition to bad conditions brought about by destruction mentioned in the preceding paragraph organic mate-

rials are burned up and nitrogen in the soil is deliberated, thus, plant succession may be set back to the primary denudation stage. On the other hand, if the fire is not too severe the burning may be of beneficial to forest succession, as light fires usually help to kill back the underbrush, open up resinous cones, stimulate germination, and encourage the development of the major forest tree species. A best illustration for that is the Douglas Fir forest in the Pacific Northwest; Hoffmann (6) says, "the principal combination of factors responsible for the preponderance of the Douglas Fir formation is the presence of seed stored in the forest floor, and of fire! When the forest is removed by fire, the stored seed gets a favorable condition for germination and immediately responds to the stimuli. He further concludes that " the Douglas fir formation (*Tsuedetsuga-hylium*) is not, as might appear, a retrogression from the Cedar-hemlock climax, but is rather the stage of succession preceding the climax".

After all a destructive lumbering and severe fire would always cause retrogression in forest succession. The dotted lines on figure 7 indicate the ways toward which the retrogression of different stages of succession on various habitat may fall. The development of the secondary succession, like that of the primary, depends upon the ability of aggregation, migration, establishment, and competition of the different individuals species and the difference in initial stages from which the secondary succession commenced. The

(28)

principles or the story of the vegetational cycle. of primary successions will, then. be followed and repeated again.

PART III.

CONTROLLING FACTORS IN FOREST
SUCCESSION.

In the foregoing discussion, for the sake of simplicity in presenting the whole story of forest successions in this region, the writer has taken only a few of the more prominent factors to outline its sequence. It is obvious that forest successions are controlled not by a single or by a few factors as may have been indicated, but a complex of factors, hence, a detailed treatment of all the possible factors together with some instrumental evidence secured from this region should be presented. Among the complex of factors three main divisions are commonly recognized as follows;

- A. Climatic. a/ Direct factors.
 b/ Indirect factors.
- B Edaphic or Physiographic.
 a/ Direct factors.
 b/ Indirect factors.
- C. Biotic. a/ Phyto-biotic factors.
 b/ Zoo-biotic factors.

By a process of elimination following the above classification, the controlling factors in forest succession at this region may be determined with same accuracy.

A. Climatic Factors.

The climatic set comprises all those atmospheric components such as the atmospheric humidity, precipitation,

temperature, etc., which may be termed as direct factors. The evaporating power of the air, which is a factor of complex of all the climatic components, which influence the atmospheric control of the water supply, may be termed an indirect factor. All the direct climatic factors usually influence the forest successions uniformly over a widespread region. The plant succession that takes place in response to the widespread climatic influence, Cowles (7) has defined, as regional succession. This takes place over long periods of time and through the operation of climatic agencies, Cowles further stated, may be expressed in terms of eons. Because of the influences and the widespread uniformity of the climatic factors to the dynamic plant succession, it seems to be, Nichols (8) stated too, much more to be gained than lost by ignoring some of the climatic agencies and directing our attention to the nearer physiographic and biotic factors, whose operation, according to Cowles, (7) may occur within periods of centuries and decades respectively. Nichols (9) also calls attention that " in applying the Law of the Minimum to problems in local physiographic ecology, climatic factors need not be taken into account since they are essentially constant throughout the region."

Evaporating power of the ^{air} ~~region~~.

Due to the great variation ⁱⁿ ~~of~~ vegetation and the lack of adequate instruments devised for measuring even the approximate amount of water lost by transpiration, and lack

of means of measuring the amount of water lost through run-off and by percolation, it seems to be impossible at present to attack the problem of plant growth in relation to the amount of the precipitation of the region. Livingston (10) tried to solve this difficult problem by devising the ^{atmo-}auto-meter cups to measure the evaporating power of the air, which is the summation of all the atmospheric factors that determine and limit the water loss by plants. The researches of Livingston (10), Fuller (11), Thone (12), and others have shown some satisfactory results. According to Fuller (11), the differences in evaporating power of the air alone would be sufficient to account for certain advances in successions. Thus, the evaporating power of the air in different types of forest, certainly, would help to explain the forest successions in this region.

Instruments and methods-- Livingston spherical ^{atmo-}autometer cups equipped with the rain proofing valves as devised by Livingston and Thone (13) were employed. The reservoir bottles were sunken partly under the ground, so that the cups were about 8 inches above the surface, with one exception, and that was hung on a drooping branch of about 6 feet above the ground for measuring the conditions above the undergrowths. Eight stations were established in seven different forest types scattered over the region. Six stations were visited once every five days and two irregularly. All the readings, except that of two stations that were taken

irregularly, after correction, were plotted accompanied by the amount of the rainfall in c.m. (see figure 11) The average daily evaporation rates of the different types for the whole period was reduced and these together with mean daily precipitation in c.c. of the period were shown in figure 12.

Discussion -- Figures 11 and 12 show a decided contrast of the evaporating power of the air in different types of forest. The open field, due to free air movement, higher wind velocity and stronger insolation, has a rate that is, naturally, ranked as the highest among them all. The cut-over land, with scattered shrubs and primary forest trees, and checking up the air movement and wind velocity, has an evaporation rate second to the open field. The matured red pine forest, due to open canopy and lighter soils supporting only a limited undergrowth, the rate is ranked to the fourth. The records of the matured Jack pine type, owing to disturbances by animals during the course of the investigation, cannot be presented. Judging from a few days' complete records, however, it would be ranked third in the series. In the young Jack pine type, due to its thicket habit of growth, the rate of evaporation is ranked fifth. According to this investigation the rate of evaporation has, probably, less influence on succession during its juvenile stage. In the matured/white pine type, on account of very dense undergrowth, two stations, one below and the other above the undergrowth, were established. The rate of evaporation at the station

above the undergrowth is ranked the third and that of the station below the undergrowth the sixth among them all. The hardwood type, with high mesophytic condition, is ranked the seventh, and the Abies-Picea type, with its dense shade, is seen to be the most mesophytic of all the types.

These instrumental data show a marked correspondence with and give a greater emphasis to the sequence of forest succession as given in part II. of this paper. Thus, assuming that all the other factors are equal, the differences in the rate of evaporation would cause a sequence of succession as outlined. Nevertheless, the writer freely admits, that the records of the evaporating power of the air in the lowest stratum of the various forest types for one season is far from sufficient evidence upon which to base any conclusion, ^wWere it not that data of others such as Fuller (11) and ^vWeaver (20) from records extending over three consecutive years prove that while the records in a series of associations varied somewhat from year to year the same general proportionate relationship was maintained between various associations, and the sequence in mesophytism between the various forest types remained the same throughout the entire period. This unchanging order between the different types in their rate of evaporation is sufficient to justify the belief that one season's records, is in a very substantial manner truly indicative of the permanent relationship of the communities and that records extending over many years would result in

no essential difference.

B. Edaphic Factors.

This set of factors includes all those conditions of the substratum that either directly or indirectly influence the growth and development of vegetation. The former comprises (1) soil composition and soil nutrients, (2) soil acidity and alkalinity, (3) soil temperature, (4) soil moisture content, (5) depth and texture of soil, etc. The latter ~~also~~ involves (1) the surface cover, (2) topography and slope etc.

(a) Direct Operations.

Q. Soil composition and nutrients as a factor--

Broadly speaking, the soil is composed of two general classes of material--minerals and organic matter. The former may be subclassified into two groups, namely: mineralogical constituents, chiefly quartz, which makes up the bulk of the soil; and the nutrient productive particals such as compounds of aluminum, calcium, magnesium, potassium, sodium, sulphur, iron, etc. All these three kinds of soil particals are found in practically every kind of soil. The solubility, presence, or absence of a certain mineral elements determines the chemical properties of the soil and that of the organic matters has more to do with the physical and biological phases. Their relative proportion and availability determines what is generally called the soil fertility. In speaking of soil fertility all three phases must be taken into consideration. The

soils of this region have not, up to the present, been studied intensively by any soil specialist. Leverett (14) gives only general information about the surface formation and Alway (15) gives a good account on Minnesota glacial soil studies, but no detailed information for this particular region. The soils in ~~this~~ this region are too intricate and require soil specialist to make a detailed study, therefore no attempt at chemical analysis will be made in this paper, but some of the peculiar characters of the soils, that usually support special types of vegetation in this region, should be mentioned. The most striking characters are those due to the presence of rich iron compounds and calcareous elements. The former are especially abundant in coarse sterile sand and more prominent at a depth of two feet or more. This may be due to the fact that at greater depths the soil becomes coarse and the coarser particles are usually chemically inert, consequently more insoluble iron compounds are deposited. Russel (16) calls attention to the fact that soils containing ferrous compounds are generally infertile. This may explain the lack of fertility in ~~this~~ reddish, sterile sand occupied by Jack pine in this region. The calcareous materials, on the other hand, decidedly influence soil conditions. Directly they furnish plant food and indirectly they change the physical condition so as to increase the soil tenacity and soil moisture-holding capacity. The latter is especially important in this region of

moderately low precipitation and has a direct bearing on forest succession. Thus, the relative proportion calcareous materials seems to determine the forest types in this region; the sandy loam soils with less calcareous material are generally occupied by red pine; and the clay soils with a higher calcium contents are usually occupied by hardwoods and white pine type. Fernow (17) and Howe (18) also call attention to the fact that the composition and distribution of forests vary mainly according to the differences in the soils. Figure 13 shows the sensitiveness of forest types in response to soil conditions. The boundary line of the two forest types agrees so closely with that of the two soil types that the former look like an artificial plantation. The texture, structure, and composition of the soil thus plays an important role on forest succession in this region.

2. Soil acidity as a factor. -- It is a widely accepted fact that different kinds of vegetation have different acid tolerance. The correlation between the hydrogen-ion concentration of the soil and the degree of acid tolerance of the plants determine to a considerable extent the distribution of the vegetation and consequently modify the plant succession. Certain plants such as the Sphagnum, Osmunda, Vaccinium etc. are usually referred to acid soils and others like Amaranthus, Tamarix, Chenopodium, etc. are usually found in more or less

alkaline soils. On account of the supposed limitation of ~~of~~ plants like those mentioned to acid or alkaline soils, ecologists have often taken them as indicators of soil conditions. This concept of soil indicators must not be too rigidly held, because more recent investigations show that the influences drawn from the presence of such supposed indicators are not always correct, *Pinus Banksiana*, *Arctostaphylos Uva-ursi* ~~Gaultheria~~ *Gaultheria procumbens* and ~~Maianthemum~~ *Maianthemum canadense* are commonly recognized as acid indicators but the recent intensive work of Kurz (19) shows that they may be found upon soils with an alkalinity as high as that indicated by ~~pH~~ 7.5. Thus it is evident that it is not safe to adhere rigidly to the idea of acid and alkali plant indicators without taking account of such factors as aeration, soil moisture, light, etc. Kurz also points out that one must distinguish acid clay, acid sands, and acid peats, ^{which} ~~with~~ means, evidently, that the pH value probably does not account for the distributional phenomena to such an extent as does the difference in soil types. This statement quite agree with the condition of the plant association in this region; in the sterile sandy soils Jack pine is invariably associating with *Arctostaphylos Uva-ursi*, *Vaccinium canadense* and *V. pennsylvanicum*, *Maianthemum canadense*, *Uvularia grandiflora* etc; While in the loamy and clayey soils occupied by red pine and hardwoods one can hardly find a single one of them. This situation

would lead any one to believe that the sterile Jack pine soil must be more acid than the others, but the fact is not universally true. About 40 soil samples taken from a depth of six inches in various soil types of the region were tested by Dr. Kurz and about 70 samples taken from a depth of 1, 2, and 3 feet in various types were tested by the writer with the LaMotte chemical indicators. The results are listed below:

Forest and Soil type	Depth	No. of samples	P.H.
Jack pine, sterile sandy soils.	6 inches	3	5.5
ditto	ditto	5	6.0
"	"	2	7.0
"	1 foot	10	6.0
ditto	ditto	8	6.5
"	2 feet	3	6.0
"	ditto	3	5.5
"	3 feet	4	6.0
"			
Red pine, loamy soil.	6 inches	2	7.0
ditto	ditto	6	6.0
"	1 foot	12	6.0
"	2 feet	4	6.5
"	3 "	4	6.0
"	ditto	1	5.5

Forest and soil types	depth	No. of samples	P.H.
Hardwoods, clayey soil.	6 inches	7	6.5
ditto	ditto	5	6.0
"	"	1	7.5
"	1 foot	6	6.0
"	ditto	2	6.5
"	2 feet	3	6.0
"	ditto	2	6.5
"	3 feet	3	6.0
"	ditto	2	5.5
"	"	1	5.0

The above table shows a remarkable uniformity of the p.H. values throughout the region. Most of them ranges from p.H. 6.0 to 6.5 with only one or two exceptions that are p.H. 5.0 and 7.5 respectively. It may also be well to call attention to the fact that the greater the depth from which the soil samples are taken the more uniform is the hydrogen ion concentration. Because of these uniform conditions of acidity throughout the region the writer is inclining to believe that the soil acidity has probably no significance in the forest succession of this region. The invariable association of *Pinus Banksiana*, *Vaccinium pennsylvanicum*, *Arctostaphylos Uva-ursi*, etc seems to the writer to be due not to the acid influence but to the sterile condition of the soil, in which the other plants are unable to grow, thus, in any

habitat that is sterile competition between the plants is usually not keen and only those hardy species named above will survive as a natural association and mislead us into believing that they are acid soil indicators.

3. Soil temperature as a factor.--- It is a well-known fact that soil temperature does not fluctuate much during the year and a constant temperature is reached in a depth of 34 feet. The most prominent fluctuation occurs only within the upper 2 or 3 feet. In the forest, due to dense shade, the fluctuation of soil temperature is much less than that in the open. Nevertheless, it is of great significance to both soil fertility and the development of plant roots, consequently it bears a definite relation to forest succession. Weaver (20) in his work in Idaho and Washington found a marked relation between the temperature of the soil at various depths and the stage in the succession; he found that the temperature decreases as the climax community is approached; his work (21) at Lincoln, Nebraska also shows that the soil temperature becomes progressively lower at all depths from prairie through scrub to forest. From Weaver's work one can readily see that the progressive decrease of soil temperature as the climax community approached is probably due, at least, two causes; (1) the increase of shade and the consequent decreasing amount of direct insolation, and (2) the increase of soil

moisture content as the climax community is approached and the consequent lowering of the soil temperature. The kind of soil should, of course, be taken into consideration; sand soil being generally the more readily heated the more rapid in its loss by radiation; on the other hand, clay while absorbing heat more slowly loses its heat very slowly and has a very uniform temperature as a consequence. Furthermore, soil receives the heat not merely from the insolation and from the interior of the earth but also from the decay of the organic matter. Consequently rich soils supporting a dense vegetation have more organic matter subject to decay, consequently more heat would be produced by such decomposition. Thus, the lower temperature in clay due to higher moisture content may be compensated to a great extent by the function of the decay. The soil in this region, as stated before, ranges from bare sand to heavy clay. The records of the soil temperatures of this region, therefore, followed the natural sequence, that is the open Jack pine forest with little or no humus cover has a higher average soil temperature than the mesophytic hardwood. It is regretted that, due to lack of adequate instruments at hand, the soil temperature of various types could not be measured for an appreciable length of time, however, a two-week's records of various types may give a general idea of the sequence:

Average Soil temperature in Centigrade
of Sept. 3-16, 1922 inclusive.

Forest type.	6 inches	1 foot	2 feet	3feet
Pinus Banksiana.	14.31	14.09	14.16	14.20
Pinus resinosa	14.28	14.10	14.14	14.16
Acer saccharum	14.10	14.01	14.08	14.09
Abies-Picea	13.82	13.78	13.80	13.81

The above table indicates the general sequence of the soil temperature and the different forest types. One should, however, bear in mind that, although the soil temperature is very significant to forest succession, it acts only as an indirect factor, because soil temperature is determined by the kind of soil and the type of forest rather than vice versa. The sterile sand soil, with little or no humus cover, will be frozen earlier in the winter and being deficient in shade, will be heated more quickly and dried out more easily in the summer, consequently it will tend to support only pioneer vegetation; while the heavy clay soil with slower fluctuations, on the contrary, would tend to support a more mesophytic forest.

4. Soil moisture as a factor.-- The vital importance of soil moisture to the vegetation has been recognized from the very beginning of ecological sciences. Warming (22) classified the distribution of plant communities largely upon the moisture conditions. Shreve's work (23) shows that soil moisture is the factor that determines the occurrence and dis-

tribution of vegetation. Pearson (24) calls attention to the fact that ~~this~~ experiments showed, by supplying adequate soil moisture nearly all the species found in the western mountain region are capable of enduring high temperature and of growing under conditions of lower atmospheric humidity. Thus, it becomes evident that soil moisture in relation to plant growth requires critical consideration. Attempts have been made by many workers to establish a definite relation between the moisture supply and plant growth. Among the many workers Briggs and Shantz (25) first developed the idea of Wilting Coefficient. Alway (26) separates the water into available and non-available by means of the Hygroscopic Coefficient. Clements (27) classified the soil water into chresard involving the available, and echard involving the non-available portion. Since it has been proven that the ability of one plant to get water out of the soil is little different from that of another, a single-valued numerical term to express the soil moisture has been established by Briggs and McLane (28); this is known as the "Moisture Equivalent". On account of adequateness this method was used to secure soil moisture data for studying the forest succession.

The records of all the previous investigations show that the moisture equivalent varies with the different kinds of soil and with the various depths. The general situation is that moisture equivalent is usually higher on the surface and lower within the sub-soil of the same habitat. The critical depth for the development of seedlings is, probably, not more than

one foot, therefore, soil samples for this investigation were taken from various depths within a foot of the surface and from various places within the region, so that a better average for each type of soil as well as each type of forest could be secured. The samples were tested by using a centrifugal force of 1,000 times gravity. The average results and the range between the different types of soil and their occupants are given as follows:

<u>Forest type</u>	<u>Soil type.</u>	Ave. M.E. of the types.
Young Pinus Banksiana.	Coarse sand.	1.2
Matured Pinus Banksiana.	Medium sand.	2.6
ditto.	Fine sand	8.6
Abies-Picea-Betula.	ditto.	9.1
Pinus resinosa-P. Banks'na.	Sand loam	9.9
Pinus resinosa.	ditto.	10.7
ditto.	Loam.	11.2
Mixed Hardwood.	ditto.	14.2
Mixed P. resinosa and Pinus strobus.	Clay.	18.3
Acer-Pinus strobus.	Heavy clay.	22.4

Discussion-- From an examination of the above list one can readily see that the range of the moisture equivalent exhibits a distinct correspondence to the sequence of the forest succession with one exception, that is, the Abies-Picea type which, according to the successional series, should occupy the soil with the highest moisture equivalent, but, as

stated before, the Aies-Picea type is found in any kind of soil that has space and adequate moisture supply; it should be clear, then, that a high moisture equivalent does not necessarily mean an adequate moisture supply, nor a low equivalent one that is deficient. For example the sand has the lowest moisture equivalent of the series but when it is near to some of the many small lakes or ponds occurring in this region the underground source of supply provides a constant and abundant moisture content. Remote from such open bodies of water, however, it is necessary that the soil possess a considerable water-holding capacity to provide ^a reserve for the vegetation during the critical dry period of the year. Thus aside from the proximity of open bodies of water the difference in the soil type determining the amount of the moisture supply together with the difference in the rate of the evaporating power of the air would determine the forest succession of the region.

5. Depth and stratification of the soil as a factor.-- In many regions, especially in hilly countries, where the soil mantle is usually thin, the relative thickness of soil often becomes a limiting factor in plant succession. In clay country the impervious stratum known as the " Hard-pan " is generally present. The poor drainage and bad aeration of such a habitat determine a special type of vegetation. Soils in the region under consideration except in the bogs, and swamps are remarkable deep with ex-

cellent drainage and aeration, therefore this factor may be disregarded in the discussion of forest successions.

(b) Indirect Factors.

1. Surface cover as a factor-- The surface cover may be divided into two groups namely: the living cover which includes all the shrubs, herbs, grasses, etc. and the non-living cover which includes all organic debris and snow. These two groups have much indirect influence on forest successions.

Living cover as a factor-- In the forests of this region, perhaps, nothing is more striking than the abundance of the undergrowth consisting of *Corylus rostrata* and *C. americana* and *Aster macrophyllus*. The former usually form a dense first story and the latter the second story of the undergrowth. The prolific propagation by means of both the seeds and the adventitious roots enables them to develop so abundant that practically no other kind of vegetation is able to grow under them. The soil of the upper six inches is practically fully interwoven by their roots and underground stems. (see fig. 14, 15 and 16) This thicket growth of underbrush certainly has a tremendous influence on the existence and development of the forest tree reproduction. The competition for space, light, water and plant food between the tree seedlings and the underbrushes becomes very keen . The feeble pine seedlings cannot conquer the dense and thrifty undergrowth. The failure of reproduction in the pines in this region is largely due to the presence of this thicket undergrowth.

This fact is well indicated by the presence of many 1-year old pine seedlings here and there under them, and the entire absence of such seedlings of any greater age. The reason can be readily seen in the tightly interwoven roots of the undergrowth. During the spring, which is usually rather dry in this region, the soil moisture in the surface layer, which is generally of duff or humus and not very intimately connected with the capillary moisture supply, would be easily exhausted by this heavy foliated undergrowth. Then the dense shade combining with a critical desiccation would be sufficient to kill out the feeble pine seedlings. The absence of larger pine reproduction in this region is due to this very cause and consequently the undergrowth should be accounted one of the most important factors in determining the forest succession.

Non-living cover as a factor-- The amount and kind of debris has a decided influence on the radiation and on the absorption of the insolation, and as a consequence it affects the soil temperature. It also affects the water content of the soil by checking the run-off, increasing the absorption, and lowering the rate of evaporation. Here again, the Jack pine soil with little or no humus cover has wider range of soil temperature and a higher evaporation; consequently it is more xerophytic while the hardwood-Pinus-strobus forest soils, on the contrary, have thick humus cover and are more mesophytic. The duration of snow in different types of forest has also a great influence on the soil tem-

temperature and the soil moisture condition; in the dense shade of the coniferous forest the snow usually lasts longer, and keeps the ground from being frozen, and reduces the loss of water by evaporation; while in open Jack pine forest the snow melts more quickly and the soil is more subject to freezing. All these influences have a share in determining forest succession, but they are of minor importance.

2. Topography and slopes as a factor.-- Practically all the earlier work in the field of ecology recognized the general effects of topography as one of the most important modifiers of plant succession. Cowles (29) especially emphasizes the importance of topography as a general control over other factors in dynamic plant successions. The dynamic topography or slopes, that are subject to active erosion, strong wind action, and to unequal insolation, afford efficient cause for plant succession. However, in a flat country, especially with sand soil, as in this region, the topography changes slowly and consequently it has very little effect on the plant succession.

C. Biotic Factors.

Among the biotic factors two main groups may be recognized namely: (a) Phyto-biotic and (b) Zoo-biotic factors. The former include all the factors of plants themselves and the latter involve all the influences of animals and insects.

(a) Phyto-biotic Factors.

Tolerance and light intensity-- The ability of trees to endure shade is generally called, by the foresters, as tolerance. Since light is essential for photosynthesis and assimilation the relative amount required by each species and the light intensity available becomes one of the most important factors in forest succession. The tolerance of shade varies not only with different species, but even within the same species, according to the conditions under which the tree is growing. Wiesner (30) calls attention to the fact that trees increase their tolerance when they are growing in more fertile soils and under more suitable moisture conditions and the same individuals would be less tolerant to shade when they grow in precarious conditions. Beside the soil and soil moisture factors, the age, the vigor, the origin of the tree, and all the climate factors have bearings on the tolerant ability. Because of the fact that so many different factors affect the tolerance of the tree it is extremely difficult to measure the tolerance of a given species and an exact quantitative value of tolerance of a certain species of tree cannot be found. Zen (31) follows

a number of European authorities in proposing a relative scale designating the tolerance of the different tree species. Thus, instead of measuring the amount of light a certain species required, investigators generally measure the relative amount of light intensity present in the different types of forest. To measure the light intensity Wiesner (30) first devised an "Insolator" and used a sensitive photographic paper. Following the same principle Clements (27) invented a "Photometer". Recent ecological investigations such as Brown (32), Thene (12) and others have employed Livingston's "Radio-atmometer" by means of getting the light intensity through the difference in evaporation on the black and white cups. None of these instruments and means have been proven satisfactory. In this study, for the sake of convenience, two thermometers, black and white, were employed. This method is, of course, by no means accurate, but it gives the relative value of the light intensity in different types of forests with a ^{fair} degree of accuracy.

Instrument and method-- The bulbs of the ordinary thermometers were wrapped up with silk cloth, one with black and the other with white. The two thermometers were attached to a narrow and grooved board. Since we know that the black absorbs and the white reflects, the difference in readings between the black and white thermometers is supposed to be due to the light intensity. The thermometer-board was held facing horizontally upwards at about 4 feet from the ground and was carried slowly through the forest along definite

lines laid out in such a way that they would cover all the different conditions of the stand. Readings were taken at every 200 feet and in order to afford sufficient time for the thermometers to adjust themselves to the different light conditions, 10 minutes were allowed for each reading. After taking each reading the thermometer-board was put in a light-proof sack for a while, until both instruments indicate the same reading. They were then taken out and the next reading made after the 10 minutes interval. The readings were taken at the same time on the different days. The days for such investigation were selected with special care of about the same approximate brightness, which was judged by exposing this thermometer-board to direct sunlight at the same spot and the same time of the day. The readings thus indicate the difference in brightness. Fifty readings were made in each type of the forest. The average results of the different types are shown graphically by the figure 17. The relative light intensity between the different types is expressed quantitatively in the following table:

Forest type.	The ave. difference between the black and white thermom- eter readings.	Ratio	The relative intensity in various types.
Matured Jack pine	1.56	100.0	1.00 (standard)
" red "	1.02	65.3	2/3 +
" white "	.80	51.2	1/2 +
Young red "	.62	39.8	2/5 -
" Jack "	.57	36.5	1/3 +
Pure hard-wood	.215	13.7	1/7 -
Abies-Picea.	.166	19.6	1/19 +

Discussion -- As can be seen from the above table by taking the matured Jack pine type as a standard and its ratio as 1, the intensity in the hardwood type is $1/7$ and that of the Abies-Picea type only $1/10$. The weak light intensity in hardwood and Abies-Picea type would, apparently eliminate the reproduction of pines. The experimental records of the Cloquet Forest Experiment Station (33) show that the "no Shade" plots of Pinus strobus seedlings developed much better than those "Quarter shade" and the "Quarter shade" still better than "Half-shade"; for red pine " $1/4$ shade" and "No-shade" plots were much superior than those of " $1/2$ shade"

General observations on pine reproduction in northern Minnesota indicate the same situation; in open places where seed trees are available one always finds abundant red pine reproduction (see fig. 18); while in a dense stand one can hardly find any. Brown (32), too, calls attention to the fact that light is one of the limiting factors for plant succession on the Philippine mountains. In this region, although there are many other factors, the ability to tolerate shade and the light intensity under the forest cover should be accounted one of the most important factors in determining forest succession.

Frequency of seed reproduction as a factor. -- The frequency of seed reproduction depends upon two main factors namely; environmental conditions especially of those of soil fertility, and the hereditary character of the different species

Despite the former the difference in the latter may be the limiting factor in determining forest succession. Most of the pines bear seed with definite periodicity. The length of the period is quite irregular, but on the average, *Pinus strobus* has a seed year in every four years and *Pinus resinosa* every 7; while *Pinus Banksiana*, *Abies balsamea*, *Picea canadensis*, and a number of hardwoods bear seed almost every year. The infrequency of seed reproduction in *Pinus strobus* and *P. resinosa* results in a decided advantage to *Acer*, *Abies*, and *Picea canadensis* and aids them to dominate the succession in this region.

Motility, adaptation, and establishment as a factor.

-- The ability of a species to move out from the parent tree determines its extent of aggregation, and this has a special bearing upon the nature and course of succession. Motility is determined chiefly by the character of the seed and nature of its dissemination; thus seeds of *Populus*, *Acer*, *Ulmus*, etc. . . being light and disseminated mostly by the wind, are able to spread much more widely than those of pines. On the other hand, the larger seeds are apt to be carried away by animals to a much greater distance than are the light seeds blown by the wind. After the migration of the seeds the ability of different species to adjust themselves to the new habitat determines their establishment. For the adjustment of a plant to new conditions Clements (34) introduced the term "Ecesis", which consists of

several processes viz: germination, growth, competition, reproduction, etc. Here again, the three main sets of factors discussed previously have their affect. After all, the motility adaptation, and establishment are important factors to plant succession during the pioneer stages on areas ^{of} denudation and of relatively little significance in advanced stages of succession like those existing in this region.

Longevity of trees as a factor. -- Theoretically speaking a tree should not die, since a new layer of tissues is always being formed each year. The death of a tree is simply caused by destructive agencies such as fungi, insects, fire, wind, and other unfavorable conditions that reduces the vitality of the tree. The longevity of a tree is, then, determined by its ability to resist the destructive agencies and to withstand unfavorable conditions. As a general rule, most of the pioneer species such as *Populus*, *Betula*, *Pinus Banksiana*, etc. are very mobile but less resistant to the destructive agencies, consequently they have shorter life cycle than those advanced tree species such as *Pinus resinosa*, *P. strobus*, *Acer saccharum*, etc. Those that have the greatest longevity are generally able to dominate the region, but they do not necessarily form the climax of the region, because, as previously stated, the climax of the region is determined not merely by the predominance but by the persistence and continuity of their regeneration.

(b) Zoo-biotic Factors.

The Zoo-biotic factors may be divided into two groups namely: the human influences, which consists of cuttings, silvicultural treatment, etc.; and the animals and insects. Some of these factors are beneficial and some detrimental to forest succession.

Human influences as a factor.-- Cuttings and silvicultural treatment may bring about progressive succession or may cause retrogression depending upon the region and the method of cutting and treatment. In Adirondack Mountain region, where the virgin forests are mostly mixtures of conifers and hardwoods., the lumberman usually takes out the conifers and leaves the hardwood. Cuttings like this generally advance a stage of succession, because soon after the removal of the conifers the maple reproduction takes place and develops its climax much quicker than would otherwise happen. Silvicultural treatment, on the other hand, usually takes out the inferior species such as maple, birch, etc. and makes more room for the pines. Treatment like this generally brings about a mechanical retrogression. Cutting in region under discussion has been stopped since the creation of the park and silvicultural treatment has not yet been practiced. Thus, for the time being these factors may be disregarded.

Animals and insects as a factor.-- The effects of animals and insects on ^{forest} first succession, like those of the human influences, may be to cause progressive succession or

retrogression depending upon the region and the degree of the influence. In the west overgrazing usually causes retrogression. In southern pine region grazing generally helps to keep down the undergrowth and encourage the development of the pines, which are generally the climax trees of the region. In the northern woods, during the winter when the ground is covered by snow, deer, rabbits, etc. usually feed on the coniferous seedlings that are uncovered by the snow. In region like Itasca which is under game preservation these animals are abundant enough to play a part as the limiting factors of forest succession. Insects are another factor that may influence forest succession. Among the important insects the spruce budworm may be cited. It has been reported that the last outbreak of this insect was 1910-1919, within this period practically all the spruce and balsam fir within an area of more than 1,000 miles from Quebec eastward to the Atlantic were killed back and birches were left as the dominant tree of the region. A destruction like this certainly would modify forest succession. In this region, however, neither grazing nor such insects outbreaks seem to have been sufficient to affect succession.

General Conclusion.

The distribution of the larger plant communities is controlled by climatic factors. The demarkation between the climatic types is by no means sharp, transitional belts of varying widths are usually present. The forest successions within this transitional belt are not controlled by a single factor nor by any one of the three sets of factors but by complex of factors. IN this factor-complex the edaphic factors, especially the soil composition and the soil moisture content combining with the differences of the evaporating power of the air in different types of forest indicated by the figures 11, 12, and 13 are the limiting ones on forest succession; the biotic factors, especially the tolerance to shade, the relative light intensity within each type of forests, and the thicket growth of under shrubs which enter into serious competition with tree seedlings for all the necessaities of life indicated by the figures 14, 15, and 16, also play a most important rôle in forest succession; and the climatic factors, with the exception of their indirect action through the evaporatång power of the air, have very little bearing on the local successions.

Owing to the presence of diversified soil types in this region. a series of edaphic climax types has been, is being, and will in the future be developed. Of these the *Pinus Banksiana* on the sterile sand soils, the *Pinus resinosa* on the sand loam, and the hardwood-*Pinus Strbus* forest on the calcareous clay, are the typical types ameliorated and advanced

simply by soil conditions of the region. As time goes on, the soil conditions are improving and this would enable a progressive succession to take place or a transformation from one edaphic climax to the other. The failure of *Pinus resinosa* and *Pinus Strbus* to regenerate themselves under their own shade together with the unfavorable conditions of the presence of the thick undergrowth indicates the impossibility of the pines culminating the forest succession of the region. *Acer saccharum* is able to reproduce itself but is limited to heavy soils. The slowness in the improvement of the sterile sand soils and the limited area of heavy soils in the region make it diffecult for *Acer saccharum* to become a climax over the entire area, however, it may develop an edaphic climax and last longer. The great shade tolerance of the *Ahies-Picea* typewith its prolific reproduction on any kind of soil that has adequate soil moisture, as indicated by quadrant study, makes it one of the forests best suited to the region and the good water supply due to the presence of numerous small lakes favors it to such an extent that it seems both possible and probable that it may develop into the true climax of the region.

Summary.

1. This paper is a report of an ecological study of the controlling factors in forest succession within a transitional belt between a coniferous and deciduous forest, at Lake Itasca, Minnesota, made during the growing season of 1922.
2. Three main sets of factors; climatic, edaphic (or physiographic) and biotic, were studied. Of these the following important ones may be listed: (a) evaporating power of the air. (b) temperature of the air and soil. (c) type, composition, and acidity of the soil. (d) Soil moisture. (e) light intensity within each type of forest. (f) living surface-cover or under-growth. (g) reproduction in quadrant areas.
3. The distribution of large forest communities is controlled by climatic factors. Of these the most efficient ones are the temperature, which controls the survival and growth of the seedlings and the consequent advance or retrogression of a given species and the precipitation, of which not merely the amount but the character of the seasonal distribution is important.
4. At the transitional belt the controlling factors in forest succession are chiefly the edaphic ones. In this particular region, biotic factors, especially the tolerance to shade and the thicket growth of underbrush, etc. are probably of equal importance in controlling the forest succession. The light intensity within the different types of forests was

found to be decreasing with increasing of mesophytism.

5. Climatic factors, with the exception of the evaporating power of the air, have very little bearing on local succession. The evaporating power of the air was found to decrease with increasing mesophytism.
6. Among the edaphic factors, the differences in soil type and in their consequent soil moisture-holding capacity are the limiting ones in forest succession. The heavier the soil is the higher the moisture-holding capacity, and the more mesophytic the forms supported.
7. The average temperature of the soil was found in the coarse sand type higher than that in loam and in the loam soil than that in the clay at all depth.
8. The soils, regardless the type, are practically all slightly acid throughout the region. The range of the hydrogen-ion Concentration is ~~is~~ mostly pH. 5 - 6.5 and the deeper the soil is, the more uniform the acid content was found.
9. The presence of abundance of so-called acid indicators such as *Arctostaphylos Uva-ursi*, *Vaccinium pennsylvanicum*, *V. canadense*, etc. in association with *Pinus Banksiana* and not with the other type of forest in the region, is probably due to such factors as light intensity, poor soil, and other precarious conditions that the other plants cannot withstand rather than to the factor of soil acidity.

10. The diversified soil types have resulted in an intricate of forest communities. The forest succession are, thus, progressing as the soil conditions are improving.
11. Each particular type of soil is usually occupied by a special type of forest, as a consequence a series of edaphic climax forests of the different types are being developed.
12. Due to the various factors such as (1) the incapability of pines to reproduce themselves under their own shade, (2) the presence of dense undergrowth, (3) the sensitiveness to soil of the hardwood-Pinus Strobus type and the limited area of heavy soils in the region, (4) the prolific reproduction of the most shade-enduring Abies-Picea type on any kind of soil, and others, leads to a conclusion that the Abies-Picea type would probably be able to replace the others and develop the true climax of the region.

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Description of Figures.

1. Map of Minnesota showing Distribution of Forest and Prairie. (After map by Warren Upham and by F.K. Butters).
2. Map of Minnesota showing the average annual precipitation.
3. Map of Minnesota showing the first and last killing frost dates. Line A showing the number of days of the average growing season. Line B showing the mean annual temperature of 42°F. Arrow points Lake Itasca.
4. Map of Minnesota showing the distribution of glacial drifts. Arrow points Lake Itasca.
5. Map of Lake Itasca showing the distribution of numerous Lakes. (After Minn. Forest Service Bull. 4)
6. Virgin red pine forest in Lake Itasca showing three stories of forest; red pine, birch, and Abies-Picea, and the invasion of Abies-Picea reproduction near the lakeshore.
7. Classification of stages of Xerarch successions.
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10. Curve showing the percentage of Abies-Picea reproduction from lakeshore inlandward.
11. Evaporating power of the air in different types of forest in 5-day periods and the amount of rainfall of equivalent length of time.
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13. Calcareous substratum underlying the coarse sand soil supporting a Pinus resinosa type on the right and the same soil without calcareous substratum supporting Pinus Banksiana type on the left.
14. The adventitious roots of Corylus rostrata within an area of three square feet.
15. The adventitious roots of Aster macrophyllum within an area of 3 square feet.
16. Mixed stand of Pinus resinosa and Pinus Strobilus showing the density of undergrowths.
17. The relative light intensity in different types of forest.
18. The prolific reproduction of Pinus resinosa in the open near Cloquet, Minn.

MAP OF MINNESOTA SHOWING DISTRIBUTION OF FOREST AND PRAIRIE. (AFTER MAP BY WARREN UPHAM AND BY FREDERIC K. BUTTERS)

Fig. 1.

MAP SHOWING THE AVERAGE ANNUAL PRECIPITATION FOR MINNESOTA

Fig. 2.

Map of Minnesota showing Distribution of Prairie, Coniferous and Deciduous Forests. Heavy lines showing the First and last Killing Frost date and line A. showing the number of days of the average growing season. The arrow points Lake Itasca.

Fig. 3.

MAP OF GLACIAL DRIFTS, LOSSES, AND GLACIAL LAKES IN MINNESOTA

Fig. 4.

Fig. 5.

Fig. 6.

Fig. 7.

Fig. 8.

Fig. 9.

Fig. 10.

Fig. 11.

Fig. 12.

Fig. 13.

Fig. 14.

Fig. 15.

Fig. 16.

Fig. 17.

Fig. 18.

FACTORS CONTROLLING FOREST SUCCESSIONS AT

LAKE ITASCA, MINNESOTA.

Abstract of a Dissertation
Submitted to the Faculty of the
Ogden Graduate School of Science
In Candidacy for the Degree of
Doctor of Philosophy.

In the Department of Botany.

by
Shun Ching Lee.

This paper is a report of an ecological study of the controlling factors in forest succession within a transitional belt between a coniferous and deciduous forest, at Lake Itasca, Minnesota, made during the growing season of 1922. The paper has been divided into three parts:

Part I. The introductory -- dealing with (a) the controlling factors in the distribution of major divisions of vegetation. The fact has been widely recognized that the main control of the distribution of the climax formation of prairie, coniferous, and deciduous forest has been determined by climate. Among the efficient climatic factors low precipitation combined with high evaporating power of the air is the limiting one in the distribution of prairie and the temperature is the limiting one in the distribution of conifers and hardwoods, because the geographic distribution of any plant, at its zero point, depends upon its ability to reproduce itself; the survival and growth of seedlings and the consequent advance or retrogression north or southward of the particular forest type is determined largely by temperature. (b) Location this study

made and the general physiographic features of the region, which involve the topography, soil, climate, forest condition, etc.

Part II. The forest succession of the region and quadrat studies in the reproduction of *Abies balsamea* and *Picea canadensis*. --- Taking the region as a physiographic unit and basing upon the soil conditions supporting various forest types, and other factors the forest succession has been studied. The whole story of forest succession of the region has been divided into three periods namely: past, present, and future; from the stage of denudation leading to the climax formation ten stages have been classified. The sequence of primary and secondary successions on the different types of soil was indicated diagrammatically. The hydrarch succession of pre-forest stages was not described since the attention of the investigation was directed on the forest succession. The xerarch succession started from the denudation of bare soil, which was laid down by glaciers. The initial substratum in this region, unlike that of many others, was bare soil instead of hard rock surface, as a consequence the first stages of vegetation would be grasses and herbaceous forms instead of lichens and mosses. The availability of soil for a foothold for vegetation would shorten very decidedly the earlier stages of succession. Soon after the development of herbaceous forms xerophytic shrubs such as willows, birches, hazels, and other northern shrubs left behind by glaciers would have developed, driving out the herbaceous forms, and developing a shrubby stage. By the gradually increasing density of shrubby growth the soil surface was shaded and the evapo-

3.

rating power of the air was reduced. This resulted in a condition favorable for the germination of some of the pioneer forest tree species notably, *Populus tremuloides*, *Betula alba* var. *papyrifera*, *Pinus Banksiana*, and others that would be the first members of the forest succession. After the establishment of forest trees the successional development in the region was controlled largely by the kind of soil and the tolerance to shade of different species. At this stage two principal types of soil may be recognized. (a) The sterile sandy areas resulting from glacial outwashes, which are occupied mostly by *Pinus Banksiana*. (b) sandy loam and clay soils, which are fertile enough to support a dense tree population, upon which a mixture of hardwoods and three native pines developed. The struggle for existence among species of this mixture on such heavier soils was very keen. The degree of sensitiveness to soil moisture, the supply of mineral salts and the ability tolerate shade would mark a step in the succession. Consequently at this stage two types of forests occupying two types of soil would, naturally, be segregated: clay soils with higher moisture-holding capacity and with higher percentage of nutritive salts would be dominated by the more shade tolerant species such as *Pinus Strobus*, *Acer saccharum*, *Tilia americana*, *Quercus rubra*, etc. and the sandy and sandy loam soils with lower moisture and salt content would be occupied by less shade tolerant and less moisture and nutrition exacting species, notably *Pinus resinosa*, the timber crop tree of the region.

On account of the slow improvement of soil conditions in the sterile sand soils *Pinus Banksiana* was free from competition and hence able to permanently occupy the areas where it became originally established. This permanent development may be called the edaphic climax of the *Pinus Banksiana* type.

A large percent of the soils of this region being rather fertile sand and sandy loam well suited to *Pinus resinosa* and a gradual increase in the areas of improved sterile sandy soils in the region made the conditions favorable for the regional dominance of *Pinus resinosa*. This situation might lead one to conclude that the climax formation of the region is pine, however, one should bear in mind that a true climax forest is determined not merely by the present quantitative predominance of a certain species but also the continuity of its reproduction in the habitat which it is occupying. As a matter of fact both, *Pinus Strobus* and *Pinus resinosa* in this region not only are failing to reproduce themselves but they are being replaced by either *Acer saccharum*, *Abies balsamea*, or *Picea canadensis*. The present predominance of *Pinus resinosa* in the region is simply due to the amelioration and the suitability of soil conditions of the present stage, consequently the writer would consider it an edaphic climax stage of *Pinus resinosa*. *Acer saccharum* is able to reproduce itself, but it is too exacting in soil fertility. On account of the limited areas of heavy soil in the region it would be difficult for *Acer saccharum* to develop a regional climax, however, an edaphic climax may be developed and may endure for considerable time, eventually it may be crowded out by *Abies balsamea* and *Picea canadensis*, since evidence secured from quadrat studies in the reproduction of these species indicates that they are capable of

invading any habitat that has adequate soil moisture. Since the region is thickly spotted with lakes that furnish the adequate water to the adjacent land it is possible and probable that this may enable *Abies* and *Picea* to develop a regional climax.

Part III. The controlling factors in forest succession and the presentation of instrumental data secured in this region. ---- Among all the ecological factors three main sets have been classified and studied. They are: climatic, edaphic or physiographic, and biotic factors. of these the following important ones may be enumerated: 1. Evaporating power of the air in different types of forest measured with Livingston atmometer cups. 2. Temperature of the air and the soil. 3. Soil acidity tested by using LaMotte Chemical Indicators. 4. Soil moisture content measured by determining the moisture equivalent of the different soil types. 5. Light intensity in different types of forest measured by using the black and white bulb thermometers. 6. The influence of undergrowth on the survival of the forest tree seedlings. By a process of elimination following the above classification the controlling factors in forest succession at this region may be determined with some accuracy.

Conclusion.

The distribution of the larger plant communities is controlled by climatic factors. The demarkation between the climatic types is by no means sharp; transitional belts of varying widths being usually present. The forest successions within this transitional belt are not controlled by a single factor nor by any one of the three sets of factors but by complex of factors. In this factor-complex the edaphic factors, especially the soil composition and

the soil moisture content, combining with the differences of the evaporating power of the air in different types of forest, are limiting ones on forest succession; the biotic factors, especially the tolerance to shade, the relative light intensity within each type of forest, and the thickened growth of undershrubs which enter into serious competition with tree seedlings for all the necessities of life also play a most important rôle in forest succession; and the climatic factors, with the exception of their indirect action through the evaporating power of the air have very little bearing on local succession.

Owing to the presence of diversified soil types in this region, a series of edaphic climax types has been, is being, and will continue to be developed. Of these the *Pinus Banksiana* on the sterile sand soils, the *Pinus resinosa* on the sand loam, and the hardwood-*Pinus Strobus* forest on the calcareous clay, are the typical types, ameliorated and advanced simply by soil conditions of the region. As time goes on, the soil conditions are improving and this would enable a progressive succession to take place or a transformation from one edaphic climax to the other. The failure of *Pinus resinosa* and *Pinus Strobus* to regenerate themselves under their own shade, together with the unfavorable conditions of the presence of the thicket growth, indicates the impossibility of the pines to culminate the forest succession of the region. *Acer saccharum* is able to reproduce itself but is limited to heavy soils. The slowness in the improvement of the sterile sand soils and the limited area of heavy soil in the region make it difficult for *Acer saccharum* to become a climax over the entire area. The great shade tolerance of the *Abies-Picea* type with its prolific reproduct-

ion on any kind of soil that has adequate soil moisture, as indicated by quadrat studies, make it one of the factors best suited to the region and the good water supply due to the presence of numerous small lakes favors it to such an extent that it seems both possible and probable that it may develop a true climax of the region.