

HARVARD FOREST

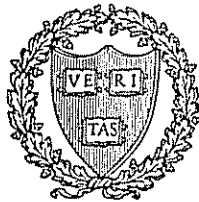
BULLETIN No. 21

THE VIRGIN UPLAND FOREST OF CENTRAL NEW ENGLAND

A STUDY OF OLD GROWTH STANDS
IN THE PISGAH MOUNTAIN SECTION
OF SOUTHWESTERN NEW HAMPSHIRE

By

A. C. CLINE and S. H. SPURR



HARVARD FOREST
PETERSHAM, MASSACHUSETTS

1942

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PREFACE

Studies of the virgin forest remnants in the Pisgah Mountain section of southern New Hampshire began some twenty-five years ago when, under the guidance of Professor R. T. Fisher, first director of the Harvard Forest, students and staff members made yearly trips to see the veteran trees and to try to locate remnants of old stands not previously discovered. The rugged topography and numerous slash-covered areas made it a difficult country to explore, and occasionally the party failed to relocate some of the remnants found on previous trips. At first these field excursions served chiefly to gratify the curiosity of those who had never before seen central New England virgin timber and to obtain rough notes and measurements on the character of the stands and the size of the trees—always with the accompaniment of picture taking. As time went on, however, it became more and more evident that the soundest basis for the development of the art of silviculture lay in an understanding of the “natural” forests of the region—the complex of trees, shrubs and herbaceous plants which would occupy a given piece of ground when free from interference by man. Thus, interest in the Pisgah old growth grew, and with it a feeling of urgency to make a thorough study lest the old stands be cut or accidentally destroyed. It was through this interest and the generous contributions of a number of persons that Harvard University in 1927 was able to acquire twenty acres of one of the choicest remaining stands.

Beginning at about the time of this acquisition, a series of studies was undertaken. Those directing the work, besides Professor Fisher, were A. C. Cline, P. R. Gast and N. W. Hosley of the Harvard Forest staff. In 1927, C. S. Herr and Hollis A. Smith, graduate students, assisted in making a stump analysis in a recent cutting of virgin timber, in this way determining certain age and size relationships and growth rates. In 1929, B. G. Griffith, E. W. Hartwell, and T. E. Shaw participated in a study of soil conditions under virgin stands, the results of which have been published in another bulletin of the Harvard Forest. In 1929-30, sixty-eight remnants of old growth and twenty-three recently cutover areas of old growth were included in a comprehensive unpublished study by W. C. Branch, R. K. Daley, and Thomas Lotti under the immediate direction of A. C. Cline and N. W. Hosley, in partial fulfillment of the requirements for the degree of Master in Forestry. The Harvard tract of twenty

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acres formed only a part of this study. Most of the remnants were located some distance away, though within the same general area.

During the next few years certain supplementary information was gathered, and in 1937 the senior author reworked the field data and revised the manuscript which had been prepared by the students in 1930. On September 21, 1938, the great hurricane almost completely destroyed all that remained of the old growth stands, including that owned by the University.¹ Thus came to an end the current series of studies of standing virgin timber.

Within the past year, and with the use of new techniques in analyzing the field data, the junior author, a member of the Harvard Forest staff, reduced the material to its present form and revised the manuscript accordingly.

The field studies of 1929-30, which form the basis of this publication, were made possible through a generous grant by the Massachusetts Society for Promoting Agriculture. This enabled instructors and students to live in the field and carry on the work without interruption for a period of several months, for which all members of the field party are very grateful. The printing of this bulletin was financed by a friend of the Harvard Forest who wishes to remain anonymous.

The authors and others who contributed to this study are particularly appreciative of the permission generously given by the owners of most of the Pisgah Mountain area, the Ansel Dickinson heirs, to enter upon their property at will, of the advice given by Professor Hugh M. Raup, forest ecologist and a member of the staff of the Arnold Arboretum, and of the cooperation extended by the Division of Soil Survey of the U. S. Bureau of Plant Industry which, through the services of Charles S. Simmons, identified and described the soils of the Pisgah Mountain Area.

A. C. CLINE
S. H. SPURR

Petersham, Massachusetts
November 1, 1942

¹ Even in their prostrate position, these veteran trees are an impressive sight. In the small openings among the fallen trunks and branches, the new generation is already becoming established. In accordance with the purpose of acquisition of the Harvard tract, no salvage of the down timber has been permitted. It remains a place where one may study nature undisturbed by man.

INTRODUCTION

The principal object of the forester is to maintain the forest in its most productive condition. In the early years of the development of silviculture in a new country, the measures taken towards this end exhibit wide differences. Lacking a background of experience and a sound ecological foundation, foresters resort to the trial and error method—almost invariably with the same results. While some trials are promising, most are failures, and shortly turn out to be costly to the forest owner and detrimental to the forest itself (Spurr and Cline, 1942). The history of forestry in central New England has been no exception.

The very beginning of forestry in the region, near the turn of the century, happened to coincide with the peak of white pine production. To the early foresters, surrounded by thousands of acres of solid pine and scores of dependent industries, central New England was indeed the "white pine" region, and should be perpetuated as such. Thus, a great wave of enthusiasm arose for planting—mostly white pine, but also red and Scotch pines, Norway spruce and almost every other conifer that was readily available. Difficulties followed shortly. Repeated weedings were often necessary to save young plantations from competing volunteer hardwoods. Many areas were planted and promptly forgotten, until the owner returned to find the trees crowded and overtopped by hardwoods or ravaged by insects and diseases. Most white pine plantations were severely damaged by the white pine weevil, a native insect which reached epidemic proportions under conditions of a highly concentrated food supply. Many of the plantings, especially those composed of exotics, were complete failures, because too often the wrong species was planted on the wrong site under the wrong conditions. Few met with more than partial success. Similar results attended all efforts to reproduce even-aged white pine stands on upland soils by natural means.

As time went on, ecological studies pointed out the underlying fallacy of these practices. The natural upland vegetation of central New England was shown to be composed largely of hardwoods and hemlock. The prevalence of pure stands of white pine was a temporary phenomenon due solely to the seeding in of this species on fields and pastures abandoned during the previous century. "Old field" pine cuttings—as well as all other kinds of cuttings on heavy, upland soils—have been followed by the establishment of hardwoods, until, today, hardwoods are once more

dominant in the region. It is indeed unfortunate that, despite ecological advances, the concept that forestry is the planting of pine has persisted so long and has so completely dominated forest policies and practices.

It is not quite true to say that everyone—foresters and laymen alike—blindly followed this concept. One outstanding exception was R. T. Fisher, who, more than thirty years ago, adopted a policy of favoring volunteer stands following the harvesting of old field white pine and of improving, on each area, the stands that naturally developed. This basic philosophy of working in harmony with nature has time and again proved its soundness and has become firmly fixed as the foundation of silvicultural policy at the Harvard Forest.

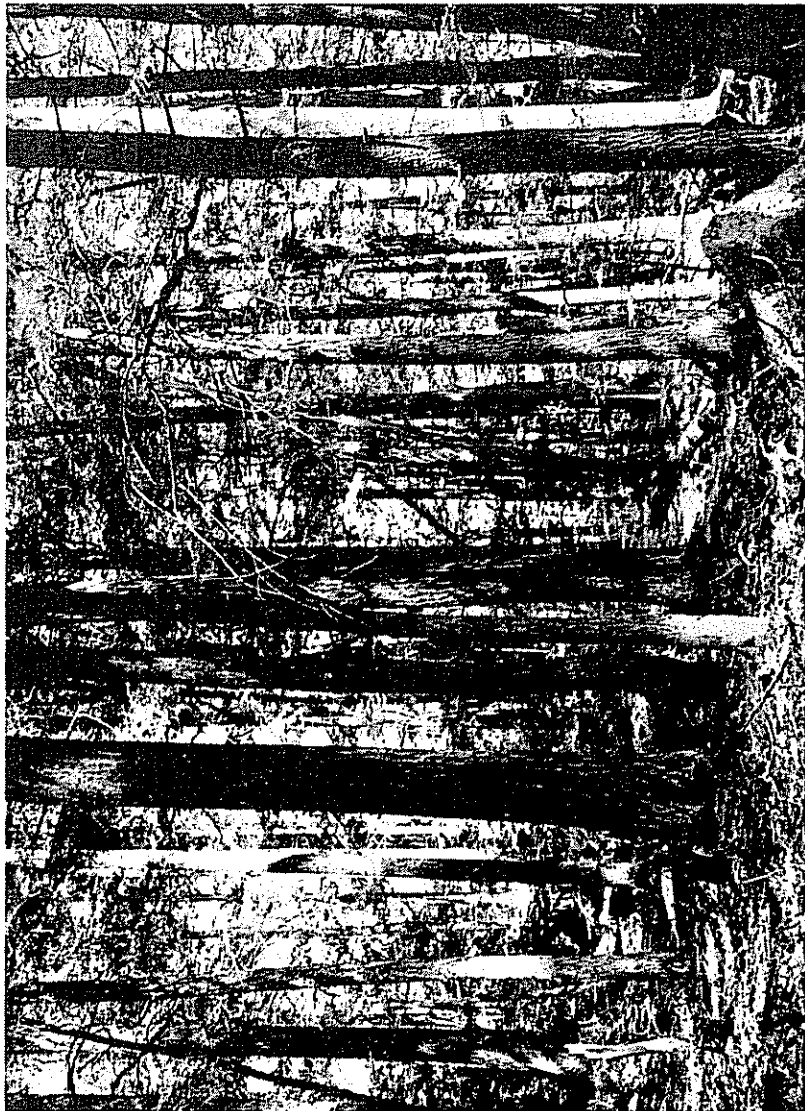
Although the concept that forestry is planting pine still persists, we may look forward to a more general recognition of the importance of studying nature as a basis of silviculture. In developing new and better techniques for use in the days ahead, it is necessary that foresters gain a better understanding of the natural forces forever at work in the forest. The natural stand is the product of the effect of climate, site and other external influences upon a community of plants, each species of which reacts according to its own inherent characteristics. Such relationships can best be studied where man has not interfered.

Thus, it was with the purpose of acquiring further knowledge of the original forests of central New England, and particularly of the successional and environmental relationships of the various associations found therein, that this study was undertaken. The few remnants of primeval forest which still exist are invaluable guides and deserve the most careful study. Such were the Pisgah Mountain old growth stands (Fig. 1).

* * * * *

Records of old growth forests fall into four major categories: (1) historical references, (2) extensive studies of virgin forests throughout a given region, (3) intensive floristic studies of specific remnant stands, and (4) general discussions of the subject. All phases, of course, are highly interrelated in modern ecological work.

Early contemporaneous records of the original forest have been discussed competently by many of the recent investigators herein referred to. It should be noted, nevertheless, that ever since the arrival of the white man, fragmentary notes concerning the forest have been recorded and preserved. These may be found in the writings of early chroniclers, in the narratives of learned travelers such as President Timothy Dwight of Yale, in the notebooks of frontier surveyors, in town and colonial records, and in local gazetteers and histories. Historical information concerning the original forests and forest history of southwestern New Hampshire was



Harvard Forest photograph

FIG. 1. A PORTION OF THE PISGAH OLD GROWTH FOREST

The trees pictured include hemlock, red oak and white pine

found chiefly in Child's gazetteer of Cheshire County (1885), Hurd's History of Cheshire and Sullivan Counties (1886) and in local town histories.

By bringing together fragments of historical data and adding to these a knowledge of such virgin stands as still exist, several excellent regional surveys have been produced. Nichols (1913) studied remaining Connecticut old growth stands, while Hawes (1923) recorded additional historical material and descriptions of similar remnants. Bromley (1935) stressed the importance of fire in the primeval forest, particularly in perpetuating the pre-climax oak-hickory stands of southern New England. The writings of Raup (1938, 1941) and of Gordon (1940) have added further to our knowledge of the original forest.

The application of recently developed precision methods in ecology to individual stands has resulted in reports by Lutz (1928, 1930), Hough (1936) and others in the Northeast. The present study falls into this category. Such studies rely upon the statistical analysis of sample plots, in addition to the general observation, description, and interpretation required in all scientific work.

Prominent among the papers presenting a general discussion of the original forests of central New England are those by Fisher (1933), Nichols (1935) and Raup (1937).

The very substantial amount of material already published on the original forests of the Northeast has been of great value in the investigation of the old growth forests of the Pisgah Mountain section. In this work the authors have ventured beyond the point of describing the variations in the composition within the virgin forest. Emphasis has been placed upon the relationships between the different associations, particularly in regard to the influence of site and to the influence of fire, wind and other natural disturbances.

DESCRIPTION OF THE PISGAH MOUNTAIN AREA

LOCATION AND OWNERSHIP

The study was confined to an area of privately owned forest land situated in Cheshire County, New Hampshire, in the northwest corner of the town of Winchester (Fig. 2). Winchester is in the extreme southwest portion of the state, bordered by Massachusetts on the south and separated from Vermont only by the narrow town of Hinsdale on the west. The Pisgah forest covers an area of approximately 5,000 acres, at present owned by the Ansel Dickinson heirs, with the exception of 20 acres belonging to Harvard University.

TOPOGRAPHY

Central New England is dominated by an ancient plateau-like upland which has been dissected and recently heavily glaciated. The topography, consequently, is rough and hilly, with the main ridges running in a general north-south direction. Elevations in the Pisgah area range from about 700 feet above sea level to a little more than 1300 feet, which, incidentally, is approximately the same range as that represented within the boundaries of the Harvard Forest in Petersham, Massachusetts, some twenty-five miles distant to the southeast. The summits of the highest ridges are of bare rock or are covered with a layer of soil so thin that only very insecure anchorage is afforded the trees found growing upon them (Fig. 3). The slopes are generally steep, and often broken by rocky outcrops. Swift-running streams in the narrow valleys quickly drain into the nearby Ashuelot River, which flows westerly along the southern border of the area and empties into the Connecticut River several miles beyond.

SOILS

Over most of the area the soils are thin and stony. The soil survey of the region (Simmons, et al., 1942) classifies most of the area as "rough stony land, Hermon soil." Hermon soils are true podzols¹ developed from

¹ A podzol is a soil in which the uppermost mineral portion has been altered by leaching of iron and other elements through weathering. A very light gray layer is left. It is a soil characteristic of northern temperate humid regions.

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granitic material. They have from two to four inches of organic material overlaying from one-half to two inches of light gray or nearly white sandy loam. This leached sandy loam varies from fine to coarse and gravelly in texture. Beneath this is the dark brown, enriched horizon, a smooth fine sandy loam that may become sticky when wet. The deeper subsoil is a brownish-yellow fine sandy loam that becomes lighter colored and coarser with depth until, at about 30 inches, gray sandy glacial till, from which the soil has developed, is found. The soil mantle is especially thin on the ridge tops and upper slopes, and the parent material (glacial till) is absent in many places. The bedrock and most of the rock fragments are a very coarse granite, although the soils of the Pisgah area are somewhat finer than the Hermon soils found in other parts of the region. This may be due to the inclusion in the parent material of some schist fragments from outcrops to the north and west of Pisgah Mountain.

CLIMATE

No weather data are available for the Pisgah Mountain area, but records made over a period of forty years at the private weather station of Samuel Wadsworth in Keene, New Hampshire, some 12 miles distant, are applicable to this area (U. S. Dept. Agric. 1941).

The mean annual precipitation is about 38 inches, fairly well distributed throughout the year. The average annual snowfall approximates 63 inches, most of it falling during January and February. The average date of the first frost is September 20, and of the last, May 26. The earliest frost recorded was August 29, and the latest, June 21. The growing season lasts about 120 days. The prevailing winds are northwesterly. Excessively high winds, sometimes in connection with severe electrical storms, and ice storms of destructive character occur at infrequent intervals.

HISTORY

The town of Winchester was granted in 1733 by the Massachusetts Bay Colony to Colonel Josiah Willard, for many years commander of Fort Dummer just across the Connecticut River, and sixty-three associates. The Squakheag Indians who formerly occupied the region had sold about 65,000 acres known as Nawelets country to the whites in 1687 and had subsequently (1720) moved to Canada. The town was abandoned in 1745 because of the French and Indian War, but was resettled eight years later (Child, 1885).

Information as to the early development of the lumber industry is meager, but it is known that Colonel Willard erected the first sawmill at

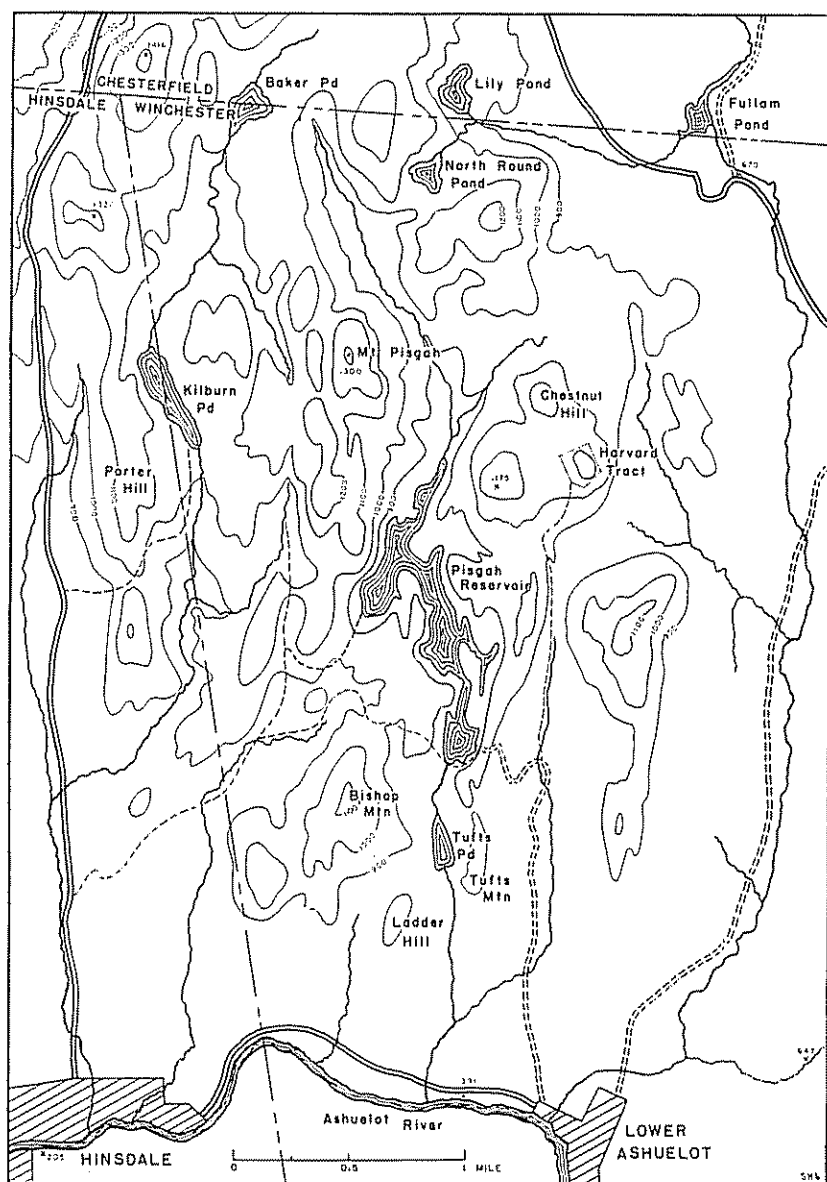


FIG. 2. TOPOGRAPHIC MAP OF THE PISGAH MOUNTAIN AREA

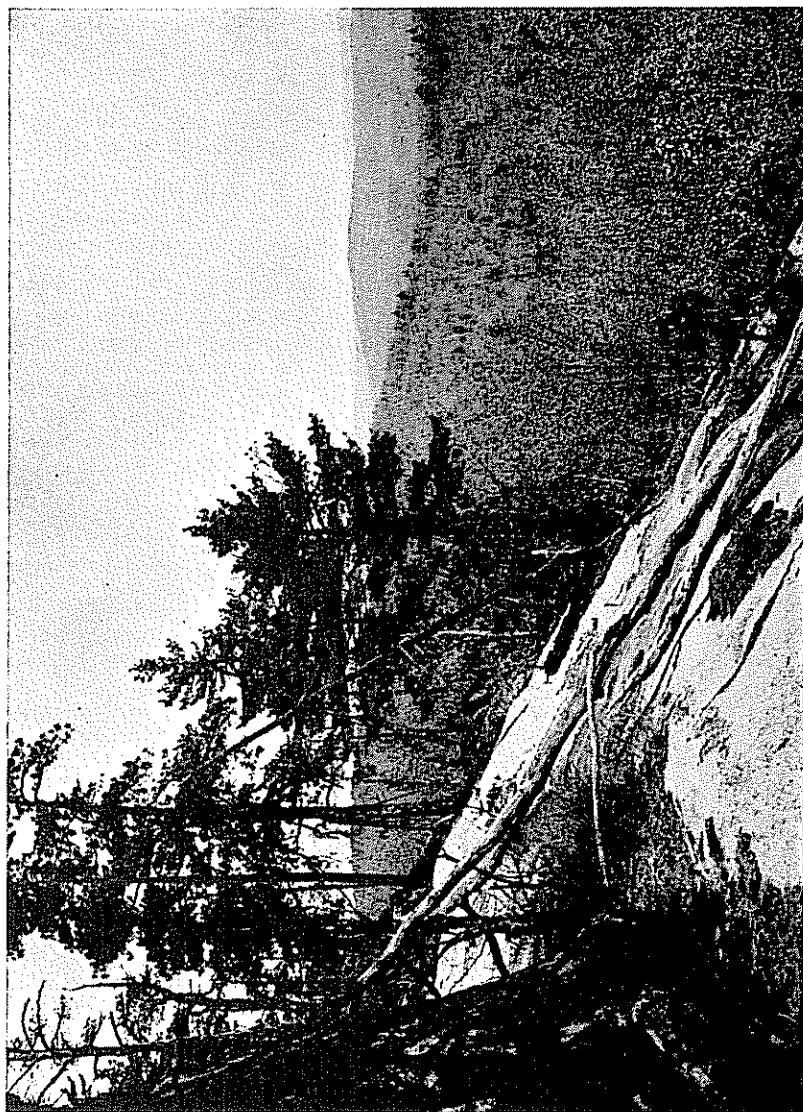
Contours not shown below 900 feet

Adapted from the Keene Quadrangle topographic map by the U. S. Geological Survey (1935)

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Winchester in 1734, for the purpose of supplying the settlers with construction materials. From this time on lumbering gradually increased in importance until it reached its peak in the latter part of the nineteenth century. In the year 1885 there were eight sawmills and four box factories dependent upon the forests in the vicinity of the villages of Winchester and Ashuelot. The annual cut of these was more than six million board feet, the largest portion being second-growth "old field" white pine. Since then the industry has declined until in recent years but one or two small stationary sawmills have been in operation. With the exception of the small scattered stands which comprise part of the Pisgah forest, all of the local virgin timber was cut many years ago, much of the best and most accessible of it in the first decades following settlement.

That the timber in the Pisgah area was not completely exploited long ago is due to its relative inaccessibility and to its ownership by one family which for generations has retained interests in local wood-using industries and looked upon the Pisgah forest as a reserve to be used sparingly and at such times as their needs could not be as well met from other timber lands.



Harvard Forest photograph

FIG. 3. BEDROCK EXPOSED ON A RIDGE TOP, AND A VIEW OF THE AREA

METHOD OF STUDY

The first step in the project was to locate remnants of old growth stands in which no signs of human disturbance were evident, following which sample plots one-tenth acre in area were laid out for intensive study. Such remnants as could be located were mostly small in area, representing only portions of the original stands. Clues to past composition were afforded by an examination of dead trees, by stump studies in nearby cutover areas and to some extent by increment borings in living trees. As a basis for determining the composition of present stands and any tendencies toward changes in the future, the tree cover on each plot was analyzed according to three height levels—overstory, middlestory and understory.

The overstory record included an individual tally of all trees whose crowns were in the main canopy, classified according to species, diameter and height. The composition of this crown level was used as a basis for the segregation of forest cover types according to the criteria laid down by the Society of American Foresters (1940). Thus, if a single species comprised 80 percent or more, by number of stems, of the overstory, the type was considered "pure"; otherwise, a mixture designated by the common names of the predominant species.

The middlestory comprised all trees growing beneath the main canopy down to a height of fifteen feet above ground, and these also were tallied by species, diameter and height.

The trees in the understory were subdivided into two classes, one including reproduction up to one foot in height, and the other seedlings and saplings from one to fifteen feet in height. The purpose of this was to distinguish between species that were able to survive only the first few years and those which could withstand prolonged suppression by overtopping trees. It was assumed that those which had attained a height of over one foot were potential members of the upper stories. An estimate of the understory was obtained from ten mil-acre quadrats (each 6.6 feet square) laid out along the center line of each sample plot.

Stand form, density of crown canopy, vigor and age were recorded. Age determination through increment borings was limited to a few trees in each plot. Further knowledge of age relations was obtained by an examination of nearby recently cutover areas, but here difficulties were encountered in reconstructing the former canopy levels.

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In addition to the record of tree cover, notes were taken on (1) topography of the plot, (2) evidences of past disturbances, (3) soil profile and (4) shrubs and herbs.

Under topography were recorded the plot location, elevation above sea level, relative elevation (ridge top, high slope, mid-slope or low slope), aspect and degree of slope.

Past fires were evidenced by fire scars on the trees and the occurrence of charcoal in the soil. The approximate severity and time of occurrence of destructive winds was indicated by the relative numbers of fallen trees and their stage of decay. Even extremely ancient disturbances could often be detected through the occurrence of several parallel and barely perceptible "ridges" containing much rotted wood, each terminated by a depression caused by the upturned root system. Damage resulting from lightning, fungi, insects and other agencies was also noted.

The soil profile was determined from three samples in each plot, with measurement to the nearest tenth inch of the thickness of the various organic layers, and the leached (A) and dark brown (B₁) horizons of the mineral soil.

Shrubs and herbs were tallied according to species and three classes of abundance: few, many and abundant.

Sixty-eight plots were taken in virgin forest remnants, and an additional twenty-three in recently cutover old growth areas. Only forested upland sites were studied; no plots were taken in swale or swamp types, or on rock outcrops where lack of soil and extreme exposure precluded the development of a full forest stand.

In the analysis of the data, the abundance of the individual tree species in each height level was expressed as the percent of the number of stems in that level. The plots were then grouped into seven cover types according to the composition of the overstory. As a result of this, certain relationships between composition and both topographic location and successional position could be observed. A considerable amount of the variation in stand composition, however, still remained unexplained.

The data were then resorted on the basis of (1) elevation and (2) history of the stand. The composition of the associations thus segregated is given in Appendix A and is the basis of Tables 3 to 7 in the text. The stands within each association were similar in structure and floral characteristics. Consequently, under this treatment, a large proportion of the variation in composition could be explained.

The data for the cutover areas, for the shrubs and herbs and for the soil profiles were analyzed in a similar manner.

THE ORIGINAL FOREST

The original forest of Cheshire County is described in an early gazetteer (Child, 1885) as including "dense bodies of the finest white pine timber" along the valleys of the Connecticut and Ashuelot, "an abundant growth of hemlock" on higher lands, "belts of heavy spruce timber on the highest portions" and maples, beech, birches and red oak on the best-drained tracts. This agrees closely with the average composition of the stand remnants sampled in the present study. Hemlock and white pine were found to comprise over sixty percent of the total stand (Fig. 4), and trees of these species taken together with the others listed by Child made up ninety-seven percent of the dominant trees tallied. Red spruce was found to be rather uncommon in the Pisgah area. There is no reason, however, to believe that it was not as common in the original forest on Mount Monadnock and in the northern part of the country as it is at the present time.

The average composition of the overstory on all the plots is shown in Table 1. The number of trees on individual plots ranged up to 220, and

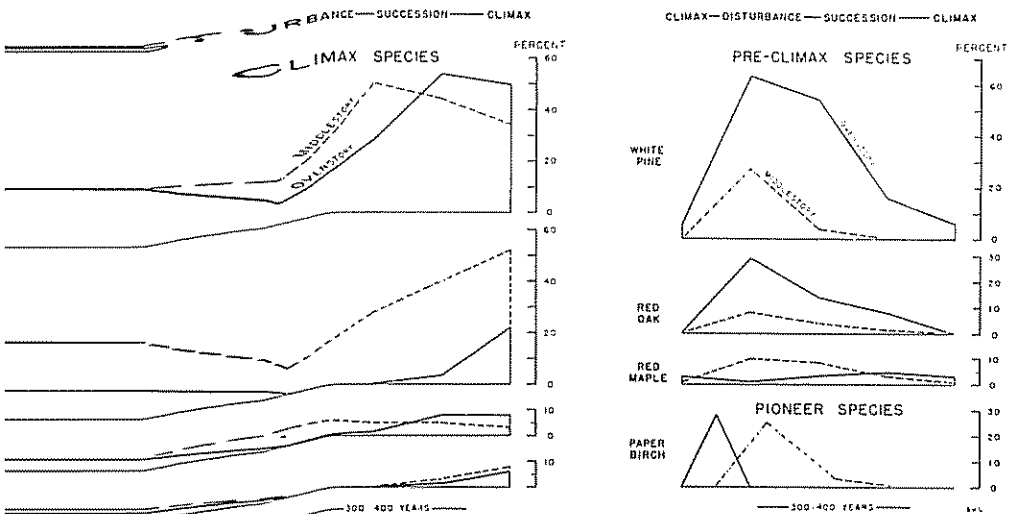
TABLE 1
AVERAGE COMPOSITION AND VOLUME OF THE OVERSTORY

<i>Species</i>	<i>Number of trees per acre</i>	<i>Volume in board feet per acre</i>	<i>Approx maximum age in years</i>	<i>Approx maximum diameter in inches</i>	<i>Approx maximum height in feet</i>
Hemlock	31.8	14,700	380	36	110
White pine	21.1	12,500	280	48	150
Red oak	9.5	1,500	270	32	80
Beech	6.2	1,200	280	24	80
Black birch	5.4	1,000	150	30	90
Paper birch	3.6	600		22	90
Red maple	3.3	1,000		26	80
Sugar maple	1.2	600		27	90
Red spruce8	100	260	18	80
White ash4	100	160	22	90
Others7	100		18	80
Yellow birch					
White oak					
Basswood					
All species	84.0	33,400	380	48	150

ECOLOGICAL STATUS OF THE TREE SPECIES

ecological viewpoint, the trees in the central New England may be grouped into three classes: (1) pioneer species, (2) pre-climax species and (3) climax species.

Figure 11 shows the changes in abundance of the most common species during the gradual restoration of the climax following its complete destruction. The values were obtained by averaging the composition of samples from various elevations and aspects. Pioneer species establish themselves in the first openings, are shortly overtopped by pre-climax trees and disappear until other openings are created. Early in the succession pre-climax species become prominent but thereafter gradually decrease in abundance. The climax species are most numerous in climax associations and are least numerous in recently disturbed stands.



11. CHANGES IN ABUNDANCE OF THE MOST COMMON SPECIES DURING THE PERIOD REQUIRED TO RESTORE THE CLIMAX ASSOCIATION FOLLOWING ITS DESTRUCTION

PIONEER SPECIES

Pioneer species are rapid-growing, short-lived trees which come in when the forest has been destroyed. Gray birch (*Betula populifolia*), pin and aspen are characteristic pioneer species, while paper birch and

ECOLOGICAL STATUS OF THE TREE SPECIES

From an ecological viewpoint, the trees in the central New England virgin forest may be grouped into three classes: (1) pioneer species, (2) pre-climax species and (3) climax species.

Figure 11 shows the changes in abundance of the most common species during the gradual restoration of the climax following its complete destruction. Values were obtained by averaging the composition of samples taken at all elevations and aspects. Pioneer species establish themselves in newly created openings, are shortly overtopped by pre-climax trees and then disappear until other openings are created. Early in the succession pre-climax species become prominent but thereafter gradually decrease in importance. The climax species are most numerous in climax associations and least so in recently disturbed stands.

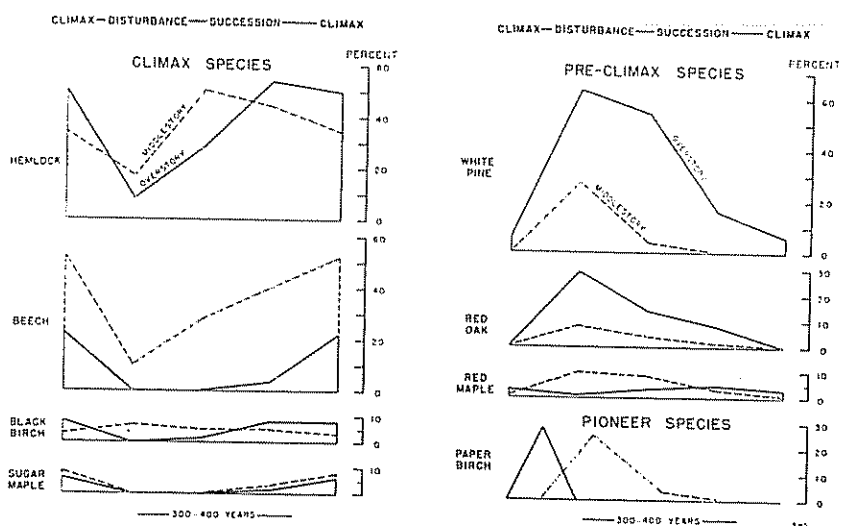


FIG. 11. CHANGES IN ABUNDANCE OF THE MOST COMMON SPECIES DURING THE PERIOD REQUIRED TO RESTORE THE CLIMAX ASSOCIATION FOLLOWING ITS DESTRUCTION

PIONEER SPECIES

Pioneer species are rapid-growing, short-lived trees which come in where the forest has been destroyed. Gray birch (*Betula populifolia*), pin cherry and aspen are characteristic pioneer species, while paper birch and

Each group of associations characterized by a similar history therefore may be regarded as representing a successional stage in the life history of a stand. These are designated with roman numerals in the following discussion. Thus, associations following *old partial* disturbances (stage II) most closely approach the climax (stage I) both in composition and in the long absence of severe disturbances. Stands comprising these associations have reached a late pre-climax stage in the succession which originated in the disturbance of the forest by fire, wind and other natural causes. Associations following *old severe* disturbances (stage III) are early pre-climax in character, while associations following *recent* disturbances (stage IV) are composed of late pioneer stands.

Following the destruction of the forest on a given site, the ensuing stand will at first be composed largely of pioneer species. Within 50 years, however, the stand composition will be comparable to that of stage IV. This in turn will develop through stages III and II until stage I, the climax, is reached. Use is made of this concept in interpreting the ecological status of tree species and the effect of composition changes on the soil profile.

Because the former chestnut association constitutes a special case, it is omitted from the above successional series. This association is the product of a specific, unduplicated set of conditions, among which the recent eradication of the principal species is unique in the forest history of the region.

The climax composition cannot be attained until after the death of most of the non-climax trees in the stand. Since the maximum age reached by white pine, the longest-lived pre-climax species in the Pisgah forest, is not far beyond 300 years, it may be assumed that a lapse of nearly 400 years was necessary for the reestablishment of the climax following a severe disturbance. During this time, the stand was exposed to recurring hurricanes and other disturbances which often destroyed the existing stand, thereby initiating a new succession toward the climax.

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ponent of pioneer and pre-climax associations on a wide variety of sites, it was abundant in the Pisgah Mountain area only under a single set of conditions. Stands that formerly contained much chestnut were found on north and east slopes, and practically all the chestnut was the same age, 180 to 190 years. No trees were older. This chestnut association appears to have been an even-aged pioneer following a single northeasterly storm and associated fire. During the lapse of the more than 190 years since this storm, the stand had developed into a pre-climax association (Fig. 9). Besides chestnut, the overstory included paper birch, a tree whose presence usually indicates past disturbances, and a mixture of both intolerant and tolerant species (Table 7).

TABLE 7
THE FORMER CHESTNUT ASSOCIATION
Percent Composition by Crown Level

Species	Overstory	Middlestory	Understory	
			15'-1'	1' or less
(9 samples)				
Paper birch	28		1	
Black birch	23	7		1
Beech	17	67	63	37
White pine	12	1		4
Red oak	7	3		12
Red maple	5	3	6	17
Sugar maple	5	2	20	18
White ash	3			
Hemlock		17	10	11
	100%	100%	100%	100%

The understory was primarily composed of such tolerant species as hemlock, beech and sugar maple. With the opening of the stand following the death of the chestnut, trees of these species were pressing up into the openings in the overstory. These stands appear to demonstrate that under certain conditions the disturbance of a pre-climax association may actually hasten rather than retard forest succession toward the climax.

EFFECT OF ASPECT ON STAND COMPOSITION

It must not be assumed that all differences in stand composition can be explained on the basis of relative elevation and of climatic or other disturbances. Among the other factors which markedly influence com-

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TABLE 6

ASSOCIATIONS FOLLOWING RECENT DISTURBANCES
Percent Composition by Location and Crown Level

Species	Overstory	Middlestory	Understory	
			15'-1'	1' or less
RIDGE TOPS (5 samples)				
White pine	64	32	18	41
Red oak	31	2	.	3
Hemlock	5	9	58	23
Paper birch	.	34	4	3
Red maple	.	12	10	8
Black birch	.	10	1	22
Others (Be, Pop, PC)	.	1	9	..
	100%	100%	100%	100%
HIGH SLOPES (4 samples)				
White pine	61	25	53	11
Red oak	27	15	7	.
Hemlock	12	26	18	31
Paper birch	.	16	3	5
Red maple	.	8	9	.
Black birch	.	3	4	53
Others (RP, SM, Be)	..	7	6	..
	100%	100%	100%	100%

even-aged overstory of pre-climax species evidently had originated following an earlier severe disturbance.

The middlestory contained the same species as found in the overstory, but paper birch was the most abundant tree, while red maple and black birch were other important components. The abundance of paper birch confirms the other indications of recent fires, namely, fire-scars on the residuals and abundant charcoal in the humus. Pioneer and pre-climax species are the characteristic components of these associations and little indication is afforded of progress toward the climax.

THE FORMER CHESINUI ASSOCIATION

Until destroyed by the blight a quarter of a century ago, chestnut was an important species in the virgin forest. Although an occasional com-



Harvard Forest photograph

FIG 8. WHITE PINE AND HEMLOCK ON HIGH SLOPE

A late pre-climax association following wind and fire

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TABLE 5
ASSOCIATIONS FOLLOWING OLD SEVERE DISTURBANCES
Percent Composition by Location and Crown Level

Species	Overstory	Middlestory	Understory	
			15'-1'	1' or less
<div>RIDGE TOPS</div> <div>(9 samples)</div>				
White pine	51	6		19
Hemlock	24	58	56	45
Red oak	18	5		1
Red maple	3	13	15	14
Black birch	1	9	8	13
Beech		6	12	5
Others (PB, RS, YB, WO)	3	3	9	3
	100%	100%	100%	100%
<div>LOW AND MID-SLOPES</div> <div>(3 samples)</div>				
White pine	58	1		32
Hemlock	30	43	28	66
Red oak	9	2		
Red maple	3	5	1	1
Beech		49	43	
Others (BB, SM)			28	1
	100%	100%	100%	100%

ASSOCIATIONS FOLLOWING RECENT DISTURBANCES

Evidence of disturbances within the last fifty years was confined to high slopes and ridge tops, where nine areas were found on which the combined action of wind and fire had initiated a new forest succession (Table 6). These recent disturbances had resulted in the partial destruction of the overstory, leaving in most cases less than 60 trees per acre. Under this partial canopy the middle and understories consisted of trees less than 50 years old, which had come in following the disturbance. On the forest floor were many fallen trees, formerly of the overstory, with upturned roots.

The composition of the overstory at the two elevations was strikingly similar, consisting of 61 to 64 percent white pine, 27 to 31 percent red oak and 5 to 12 percent hemlock. No other species were represented. This

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overstory. This is as would be expected, since fires are more destructive on high ridges than at lower elevations.

Associations following old partial disturbances at the lower elevations contained more hemlock and black birch and less sugar maple and beech than did climax stands on similar sites. Red maple, absent in the climatic climax, was present in all crown levels. Since the bark of hemlock is among the most fire resistant in the virgin forest and beech the least (Stickel, 1937), the increase in abundance of hemlock and the decrease in beech is to be expected on lower slopes where the stand has been partially disturbed by fire.

On the higher slopes hemlock had decreased in abundance as compared with the climax. This is possibly due to the thinner soil on the high ridges and the consequent root injury when the organic layers are destroyed by fire. Although the bole of the mature hemlock is highly resistant to fire, the roots, being very shallow, are quite susceptible to damage (Stickel, 1937). At the higher elevations paper birch and red oak were prominent components of the association; both are relatively intolerant and neither is abundant in the climax forest. The association, however, consisted primarily of hemlock and white pine, the former being less abundant and the latter more so than in the ridge top physiographic climax.

ASSOCIATIONS FOLLOWING OLD SEVERE DISTURBANCES

Where old signs of both fire and windstorms indicated old disturbances severe enough to largely or completely destroy the stand, the resulting associations were even-aged and bore less resemblance to the climax than did associations following partial disturbances. Due to the lapse of fifty or more years since the catastrophe, however, forest succession had progressed considerably and the composition of the subordinate crown levels indicates the approach towards the climax (Table 5). Such associations following old severe disturbances were most common on ridge tops, where windthrow is most frequent.

At all elevations, the destructive action of wind and fire resulted in a more or less even-aged stand of white pine with about half as much hemlock and smaller amounts of red oak and red maple (Fig. 8). White pine and red oak were poorly represented below the crown canopy. White pine seedlings less than one foot high were abundant, it is true, but none had survived to attain a greater height. On the other hand, the more tolerant species of the overstory, hemlock and red maple, were represented in all crown levels. As in the climax associations, red maple was more prominent on ridge tops than on low and mid-slopes.

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differences in stand composition reflecting their history (Table 4). Stands at the higher elevations deviated from the climax composition to a greater degree than those lower down and also possessed fewer age classes in the

TABLE 4
ASSOCIATIONS FOLLOWING OLD PARTIAL DISTURBANCES
Percent Composition by Location and Crown Level

Species	Overstory	Middlestory	Understory	
			15'-1'	1' or less
RIDGE TOPS (5 samples)				
Hemlock	30	25	10	41
White pine	24			1
Paper birch	19	3		
Red oak	18	2		14
Red maple	5	1	3	26
Beech		61	67	11
Others (BB, SM)	4	8	20	7
	100%	100%	100%	100%
HIGH SLOPES (7 samples)				
Hemlock	41	50	47	50
White pine	36			3
Red oak	15	1		4
Red maple	3	7	2	23
Black birch	2	2	4	18
Beech		28	5	
Others (SM, RS, WA, etc.)	3	12	42	2
	100%	100%	100%	100%
LOW AND MID-SLOPES (10 samples)				
Hemlock	71	47	51	61
Black birch	14	8	1	17
Beech	6	39	41	5
Red maple	4	3	3	8
Others (YB, SM, WP, RS)	5	3	4	9
	100%	100%	100%	100%

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CLIMAX ASSOCIATIONS

In the Pisgah Mountain area the climax forest is represented by certain all-aged stands in which no evidence of severe disturbance was detectable, and whose composition was generally the same in all the crown levels. Fourteen plots were classified as representing climax associations. For these, the percent composition of the crown levels was determined for plots found on the high slopes and ridge tops in one group, and for the low and mid-slopes in another (Table 3). This grouping was indicated by the plot compositions and was necessitated by the inadequate number of plots at each elevation.

The climatic climax association as represented by the low and mid-slope stands consists primarily of hemlock, beech and sugar maple, with black birch and white ash as other major components, and yellow birch, basswood and red spruce as species of minor importance. This hemlock-beech-sugar maple association (Fig. 7) is essentially the same hemlock-northern hardwoods climax recognized by the majority of field investigators as existing throughout the northeastern United States.

At high elevations—on or near the tops of ridges—the composition of undisturbed stands differs from that of the climatic climax, and a physiographic climax may be delineated. This consists primarily of hemlock and white pine with lesser amounts of beech, black birch and red maple. Contrasted with the climatic climax, this ridge top association is generally simpler in composition and shows marked differences in both the species present and their abundance. Hemlock, beech and black birch characterize both climaxes. Certain species (sugar maple, white ash and basswood) are entirely lacking at the higher elevations, while others, such as white pine and red maple, are common at the higher elevations but absent in the climatic climax.

It will be noticed that white pine, here considered a major component of the ridge top physiographic climax, is the only species that is not present in all stories of the stand. White pine does not possess the high degree of tolerance¹ and the ability to reproduce and maintain itself in the deep layer of duff and litter ordinarily associated with climax species (Graham, 1941). The ultimate requirement of a climax species, however, is that it must be able to occupy the opening caused by the death or decadence of a tree in the overstory. On better soils, a white pine seedling germinating after the formation of a small opening in the overstory cannot compete with the advance growth of hemlock and hardwoods beneath. On exposed ridges, however, with smaller, broader trees and relatively infertile

¹ A tolerant species can survive under a dense forest cover for prolonged periods; an intolerant one requires full light for survival.

ASSOCIATIONS WITHIN THE PISGAH VIRGIN FOREST

An association is a community of plants which has distinguishing characteristics, usually with respect to composition, location, structure and history. In contrast, a "cover type" merely characterizes stands with a similar composition of the overstory without regard to internal structure or history. When an association has reached a condition of stability, and is capable of perpetuating itself from generation to generation without marked changes, it is known as the climax. All other associations are at some stage in the process of development towards the climax. Thus, the vegetation on any given area in the absence of disturbances develops through various successional stages, constantly becoming more and more stable.

Two types of climax are distinguished (Nichols, 1923): (1) climatic climax and (2) physiographic climax. The climatic climax is that self-maintaining association that "most fully expresses the influence of *climate* as a differentiating factor of the environment." Since this condition is best fulfilled in habitats where localized climatic influences are minimized and where vegetative development is least inhibited by adverse soil or topographic conditions, the climatic climax in the Northeast will tend to develop on the better soils and under favorable climatic conditions. Topographic and allied local climatic and soil conditions often preclude the development of the climatic climax. On certain sites such as ridge tops, sand plains and swamps, therefore, it is necessary to recognize physiographic climaxes,—associations which constitute a climax for the site but which differ in composition from the climatic climax. Examples of these are the pitch pine-oak climax on dry sandy outwash soils (the sand barrens of central New England) and the white pine-hemlock association on outwash soils which are somewhat more moist and fertile than those which support pitch pine.

Pioneer associations consist of the first forest stands to invade an area devoid of tree growth for any reason. These are followed by pre-climax associations, which in the absence of disturbances develop into the climax.

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to which the native species of chestnut had no resistance, and the loss sustained is without parallel in the recorded history of local forests.

Otherwise, the incidence of disease and decay in erstwhile vigorous trees generally may be traced to other causes, such as lightning, fire or drought. For example, in the Pisgah forest several areas were found, varying from one-half to two acres in size, where *Armillaria mellea*, a fungus causing root rot, was associated with the death of all the hemlocks in the dominant stand, the trees having been weakened by surface fires some fifteen years previously. Similarly, small groups of pine struck by lightning had subsequently been severely attacked by this same fungus.

Death of trees from insects and fungi as a primary cause in the mixed original forests of central New England appears to have been generally limited to groups of trees or to small portions of stands. Only minor changes in composition, therefore, probably have resulted from these causes.

These in turn fall, exposing still others. Large openings caused in this manner afford favorable conditions for the establishment of such light-demanding species as characteristically occupy clear cuttings or severe burns.

The foregoing paragraph was written in 1937. The hurricane of September 21, 1938 (Fig. 6) demonstrated its truth, and emphasized the importance of wind as a factor affecting forest succession. In this storm, practically all the mature trees in Cheshire County were destroyed. Other storms of similar violence occurred in New England in 1815, 1635 and undoubtedly in previous centuries (Brooks, 1939).

Although windfalls can often be identified as long as 150 years after the catastrophe, stump analyses on cutover areas of virgin growth give us evidence of even earlier storms. The common occurrence of old even-aged stands, particularly those containing pine, which originated before the arrival of white man, testify to early catastrophes, either severe wind storms or fires.

As would be supposed, extensive wind damage is commonest at the higher elevations. Of the 21 samples in which wind had exerted an appreciable effect on forest composition, 17 were located on high slopes or ridge tops (13 on ridge tops alone), and only 4 occurred on low or mid-slopes.

Evidences of fire were almost invariably found together with evidences of wind. These two agencies are mutually favorable to one another. Fire weakens the trees, particularly the root systems, and makes them more liable to windthrow, while wind storms produce a tangled mass of brush and fallen trees in which severe fires may easily develop.

Sleet storms constitute another important disturbing influence bringing disaster to forests. Trees heavily coated with ice often suffer injury through the loss of top or branches, their exposed parts and weakened condition thereafter paving the way for the entrance of fungi or the attack of insects.

INSECTS AND FUNGI

Both insects and fungi play an important role in speeding the decline and death of trees damaged by other agencies, but little is known of their activities as primary causes of mortality in virgin stands on trees not yet decadent or otherwise weakened. Insect epidemics have been known to inflict heavy losses in extensive stands composed of a single or a few species, but there is reason to believe that the mixed composition of the stands in central New England served to hold insect damage to low limits. In the case of fungi, at least one organism, *Endothia parasitica*, the chestnut blight, has altered the composition of virgin stands to the extent of eliminating one species, the chestnut. This was a disease of foreign origin



Harvard Forest photograph

FIG. 6. A VIEW OF THE HARVARD TRACT THREE YEARS AFTER
THE HURRICANE OF SEPTEMBER, 1938

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underbrush for cultivable fields. These fires were generally set in the fall after the leaves and seed had fallen, and in this way not only the smaller trees were destroyed, but the larger ones were also sooner or later killed. By this method they kept quite large areas treeless for the purpose of cultivation." Similar practices on the part of the Indians to improve agricultural lands and to increase visibility in hunting have been recorded by others (Hawes, 1923; Lutz, 1930; Bromley, 1935).

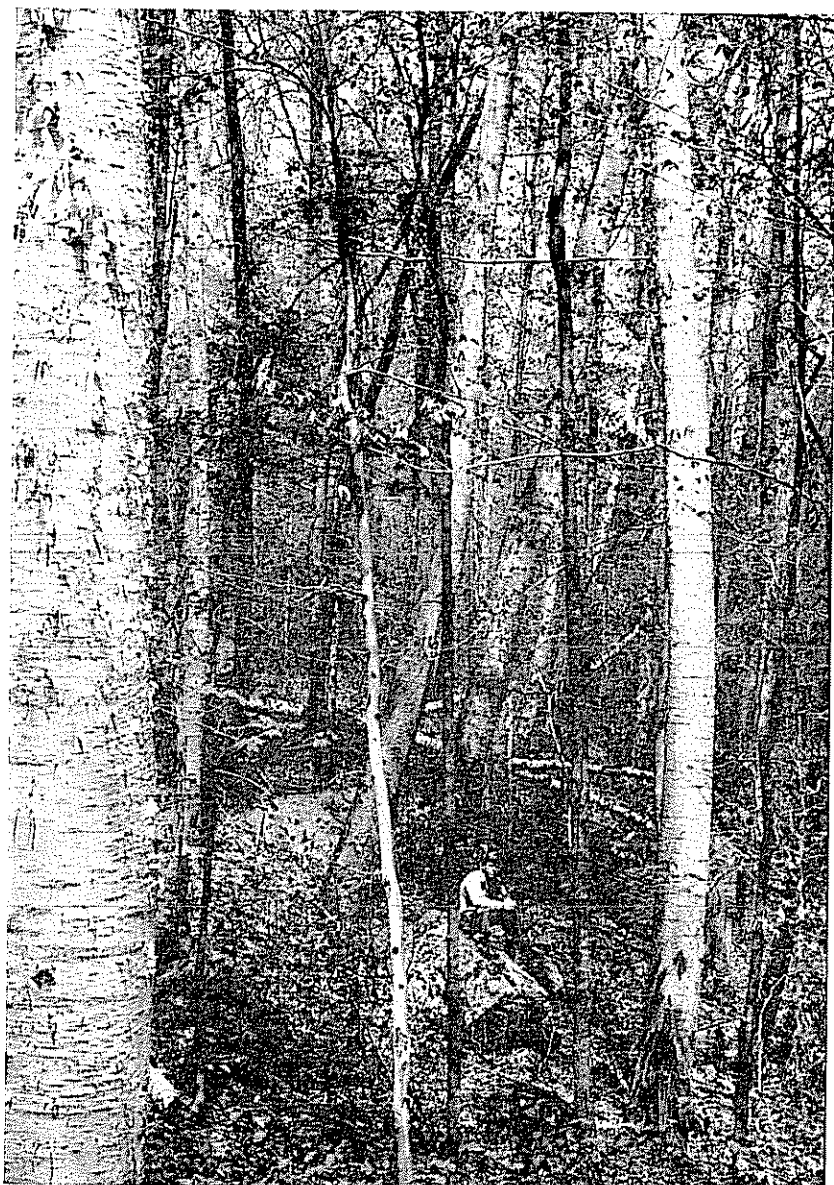
Fires set by early white settlers may be placed in nearly the same category as Indian fires. Child (1885) states that "the settlers' methods of clearing the land was to cut the trees and let them lie upon the ground until fairly well seasoned. They then burned them as they lay, afterwards drawing together the remnants of the unburned logs and again subjecting them to fire until completely consumed." Doubtless, even as today, many such brush fires became uncontrollable and developed into extensive conflagrations. Furthermore, little effort was made towards controlling such fires, since in the early years of settlement the forest was generally looked upon as a hindrance to progress and something to be rid of by the quickest means available.

Mount Monadnock (3166 feet), some fifteen miles to the east of the Pisgah forest, furnishes a spectacular (and, therefore, well-documented) example of the effects of early fires. Successive fires before and during the days of early settlement of the locality not only destroyed the original forest but also consumed the organic soil supporting tree growth at the higher elevations, thus laying bare a large part of the summit (Nutting, 1925).

When restricted to the surface litter, a fire may cause no more damage than the death of the smallest seedlings and ground plants, and with the passage of a few years its effect is scarcely discernible. With the more destructive types of fire, however, the species composition of the stand may be drastically altered and fire becomes an important agency influencing forest succession (Fig. 5).

WIND AND SLEEP

Trees felled and uprooted by the wind are common in the virgin forest, particularly on high ridge tops where the soil is thin and the trees are exposed to the full force of the gale. As the stand grows older and the trees become taller, the likelihood of windthrow increases. Wind is perhaps the commonest cause of death of overmature trees. Storms of unusual violence may at times prostrate the larger part of a stand on an exposed site, as was observed during the present study. Once a few trees are felled on the windward side, their immediate neighbors are exposed.



Harvard Forest photograph

FIG 5. EVEN-AGED PAPER BIRCH STAND WHICH BECAME
ESTABLISHED AFTER A FIRE

DISTURBING INFLUENCES IN THE VIRGIN FOREST

Destructive agencies, independent of man, have always exercised a considerable effect on forest composition. Foremost among these are fire, wind, ice, insects and fungi. In the Pisgah forest these influences had been sufficiently common and severe to affect markedly the composition of about eighty percent of all the samples studied.

FIRE

The occurrence of fire in the original forest is evidenced by written history, by the trees themselves and by the soil. Whether started by lightning or by man, there is every reason to believe that fires were perhaps less numerous but at the same time more extensive and more destructive in the original than in the present forest. This greater severity of fires was due to the absence of artificial barriers, such as roads and cleared land, to the lack of organized forest fire control and to the heavy accumulation of organic matter under the original forest, which was highly inflammable during periods of drought.

During dry times lightning undoubtedly causes an occasional forest fire. In the present study many veteran pines were observed that had been struck by lightning. In one instance a large pine snag had been consumed by a lightning-caused fire, which had penetrated a foot below the ground level. Only a few charred limbs and pieces of bark remained. One may readily picture such a snag smoldering for a day or more after a storm, eventually starting a surface fire when the litter and duff dry out sufficiently to become inflammable.

Lightning may cause openings in the canopy even when no fire results. The death of trees from electrical shock, occasionally several in a group, has been noted in second-growth stands in the Harvard Forest, as well as in those included in the present study. In some cases the openings so formed are large enough to encourage the establishment of a new generation.

For generations before the arrival of the white man, the Indians started forest fires. Hurd (1886) states that the Squakheag Indians, before 1720, "set frequent fires in certain portions of the domain to keep down the

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predominant on the low and mid-slopes; three others (white pine, white pine-hemlock-red oak, and red oak) characterized high slopes and ridge tops; while one type (white pine-hemlock) occupied a somewhat intermediate position with respect both to site and composition.

In all cases where types containing white pine were found on low and mid-slopes, the plots were on the warmer and drier south and west slopes. These types showed a similar affinity for the warmer and drier aspects at higher elevations. The red oak type characteristically occupied the extreme top of the ridges (aspect, all sides).

Variations in relative elevation and aspect, nevertheless, do not wholly account for differences in stand composition. Since other factors of the site, such as soil and climate, were relatively constant for all samples, it would appear that these differences are due in part to stand history, in particular to the disturbing influences that have always been operative. A consideration of these catastrophic or destructive agencies is essential to an understanding of the old growth forest.

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averaged 84 trees per acre. In only four plots, however, were there less than 30 trees per acre, and in only six were there more than 130.

Volumes ranged up to 85,000 board feet and averaged 33,400 board feet per acre (Scribner Decimal C scale). Of this volume, over 80 percent was in hemlock and white pine—species which also attained the largest size and the greatest age.

Seven cover types, named after the species predominant in the overstory were recognized (Table 2). Of these, six can be readily classified as cover types or variants standardized by the Society of American Foresters (1940), while the red oak type delineated in the present study occupies a somewhat anomalous position. In character and distribution it is similar to the S.A.F. red oak type (No. 52) described for the southern Appalachians. The associates differ, however, and consist of paper birch, hemlock and red maple in the Pisgah forest, but of chestnut, other oaks and yellow poplar (*Liriodendron tulipifera*) in the Appalachians.

The names assigned to the several cover types, based as they are on the composition of the overstory alone, are misleading in those types where the composition of the middlestory and understory is unlike that of the overstory. For example, stands classified under the hemlock type almost invariably contained beech as a leading element in the middlestory.

The distribution of the cover types was related to elevation and aspect. Three types (hemlock, hemlock-beech and beech-birch-sugar maple) were

TABLE 2
FOREST COVER TYPES AND THEIR DISTRIBUTION
ACCORDING TO LOCATION

S. A. F. standardized cover types ^a	Types recognized in present study	Number of samples			
		Low and mid- slopes	High slopes	Ridge tops	Total
9. White pine	A. White pine	1	2	9	12
10. White pine-hemlock	B. White pine-hemlock	1	4	0	5
	C. White pine-hemlock- red oak	1	3	6	10
11. Hemlock	D. Hemlock	8	4	4	16
	E. Hemlock-beech	7	1	1	9
12. Sugar maple-beech- yellow birch	F. Beech-birch-sugar maple	8	1	2	11
52. Red oak	G. Red oak	0	2	3	5

^a Society of American Foresters, 1940.



Harvard Forest photograph

FIG. 4. OLD GROWTH HEMLOCK AND WHITE PINE IN THE
HARVARD TRACT

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chestnut are longer-lived pioneers that persist into pre-climax associations. Since the present investigation was confined to "old growth," few of the shorter-lived pioneers were encountered. Pin cherry, aspen and gray birch undoubtedly sprang up in each new opening in the original forests and persisted for a few decades.

In the Pisgah forest, paper birch was primarily a pioneer that followed fire, especially at the higher elevations. Evidence of fire was associated with the occurrence of paper birch on 94 percent of the sample plots where it occurred. This species was abundant throughout the former chestnut association.

The occurrence of chestnut in the Pisgah area is somewhat enigmatic. Inasmuch as it has been eradicated, the methods adopted in this study fail to explain fully its former position in the virgin forest. A tree of the central forest at the extreme northern limit of its range in the New England upland (it occurs farther north in the Connecticut and Merrimac valleys and in similar habitats), it appears to have been an occasional component of late pioneer and early pre-climax stands, generally being associated with paper birch, red maple and red oak. Associations in which chestnut was formerly the predominant species are described in the preceding chapter, and are thought to have originated as a result of a single northeasterly storm and associated fire in about 1726.

It is possible that chestnut in the Pisgah forest may be a relict of times when the local climate was milder. The hypothesis that recent climatic changes affect the distribution of plants has been developed by Raup (1937).

PRE-CLIMAX SPECIES

Species that occupy an intermediate position between pioneer and climax species in the Pisgah forest include white pine, red oak, red maple and red spruce. Becoming established soon after the disturbance, often under a nurse crop of pioneer trees, they persist until shortly before the climax is reached. On exposed sites certain of them occur as components of the climax.

The ecological status of white pine has been the subject of much controversy. While the majority of investigators have excluded it from the hemlock-northern hardwoods climatic climax, others have considered it as a true climax species. Nichols (1935) has summarized the latter view. The present study contains no evidence that white pine is a member of the climatic climax, but does indicate that it is a characteristic component of the physiographic climax at higher elevations. Its occurrence in the ridge top physiographic climax, as in the sand plain physiographic climax,

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can be explained on the basis of the relatively greater vigor of pine in comparison with hardwoods when growing on the drier and more infertile soils.

Red oak, another characteristic species of the transition forest, occupies a similar ecological position. Less vigorous than white pine in the virgin forest, it is generally confined to the higher elevations, particularly to sunny exposures on dry ridge tops.

Red maple is more tolerant than either white pine or red oak, but is less vigorous than either when grown in the open. It seeds prolifically under most old growth associations, but few seedlings survive.

Although neither frequent nor abundant, red spruce was found at all elevations in the less disturbed associations. Farther north it is an important climax species, but in the Pisgah area it cannot successfully compete with its associates and is reduced to a pre-climax status.

CLIMAX SPECIES

Hemlock, beech, black birch and sugar maple are the most important climax species in the Pisgah virgin forest. Others classified in this category include white ash, yellow birch and basswood. Of these, hemlock, beech and black birch occur in climax associations on all sites. The others are largely confined to the more protected places.

Hemlock is the most abundant and aggressive climax species. It is the first climax tree to invade the pre-climax stand, preempting some space ultimately filled by other species. In the Pisgah area beech is not as aggressive as hemlock. Although it comprises a large part of the middle-story, few trees succeed in attaining a place in the overstory and then largely in climax stands (Fig. 11).

Despite the fact that black birch reproduction is abundant on the forest floor, mature trees are not often found in the overstory. This species has seldom been considered an important member of the climax by other investigators. Its position in the Pisgah forest, however, is analogous to that occupied by yellow birch in northern New England.

Sugar maple was the fourth most numerous climax species in the area studied. It was confined to low and mid-slopes and was equally abundant in the middle and overstories.

The above discussion is confined to the more common species. Others, such as red pine, white oak and black cherry were so infrequent as to preclude generalization of their ecological status. The first two are probably late pioneer or early pre-climax species on high, well-drained sites. Trees such as hophornbeam, striped maple and mountain maple, which are incapable of gaining a dominant position in the stand, are omitted from the

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discussion or are considered as shrubs. Still other species occurred in the Pisgah old growth, but were confined to extremes of habitat. Examples of these include elm (*Ulmus americana*) and black gum (*Nyssa sylvatica*) in swales and swamps, and pitch pine (*Pinus rigida*) on highly exposed ridge tops.

SHRUBS AND HERBS

With very few exceptions the ground cover was found to be scanty throughout the stands studied. Altogether, only thirty-five common species of shrubs and herbs were recorded in addition to six genera not broken down into species. Although an effort was made to tally all species, the list is undoubtedly far from complete. Lutz (1934) has shown that the same area must be visited often during all portions of the growing season to complete an accurate check-list. This was not done in the present study, but sufficient information was obtained to characterize the ground vegetation and to show its relationship to forest trees, site and land-use history.

The species recorded are listed in Appendix C in order of descending frequency. Three species (checkerberry, partridge berry, and witch hobble) occurred on more than half of the sample plots, while thirteen additional species occurred on more than ten percent.

The occurrence and abundance of shrubs and herbs were definitely related to forest cover types (Appendix D), each of the seven cover types being associated with a characteristic composition of ground cover. A few plants were confined to one cover type. Of these, dockmackie, or maple-leaved viburnum, occurred in eighty-two percent of the northern hardwood (beech-birch-sugar maple) samples, but in less than ten percent of those of other types. Other common plants generally specific to one type included asters in the northern hardwood type and club mosses in the hemlock-beech type. Bracken, raspberry and blackberry were largely confined to areas of recent disturbances.

Other plants were largely associated with certain predominant over-story trees. Among these, mountain maple and pipsissewa were found under hemlock, mayflower under white pine and striped maple under types containing considerable hardwoods. Still other plants were common in many types, but strikingly absent in others. This is perhaps the most common relationship of ground cover species to forest types (for example, the first five species listed in Appendix D). No plant was uniformly abundant under all cover types.

Little evidence is apparent that, in the Pisgah old growth forest, the ground cover was of any direct indicator value for either site or early stand history. Instead, the relationship between these factors is of a secondary nature, since the shrubby and herbaceous vegetation is largely controlled by the trees under which they grow which, in turn, are determined by factors of environment and stand history.

SOILS

A previous publication of the Harvard Forest (Griffith, Hartwell and Shaw, 1930) included observations and analyses of soil profiles taken in the Pisgah mountain virgin forest. In that study the depth of the horizons of over one hundred profiles was measured, and many of the soils were analyzed for consistency and structure, texture, acidity, and nitrogen content. Certain differences were found, but these were not considered particularly noteworthy. Both the organic layers and the leached horizon were found to be thicker under coniferous stands than under hardwoods. The soils under both types of stands were distinctly acid, particularly the leached horizons. Each layer of soil under conifers, however, was more acid than the same layer under hardwoods. Similarly, more nitrogen was found in each mineral horizon under hardwoods than in the corresponding stratum under conifers.

In the present study, soil observations were confined to the measurement of the depth of each horizon on three profiles within each plot. The mean depth of each horizon was then computed for each of the five groups of associations described above and for the different cover types.

In Figure 12, the depth of the horizons is contrasted with the average composition of the stand at each successional stage. The stages are arranged according to their relationship to the climax (stage I) from the standpoint of forest composition. Since soil changes necessarily lag behind changes in composition, and since the stand composition itself generally is continually changing, it is evident that the soil profile under any association is an expression not only of the composition of that particular association but also of all previous stands which have occupied the same site.

In general, differences in the soil profiles appear to be related to the composition of the dominant stand. The greater the proportion of conifers, particularly white pine, the thicker are all the layers of the organic soil and the leached horizon. Contrariwise, the dark brown enriched horizon attains its greatest depth in the soils which support the greatest proportion of hardwoods in the overstory. This conclusion is substantiated by Appendix E, which presents the average depth of each horizon under coniferous, mixed and hardwood stands.

Most of the soil horizons were of approximately the same depth at the different elevations. The dark brown layer was an exception to this, being thickest (0.97 inch) on low and mid-slopes, intermediate in depth (0.79 inch) on high slopes, and thinnest (0.57 inch) on ridge tops.

Although both studies (Griffith, Hartwell, and Shaw, 1930, and the present one) reveal similar trends in soil horizon thicknesses with changing composition of the stand, the quantitative results do not agree very closely. This is probably due in part to personal bias in identifying horizons (no individual was common to both field parties) and in part to the fact that, while the two studies overlapped, the present one covered a considerably larger area and a greater variety of conditions.

The soil profiles under the old growth stands differ markedly from those of similar soils under second-growth stands in the Harvard Forest. Under the old growth, a thick leached horizon overlain by a compact layer of unincorporated humus (mor) is characteristic, while under second-growth stands the leached layer is thin or absent and the organic material is ordinarily mixed with the upper portion of the mineral soil (mull). Part of this difference is undoubtedly due to the fact that, although separated by only 25 miles, Pisgah Mountain lies in a region of true podzols or leached soils, while Petersham is located in a different major soil region, that of the brown podzolic soils (U. S. Dept. Agric., 1938). Nevertheless, soil conditions under old growth stands are evidently not ideal and are, in fact, less favorable to tree growth than those generally found under second-growth stands.

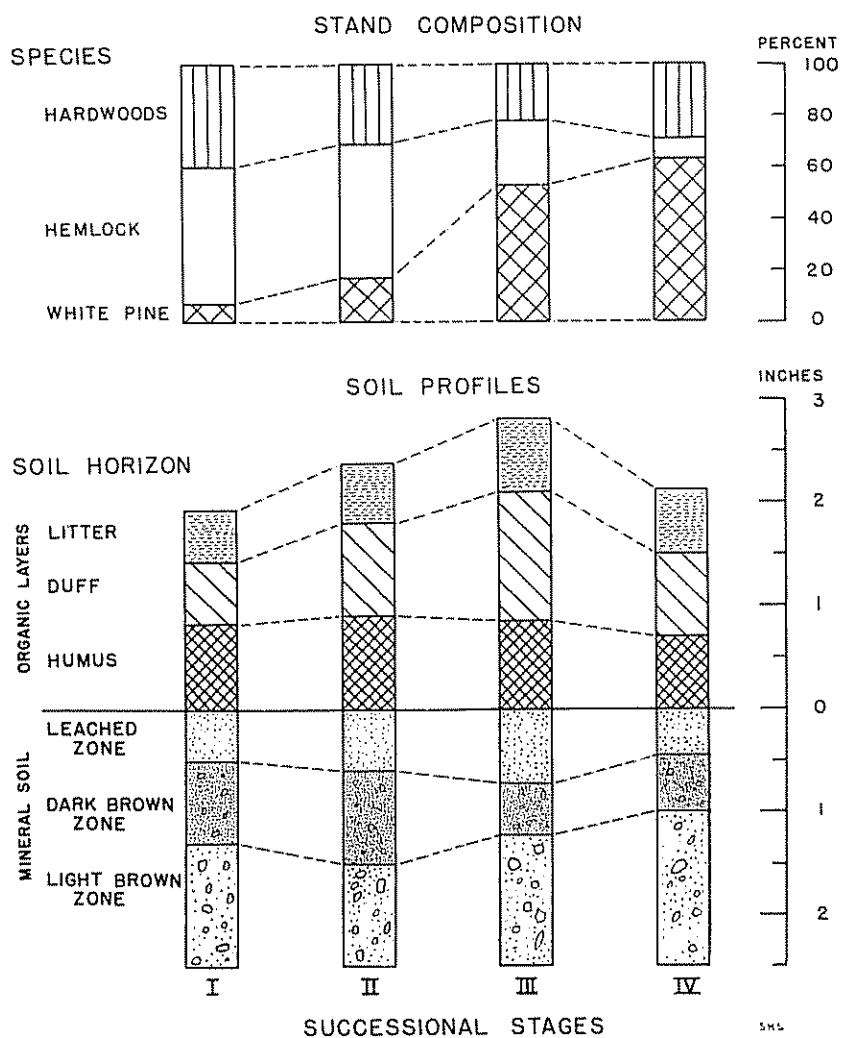


FIG. 12. RELATION OF SOIL PROFILES TO COMPOSITION OF THE OVERSTORY

SUMMARY AND CONCLUSIONS

The virgin forests of central New England exhibited wide variations in composition. Seven distinct forest cover types were represented among the sixty-eight remnants of primeval stands studied, not to mention minor variations.

The variation in composition can be partly explained by differences in the elevation and aspect of the stands. To more fully account for it, however, one must utilize evidence of past stand history, giving particular attention to the occurrence and severity of fire, wind, and other natural forces of destruction. When all these factors are considered, few important differences in composition remain unexplained.

Two climax associations were recognized. The first, the climatic climax, found on lower slopes, consists primarily of hemlock, beech, sugar maple and black birch. The second, the ridge top physiographic climax, is a hemlock-white pine association, with beech, black birch and red maple as minor components. This latter climax also occurs on dry outwash soils in the lowlands, where the habitat is ecologically similar to that of the ridge tops of the Pisgah Mountain forest.

Natural disturbances of greater or less violence had markedly affected composition in over eighty percent of the stands. Fire and wind were the most frequent and disastrous, while lightning, sleet, insects and fungi were also influencing factors.

In general, the more severe any disturbance and the shorter the lapse of time since its occurrence, the greater is the difference in composition between the ensuing stand and the climax.

The complete destruction of a stand, an occurrence often brought about by the combined action of wind and fire, was generally followed by the establishment of even-aged stands of white pine, red oak, and some hemlock. Under certain conditions chestnut and paper birch were prominent in these temporary associations. As such stands approached old age, hemlock, beech, and black birch gradually replaced the pre-climax species. Supplementing these species on the best sites were sugar maple, yellow birch, white ash, and basswood.

Not in all cases does a natural disturbance increase the period of time necessary for the development of the climax. In associations where pre-climax species form an overstory over climax species, a disturbance may hasten the succession toward the climax. This happens when the over-

CENTRAL NEW ENGLAND VIRGIN FOREST

story is largely destroyed, such as by wind or disease (for example, the chestnut blight), and much of the understory survives to form the new stand.

The climax composition will be reached after the death of most of the longest-lived pre-climax trees. In the Pisgah forest, it was reached in a period of about four hundred years during which no severe disturbance took place.

The distribution of shrubs and herbs appears to be governed to some extent by the composition of the forest cover. Most species, however, occurred under a variety of overstory types.

True podzol profiles had developed throughout the virgin forest under all cover types. The depth of the soil horizons was related to the composition of the stand. In general, the accumulation of organic matter was greatest and the leached horizon the thickest under conifers, particularly white pine; while the dark brown, enriched horizon reached its greatest depth under stands containing a large proportion of hardwoods.

* * * * *

The primeval forests, then, did not consist of stagnant stands of immense trees stretching with little change in composition over vast areas. Large trees were common, it is true, and limited areas did support climax stands, but the majority of the stands undoubtedly were in a state of flux resulting from the dynamic action of wind, fire and other forces of nature. The various successional stages thus brought about, coupled with the effects of elevation, aspect, and other factors of site, made the virgin forest highly variable in composition, density and form.

These same natural forces and factors of site are exerting equally powerful influences today, and will continue to do so in the future. Although obscured by the destructive action of man, the same successional trends are none the less ever present in our second growth forests, and the same tendency of stand composition to develop in the direction of the stable climax association is as operative now as it was four hundred years ago.

The forester who is capable of analyzing a given site in terms of the climax composition which will naturally develop there, and of determining the successional stage reached by the stand now on the ground has it in his power to practice silviculture in harmony with natural forces. In so doing, the authors believe, lies the greatest promise of minimizing the costs of crop production and maintenance, of affording the greatest security against destructive agencies and of building up a sound and enduring enterprise in forestry.

APPENDICES

- A. SUMMARY OF SAMPLE PLOT COMPOSITION
- B. FREQUENCY OF OCCURRENCE OF TREE SPECIES BY CROWN LEVEL
- C. FREQUENCY OF OCCURRENCE OF SHRUBS AND HERBS
- D. FREQUENCY OF OCCURRENCE OF THE MORE COMMON SHRUBS AND HERBS
BY FOREST COVER TYPES
- E. SOIL PROFILES UNDER CONIFEROUS, MIXED, AND HARDWOOD STANDS

APPENDIX B
FREQUENCY OF OCCURRENCE OF TREE SPECIES
BY CROWN LEVEL

Common name ^a	Scientific name ^a	Frequency ^b			
		Over- story	Middle- story	Understory 15'-1'	1' or less
Hemlock (Hem)	<i>Tsuga canadensis</i>	59	87	74	74
White pine (WP)	<i>Pinus strobus</i>	44	16	9	41
Black birch (BB)	<i>Betula lenta</i>	32	47	22	46
Chestnut (C)	<i>Castanea dentata</i>	32 ^c		6 ^c	1 ^c
Red oak (RO)	<i>Quercus borealis</i>				
	<i>maxima</i>	28	22	4	19
Beech (Be)	<i>Fagus grandifolia</i>	25	79	68	46
Red maple (RM)	<i>Acer rubrum</i>	25	43	24	57
Paper birch (PB)	<i>Betula papyrifera</i>	15	16	10	4
Sugar maple (SM)	<i>Acer saccharum</i>	7	15	28	28
Red spruce (RS)	<i>Picea rubens</i>	7	4	15	15
White ash (WA)	<i>Fraxinus americana</i>	4	3	4	6
Yellow birch (YB)	<i>Betula lutea</i>	3	7	7	7
White oak (WO)	<i>Quercus alba</i>	1	3		
Basswood (Ba)	<i>Tilia glabra</i>	1	1	3	3
Red pine (RP)	<i>Pinus resinosa</i>		1	4	
Black cherry (BC)	<i>Prunus serotina</i>				
Pin cherry (PC)	<i>Prunus pennsylvanica</i>				
Aspen, poplar (Pop)	<i>Populus tremuloides</i>				
Hophornbeam (H)	<i>Ostrya virginiana</i>				

^a Nomenclature follows that of Harlow and Harrar (1941).

^b Frequency refers to percent of the total number of plots in which the species was observed. For example, hemlock was found in the overstory on 59% of the plots.

^c Overstory chestnuts are blight-killed; understory trees are sprout clumps.

APPENDIX C

FREQUENCY OF OCCURRENCE OF SHRUBS AND HERBS

<i>Common name</i> ^a	<i>Scientific name</i> ^a	<i>Frequency</i> ^b
Checkerberry	<i>Gaultheria procumbens</i>	75
Partridge berry	<i>Mitchella repens</i>	63
Witch hobble	<i>Viburnum alnifolium</i>	60
Blueberry	<i>Vaccinium</i> spp.	47
Striped maple	<i>Acer pennsylvanicum</i>	44
Polypody	<i>Polypodium vulgare</i>	38
Common wood fern	<i>Aspidium spinulosum</i>	35
Sarsaparilla	<i>Aralia nudicaulis</i>	34
Pipsissewa	<i>Chimaphila umbellata</i>	24
Dockmackie	<i>Viburnum acerfolium</i>	22
Mayflower	<i>Epigaea repens</i>	21
Aster	<i>Aster</i> spp.	19
Indian cucumber-root	<i>Medeola virginiana</i>	19
Club moss	<i>Lycopodium</i> spp.	16
American fly honeysuckle	<i>Lonicera canadensis</i>	15
Mountain laurel	<i>Kalmia latifolia</i>	12
Goldthread	<i>Coptis trifolia</i>	9
Bracken	<i>Pteris aquilina</i>	9
Marginal shield fern	<i>Aspidium marginale</i>	7
Bunchberry	<i>Cornus canadensis</i>	7
Nannyberry	<i>Viburnum lentago</i>	7
Witch-hazel	<i>Hamamelis virginiana</i>	6
Wild lily of the valley	<i>Maianthemum canadense</i>	6
Raspberry, blackberry, etc.	<i>Rubus</i> spp.	6
Christmas fern	<i>Polystichum acrostichoides</i>	4
False Solomon's seal	<i>Smilacina racemosa</i>	4
Violet	<i>Viola</i> spp.	4
Mountain maple	<i>Acer spicatum</i>	
Sedge	<i>Carex</i> spp.	
Rattlesnake plantain	<i>Epipactis pubescens</i>	
Sheep laurel	<i>Kalmia angustifolia</i>	
Twin-flower	<i>Linnaea borealis</i>	
Indian pipe	<i>Monotropa uniflora</i>	
Mountain holly	<i>Nemopanthus mucronata</i>	
Wood sorrel	<i>Oxalis acetosella</i>	
Grass	<i>Poa</i> spp., etc.	
Wild gooseberry	<i>Ribes prostratum</i>	
Common elder	<i>Sambucus canadensis</i>	
American yew	<i>Taxus canadensis</i>	
Star flower	<i>Trientalis americana</i>	

^a Nomenclature follows that of Gray's Manual of Botany (7th edition).

^b Frequency refers to percent of the total number of plots in which the plant was observed. For example, checkerberry was observed in 75% of the plots.

APPENDIX D
FREQUENCY OF OCCURRENCE^a OF THE MORE COMMON
SHRUBS AND HERBS BY FOREST COVER TYPES

<i>Species</i>	<i>Coniferous types</i>			<i>Mixed types</i>		<i>Hardwood-types</i>	
	<i>Hem</i>	<i>WP</i>	<i>Hem-WP</i>	<i>Hem-Be</i>	<i>WP-Hem-RO</i>	<i>RO</i>	<i>Be-B-SM</i>
Witch hobble ^b	94	50	60	82			64
Partridge berry	75	83	60	78		60	36
Checkerberry	87	92	100	89	90	60	
Blueberry	37	58	40		80	60	
Polypody	50	67	60		50		
Striped maple	31			67	60	60	82
Pipsissewa	31		40	33			
Mayflower		33			60		
Mountain maple	62			56			
Sarsaparilla		75					45
Aster							54
Dockmackie							82
Club moss				56			

^a For convenience in interpretation, low percent frequencies have been omitted.

^b For example, witch hobble occurred in 94% of the hemlock stands, 50% of the white pine stands, etc.

APPENDIX E
SOIL PROFILES UNDER CONIFEROUS, MIXED AND
HARDWOOD STANDS

<i>Soil layer</i>	<i>Coniferous stands</i>	<i>Mixed stands</i>	<i>Hardwood stands</i>
	<i>(depth in inches)</i>		
L layer (litter)	0.59	0.56	0.57
F layer (duff)	.93	.80	.78
H layer (humus)	.97	.75	.57
Total organic layers	2.49	2.11	1.92
Leached (A) horizon	.68	.48	.44
Dark brown (B ₁) horizon	.73	.67	.88

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APPENDIX A. SUMMARY OF SAMPLE PLOT COMPOSITION

Stand description and history	Aspect Sample & Slope plot no. degrees	Number of trees per acre U° M° 15'-1' 1' minus				Percent composition of crown levels by species ^a												Other species ^b																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																							
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* Percent composition is calculated for the entire understory in this table. In tables in the text, the percent composition is calculated for each layer of the understory.

^b C—chestnut (number in parentheses is number of dominant chestnuts formerly in 0.1 acre plot); WO—white oak; PC—pin cherry; BC—black cherry; Pop—quaking aspen; H—hophornbeam; Ba—basswood; RP—red pine.^c O—overstory; M—middlestory; U—understory.