THE PISCAH FOREST: 300 Years of Change

by

J. David Henry

Submitted in partial fulfillment of the requirements for the degree of Master of Forest Science at Harvard University

HARVARD FOREST PETERSHAM, MASSACHUSETTS

TABLE OF CONTENTS

	Page
ABSTRACT was a set and all the set of the	I
ACKNOWLEDGMENTS	II
LIST OF ILLUSTRATIONS	III
LIST OF TABLES (and seem to the control of the cont	IV
INTRODUCTION	1
DESCRIPTION OF AREA	4
METHODS	7
Selection of Study Quadrat	7
Approach	7
Field Methods	10
Laboratory Methods	12
Age and Growth Rates	12
Wood and Charcoal Fragments	13
RESULTS — in the second control of the secon	14
General History of the Forest on the Quadrat	14
Behavior of Forest Tree Species	23
The Post-fire Forest	24
The Present Forest	29
Conclusion as we do not see the see that the see the s	44
DISCUSSION ON THE PROPERTY OF	45
LITERATURE CITED	49
ADDENDTY	F. /

ABSTRACT

The change of vegetation over time is particularly difficult to document and research on this subject has consequently lagged. The purpose of this study is to analyze the changes in the behavior of' forest tree populations that occur in one forest over a long period of time. The study area was a tenth acre square plot, the forest of which had never been cut. It is located within the Harvard Pisgah Tract, southwestern New Hampshire. The vegetational history of the plot was reconstructed for the period 1665 to 1967 from a minute examination of all living trees, fragments from dead trees, and microtopography. The forest was destroyed by a severe fire prior to 1665 and by a hurricane in 1938. Between the disturbances a white pine-hemlock stand became established which changed but little in its composition during the 273 years of its growth. However, the composition of the forest changed considerably after the hurricane and is now dominated by hemlock, red maple, black birch, and beech. Thus autogenic succession did not contribute significantly to structural change over the time period examined, but disturbance was very important in this regard. Specifically, changes in forest structure were often found to be manifestations of rystica species behavior; each tree species has a distinctive locational pattern, mode of germination, and growth. Studies of species population behavior seem to be fundamental to understanding changes in forest structure. Their thorough documentation in other areas should produce regionally valid concepts of forest structure and dynamics.

ACKNOWLEDGMENTS

For guidance and continued tutelage I am obliged to
Dr. J. M. A. Swan. For interested support, I am indebted to
the staff of the Harvard Forest under the direction of Dr. M. H.
Zimmermann. To you, gentlemen, I express my thanks for the
opportunity to carry out this study.

LIST OF ILLUSTRATIONS

		Page
Figure 1.	Location of Harvard Tract.	5
Figure 2.	Paper Birch Growing in the Center of a Crown of	
	Salvaged Chestnut Sprouts.	9
Figure 3.	Estimated Heights of the Forest Trees in 1907.	19
Figure 4.	Charcoal Deposits from a Burnt Tree Located in the	
	Bottom of the Organic Layer.	22
Figure 5.	Diameter Growth of Hemlock and White Pine.	28
Figure 6.	The Growth and Germination of Beech.	32
Figure 7.	The Growth and Germination of Hemlock.	35
Figure 8.	The Growth and Germination of Red Maple.	39
Figure 9.	The Growth and Germination of Black Birch.	42

LIST OF TABLES

		Page
Table 1.	Composition and Size Structure of the Forest in 1967.	15
Table 2.	Composition and Size Structure of the Forest in 1907.	18
Table 3.	Distribution of Beech.	31
Table 4.	Distribution of Hemlock.	34
Table 5.	Distribution of Red Maple	38
Table 6.	Distribution of Black Birch	41

į.

INTRODUCTION

We see a forest at a particular point in time. It is actually the product of environmental and biological processes that are active and changing not only in space, but also through time. The effects of these processes are manifested in the changing character (species, number of stems and their sizes) of the forest. The study of forest change with time has lagged because of the inherent difficulties of observing it but I choose to study this aspect here because of its fundamental importance.

The problem directly facing such a study is that the long life span of forest trees often makes impossible the direct observation of the changes that take place over several generations. Hence indirect approaches have often been used. For example, one method sets out a number of plots on areas which have progressively more recent origins for their forest vegetation, and compares these as if they were different stages in a time sequence (Cowles, 1899; Spurr, 1956: Flaccus, 1959; Viereck, 1966). However, one of the most important deficiencies of this technique is that the variation found in the vegetation (concerning species, number of stems and their sizes) cannot be clearly credited to a change over time unless the different habitat conditions on the plots are assumed to have little or no effect upon the vegetation: there is an unfortunate substitution of space for time. A second technique is to use available historical records (traveler's journals, surveyor's notes) to indicate the state of a second forest at some time in the past and then contrast this to the present forest (Sears, 1925; Stearns, 1949). General

changes are indicated. However, with this technique the dynamics of population changes over time cannot be followed in detail. A third rechnique is to take increment cores of all trees in a stand in order to establish the time relationships between the various sizes and species (Swan, 1966; Newsome, 1966). With this technique, age structure can be studied in great detail but only for the living vegetation. However, much information about the past vegetation can be collected from a study of rotting tree fragments found in or on the forest floor. fragments can usually be traced to locate the place where the tree germinated and can often be used to obtain diameter-size and age counts. Stephens (1955) first used this evidence to reconstruct the forest history of an old woodlot on the Harvard Forest. From this history, he was able to document the distruction wrought upon the forest by catastrophic disturbances (specifically hurricanes). I thought that this approach might also be used to analyze forest tree population changes in detail over a long period of time (i.e. several hundred years involving several generations of forest trees).

Specifically, the aim of this study is to investigate, over time, changes in tree species composition (all trees over 6" in height), their times of germination as related to environmental conditions, diameter growth for the life of each tree, and the development of the overstory strata. The analysis of this data should be helpful in understanding changes in tree species populations that have been brought about by the vegetation itself as well as changes that were initiated by environmental crises (windstorms, fires, droughts, etc.).

For this study, an area was required that had a long vegetational history undisturbed by man. This is partially because the analysis depends on the discovery, in place, of wood fragments and on the interpretation of microrelief. Yet, there was a more fundamental reason for selecting an area undisturbed by man. Although man can greatly affect the forest, he is clearly not essential to its continued growth and survival. That is, the New England forest is a biotic system which, when left to its own resources, will maintain itself indefinitely. It is the structure of this self-maintaining system that I wish to study. Harvard University acquired a twenty acre tract of land in the Pisgah Forest of southwestern New Hampshire in 1927, because it was one of the rare old growth stands still undisturbed by man in central New England. Because of the lack of human disturbance this tract was selected as the study area.

^{1/} Structure is used here as a general term to include the number of trees, their species composition, their height and diameter sizes.

DESCRIPTION OF AREA

The Harvard Tract of the Pisgah Forest is seven miles northwest of Winchester, New Hampshire, only a few miles from Vermont to the west and Massachusetts to the south. The Tract is located within the 5,000 acre Pisgah Forest (Figure 1), owned by the Ansel Dickinson Heirs (owners of the New England Box Co.).

The elevation of the Pisgah Forest ranges from 700 ft. to 1300 ft. above sea level. It was heavily glaciated 12-14,000 years ago (Schafer and Hartshorn, 1965). The topography is rough and hilly. The summits of the ridges are mostly bare rock although in places they are covered with a thin layer of soil that affords shallow anchorage to trees. The soils of the Harvard Tract are classified as rough, stony land (Gloucester soil material, Simmons et al., 1949). These soils were studied by Griffith, Hartwell, and Shaw (1930). Their study is often cited as evidence for the influence of vegetation on soil genesis.

The climate of the Tract is indicated from the weather data collected for over forty years by Samuel Wadsworth at his private weather station in Keene, New Hampshire, located some 12 miles to the northeast. The mean annual precipitation is 38 inches which is usually well distributed throughout the year. The average annual snowfall is 63 inches, most of which falls during January and February. The frost free season usually extends about 120 days (calculated from the average last frost of May 26 to the average first frost of September 20). The prevailing winds are

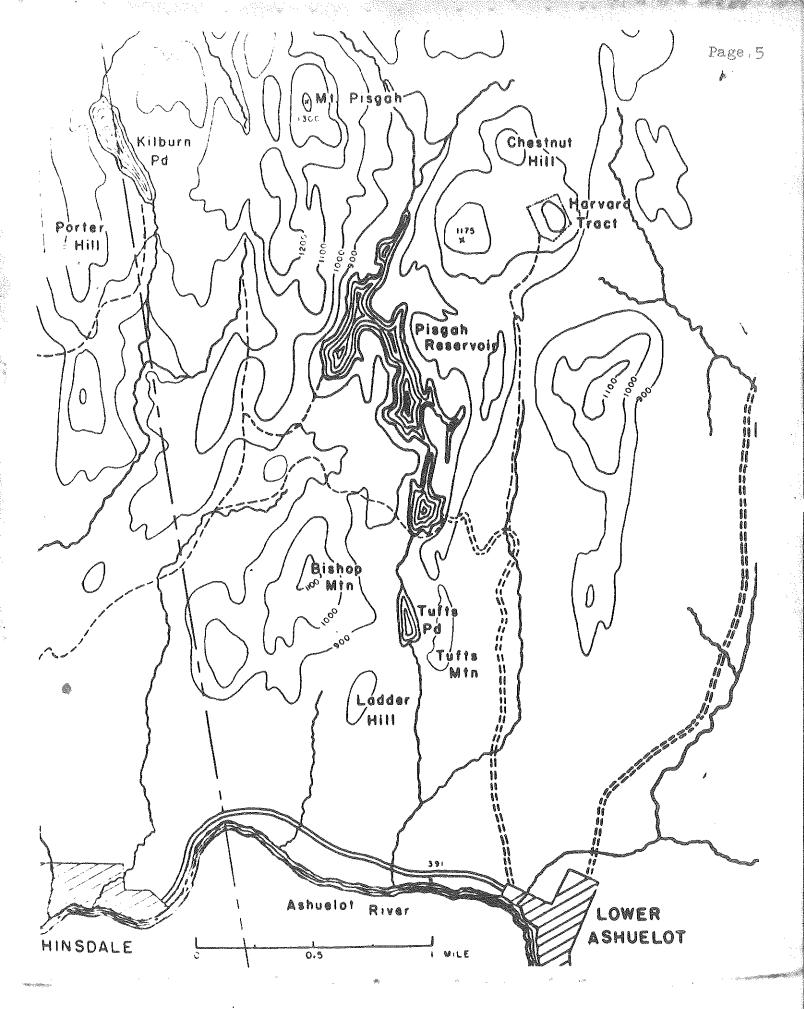


Figure 1. Location of the Harvard Tract

northwesterly. Excessively high winds, occasionally of hurricane force, occur at very infrequent intervals, sometimes in connection with severe electrical or ice storms (Cline and Spurr, 1942). Belknap(1792) and others (Hurd, 1886; Nutting, 1925) also report the occurrence of infrequent severe fires in this area.

METHODS

Selection of Study Quadrat

Because Stephens' technique involves a great deal of work, a restriction must be placed on the size of the study plot. I therefore chose a tenth acre square quadrat within the Harvard Tract. This was the largest area I could expect to thoroughly process in the time available (one summer's field work). Because of the small size of my quadrat, this is a point study and not a regional one.

Approach

In order to clearly understand the methods that were employed, their conceptual basis must first be explained. The time of establishment and diameter growth of each tree on the study quadrat can be examined. Then all these trees can be placed in a single diagram which would represent the change of vegetation over time. To do this, I must know two things about each tree: a) how did that tree grow during its lifetime and b) at what time did that life occur?

The first question can be partially answered by examining the growth record present in the tree itself. By cutting a cross-sectional disk from low in the trunk of a tree, its age can be determined and its growth history examined. Further information about each tree is also collected. The place of germination is examined; and evidence of the probable cause of death is noted, such as scars from fire or disease, windthrown mounds, or entrapment under fallen trees.

The second question (when did this lifetime occur?) is only a problem for the dead trees. It is answered by a number of approaches

that vary in the accuracy of the information they produce. For example, if a tree, that has been injured by another in its fall has survived to thepresent, the year in which the dead tree fell can be dated precisely. Another approach is to use fallen boles as "date-lines". If a tree fell in 1921, all trees that pass under its bole must have fallen in 1921 or earlier, and all the trees that pass over the bole must have fallen in 1921 or later. Each stem is an individual case in which the various lines of evidence are pieced together in the most coherent way. Usually the year that the tree died becomes evident from these analyses so that its lifespan and individual growth record can be extended back in time from this date.

An example of the application of this technique should give an idea of the type and amount of information that can be obtained. The example comes from the culled woodland section of the Pisgah Forest outside the Harvard Tract (Figure 2). The paper birch (Betula paperifera Gray) grows in the center of the sprout crown and minimally dates its death to 1935. No bark is found under the place of germination of the paper birch, so these sprouts were probably dead for some time before the paper birch germinated. Saw lines indicate that logging is one possible agent of death. However, the sprouts were anatomically identified as chestnut (Castanea dentata Marsh), so death was probably caused by the chestnut blight (Endothia parasitica) and the time of death can probably be estimated from local newspaper accounts of the parasite attack. The death of the parent tree can be dated from the ages of the sprouts. The size of the parent tree is estimated from the sprout crown's inner circumference.



Figure 2, Paper birch growing in the center of a crown of salvaged chestnut sprouts. (This location is in the culled woodland section of the Pisgah Forest, outside the Harvard tract.)

Using the larger growth rings from wood fragments of the parent tree, a conservative estimate of the parent's age can be obtained. Thus, the trees that grew on this spot can be traced back three complete lifespans.

Field Methods

To accurately map stems and stem fragments so as to be able to date their time of death (see p. 3) a string grid system was established with coordinates at 11' intervals in the 66' x 66' square. Because of the volume of living, dead, and rotten material on the quadrat the collection of data was divided into three arbitrary parts treating first the living forest, second the dead but unburied material, and third the dead material buried in the forest floor.

For the living vegetation, the following data were collected for each tree. First, the tree was numbered. Then its species, location in the quadrat, height, diameter (at breast height, outside bark), origin (seedling or sprout), place of germination, and past growing conditions (any evidence of injuries or diseases, evidence from branch scars of its past branch morphology) were examined and noted. An increment core at a height of 9 inches was taken from every tree to permit the determination of age and growth rate. Ten trees of each species were cored at ground level and at 9 inches to determine the number of years by which the cores taken at 9 inches were short of the true age of the tree (estimated at the stem base). The averaged differences between samples from 9 inches and ground level were 6 with an average deviation from the mean of \pm 3 years for hemlocks, 5 ± 2 years for beech, 3 ± 1 years for black birch and 3 ± 1 years for red maple. One of these corrective values was then added to the core count of each tree in order to get the total age of each tree.

Information on location, species, size, origin, and injuries was likewise collected for the dead, unburied trees. In addition the fallen position and direction of each tree was mapped. I then determined the year of death for each tree as accurately as possible (see page \(\text{?} \)). Finally, a cross-sectional disk from low in the bole of each tree was cut so that its age could be determined and its growth rings could be examined. An age correction for the height of the disk above the stem base was calculated and added to these readings whenever necessary.

To discover old buried boles and old windthrow mounds, the quadrat was raked clean of all litter and duff. Then the entire organic layer of the soil was systematically and very carefully overturned until a fragment of wood or charcoal was located. A sample of each remnant was collected so that anatomical identification of species and possible age and size estimations could be made in the laboratory. The remains of the stem were followed in the soil as far as possible, and their position precisely mapped. All possible information concerning the size of the tree, date of fall, or cause of death was collected.

I want to clearly point out the limitations of my data before proceeding to the analysis. The investigation of the dead trees depends on the detection and evaluation of dead and rotten wood fragments. Little information is available on decay rates but they must vary with (among other things), the micro-conditions around the fallen tree, as well as the amount of time decay has been active (McFee and Stone, 1966). Hence, if I discover a very old tree, it may be because it has been in a position subject to little decay or very large. Therefore the record of the past vegetation probably becomes less complete the further it extends back in time.

Laboratory Methods

The laboratory work consisted of two different activities: 1)

determination of age and growth rates whenever this was possible, and

2) identification of species from the small wood and charcoal fragments
found in the forest floor (using anatomical characteristics of the wood

structure).

Ages and Growth Rates

The increment cores of the living vegetation and the cross-sectional disks cut from fallen, unburied trees were examined for ages and growth rates. The age of each tree was counted 3 times to obtain an average age and estimated error. The entire growth radius was examined for major, abrupt suppressions or releases in growth. Criteria were established to determine their occurrence. For a suppression or release to be recorded, a changed growth rate had to extend for at least four consecutive growth rings. Also only changes that were more than double or less than half the previous growth rate were recorded. In practice, only an increase of 2.5 or more over the previous rate was recorded as a release and only a decrease to 0.4 or less of the previous rate was recorded as a suppression.

When the growth rings were indistinct due to rot, the material was specially treated. Increment cores were stained with safranin and viewed under transmitted or reflected light (New some, 1963). This was often necessary for hardwoods, less so for conifers. Rotten cross-sectional disks were cut with a high quality cabinet-maker's planar saw and a readable surface was easily obtained.

In several instances a portion of the disk had rotted away completely and the number of years missing from the radius had to be estimated. This was done by estimating the missing portion of the radius from the arc of curvature of the disk. This distance was divided by an average ring width obtained from the readable surface to give an estimate of the number of years missing. Throughout this study estimates are used as supplimentary information and no interpretations are based solely on them.

Wood and Charcoal Fragments

Wood and charcoal samples were embedded in paraffin and 10 micron sections were prepared. Species identification was made by using the anatomical characteristics of the wood structure (Johansen, 1940; Brown and Panshin, 1940; Sen, 1963). When a fragment was sufficiently large for an arc of curvature to be calculated, a minimal size for the tree was estimated. Minimal ages were counted or estimated whenever possible. Since I did not know how much wood had rotted from the outside of the fragment, a maximum estimate of size or age could not be made. Identification of the charcoal fragments is not completed, and this information cannot be included in the following presentation.

All this information was assembled into two master diagrams, the first shows tree growth over time while the second shows all stem locations on the plot. The diagrams are presented and explained in Appendix A. Statements made and figures presented in the results are all extracted from the information in these diagrams.

RESULTS

The results are given in 3 main parts: a) the establishment of the general history of the forest on the quadrat, following it back from what we see now to what can be detected from the available older evidence, b) a closer look at the changes that the forest has undergone to see what can be understood about the changes that take place over time in tree populations, c) a final synthesis to draw together the main conclusions of sections a) and b).

General History of the Forest on the Quadrat

The living forest on the quadrat is a very dense growth of small trees (261 trees per tenth acre). Its structure is summarized in Table 1. Hemlock (Tsuga canadensis L.) is well represented in all the 1" diameter size classes of the forest. Thus, it is the most frequent large tree as well as the most frequent small stem and is well represented in all the intermediate size classes. On the other hand, black birch (Betula lenta L.), although very well represented in the intermediate sizes, is not represented in the smallest classes at all: it is no longer entering the quadrat. Red maple (Acer rubrum L.) has more individuals in the intermediate sizes than the smaller: its entrance into the quadrat appears to be slowing down.

On the forest floor, there are many windthrown trees: 10 of these fell in 1938, 6 in 1921, 3 in 1908,

Table 1. Stand Table of the Forest in 1967.

Diameter Class (dbh)	Total per class	Hemlock	Black Birch	Red Maple	Beech	Sugar Maple	Paper Birch	Striped Maple
above 6" tall below .5" dbh	26	24		2		49 czywowa sowonie o wodanie do nie obsząż		1944 (Annie 1944) (Annie 1964)
.5"-1.0"	24	11	4	6	3			
1.0"-2.0"	74	23	21	22	5	3		
2.0"-3.0"	54	16	19	13	4	1		1
3.0"-4.0"	33	9	12	7	3		2	
4.0"-5.0"	20	6	7	4	3			
5.0"-6.0"	9	7		1	1			
6.011-7.011	10	6	4	2	2			
7.0"-8.0"	4	1			3			
8.0"-9.0"	1	1						
9.0"-10.0"	2	1			1			
10.0"-11.0"	1	1						
11.0"-12.0"	2	1			1			
12.0"-13.0"	1	1						
Total per species	261	108	63	57	26	4	2	1

k

3 in 1898 (this includes all windthrown trees that had germinated in the quadrat as well as those that germinated outside the quadrat but fell into it). The time of death of all these trees was usually dated by a combination of observations: by trees growing on the windthrow mounds, by the fallen tree that is to be dated passing over or under other dated windthrown trees, by the year in which they injured other living trees (see p. 7). Because times of tree fall are clustered into four separate years, rather than a few trees falling every year, four windstorms probably affected the vegetation on the quadrat in the course of forty years (1898-1938). Weather records (USDA Climatological Data Annual) show that the following very destructive storms have occurred in the Pisgah Forest area: 1938 hurricane: 1921 tornado: windstorm in February, 1909 (there is a one-year inconsistency between the evidence on the quadrat and the information gathered from the weather data,) wind and rain storm. August 1898, These storms were probably responsible for the disturbances to the vegetation on the quadrat. Table 2. summarizes by size class the composition of the forest as it was in 1907 before 3 of the storms. This year was chosen because it is one of the earliest years for which all strata above the advance growth (above 6 inches tall) are comprehensively represented in the data. The forest was dominated by white pine (Pinus strobus L.) and hemlock with their distributions intermixed (see distribution map of old growth stand in Appendix).

Figure 3 shows the approximate heights of the trees that were growing on the quadrat in 1907. No definite strata within the forest structure can be recognized. This is primarily because there is a continuous gradient in the heights of the hemlocks. When we look at the species,

we can see that all the white pines were among the tallest trees (ranging from 79 feet to 101 feet). In contrast, beech stems vary from 6 feet to 35 feet. The two paper birch on the quadrat were 53 feet and 66 feet high while, as I have stated, hemlock was represented by stems that covered almost the entire height spectrum. Its representation in each class was more or less constant: 2 trees in the smallest class, 3, 2, 3, 4, 3, 3, in successive heights classes and, finally, 6 trees in the 75 foot to 85 foot class. Thus, with the exception of hemlock, the stems of each species fall within a different but narrow range of heights. I also infer from the Figure that the top surface of the crowns of the dominant trees must have had an uneven two layered appearance with white pine crowns projecting above a rather dense layer of hemlock (6 trees in the 75 foot to 85 foot height class).

A comparison between Tables 1. and 2. shows how the pre- and post-windstorm forest differs. The largest size class shown in Table 1. is 12.0" dbh whereas it is 34.0 dbh in Table 2. Also the two forests differ somewhat in species composition. They share some species, i.e. hemlock, beech (Fagus grandifolia Ehrh.), paper birch; but the present forest also contains red maple, black birch, sugar maple (Acer Saccharum Marsh.), striped maple (Acer pennsylvanicum L.) and contains no white pine. I cannot say how much of the advance growth of the pre-storm forest survived to the present. Some idea of its nature can be obtained from the work of Branch, Lotti, and Daley on the Harvard Tract in 1929 (Harvard Forest Records). On similar sites to this quadrat they reported the advance growth to be abundant (on an average, 500 stems per tenth acre) with

Table 2. Stand Table of the Forest in 1907.

Diameter Class (dbh)	Total per class	Hemlock	White Pine	Beech	Paper Birch
Above 6" tall					
below .5" dbh	4	3(3)		1(1)	
.5"-1.0"	6	5(5)		1(1)	
1.0"-2.0"	4	3(3)		1(1)	
2.0"-3.0"	2	0(0)		2(2)	
3.0"-4.0"	3			3(2)	
4.0"-5.0"	_			~ (-)	
5.0"-6.0"	1			1(1)	
6.0"-7.0"				- \ - <i>/</i>	
7.011-8.011					
8.0"-9.0"	2	2			
9.0"-10.0"	2	2			
10.0"-11.0"	1				1
11.0"-12.0"	3	2			1
12.0"-13.0"					_
13.0"-14.0"					
14.0"-15.0"	4	4			
15.0"-16.0"	2	1	1		
16.0"-17.0"		_	_		
17.0"-18.0"					
18.0"-19.0"	1	1			
19.0"-20.0"	1	1			
20.0"-21.0"	3	2	1		
21.0"-22.0"	_		_		
22.0"-23.0"					
23.0"-24.0"	1		1		
24.0"-25.0"			-		
25.0"-26.0"					
26.0"-27.0"					
27.0"-28.0"					
28.0"-29.0"					
29.0"-30.0"					
30.0"-31.0"	1		1		
31.0"-32.0"					
32.0"-33.0"					
33.0"-34.0"					
Total					
per species	41	26	4	9	2

The numbers in parentheses are the number of trees in each size class that have survived to the present.

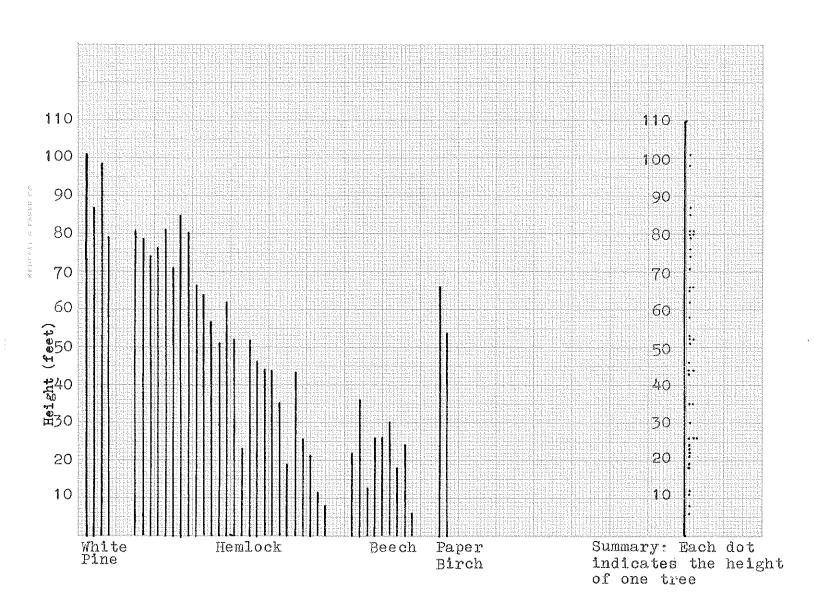


Figure 3. Estimated heights of the forest trees in 1907. (Each line represents one tree.)

hemlock reproduction comprising 60 per cent of this. The advance growth of the present forest although still predominantly hemlock by composition is much less abundant (26 stems per tenth acre). From all these comparisons, I conclude that the windstorms have brought about a radical change in all major strata of the forest in the course of forty years.

The fact that white pine was consistently larger than the hemlock suggests that the tree species may have originated at different times. We can answer this question by examining the age structure of the old growth forest. All six white pines (all of which project through the top surface of the hemlock crowns in the old growth stand) became established within 20 years of each other (1667-1687) with five of them becoming established in the first eleven years. If any white pine germinated after 1687, it did not grow large enough to leave traceable remains in or on the forest floor.

Eleven of the fourteen hemlocks that formed the dense top surface of the crowns (or 80 per cent of the hemlocks in this layer) germinated within thirty-seven years (1665-1702). Thus the two layered upper crown surface of the old growth forest was essentially produced by trees germinating within a thirty year time period. Branch, Lotti, and Daley found a similar age structure in other parts of the Pisgah Forest when they completed their stump analysis in 1930 (Harvard Forest Records).

The growth rings of the white pine and hemlock that germinated between 1665 and 1690 are consistently very large for the first 15 or 20 years (an average of 3.1 mm. for white pine, 2.4 mm. for hemlock). Because of the even-age of the white pine, and the initially large growth rings of

all trees that germinated during the first 25 years, and because there is no evidence that any large trees grew on the quadrat between 1665-1700, I believe these conifers were part of a post-disturbance stand that came up in the open following an environmental catastrophe that occurred prior to 1665.

There is other evidence about this environmental catastrophe. every part of the quadrat, charcoal fragments were found in the organic layer of the soil, and always in the lowest part of the humus layer, directly above the mineral soil (see Figure 3, in which the charcoal deposits are outlined by pins). In six places these charcoal deposits were so large that they could be traced along the forest floor in broad continuous lines, extending up to 25'. These would appear to be charred boles lying in the forest floor. All but one of the fragments were thoroughly charred. Three fragmented boles were charred to the center. I conclude that a very severe fire occurred in this area; that it was intense enough to completely char many of the trees on the quadrat and that it completely removed the organic layer of the soil in many places so that the present organic layer post-dates the fire. Furthermore, this fire can be dated. The large trees of the old growth stand were cut cross-sectionally at intervals along their boles to check for fire scars. On no occasion was any evidence of fire found on these trees. Beneath the root butts of four out of seven wind thrown trees, I found small amounts of charcoal. Both lines of evidence indicate that the fire occurred before the white pine and hemlock germinated. Therefore it predates 1665.



Figure 4. Charcoal deposit from burnt tree located in the bottom of the organic horizon. (Pins outline deposits.)

The charred logs are remnants of the pre-fire forest (not yet analysed). However, it is interesting that many of the trees were burnt to the core. It seems unlikely that living trees would have burnt so intensely. Thus, these trees were probably dead and down at the time of the fire. We know that a severe hurricane passed through this part of New England in 1635 (Channing, 1939), so it is tempting to speculate that the living forest was blown over at this time. The twenty year period between the hurricane and fire would allow the fallen trees to dry sufficiently to be almost completely consumed by the fire. This is not an unreasonable hypothesis since a major fire hazard also existed for some years following the very severe 1938 hurricane (Brooks, 1939).

Therefore in the quadrat's history there have been two radical, abrupt changes in structure brought about by environmental catastrophes. After each kind of catastrophe, a distinctive forest has developed. The post-fire forest was an even-aged hemlock-white pine stand. It gradually and autogenically evolved into an old growth conifer stand. The post-windstorm forest that came up after 1938 is a hemlock-black birch-red maple forest and also appears to be undergoing structural change. This sequence of events permits a study of the behaviors of tree species populations in a forest over time: the subject of the next section.

Behavior of Forest Tree Species:

Because of the differences in pre-and post-windstorm forests, this analysis can conveniently be divided into two parts: the young post-fire forest and its development into an old growth stand, the young post-windstorm forest (there is, of course, some overlap as already indicated).

The Post-Fire Forest

The behavior of each species population in the post-fire forest can be studied in considerable detail.

Apparently, all the white pine became established within twenty years (1667-1687). This perhaps indicates that habitat conditions during the period 1665-1687, were very different from those that followed. As I have shown, the fire probably exposed the mineral soil over much of the area and because of its severity must have killed any living vegetation at that time. Jones (1945), Lutz (1930), Maissurow (1941), Spurr (1954) all suggest a post-fire origin for white pine in pre-settlement forests, but present little or no evidence supporting their claim. Although the evidence presented here is far from conclusive, it does suggest that this theory is probable.

Cline and Spurr (1942), Oosting (1956), and Marshall (1927) propose that white pine is a pioneer species and that hemlock will only germinate and grow successfully after a canopy is already partially formed. Thus, they thought hemlock was a second stage in succession. Yet, the evidence from the quadrat presents a clearly different view. The white pine and hemlock both came up together; no successional relationship was expressed. Furthermore, the first fifteen or twenty years of growth are consistently the most rapid years of growth for those trees of both species that germinated between 1665-1690. Thus, it seems that both species are well adapted to the invasion of burnt ground.

Since both species originated at about the same time, we might expect to find a uniform top surface to the crowns of the old growth stand. Yet at the time of its final distruction in 1938 a two layered

crown surface existed, white pine consistently projecting through a rather dense hemlock crown surface. Because the stems of both species are approximately the same age, the two layered crown surface probably resulted from a difference in growth behavior. In fact, a difference in growth behavior for these two species is shown in Figure 5 as annual changes in diameter. Clearly, the white pine grew faster than the hemlock during the entire time they were together on the quadrat. Thus, the white pine formed the upper layer of the canopy, and the hemlocks a lower layer. (The height of each tree at the time of death is indicated in a column at the lefthand side of the Figure.)

At its final destruction in 1938, 90 percent of the forest crown top surface was made up of trees that had germinated within 37 years of each other (from 1665 to 1702). Thus, for 236 years the dominant tree layer of the forest was relatively quiescent as regards compositional changes. The remaining 10 percent of the canopy composition consisted of four hemlocks and three paper birches which germinated beneath the canopy and grew into its lower reaches, during the 236 years. Thus, it seems that a) succession had little effect upon the composition of the dominants in this old growth stand during the course of its existence, b) the composition of the dominant trees could best be understood as a product of a severe fire and its subsequent undisturbed development. In short, after 236 years the impression that this fire disturbance made on the forest was still very apparent.

Because the surviving hemlocks are of many ages, this species must have germinated continuously under the canopy. Furthermore, it seems

to have occupied all 1" diameter classes and slowly entered the lower part of the dominant forest crown surface (Table 2 and Figures 3 and 5). This agrees with the data of Branch, Lotti, and Daley (1929), who also found hemlock in all size classes and particularly abundant in the reproduction beneath canopies of hemlock and white pine in the Pisgah Forest.

Beech first appeared in 1815. Since then and until the final became successfully established destruction of the canopy in 1938, it reproduces at a slow and constant rate of approximately one tree per tenth acre every decade. All these trees originated under a mature canopy which was not disturbed until 1898.

Judging from their present heights, these stems always remained well beneath the canopy in the intermediate stratum of the forest (see Figure 3).

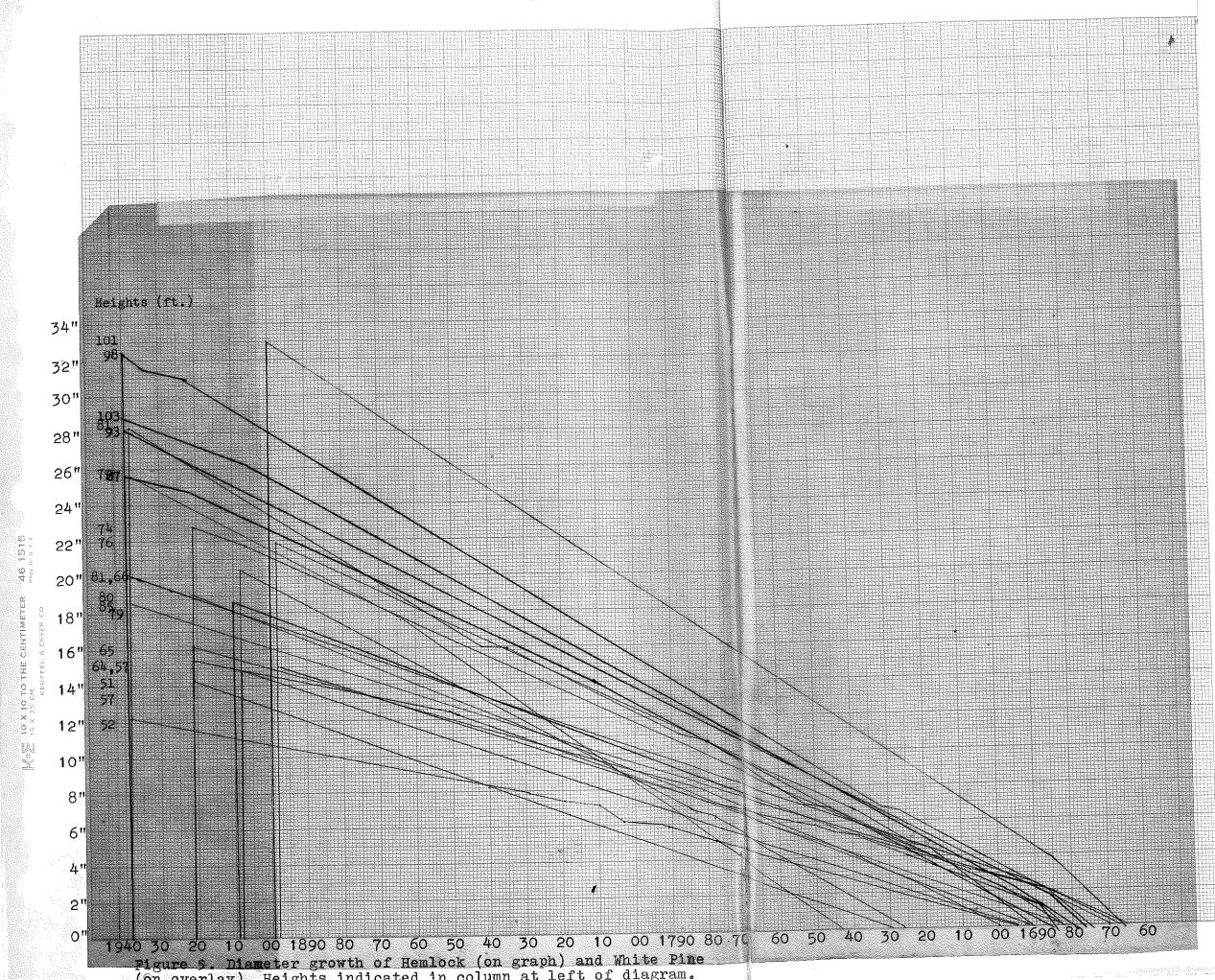
During the period 1790 to 1860, three red oaks (Quercus borealis Michx.) entered and disappeared beneath the undisturbed dominant tree layer. Those stems that became established grew to be 5.2", 6.1", and 8.5" dbh. Measurements of stem length shows that these trees never grew tall enough to enter the canopy. Their reproduction must have been slight, for when they died out there were no other red oak to take their place. Their entrance and disappearance remains an enigma. There is no evidence of disturbance or disease that might have caused their death. They seemed to germinate independently under the maturing canopy, grow successfully for a time, and die without any evident reason for it. All this happened without any other major changes taking place in the forest on the quadrat.

Three paper birches became established between 1742 and 1770. No others were found on the quadrat until the windstorm disturbances.

These three trees grew to be fairly large and reached the lower layer of the

canopy, judging from their heights at the time of death. At their death (2 paper birch were blown over in 1921, one was blown down in 1938) they measured 13.0", 12.8", and 13.7" dbh. This is the only new species to enter the canopy over the 236 years. Paper birch is often regarded as a pioneer species, because it is believed to be one of the first to invade a barely habitable site (Fowells, 1965). However, here it entered beneath an established canopy. One possible explanation of this is that all 3 paper birches germinated on very shallow buried outcrops (the organic cover on these outcrops ranged from 3" to 5" in depth). Perhaps these outcrops represent microsites made inacessible to tree species when the fire destroyed the organic layer covering them. However, after 80 years sufficient litter may have accumulated for paper birch, but not other species, to germinate there.

Two important conclusions can be derived about population behavior from the old growth forest. First, the process of autogenic change has produced no ordered sequence of succession between the fire prior to 1665 and the windstorms of the 20th century. Indeed, the composition of the dominant trees has remained essentially the same throughout this period. In the understory several new species have become established (red oak later dying out). These new establishments are the only possible successional activities taking place in the forest. These are minor and show little directional development. Second, each tree species appears to germinate, grow and die in its own distinctive manner. Better information on this can be obtained from the living forest for which more complete data are available.



The Present Forest

I studied three aspects of the growth of the living forest trees

(all stems over 6 inches in height were studied): the time of germination

for all living stems, their diameter growth rate, their spatial distribution

on the quadrat. Interestingly, different modes of behavior were expressed

by the different species and therefore these analyses are presented

according to species. How each aspect was studied will be explained

separately.

First, I wished to develop a diagram to illustrate the number of successful germinations that occurred each year (Figures 6b, 7b, 8b, 9b). To do this I placed along the abscissa a time scale extending from 1967 to 1890. On the ordinate are the number of successful germinations (those germinations that survived to the present). The same conclusions were reached regarding successful germination behavior of each species whether or not the corrective value were added to the ages of the trees. (This was added to each tree because the core for age determination was taken at 9 inches in height along the tree, see p. 10). These observations were double-checked to make sure that the corrective values had not created an artifact in the data.

Secondly, I created a diagram of tree diameter growth over time (Figures 6a, 7a, 8a, 9a). Here I have used diameter as a convenient index of growth. As with the germination diagram, the abscissa is a time scale. On the ordinate is presented stem diameter size (diameter at breast height, outside bark). Each line in the diagram represents a tree. The flow of the line represents the approximate growth

of the diameter of that tree through time. An abrupt fall of the line to zero represents the death of the tree. A change in the slope of the line indicates a major release or suppression (see page 12). Thus, from this diagram, the growth of any tree can be studied by examining its line, and the development of the entire forest can be studied by examining all these lines together. For added information, the tree heights in 1967 are recorded in a column at the left of the diagram.

Thirdly, I wished to study the spatial distribution of the living vegetation (Executed at 1, 5, 6). The stems are randomly distributed over a given area, they can grow successfully on any given point of that area equally well. If the trees are clustered or regular, we suspect that some process is active in determining their distribution (Hutchinson, 1953). So first, I wished to test for randomness in the stem distribution of the vegetation. I did this by comparing the distribution of the present vegetation with a random distribution of the same density derived from Poisson's formula (Kershaw, 1966). Using a chi-square test, if the difference between these two distributions is of no statistical importance, the vegetation is randomly distributed. On the other hand, if the difference between these two distributions is statistically significant, such things as sprouting, occurrence of trees on mounds and pits, are studied as possible explanations for this departure. This technique is well explained and adequately evaluated by Kershaw (1966).

and Tables 3-6
Four species are illustrated in Figures 5-8; beech, hemlock, red
maple, black birch. Other species were represented in the data as follows:

3 stems of sugar maple, 2 of paper birch, and 1 of striped maple. These
species are so occasional in the quadrat that their behaviors cannot
be studied.

Table 3. Rigumaxxx. The distribution of beech.

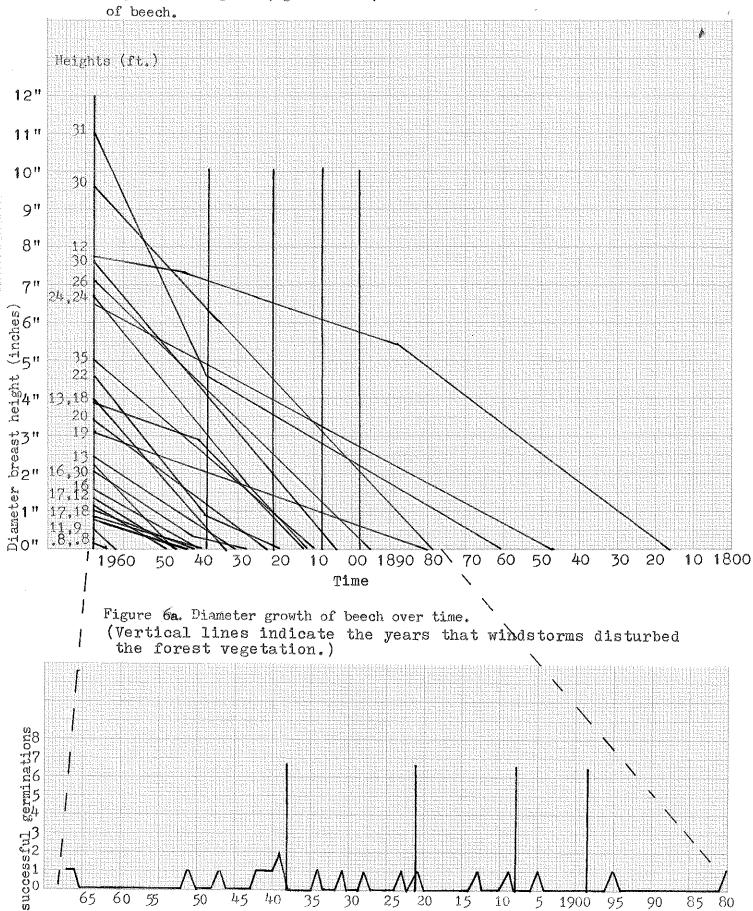
(Samples were taken with a 4 x 4 quadrat on the 66 x 66 quadrat map. In preliminary testing, this was found to be the best size for sampling, large enough to sample the vegetation adequately and small enough to expose pattern.)

Samples	containing	X	individuals:	Expected Population	Observed Population
		zer	0	627.37	617
		one		70.52	67
		two		3.96	6

Chi-square of the deviation between these two
populations (at 2df):
1.396

Conclusion: The chi-square number means that twenty-five times out of a hundred this much deviation between the observed and expected distributions will be due to chance alone. This means that there is a 1 in 4 probability that the distribution of beech is random. Using the 0.01 significance level employed here, there must be a 1 in 100 probability (or less) that the deviation between the two distributions is due to chance alone before the observed distribution is judged to be non-random.

Figure 6. The growth, germination, and distribution



The successful germinations of beech since 1880. (Dash lines indicate correspondance of time scales in Figures 5a and 5b.)

Time

Beech: 45 percent of the beech now living on the quadrat germinated within the five year periods that followed each of the four windstorm disturbances (Figure 6b). These twenty years represent 27 percent of the total time period since the first windstorm in 1898. Thus, for beech there is a slight increase in the rate of successful germination after each disturbance. This is clearest after the 1938 hurricane, but even here the increase is slight. Five of the fifteen trees that were growing on the quadrat at the time of the disturbances show a marked change in growth rate that approximately coincides with the windstorms (Figure 6a). There were three suppressions in diameter growth (one tree having been suppressed twice) and three releases. However, two thirds of the beech (ten of the fifteen trees) exhibit no major or abrupt changes in growth rate around the time of these disturbances. Finally, beech is the only species that is randomly distributed on the quadrat (Table 3). Since I can find no process actively determining the distribution of beech I conclude that it appears to be able to occupy any part of the quadrat with equal facility. Because the disturbances have brought about no significant major change in beech's rate of establishment, overall growth rate, or distribution, I conclude that the species is rather insensitive to the drastic changes in habitat caused by such disturbances.

Hemlock: From its germination behavior hemlock seems to have been constantly reproducing in the old growth forest as well as in the new (Figure 7b). In fact from my data and that of Branch, Lotti, and Daley (1929), it appears to have been the predominant advance growth found in the old growth forest. Thus there was a constant supply of seedlings and saplings on the forest floor. When a disturbance occurred, the 1 to 3 year old seedlings were particularly favored (peaks of successful germinations a few years before the disturbances). There is also an increase in hemlock establishment shortly after the time of the disturbances. This is quite different from

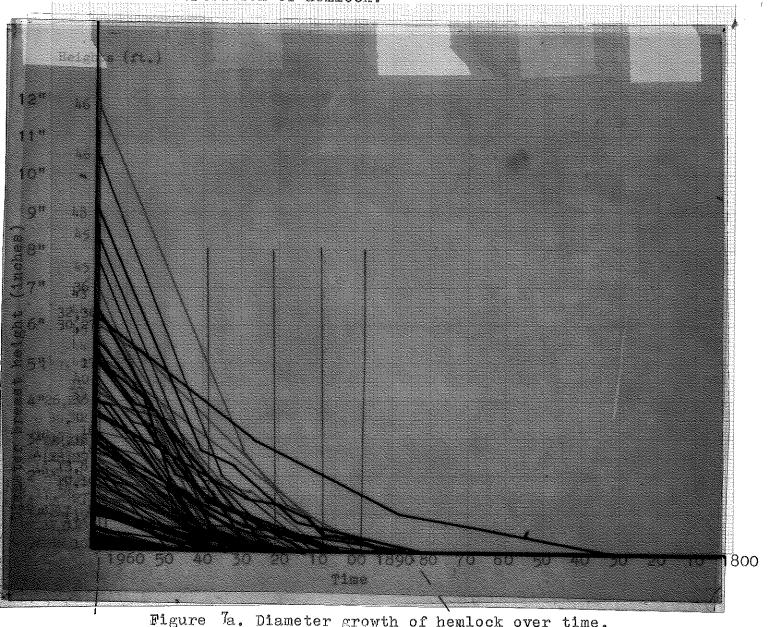
Table 4. The distribution of hemlock.

samples	containing	X	individuals:	Expected Population	Observed Population
		zero		448.34	503
				199.51	122
		two		45.59	48
		thre	ee	6.64	20
		four	r	0.72	4
		Five	2	0.066	3

Chi-square value of the deviation between these two populations (at 2df): 112.5 **

Conclusion: There is essentially no chance that the deviation between these two populations is due to chance alone. Hemlock has a clustered distribution.

Figure 7. The growth, germination, and distribution of hemlock.



7a. Diameter growth of hemlock over time.

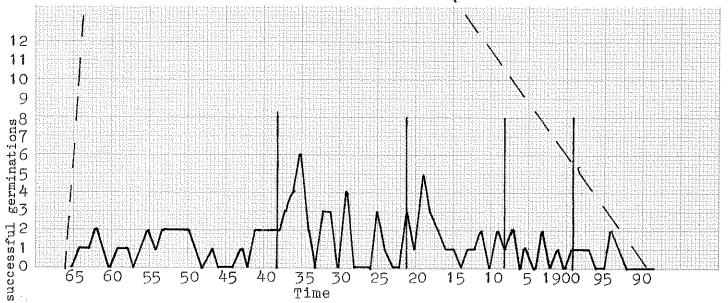


Figure 7b. The successful germinations of hemlock since 1890.

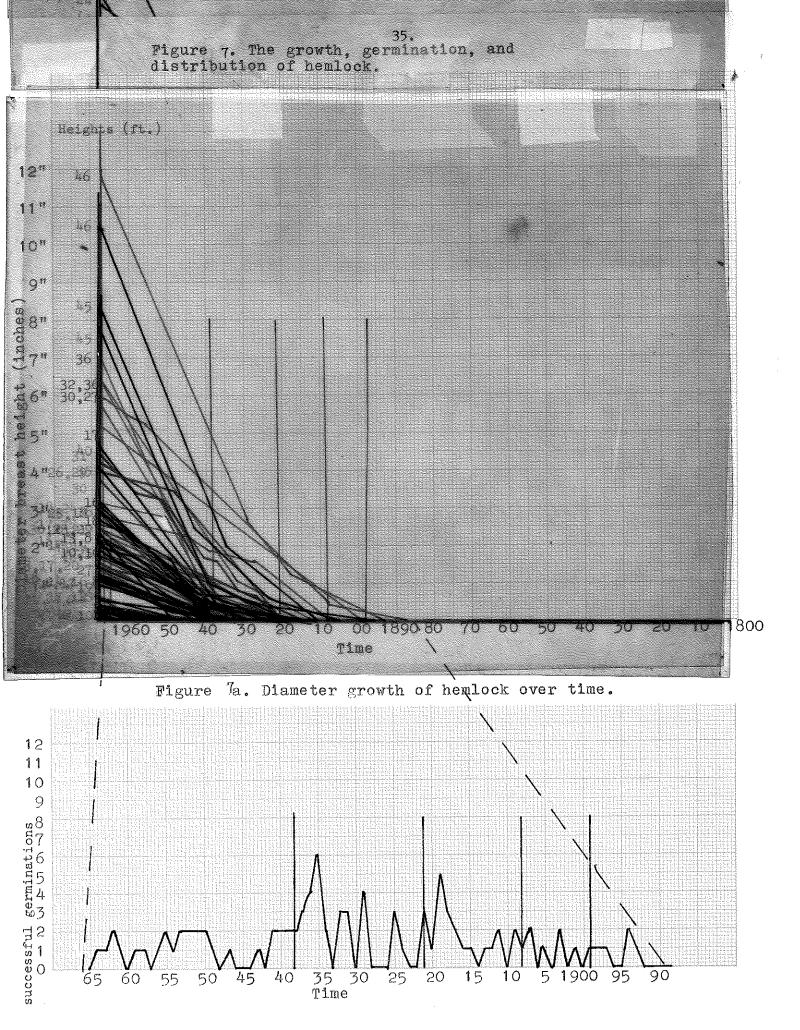


Figure 7b. The successful germinations of hemlock since 1890.

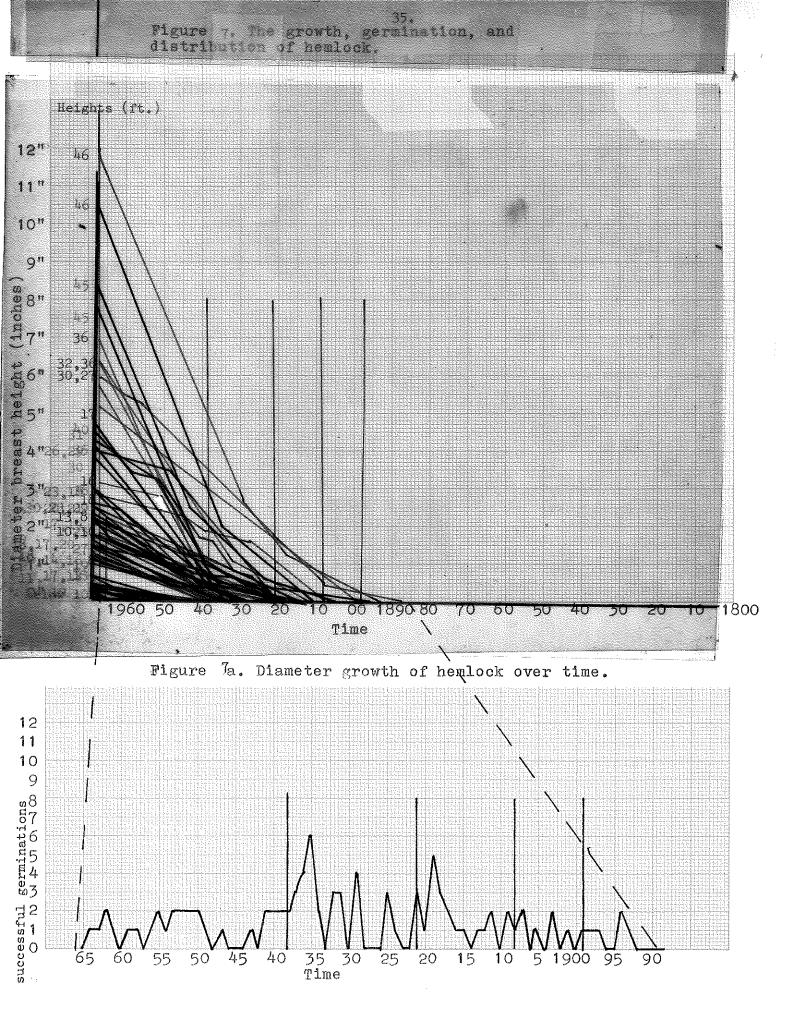


Figure 7b. The successful germinations of hemlock since 1890.

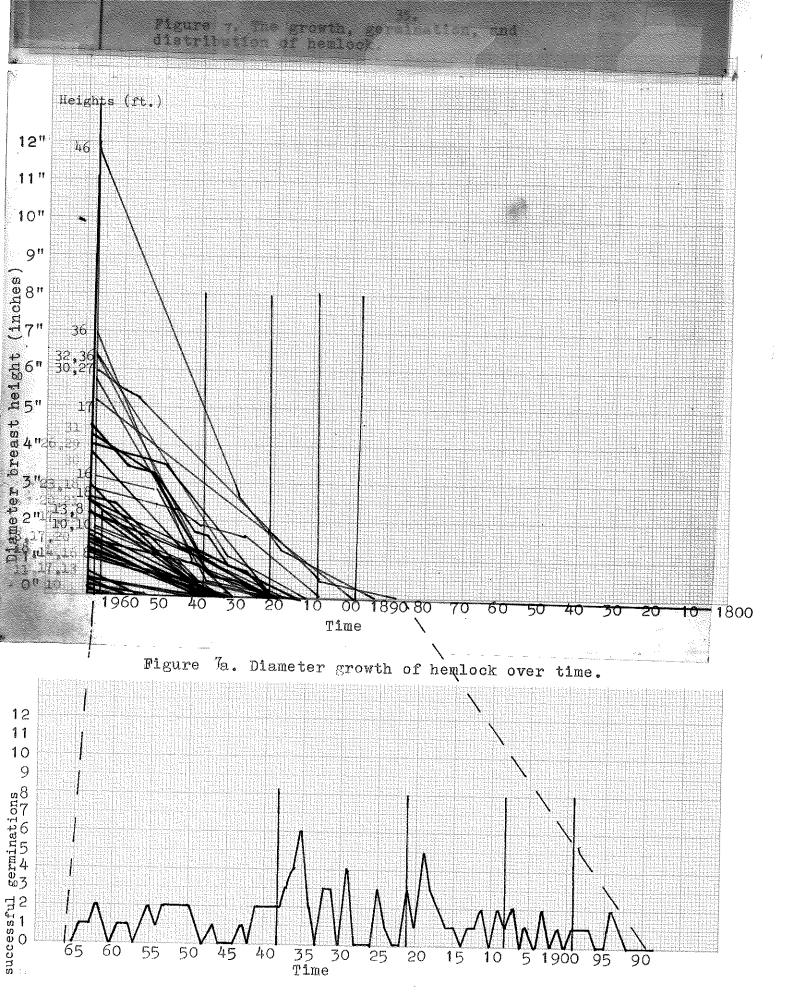
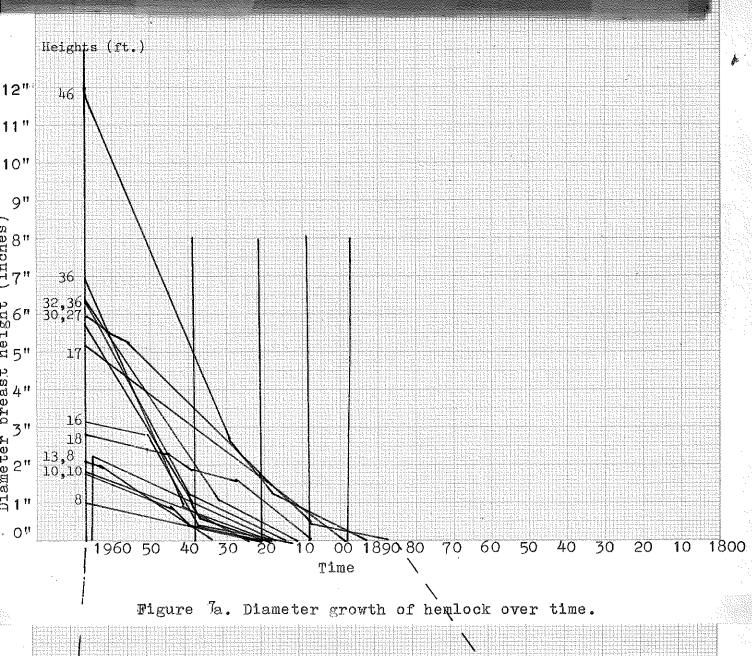


Figure 7b. The successful germinations of hemlock since 1890.



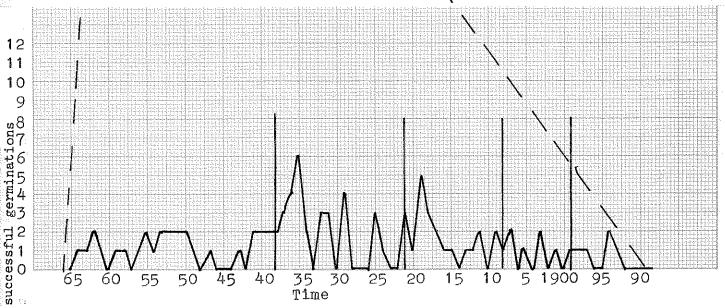


Figure 7b. The successful germinations of hemlock since 1890.

the way beech germinated and is also different from the germination characteristics of black birch and red maple, as will be shown later.

Many hemlock stems were greatly released after the disturbances (Figure 7a). For example, 23 percent (14 out of 61) of the stems that had germinated prior to 1938 were released after the hurricane, 17 percent (6 out of 38 stems) were released in 1921, and 23 percent (3 out of 13 stems) in 1909. Thus, stems that were suppressed for a long time are now among the largest trees presently on the quadrat. A number of hemlock were suppressed (four stems in 1938) often associated with injury by falling stems. However, most of these recovered after a few years and sometimes showed a marked release in growth rate. Thus, hemlock has considerable ability to recover from suppression. Also, as the new canopy closes, the growth rate of the hemlock reproduction decreases proportionately. This means that the growth rate of hemlock, unlike that of beech, is sensitive to changes in canopy closure.

Finally, we can see that hemlock's distribution is very clustered (Table 4). It seems that the freshly fallen trees occupy much of the quadrat and thereby restrict the living hemlock to the remaining free areas. This idea might be tested by eliminating the area occupied by fallen trees from the sample, and testing for non-randomness once again. The non-randomness of hemlock also may partially be explained by sprouting since, contrary to current silvicultural thought (Fowells, 1965), hemlock produces root sprouts: in the quadrat. In one case nine sprouts were produced from one disturbed root.

At this point it is interesting to compare hemlock's behavior with beech's. Hemlock reproduces constantly; beech does not. The establishment of hemlock increases greatly after the disturbances; beech shows

little increase. Hemlock's growth rate is very sensitive to the condition of the forest canopy; beech's much less so. Finally, beech has a random distribution while hemlock is very clustered. Thus, each species has a distinct and different germination pattern, growth behavior, and spatial distribution on the quadrat.

Red Maple: We know that there were disturbances in 1908 and 1921 which partially opened the canopy and another in 1938 which destroyed it completely, since then the canopy has been gradually closing once more. There is an interesting parallel between the openness of the canopy caused by the disturbances and the time red maple established itself (Figure 7b). The first of fifty-three red maples appeared in 1910; but it was between 1926 and 1952 that the most intense period of establishment occurred. Thus, it seems that red maple took advantage of the openings that were caused by the windstorms disturbances.

An explanation for the opportunistic establishment of red maple is partially provided by its spatial distribution which is clustered (Table 5). Almost a third of the young stems (18 out of a total 57 red maple stems on the quadrat) occur in the pits left by wind-thrown trees and other microswales, which together represent only about 9 per cent of the total quadrat area. Thus, red maple seems to be particularly favored by these depressions perhaps because they tend to be higher in moisture (Lyford and MacLean, 1966) and in organic matter content (Stephens, 1955) than the surrounding terrain.

Table 5.4. The distribution of red maple.

two populations (at 2 df):

samples	containing	X	individuals		Expected Population	Observed Population
		zero	o	:	545.17	577
		one		;	135.52	88
		two			16.84	27
		thr	ee		1.40	5
four				0.80	3	
Chi-squ	are value of	E th	e deviation	between	n these	

Conclusion: There is essentially no chance that the deviation between these two populations is due to chance alone.

Red maple has a clustered distribution.

53.49 **

Figure 78. The growth, germination, and distribution of red maple

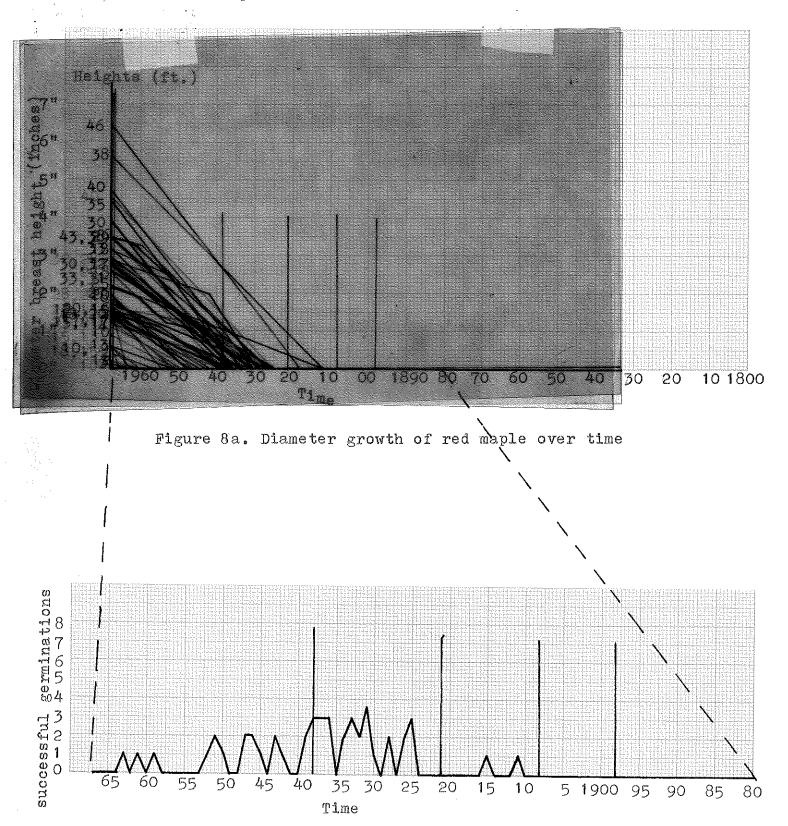


Figure 8b. The successful germinations of red maple.

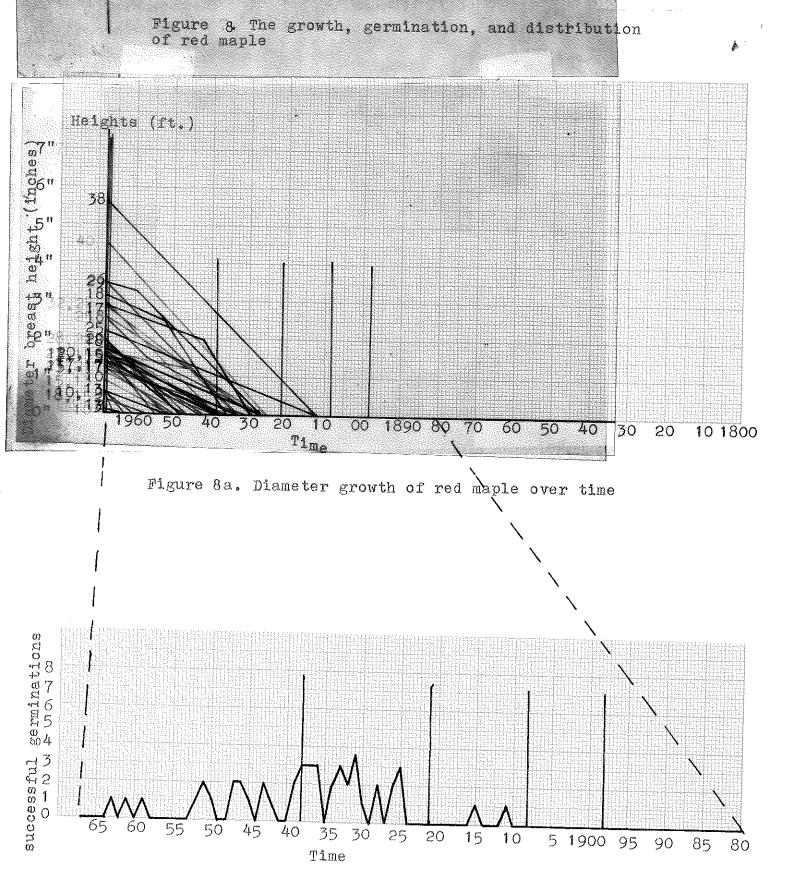


Figure 8b. The successful germinations of red maple.

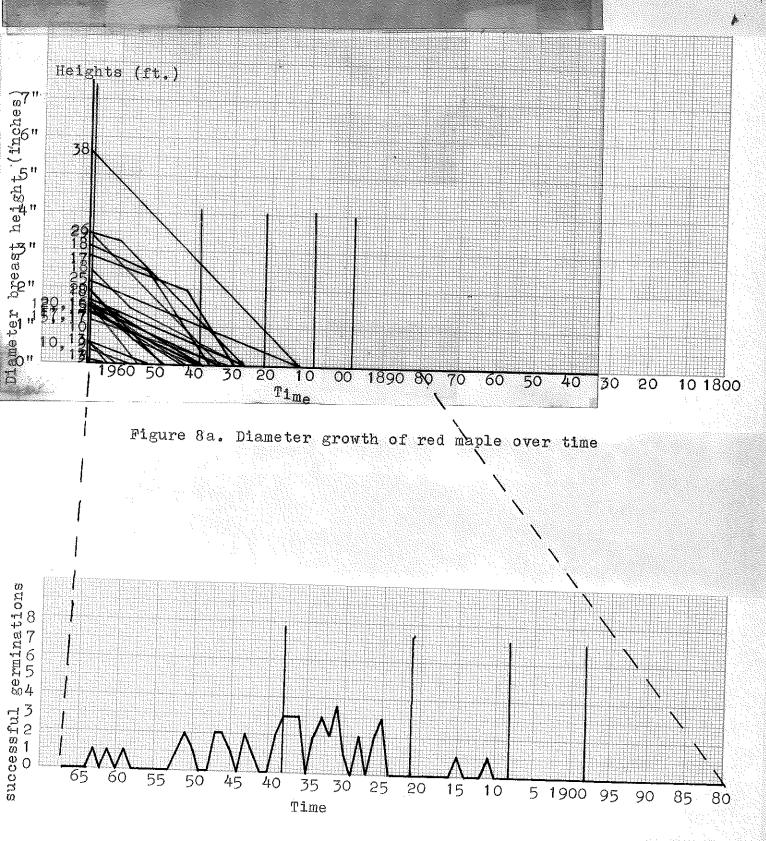


Figure 8b. The successful germinations of red maple.

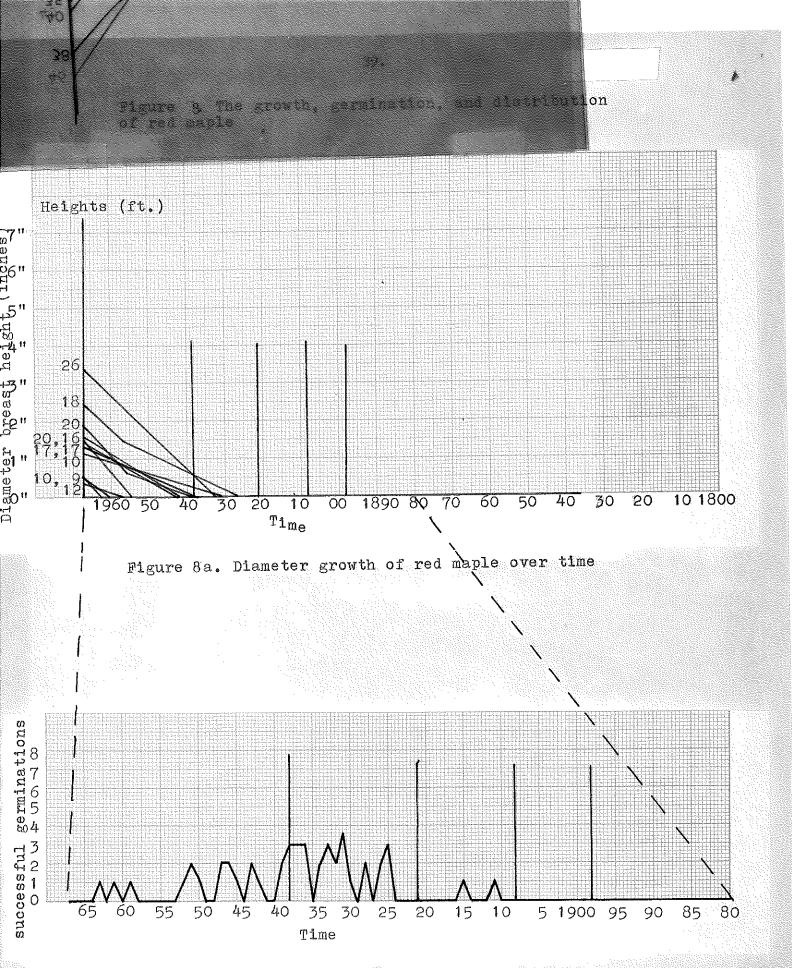


Figure 8b. The successful germinations of red maple.

The distribution of red maples in the pits is one possible explanation for the observed clustering. However, there is also another process active. Of all species on the quadrat, red maple produces sprouts most frequently. In fact, about a quarter of the red maples are of sprout origin (15 out of 57 stems). Since only one red maple sprout occurs in a pit, these two processes concern different stems and together affect a little more than half of all the red maples (33 out of 57 stems).

With the exception of the sprouts, the oldest red maples seem to have the most rapid growth (Figure 8a). This indicates that red maple grows best when it is part of the forest canopy. Trees beneath this developing canopy have a slower growth rate. This sensitivity to canopy conditions is similar to hemlock's growth behavior. In contrast to hemlock stems which germinated before the 1938 hurricane were not released by this opening of the forest.

Black Birch: Nearly half (30 stems out of a total of 63 black birch stems on the quadrat) of the black birch now living on the quadrat germinated less than three years after the disturbances of 1921 and 1938 (Figure 9b). These six years represent only 5 percent of the time that black birch has been present on the quadrat. The successful black birch were often the ones that germinated immediately after the windstorms. In fact this species has now completely stopped entering the quadrat. Thus it is intensely opportunistic and quickly takes advantage of the openings caused by the disturbances. Although black birch and red maple both germinate immediately following the disturbances, the reproduction

Table 6... The distribution of black birch.

samples	containing	Х	individuals:		pected pulation	Observed Population
		zero			19.74	586
		one two three		13	88.01	73
				1	.7.64	29
					1.50	7
		four	£		0.10	4
		five	.		0.0049	1

Chi-square value of the deviation between these two populations (at 2 df): 282.8 **

Conclusion: There is essentially no chance that the deviation between these two populations is due to chance alone.

Black birch has a clustered distribution.

Figure 9. The growth, germination, and distribution of black birch.

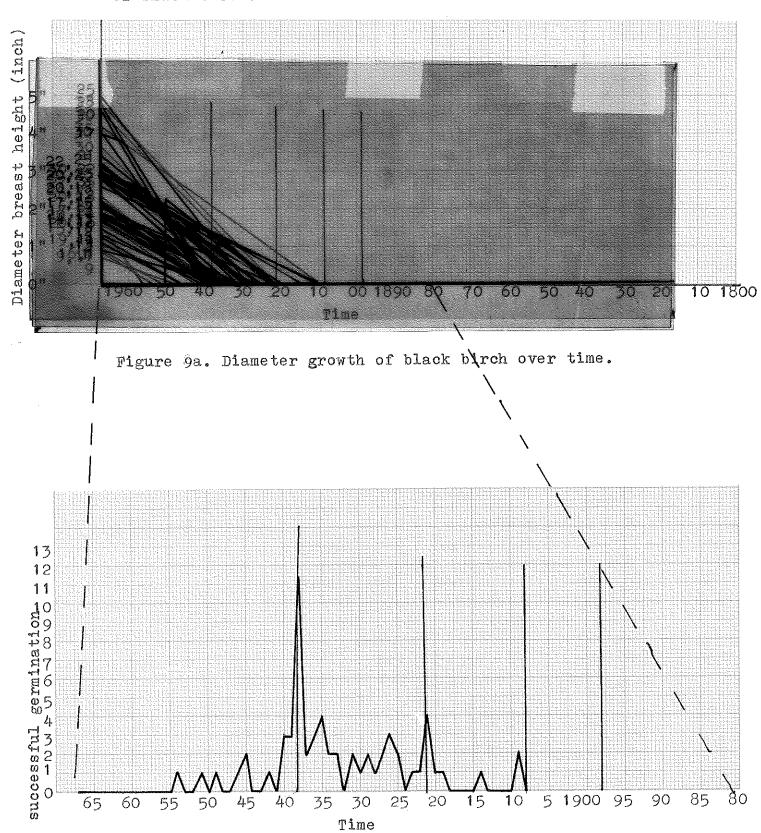


Figure 9b. The successful germinations of black birch.

Figure 9b. The successful germinations of black birch.

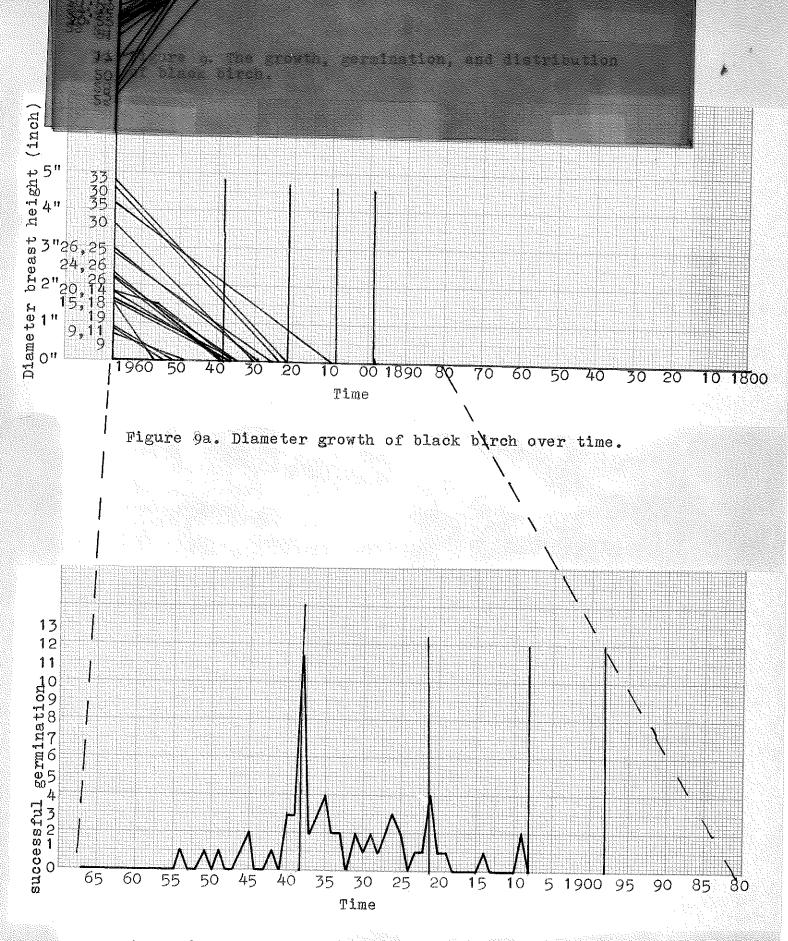


Figure 9b. The successful germinations of black birch.

of black birch is far more abundant. This difference might be partially explained by the fact that black birch has much lighter seeds than red maple and is therefore more rapidly dispersed (Egler, 1954).

The germination behavior of black birch is partially related to its spatial distribution. From chi-square tests, it has a clustered distribution on the quadrat (Table 6). Thirty-two black birch (52 percent of the living black birch) grew on the windthrown mounds although these mounds represent only about 7 percent of the total area. In addition, 13 black birch (21 percent of the black birch) occupy stony outcrops which represent another 11 percent of the total area. Thus, 73 percent of the black birch occur on 18 percent of the total area.

Black birch has the poorest overall growth rate of any species (Figure 9a). This growth rate is also rather constant. In fact, it is the least varied of any, showing no particular sensitivity to its changing environment. The slow growth rate may indicate that the microhabitats occupied by black birch are not ideal for tree growth. In fact, black birch is the only species that inhabits mineral soil mounds and rocky outcrops. These observations are compatible with the view that black birch is a 'pioneer' species (Fowells, 1965).

Conclusions

I conclude that each species population has acted in a distinctive way as regards germination, growth and distribution throughout the history of the quadrat. This is an important conclusion because it explains many characteristics of forest structure, such as the composition of the overstory in the old growth stand, its two layered structure, the composition of the reproduction beneath it, the stem distribution in the present forest as well as its composition, and finally the sizes of the hemlock and black birch in this forest. All these structural characteristics are manifestations in a changing environment of different species behaviors.

DISCUSSION

In order to evaluate a project in terms of the whole field, a researcher must make clear the limitations of his work. The first limitation of this study is that evidence about forest changes becomes less complete as we go back in time (see page 12). Yet, there seems to be no solution to this problem because no available technique can hope to resurrect a complete history when decay has been active for 100 or more years (McFee and Stone, 1966). Secondly, because site influences species behavior and since only one small area could be investigated, the results of this study cannot be generalized. study can only indicate various hypotheses that may be profitably investigated on a regional scale. The smallness of the plot has other disadvantages. Forest conditions outside the quadrat may have influenced vegetation growth within it. For example, a stem recorded as growing in the shade of the mature canopy might have actually received light through a hole in the canopy outside the quadrat. However, these influences could only be active along the edge of the quadrat.

These are the general limitations of the procedure. More specifically, my work was limited by time. First, I did not have time to process the charcoal fragments obtained from the forest that burned prior to 1665. Thus, the quadrat history is not yet complete. Second, an arbitrary criterion was employed to decide whether a growth release or suppression was a major one. Thus, certain details of species growth may have been missed. Bearing these limitations in mind, I will try to evaluate my conclusions and suggest what significance they have for future work.

My most important conclusion is that each species has its own distinct behavior over time, and many aspects of forest structure can be explained as an interaction of these behaviors. This conclusion has bearing on a long term ecological debate. Clements (1916) presented the view that each forest type in an area was a discrete and well defined unit. He believed that each principle species in the forest type was necessary for the survival of the whole: just as each organ is necessary for the satisfactory function of the human body. On the other hand, Gleason (1927), a taxonomist, said that each species acted independently and that a forest type is therefore an arbitrarily bounded mixture of species. It is my belief that Curtis and McIntosh (1950), Curtis (1959), Whittaker (1956, 1960), Whittaker and Niering (1964), and Maycock (1963) provided some crucial evidence to support Gleason's view. They showed that as the environment changed over space each species acted in its own individual way. My evidence indicates that each species also acts in a distinctive, individual manner over time. Both sources of evidence are compatible with the genetic nature of a population. Each individual of a population differs somewhat from the others, but collectively population behavior varies about a mean: each population having a different mean (Srb, Owen, Edgar; 1965).

I have been able to approach the study of forest change without making any a priori assumptions about the nature of forest processes; in essence, I have let the forest speak for itself. This is important because former studies have assumed the importance of either disturbance or autogenic change and have concentrated on one of these. For example, Clements (1916), Cline and Spurr (1942), Oosting (1956), and Daubenmire (1952) have all emphasized the importance of autogenic succession.

more

On the other hand, Raup (1957) and Olson (1958) have recently indicated the importance of catastrophic disturbance and the adjustment of vegetation to it, thereby de-emphasizing succession. I had the opportunity to evaluate both. I must conclude that disturbance in the Pisgah Forest has been the predominant occasion for change and that autogenic processes did not cause any significant alteration of forest structure over the 300 year history. The major species changes, the major behavioral changes are all initiated at the time of the disturbances.

In addition, my approach has also turned up various physiological questions that I did not anticipate. For example, why can black birch preferentially occupy mounds? Why does hemlock have such a variable growth rate while other species do not? If questions like these can be answered, we can begin to have a physiological understanding of forest structure.

So far, I have tried to evaluate the conclusions of my study. I now wish to evaluate my technique because I believe that it is very fruitful.

Owing to the complexities of studying vegetation, plant ecological conclusions and theories have often been based on speculation (Kershaw, 1966). If plant ecology is to become a critical science, it is crucial that its findings be based on evidence, and that they be testable. In this study, I have tried to restrict my findings to the evidence at hand, clearly indicating where I have speculated. To test my findings, I would compare them with those of another study conducted in the same manner on another spot in the forest. Agreement in the two sets of findings would support the ideas put forward in the first study.

Disagreement would indicate that the ideas from both studies should be combined into a more comprehensive hypothesis which could be tested once again. This approach seems intrinsically more scientific than the approaches of Clements and some other plant ecologists. For example, Clements (1916) established the "climax" theory in which he said all vegetation on any site develops through a number of stages to a self-perpetuating steady state. He then said that each stage and the final state constituted a classification system for vegetation. The only proof he ever offered for his theory was that all vegetation could be fitted into his classification scheme. Obviously, this is not a proof, and he indeed never provided direct evidence that the processes he proposed actually occurred. Thus he never tested his theory.

The technique also has two minor advantages. First, it is flexible and can be adjusted to the evidence available on the site as well as to the aims of the researcher. For example, it might be used to study remnants of past vegetation or to study the living vegetation only.

Second, the diagrams constructed from this study are simple enough to understand and the plot sufficiently small that the two can be directly related. This direct comparison makes the plot a useful teaching tool (for example, this might be done on the Harvard Forest to demonstrate ecological processes to visiting students).

Finally, there may be one interesting future use for this approach. If a number of quadrats were placed to cover the range of site variation in an area, and if each was studied as I have done here, data might be obtained which would permit us to analyze the growth of a forest over space as well as time.

LITERATURE CITED

- Belknap, J. 1792. The history of New Hampshire. Vol. III. Boston. 480 p.
- Branch, W. C., R. K. Daley and T. Lotti. 1930. Life history of the climax forest on the Pisgah Tract, Winchester, N. H. Unpublished data.

 Harvard Forest Records.
- Brooks, C. F. 1939. Hurricanes in New England: meteorology of the storm of September 21, 1938. Geog. Rev. 29: 119-127.
- Brown, H. P. and A. J. Panshin. 1940. Commercial timbers of the U. S. McGraw-Hill. 554 p.
- Channing, W. 1939. New England hurricanes. Walter Channing, Inc., Boston.16 p.
- Clements, F. E. 1916. Plant succession: an analysis of the development of vegetation. Carneg. Inst. Wash. Publ. 242. 512 p.
- Cline, A. C. and S. H. Spurr. 1942. The virgin upland forest of central New England: A study of old growth stands in the Pisgah Mountain section of southwestern New Hampshire. Harv. For. Bull. 21. 58 p.
- Cormack, R. G. H. 1953. A survey of coniferous forest succession in the eastern Rockies. For. Chron. 29: 218-232.
- Cowles, H. C. 1899. The ecological relations of the vegetation on the sand dunes of Lake Michigan. Botan. Gaz. 27: 95-117, 167-208, 361-391.
- Curtis, J. L. 1959. The vegetation of Wisconsin: an ordination of plant communities. Madison, Wisconsin.
- Curtis, J. T. and R. P. McIntosh. 1951. An upland forest continuum in the prairie-forest border region of Wisconsin. Ecology 32: 476-496.

- Daubenmire, R. F. 1952. Forest vegetation of northern Idaho and adjacent
 Washington, and its bearing on concepts of vegetation classification.
 Ecol. Monogr. 22: 301-330.
- Egler, F. E. 1954. Vegetation science concepts, I. Initial floristic composition, a factor in old-field vegetation development.

 Vegetation 4: 412-417.
- Flaccus, E. 1959. Regeneration on landslides in the White Mountains. Ecology 40: 692-703.
- Fowells, H. A. 1965. Silvics of forest trees of the United States.

 Agr. Handbk. No. 271. 762 p.
- Gleason, H. A. 1926. The individualistic concept of the plant association.

 Bull. Torrey Bot. Cl. 53: 7-26.
- Griffith, B. G., E. W. Hartwell, and T. E. Shaw. 1930. The evolution of soils as affected by the old field white pine-mixed hardwood succession in central New England. Harv. For. Bull. No. 15. 82 p.
- Hurd, D. H. 1886. History of Cheshire and Sullivan Counties, New Hampshire.
- Hutchinson, G. E. 1953. The concept of pattern in ecology. Proc. Acad.

 Nat. Sci. Philad. 105: 1-12.
- Johansen, D. A. 1940. Plant microtechniques. McGraw-Hill Book Co., Inc.
 New York.
- Jones, E. W. 1945. The structure and reproduction of the virgin forest of the north temperature zone. New Phytol. 44: 130-148.
- Kershaw, K. A. 1966. Quantitative and dynamic ecology. Edward Arnold Ltd.
 183 p.

- Lutz, H. J. 1930. The vegetation of Heart's Content, a virgin forest in northwestern Pennsylvania. Ecology 11: 1-30.
- and A. L. McComb. 1935. Origin of white pine in virgin forest stands of northwestern Pennsylvania as indicated by stem and basal branch features. Ecology 16: 252-256.
- Lyford, W. H. and D. W. MacLean. 1966. Mound and pit microrelief in relation to soil disturbance and tree distribution in New Brunswick,

 Canada. Harv. For. Paper 15. 18 p.
- Maissurow, D. K. 1941. The role of fire in the perpetuation of virgin forest of northern Wisconsin. J. Forest. 39: 201-207.
- Marshall, R. 1927. The growth of hemlock before and after release from suppression. Harv. For. Bull. 11: 1-43.
- Maycock, P. F. 1963. The phytosociology of the deciduous forests of extreme southern Ontario. Canad. Jour. Bot. 41: 379-438.
- McFee, W. W. and E. L. Stone. 1966. The persistence of decaying wood in the humus layers of northern forests. Soil Sci. Soc. Amer. Proc. 30: 513-516.
- Newsome, R. D. 1963. A report of studies preparatory to an analysis of forest stand ages. Unpublished report, Univ. of Sask. 6p.
- Nutting, H. C. 1925. Monadnock records of 3 centuries. New York.
- Olson, J. S. 1958. Rates of succession and soil changes on southern Lake Michigan sand dunes. Botan. Gaz. 119: 125-170.
- Oosting, H. J. 1956. The study of plant communities. W. H. Freeman and Co., San Francisco. 440 p.

- Raup, H. M. 1957. Vegetational adjustment to the instability of site.

 Proceedings and Paters, 6th Tech. Meeting. Int. Union, Conserv.

 Nat. and Nat'l Res., Edinburgh, pp. 36-48.
- Schafer, J. P., and J. H. Hartshorn. 1965. The quarternary of New England.

 The Quarternary of the United States. Princeton University Press 3 p.
- Sears, P. B. 1925. The natural vegetation of Ohio.
 - 1. A map of the virgin forest. Ohio Jour. of Sci. 25: 139-149.
- Sen. J. 1963. Fine structure in degraded, ancient, and buried wood II.

 Bot. Review 29: 230-242.
- Simmons, C. S., W. J. Latimer, M. H. Layton, W. H. Coates, W. H. Lyford, and P. N. Scripture. 1949. Soil survey of Cheshire and Sullivan Counties, New Hampshire. USDA Series 1937 No. 23. 82 p.
- Spurr, S. H. 1956. Forest associations in the Harvard Forest. Ecol.

 Monogr. 26: 245-262.
- Srb, A, M., R. D. Owen, and R. S. Edgar. 1965. General genetics. W. H. Freeman and Co. 557 p.
- Stearns, F. S. 1949. Ninety years change in a northern hardwood forest in Wisconsin. Ecology 30: 350-358.
- Stephens, E. R. 1955. The historical-developmental method of determining forest trends. Unpublished Ph. D. Thesis, Harvard Univ. 29 p.
- Swan, J.M.A. 1966. The phytosociology of upland vegetation at Candle

 Lake, Saskatchewan. Unpublished Ph. D. Thesis, Univ. of Sask. 166 p.
- Viereck, L. A. 1966. Plant succession and soil development on gravel outwash of the Muldrow Glacier, Alaska. Ecol. Monogr. 36: 181-199.

Watt, A. S. 1947. Pattern and process in the plant communities. J. Ecol. 35:

1-22.

Whittaker, R. H. 1956. Vegetation of the Great Smoky Mountains. Ecol.

Monogr. 26: 1-80.

1960. Vegetation of the Siskiyou Mountains, Oregon and California.

Ecol. Monogr. 30: 279-338

and W. A. Niering. 1964. Vegetation of the Santa Catalina

Mountains, Arizona: a gradient analysis of the south slope.

Ecology 46: 429-452.

APPENDIX

In this appendix I have included two different kinds of diagrams;

(1) a diagram of tree growth over time, (2) maps of the quadrat showing the locations of all trees. Each diagram will be explained separately.

Diagram of Tree Growth Over Time

On the left hand side of this diagram arranged in columns is the following information about each tree;

Column 1 - diagram position number

Column 2 - number assigned in field work

Column 3 - species

Column 4 - diameter at breast height (inches)

Column 5 - height of tree (feet)

Column 6 - Condition of tree - the following abbreviations have been used in describing conditions of trees: (1) inj. - injured,

(2) 0.M. - tree grows on windthrow mound, (3) snag - tree has died but has not fallen over, (4) W.T. - tree was blown over in a windstorm, i.e. it is a windthrown tree,

(5) 0.A.T. - tree is growing on another tree, (6) A.T. tree is growing along the length of a fallen tree.

(7) Dis. - means that tree is diseased, (8) Out - tree is growing or has grown outside the quadrat, (9) I.P. - tree is growing in a windthrow pit, (10) DEAD - means of course that tree is deceased.

A time scale is at the top of the diagram, with past to present (1500 to

1967) represented from right to left. Each line represents the life of a tree while the numbers on the line express releases and suppressions (growth rate changes expressed as a ratio). A sprout is indicated by the branching of a line. The dotted lines indicate the estimated error of the age of each tree.

Distribution Maps of Vegetation

There are three distribution maps; (1) location of living stems on the quadrat. (2) location of dead stems. (3) location and direction of the windthrown trees.