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FOREST ASSOCIATIONS IN THE HARVARD FOREST

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INTRODUCTION

THE PROBLEM

The present study represents an effort to explain so far as possible in the light of present knowledge the composition and occurrence of forest associations in the Harvard Forest.

The Harvard Forest in Petersham, Massachusetts, has been maintained as an experimental area since 1907. The long-term research program, which has been centered here for more than forty years, is based upon the belief that the history and development of forest communities can best be understood by selecting a small area—some 2,400 A in this case—and recording at intervals the composition, volume, and other characteristics of each community as well as detailing all cutting operations and other disturbances.

The study is restricted to the first 40-year period of University management, that from 1907 to 1947; and in general to those parts of the Forest which have been owned by Harvard University since the start. More specifically, it deals with Compartments I through VIII of the Prospect Hill Block, I through VIII of the Tom Swamp Block, and II through X of the Slab City Block. A total of 1,852 A of land are covered, of which 763 or 41% are in the Prospect Hill Block, 642 or 35% are in the Tom Swamp Block, and 447 or 24% are in the Slab City Block. Figure 1 shows the location of the portions of the Forest included in this study. Elevations range from 700 to 1400 ft above sea level.

The study is further confined to the composition aspects of the forest. The problem is exceedingly complex. The existing forest stands are small and highly variable. They owe their present-day existence to the interaction of a great many factors, among the most obvious of which are: the migration of tree species into the area; pre-colonial distribution of species as governed by site, fire, wind-damage, and other agencies; land-use history from the time of settlement; soil formations; depth of the water table; aspect and elevation of the site; variation in local climate between one point and another and between types of forest stands; the influence of insects and diseases such as the gypsy moth, the white pine weevil, and the chestnut blight; and the impact of fires and climatic agencies, especially the great hurricane of 1938. Many other factors could be named.

Because tree species are commonly identified by their common names, these names are used throughout. Scientific names are given in Table 4 or in the text.

During the 9 years of this study, a number of facets relating to the composition of the Harvard Forest were examined (Spurr 1946, 1950). Aspects that have been previously published, and which consequently are outside the scope of the present paper deal with the vegetational significance of recent climatic changes (Spurr 1953), stand composition following the 1938 hurricane (Spurr 1956a), the relation of local climate to forest composition (Spurr 1956b), the effect of cutting practices on forest com-

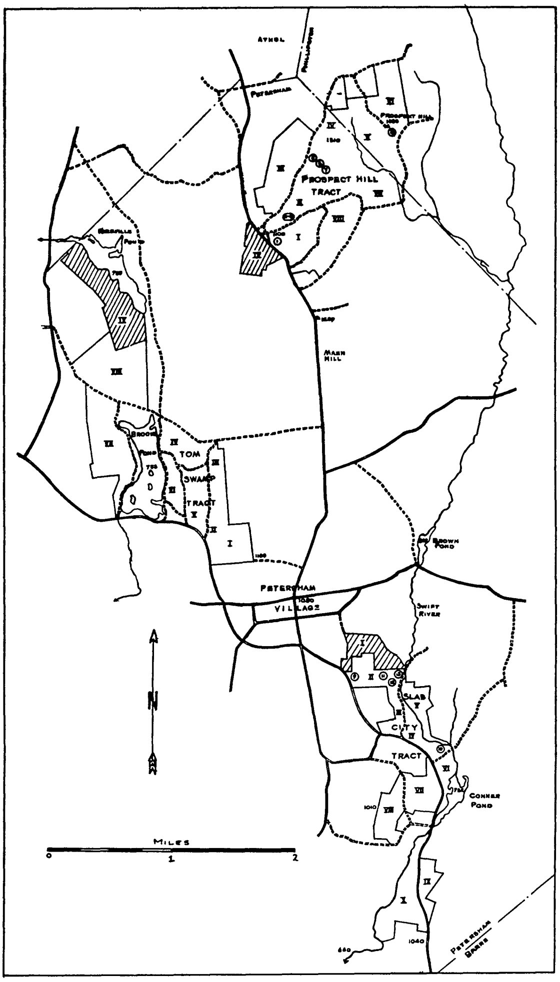

FIG. 1. Map of the Harvard Forest showing three tracts and the subordinant compartments. Numbers circled indicate location of local climate stations, 1943-45.

position (Spurr 1956c), and the success of forest planting as related to site and cleaning (Spurr 1956d). The present paper is abridged from a doctoral dissertation prepared under the supervision of Prof. Harold J. Lutz of Yale University and submitted to that University.

Basic Materials

Three sources provide much of the data: the Harvard Forest map series, the Harvard Forest stand and experimental records, and original field work.

Basic are the series of stand and type maps extending back over a 40-year period. The maps vary in quality and accuracy, but give an excellent overall picture of composition changes. Preliminary topographic maps to a scale of 1 in. to 400 ft and a contour interval of 10 ft were constructed by early students at the Harvard Forest. That part of Tom Swamp east of Harvard Pond was mapped in 1908; Tom Swamp VII and VIII were mapped about 1917; the Prospect Hill Tract in 1910; and the Slab City Tract in 1909 and 1912. The first type maps were constructed shortly afterwards. Beginning in 1919, the entire forest was mapped approximately every 5 years.

The earlier maps were constructed by compass and pacing traverses, those of 1925 through 1937 being constructed at a scale of 200 ft per in. The 1937 map is particularly valuable because it records the types on the Harvard Forest just before the 1938 hurricane and because the location of compartment lines was carefully determined for the first time by transit traverses tying in permanent boundary stakes. In the present study the earlier maps were transferred to the recent base map, with obvious errors of type-boundary location corrected in the process.

The most recent maps were prepared at a scale of 400 ft per in. by Richard C. Rose, Earl P. Stephens, and the author from aerial photographs supplemented by careful ground checking (Spurr 1948). For the first time, an effort was made to list the actual species present according to their relative importance in individual stands, and to assign height and density values to each stand. Thanks largely to the availability of recent infrared photographs of good scale (1:4,800 and 1:12,000) and to the improved techniques of mapping and classification, these maps have proved much more accurate and useful than previous map series.

The second major source of basic materials has been the Harvard Forest stand and experimental records. These records are voluminous and date back to the acquisition of the area in 1907. Although highly variable in quality and in degree of detail, they do provide a clear understanding of the cultural history of each stand over a 40-year period. Additional material pertinent to the study came from the experimental records, dealing with such topics as hardwood plantings, regeneration studies, permanent sample plots, and soil survey. The periodic inventories of the tract also yielded information of interest. Detailed case histories of 14 important stands are available (Lutz & Cline 1947), as are single-page case histories of 26 (Spurr 1944).

The third source of basic material has been original field work. The author has spent several years in the Forest in various research and management activities. He thus has participated actively in the measurement of sample plots, type mapping maintenance and development of the record system, and has obtained first-hand knowledge of practically every stand in the Forest.

THE VIRGIN FOREST OF CENTRAL NEW ENGLAND

Historical Records

Accepting the probability that the present forest species have for the most part been present and important in New England for many centuries and even for thousands of years (Spurr 1953), we still require knowledge of the virgin forests at the time of settlement by Europeans. Such information must be compiled from fragmentary historical records and from study of remnants of old-growth timber in the region.

The writings of early observers such as Thomas Morton (1632), William Wood (1634), Peter Whitney (1793), and Timothy Dwight (1795-1821) have been adequately summarized and discussed by such contemporary writers as Hawes (1923), Bromley (1935), Raup & Carlson (1941), and Cline & Spurr (1942). In general, they present a panorama of oak, chestnut, and hickory upland forests in Connecticut, Rhode Island, and eastern Massachusetts including the town of Petersham. Going north into southwestern New Hampshire, hemlock and northern hardwoods were increasingly abundant. Localized forest types such as pitch pine on sand plains, chestnut oak on xeric ridges, and spruce in bogs and at the high elevations, had approximately the same distribution as they do today. Both fire and windthrow were apparently important disturbing influences in the pre-colonial forests. The Indians habitually burned the woods at least along the coast, while lightning also may have been the cause for an undetermined number of fires. The mounds and hollows left in the ground by fallen trees were noted by Dawson (1847), as evidence of destructive pre-colonial windstorms. Destructive hurricanes were recorded in 1635 and 1815, with lesser storms being noted for intervening years.

Additional historical records of considerable interest are given by Douglass (1755) and Belknap (1792). The former gives considerable information on utilization and size of white pine, concepts of that day as to quality, sizes, and value of the wood of various species, and the scarcity of firewood around Boston, but little about actual forest composition. The latter is more specific and has been apparently overlooked by previous writers on the original forest of New England. Belknap was a keen and accurate observer of forest conditions of his time. His conclusions as to the distribution of tree species agree closely with those of present-day forest ecologists; he recognized the existence of forest succession; he is one of the earliest writers to appreciate the nature of peat and the importance of fossil wood found in it. All in all, Belknap provides the best contemporaneous description of the virgin forest that we have, and one on which we can place considerable reliance.

From these original sources, we may conclude that the pre-colonial forests of New England were made up of the same species that characterize the region today. Furthermore, specific kinds of sides were occupied by forest types generally similar to those occupying them today. The importance of any given species, or the composition of any given type within the original forest cannot be more than roughly approximated from early descriptions, and any attempt to reconstruct such evidence must of necessity be highly subjective in nature.

OLD-GROWTH REMNANTS

Perhaps the best sources of information concerning the floristic composition of the pre-colonial forest are the remnants of this forest that have persisted into recent times and which have been studied by botanists and foresters. Remnants in southern New England have been discussed by Nichols (1913) and Hawes (1923). R. T. Fisher, first Director of the Harvard Forest, was influenced by the old growth remnants in southwestern New Hampshire and elsewhere when he described in 1933 the original forest in central New England as:

> "a forest in which broad-leaved trees and hemlock formed a dense stand from eighty to one hundred feet high, above which either by small groups or single trees and varying greatly in abundance, white pines reached a height of 150 feet or more."

Old-growth remnants in the Pisgah Mountain section in the town of Winchester in extreme southwestern New Hampshire were studied in detail by various members of the Harvard Forest staff (Cline & Spurr 1942). The so-called hemlock-northern hardwoods climax forest, consisting in this case largely of hemlock, beech, sugar maple, and black birch, was found only on protected sites where fire and windthrow had apparently not occurred for about 400 years. On the more exposed sites, white pine apparently also occurred as a climax species. Most of the remnants, however, showed evidence of past disturbances which were apparently responsible for the presence of substantial quantities of white pine, paper birch, red oak, red maple, and chestnut in the stands. One paragraph from the conclusions to this study may well be repeated:

> "The primeval forest, 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."

In the Harvard Forest itself, areas that have never been cleared for agricultural use and that have always remained forested have been located as accurately as possible by Raup & Carlson (1941). None of these areas contain virgin forests today. Cutting has taken place in all the stands, and many have apparently been cut several times.

In two places, trees of considerable age still occupy the land, despite 200 years of cutting and the 1938 hurricane. These stands have been analyzed in the course of the present study.

In Slab City IX, along the east side of the highway, is an old growth hemlock stand (Fig. 2). According to Raup & Carlson (1941), the land was first assigned in 1740. Since some of the trees still standing had originated previous to this time, it is evident that the area has never been completely cleared. The present stand consists largely of hemlock, with red maple, black birch, yellow birch and other hardwoods making up about ten percent of the stand volume. A few large white pine are scattered through the stand. The average height in 1944 was 65 ft, the average basal area being about 235 ft per A and the average volume about 35,000 board ft per A. Only among the hemlock are there trees more than 110 years old, and these range up to about 90 ft in height. There is little evidence as to the composition of this stand in 1740, except that many of the large hemlock of today were small suppressed trees in the understory at that time.

FIG. 2. Old-growth hemlock stand in Slab City IX.

Analysis of increment cores of standing trees in the old growth stand indicates that the area has been culled over at least twice. In 1841 much of the stand was cut or blown down. Growth analysis of hemlocks that were left shows a marked acceleration of diameter growth beginning with this year. Of the larger white pine and hardwoods that have been bored, all originated in 1841 or within 5 years afterwards. In 1892, about 60 to 70 trees per A were cut. The stumps are still discernible. These trees ranged up to 2 ft in diameter and consisted almost entirely of white pine together with a few chestnut. It appears unlikely that hemlock predominated in this stand in 1740. Rather it would seem that white pine, chestnut, and various hardwoods occurred at this time in mixture with the hemlock, the hemlock taking over the stand after two successive logging operations had removed its competitors.

The second existing stand in which old trees predominate is in the northeastern corner of Prospect Hill II on medium to poorly drained glacial till bordering a peat bog. It consists of a small clump of large hemlock trees ranging up to 180 years old in 1946. On a quarter-acre permanent sample plot, volume per acre in 1944 was 8,300 cubic feet, or 36,700 board feet. The largest tree is 31 in. in diameter and 85 ft high. The stand apparently originated about 1765, probably following the first logging of the area. Growth-ring analysis shows that the stand was opened up by light cutting in 1790, by the 1815 hurricane, and that the trees were released again in 1838 and 1876. Large hemlock up to 3 ft in diameter were cut in 1888, and a few more trees were cut in 1894. Some release was afforded by the death of the chestnut due to the blight following 1916, and by the 1938 hurricane.

The above two cases, the only ones in the Harvard Forest where old-growth trees occupy more than one-quarter acre, tell little about the composition of the original forest on those sites. Although hemlock is currently predominant in both stands, and was undoubtedly at least a minor part of the stands in the early eighteenth century, the present stands owe their composition and structure to early windthrow and subsequent logging operations which removed the overstory, thus releasing the hemlock understory. Much the same situation was found by Marshall (1927) in the southern part of Tom Swamp IX, the Adams-Fay lot.

THE PERIOD OF SETTLEMENT: 1733-1907

The Town of Petersham was settled in 1733. The Harvard Forest was established in 1907. The uses to which the land was put during this period of 174 years have greatly influenced the forest composition. The distribution of species and forest types in the Harvard Forest in 1907 was to a large extent the function of previous use of the land, and it remains so today.

The land-use history of the area has already received considerable attention, and will be dealt with only briefly in the present study. The story in its broad outlines has been ably told by Fisher (1925, 1933) and Cline (1936), and it has been portrayed in the three-dimensional dioramas of the Harvard Forest model series. More recently, many of the details of the land-use history of Petersham and the Forest have been published by Raup & Carlson (1941).

In brief, the virgin forests were almost completely cut before the end of the eighteenth century, and much of the area cleared for farming. For a generation or two in the first portion of the nineteenth century, the area was largely agricultural. To illustrate this with a specific example, the writer prepared an agricultural land-use map of the Prospect Hill Block (Fig. 3). Areas which apparently have been always forested were mapped on the basis of the Raup & Carlson study and original field checks in which the ages of standing trees were determined and in which stumps and other evidence of former tree growth were noted. Nine percent of the tract fell into the continuously forested category. Less

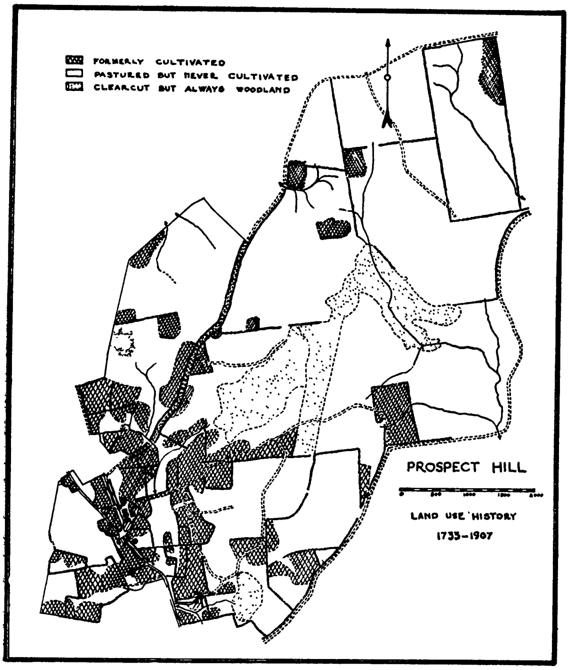

FIG. 3. Reconstruction of past land use in Prospect Hill Tract, showing areas formerly cultivated, pastured but never cultivated, and clearcut but always woodland.

than one acre is still covered with old-growth trees. The rest is occupied by hemlock, red spruce, red maple, and other species in stands less than 100 years old, although an occasional older hemlock and spruce can be found which originated under the previous stand and which was subsequently released by logging.

The remaining 91% has been cleared for agricultural use at one time or another, but not necessarily all at one time. Much of this has obviously never been cultivated repeatedly or thoroughly, but rather has been used primarily for upland pasture. To estimate how much land has been cultivated, the stone walls were followed and studied. Stone walls made up of boulders taken from cultivated fields are typically larger and contain a greater variety of stone sizes and a greater number of stones than do simple stone walls that were erected merely to mark property lines or to fence in cattle and sheep. By correlating the nature of the stone wall with the character of the ground surface on either side, it was possible to delineate those areas that had very likely been cultivated repeatedly or thoroughly. These areas covered 16% of the tract, the remaining 75% being mapped as having been cleared for upland pasture but not having been intensively cultivated.

The proportions of land in the other two tracts which have been continuously in forest, cultivated, or which have been cleared for pasture are apparently of the same general order of magnitude as in the Prospect Hill Block, but were not determined.

Following the opening of western and northern lands for settlement, much of the cleared land was abandoned, and seeded in to even-aged stands consisting largely, but by no means entirely, of white pine. These old-field pine stands became characteristic of the region, and by 1900 gave rise to a substantial logging industry. However, as Thoreau first noted (1863), and as professional foresters have since rediscovered to their sorrow, these pine stands on upland soils were succeeded after logging by even-aged hardwood stands which today constitute the principal types in the region.

Not only has the forest cover changed, but the drainage relationships of the soil have also been changed by the damming of streams and the subsequent gradual filling up of the ponds by vegetation. William S. Benninghof (personal communication) has worked out the history of Brooks Pond, Riceville Pond and the intervening Tom Swamp (Fig. 1). He found that, in the first part of the nineteenth century, only two small areas near the present highway were ponded, each of these "Meadow Water" ponds covering about an acre. By 1830, the Tom Swamp causeway had been constructed across the middle of the peat bog. Riceville Pond was formed about 1856 by damming Riceville Brook. It was drained shortly after the turn of the century and restored following the 1938 hurricane. Brooks Pond was first formed sometime after 1880, and its level was raised slightly to its present position about 1900. Each of these changes undoubtedly affected the composition and growth of the vegetation in the adjacent swamps.

Similarly, the drainage of the Swift River in the Slab City Block and several of the brooks in the Prospect Hill Block have been repeatedly modified by the construction of dams, the filling of ponds, and the destruction of dams. The ruins of the old grist mill near the Forest Cottage in Prospect Hill I are still prominent. This mill was powered by water stored in two artificial ponds in what is now Prospect Hill VIII.

COMPOSITION CHANGES: 1907-1947

THE MAP SERIES

The different stand maps vary greatly in quality. Up to and including the 1937 map, emphasis was placed on broad types. Only the changes in acreages occupied by these broad types can be obtained directly from the maps. Furthermore, there is considerable variation in the way the different types are defined. The distinction between hardwood (here defined as trees capable of forming sawlogs) and cordwood areas, in particular, has varied greatly from time to time, and these types must be grouped in the present analysis. Again, some mappers were prone to emphasize the importance of white pine, labelling stands as white pine (hardwoods or white pine-hemlock-hardwoods even) when white pine made up less than 10% of the stand. This is particularly marked in the maps constructed between 1923 and 1937. All in all, the broad trends are well defined, but any attempt to detail the composition changes must be deferred until individual areas are taken up.

The method of analysis involved transferring all type maps to a common base map prepared in 1946 from the 1937 transit survey as amended by aerial photographic data and supplementary transit surveys. Figures 4 and 5 represent the resultant maps of 1912, 1919, 1923, 1937, and 1946 for Compartments IX and X of the Slab City Block, compartments which are of particular interest because practically no cutting has been done in them since 1907, and because a minimum of damage was done there by the 1938 hurricane. In the forest type notations, WP indicates white pine; HEM, hemlock; HD, sawlog-forming hardwoods such as red oak, white ash, paper birch, and black birch; PION HD, pioneer hardwoods such as black cherry, gray birch, and aspen; and OPEN, open alluvial land. A soils map of the same area is included. Aerial photographs of this area have been published as figures 12, 13, and 14 in "Aerial photographs in forestry" (Spurr 1948).

The number of stands mapped has increased steadily in successive years. In the Prospect Hill Block alone, containing 844 A and including 763 A

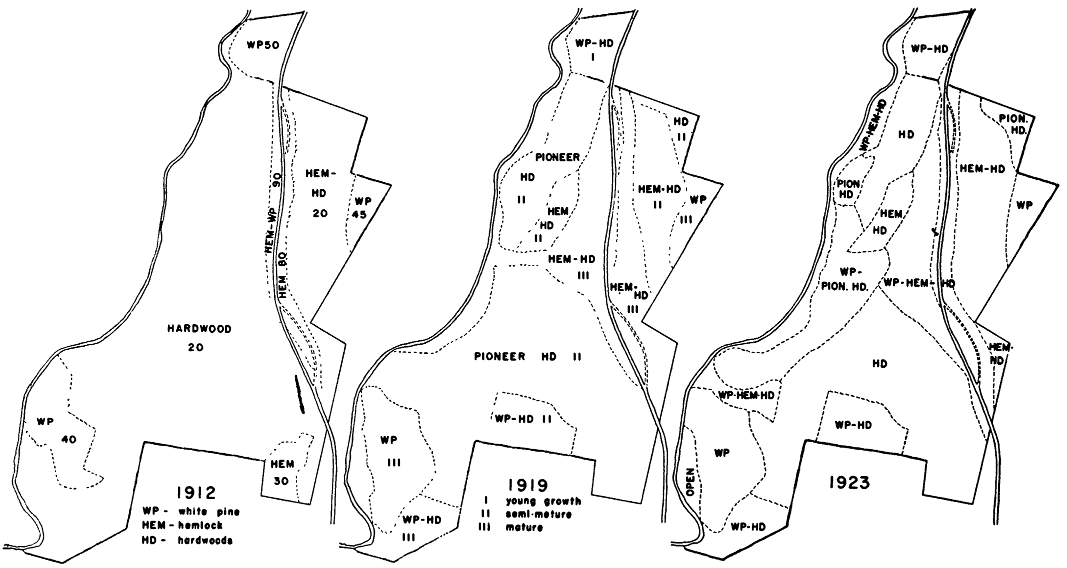

FIG. 4. Forest type maps of Slab City IX and X as of 1912, 1919 and 1923.

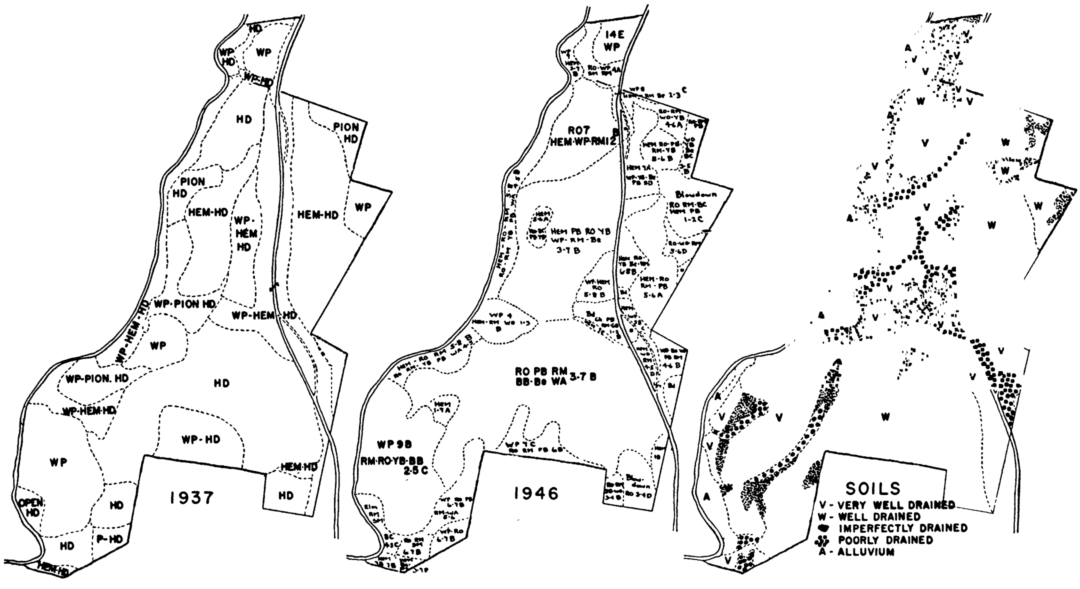

FIG. 5. Forest type maps of Slab City IX and X as of 1937 and 1946 together with generalized soils map.

considered in the present study, 90 forest stands were mapped in 1908. There were 120 stands mapped in 1919; 240 in 1929; and 280 in 1937. The 1946 map has 330 stands for this area, of which 163 are volunteer stands over 10 years old, 86 are undifferentiated blowdown and cut-over areas, and 81 are coniferous plantations. This increase in number of stands is due partly to the increasing complexity of the Forest during these years resulting from management and research activities, and partly to the gradual recognition of finer and finer distinctions within areas formerly mapped as a single stand.

The acreage occupied by each broad type in selected years is given in Table 1. In 1908-09, mapping was confined to the Slab City Block and to the eastern part of the Tom Swamp Block (Compartments I through VI), The acreages in these same compartments have been computed from the 1912-13 maps for the purpose of comparison. The 1912-13 maps included all of the study area except for Tom Swamp VII. Again for comparison, the comparable acreage values have been computed for 1919. From 1919 on, the entire 1852 A of the study area have been mapped. No acreages were computed for the maps constructed between 1923 and 1937 as these were largely modifications of the 1923 map.

TABLE 1. Acreage of forest types in the Harvard Forest study area: 1907-1947.

	15 COMPARTMENTS		24 COMPARTMENTS		25 COMPARTMENTS			
	1908	1912	1912	1919	1919	1923	1937	1946
White pine..........	238	217	395	394	480	431	208	38
Pine-hardwoods......	120	82	115	194	208	356	287	115
Hemlock-hardwoods..	34	43	79	137	164	223	306	218
Hardwoods..........	139	219	779	664	701	550	546	1046
Coniferous swamp....	...	...	82	87	87	71	73	50
Coniferous plantings..	...	...	25	67	67	81	365	330
Open...............	55	25	200	132	145	140	67	55
Total............	586	586	1575	1575	1852	1852	1852	1852

The percentage of the study area occupied by the various broad types is given in Table 2. No percentage is given for 1908-09 as less than one-third of the forest was mapped at that time. The general trends are clear. The substantial acreages occupied by white pine and old farm land in 1912-13 have been largely taken over by coniferous plantings, hardwood, and hemlock-hardwood stands.

TABLE 2. Percentage distribution of types in the Harvard Forest study area: 1912-1947.

Forest type	1912	1919	1923	1937	1946
			(Percent)		
White pine............	26	26	23	11	2
Pine-hardwood........	7	11	19	15	6
Hemlock-hardwood....	5	9	12	17	12
Hardwood...........	44	38	30	29	56
Coniferous swamp.....	5	5	4	4	3
Coniferous planting....	1	3	4	20	18
Open................	12	8	8	4	3
Total.............	100	100	100	100	100

Finally a somewhat more detailed analysis has been made for the 763 A of Prospect Hill Compartments I through VIII inclusive. The 1908 stand map was reconstructed by the author in 1944 by projecting the 1913 map backwards using information supplied by the stand records. The 1929 data have been added and the 40-year trend is illustrated in Table 3.

TABLE 3. Percentage distribution of types in Prospect Hill I-VIII: 1908-1946.

Forest type	1908	1912	1919	1923	1929	1937	1946
				(Percent)			
White pine............	17	17	17	19	17	4	1
Pine-hardwood.........	3	4	9	8	11	9	7
Upland hardwoods......	42	43	36	29	27	29	42
Hardwood swamp........	7	8	12	9	6	6	6
Hemlock...............	1	1	1	1	1	1	1
Hemlock-hardwoods.....	..	..	3	11	7	14	12
Conifer swamp.........	3	3	3	3	3	3	3
Conifer plantings.......	..	3	7	7	19	30	26
Open..................	27	21	12	13	10	5	3
Total...............	100	100	100	100	100	100	100

In general, the study of the early maps shows that the same associations have been present since 1908, but that their relative importance, distribution, and exact composition have changed greatly in the intervening period. These changes will be indicated for each broad type.

WHITE PINE TYPES

Two associations contain white pine as a major species. The first is the pine type, defined as containing 80% or more white pine by volume, or by number of trees which are free to grow. The second contains pine in mixture with red maple, red oak, and other hardwoods (Cline & Lockard 1925). These are the old-field types which follow farm abandonment. The first develops when the white pine seed supply is ample and the sod is intact; the second results when this seed supply is deficient and when bare ground is exposed.

In 1912-13, 26% of the study area was in pine, and 7% in pine-hardwoods. In succeeding years, cutting tended to reduce the area, while natural seeding on open land tended to increase it. As late as 1923, 23% of the land was classified as white pine and 19% as pine-hardwoods, although many acres of the later category actually contained few pine. Most of these stands have since been harvested, and the cut-over areas either planted or allowed to come back to hardwoods. Many residual stands were blown down in the 1938 hurricane, so that now only 2% of the study area is in natural white pine, and 6% in natural white pine-hardwoods (Table 2).

HARDWOOD TYPES

Three broad hardwood types were recognized in all the early type maps, these corresponding to the present day distinction between pioneer hardwoods, transition hardwoods, and swamp hardwoods. The acreage of these combined types show a decrease from 1912 to 1923. This decrease, however, is more apparent than real. With time, hemlock became sufficiently important in some areas to justify the segregation of hemlock-hardwood mixtures. Much of the apparent decrease in hardwood acreage, however, is attributable to the habit in the 1920's of designating stands containing a few white pine as pine-hardwoods or pine-hemlock-hardwoods. At any rate, the acreage occupied by hardwoods was nearly doubled by the 1938 hurricane, as most of the blowdown areas have come into hardwood types. At the present time, substantially more than half of the forest is in hardwood types.

Where a white pine seed source is not available at the time of land abandonment, or where mineral soil is exposed at this time, old farm land tends to come in to a mixture of light-seeded hardwoods. These pioneer hardwoods include red maple, gray birch, and black cherry as the most abundant species. Aspen, red oak, and white ash are also common. With time, the association develops into one of the transition hardwood types.

The name, *transition hardwoods,* has been given to the upland hardwood complex of central New England because this complex occupies a zone between the red oak-white oak-black oak forest of southern New England and the beech-yellow birch-sugar maple region of northern New England. Red oak and red maple characterize the zone by their extreme abundance even though they also occur over a wide region outside. Paper birch, black birch, and white ash are other commonly occurring hardwood species. Hemlock first appears as an understory species.

On the older maps, the upland hardwoods were not subdivided into specific associations, but rather mapped as "good hardwoods" or "poor hardwoods" depending upon the commercial quality of the timber. Younger stands, in which such short-lived species as gray birch, aspen, pin cherry (*Prunus pensylvanica* L.f.), and black cherry were abundant, were usually mapped as "cordwood," "poor hardwoods," or "inferior hardwoods." A few years later, after most of the short-lived species had been eliminated, the same stands were often mapped "hardwood" or "good hardwoods," or "better hardwoods."

Prior to 1916, chestnut (*Castanea dentata* (Marsh.) Borkh,) was an important and valuable species. On the 1912-13 maps, less than 2% of the study area was mapped as pure chestnut, but the species occurred as a major element in the red oak-chestnut-red maple transition hardwood type. In 1913, Kittredge noted that locally it was only exceeded in abundance by white pine and red maple. The chestnut blight disease was first noted on the Prospect Hill tract in 1910, and by 1912 the infection was uniformly distributed throughout the town (Kittredge 1913). By 1916, practically all the trees of this species were dead or infected and consequently doomed.

In the hardwood swamps, red maple is the predominant species (Fig. 6), although many other trees are located abundant. In the Prospect Hill Block (Table 3), where the acreage of hardwood swamp has been segregated from that of the other hardwood types, this acreage has remained essentially constant since 1907.

FIG. 6. Red maple swamp, Prospect Hill I.

HEMLOCK TYPES

In 1908, less than 40 A in the Forest were mapped as containing hemlock as a major species. Prominent among the stands thus designated were the two old-growth stands discussed earlier. By 1946-47, hemlock occupied substantially more than 200 A, or 12% of the study area. The slightly greater hemlock acreage indicated for 1937 in Tables 1 and 3 is due to the tendency in that year to designate stands as pine-hemlock-hardwood even when hemlock was a relatively minor species.

Practically all of the present-day hemlock and hemlock-hardwood stands have developed from transition stands either in the absence of cutting or following selective cutting in which the hardwoods were removed, freeing the hemlock understory. The former process, that of natural succession, is responsible for most of the present hemlock-hardwood acreage; although the latter process, that of silvicultural control, is currently important.

The increase in acreage of the hemlock and hemlock-hardwood types is one of the most pronounced trends in forest composition in the past 40 years. Hemlock was a minor species in 1907. It had become a major species by 1947. Apparently it will become increasingly abundant in the future. At one time largely confined to ravines and other protected spots (Figure 7), it is invading a wide variety of sites. A great many acres of hardwood forest are today developing a dense understory of hemlock.

FIG. 7. Hemlock in ravine of Swift River Valley, Slab City X.

CONIFEROUS SWAMP TYPES

Two large peat bogs in the Harvard Forest have consistently remained in coniferous swamp types. The Tom Swamp bog, of which only about 50 A are included in the present study, is forested with a mixture containing black spruce, tamarack, hemlock, red maple, and other hardwoods. The Prospect Hill bog, containing about 25 A, supports an uneven-aged mixture of red spruce, hemlock, and red maple, with smaller amounts of black gum and yellow birch. The oldest black spruce observed in the Tom Swamp bog was 125 years old, and the oldest trees found in the Prospect Hill bog were hemlock about 200 years old. Although considerable wood has been cut from the latter swamp, neither area has apparently ever been clearcut. The acreages of the coniferous types in both bogs have remained essentially constant since 1907.

CONIFEROUS PLANTATIONS

During the 40 years of existence as an experimental forest, much planting has been done on the area. No plantations were in existence in 1907, but by 1946-47, 26% of the Prospect Hill Block and 18% of the entire forest were in coniferous plantations. White pine, red pine, Norway spruce, and white spruce have proven the most successful species and predominate in the present stands. The acreage in plantations has decreased in recent years, due in part to hurricane blowdown, and in part to suppression of plantings by hardwood competition. The area actually slightly exceeds 20% of the study area.

OPEN LAND

In 1912-13, there were 200 A of open land, and in 1907 when the Forest was acquired by the University, this figure was at 230 A. Included in these values were large acreages of abandoned farm land and a lesser amount of non-forested swamp. Systematic planting of the old farm land, coupled with the natural seeding of much of that land which was not planted, reduced the amount of open land to 55 A in 1946-47. Of this amount, nearly 15 A around the Headquarters buildings have been kept open, and the remainder is largely in non-forested swamp. Practically no open upland available for planting exists today.

SUCCESSIONAL TRENDS

Even the generalized picture of stand composition changes since 1907 provided by the study of old stand maps makes it apparent that the post-agricultural succession is a dominant factor determining forest composition today. Three of the naturally occurring types—the white pine type, the white pine-hardwoods type, and the pioneer hardwoods type—originated chiefly on abandoned farm land. In addition, some of the areas mapped as transition hardwoods undoubtedly originated on old fields. All in all, these old-fields types covered about 40% of the study area in 1907 and still include approximately 12% of the area.

In addition to the natural pioneer types, the coniferous plantations, covering 18% of the study area, constitute artificial pioneer associations ecologically similar to the old-field white pine type. Thus, perhaps 30% of the present acreage is occupied by pioneer associations.

Transitional successional stages are chiefly represented by transition hardwood types, although some of the pine and hemlock stands undoubtedly fall in this category. Probably somewhat more than 50% of the forest is of this nature today.

Finally, the hemlock and hemlock-hardwood types, together with a small part of the hardwood and white pine types, represent a later stage in succession. Somewhat less than 20% of the study area was covered in 1946-47 with these "late-successional stages."

PRESENT-DAY FOREST ASSOCIATIONS

Although the information concerning stand composition from the older Harvard Forest stand maps is limited, the 1946-47 maps lend themselves to further analysis and provide a means whereby present-day forest associations can be isolated and described. A check on this technique is provided by the records of permanent sample plots.

METHOD OF STAND MAP CONSTRUCTION

The 1946-47 stand maps were the product of aerial photographic and ground reconnaissance. Various recent aerial coverages taken with panchromatic, infrared, and color film, with various filters, and at various scales, were available for the type mapping, but particular use was made of 1:12,000 photographs, taken with infrared film and a medium red (Wratten No. 25) filter, on July 5, 1944.

First, the base map constructed from transit surveys in 1937 was corrected by using the photographs in the Multiscope set up for use as a transfer device with two semi-transparent mirrors. Some supplementary transit surveying was done by C. T. Brown, Jr. and the writer. Then, the Multiscope was converted for use as a plotting stereoscope with one semi-transparent mirror, and the boundaries of all homogeneous forest areas were transferred to the base map. All stands larger than one-quarter acre were thus segregated. From the aerial photographs, the stands were classified according to (1) broad composition classes as softwood, mixed-wood or hardwood; (2) 10-ft height classes; and (3) 4 density classes. Density class A included stands having 85-100% crown closure; B, 60-85% crown closure; C, 30-60% crown closure; and D, 0-30% crown closure. Heights were coded to the nearest 10 ft, class 7 for example including trees 65 to 75 ft high.

The maps were then taken into the field, and each stand checked on the ground. To replace the broad type classification, the species making up the stand were listed in order of abundance. Trees of primary or major abundance were listed in the numerator of a fraction, and trees of secondary or minor abundance were listed in the denominator. No hard and fast line was recognized between the two groups, but trees making up more than 10% of the basal area were generally considered of primary importance, and those making up less than 10% were of secondary importance. Similarly, important understory trees could be designated in the denominator of the fraction when advisable, their height and density being indicated by separate height and density codings. Normally not more than four species were listed in either the numerator or the denominator of the type fraction.

The result of the typing and coding system was a flexible description of the stand composition and structure as it actually occurred on the ground without recourse to any arbitrary or preconceived classification system. Thus:

$$\frac{\text{T}-\text{PB}-\text{RO}}{\text{YB}-\text{Be}}\ 3-7\,\text{B}$$

would indicate a stand made up of hemlock (T for Tsuga), paper birch, and red oak in that order of abundance, with a scattering of yellow birch and beech, the trees ranging from 25 to 75 ft in height, and covering between 60 and 85% of the area with their crowns. Again:

$$\frac{\text{WP}\ 9\,\text{D}}{\text{T}-\text{RM}\ 4, 6\,\text{B}}$$

would designate a three-story stand, the highest story consisting of a scattering of white pine 85-95 ft high; and the lower two stories, one of which was 35-45 ft high, consisting of a fairly dense stand of hemlock and red maple.

Analysis of Data

In the original work on the Prospect Hill Block, the sorting of data from the stand map was based upon the primary species represented. Thus, all the white pine stands were grouped together and a frequency count made to determine the number of times each species occurred as a major and as a minor species within that group. The results were incorporated into an earlier study (Spurr 1946). In later attempting the same technique for the stands of the Slab City Tract, however, it became apparent that the technique, although informative, was generally unsatisfactory. For instance, a stand in which white pine was the predominant species might be a young stand of post-hurricane origin on a sandy site, a middle-aged old-field white pine stand, or an old-growth stand with white pine standards above a hemlock and hardwood second story. Grouping such divergent associations simply on the basis that all contained more white pine than any other species would scarcely help to define the ecological relationships and associates of white pine.

A more satisfactory approach turned out to be one adapted from a technique evolved by the writer in an earlier study (Cline & Spurr 1942). First, the study was restricted to stands covering at least 1A, to areas of natural stocking, to stands 25 ft or more in height, and with a C stocking or better (more than 30% of the area covered by tree crowns). These standards could be objectively applied to the stand maps, and served to confine the study to reasonably well-developed stands of at least moderate size. The composition of younger stands following the 1938 hurricane is discussed later.

Second, each stand was designated on the basis of field reconnaissance according to successional stage and moisture relationships of the site. Parenthetically, it should be noted that all stands meeting the requirements set up in the three major blocks of the Harvard Forest were used in this study, and not only those in the study area.

Three successional stages were recognized: (1) pioneer, (2) transitional, and (3) late successional. The distinction was relative rather than absolute. Pioneer stands included all those known to have originated on old fields and following clear-cutting and fire in the past 20 to 30 years. Such stands were subdivided into those of old field origin and those originating on cut-over land. Pioneer stands on cut-over sites were distinguished from transitional types of being younger and characterized by the presence of short-lived species such as gray birch, pin cherry, and aspen. Abundant black cherry was also frequently found in pioneer types. Transitional types included all middle-aged stands not segregated as pioneer or late successional. Late successional types included all old-growth remnants, and all areas in which no cutting or other disturbances have taken place over the past half-century or more. Although the segregation of successional stages was somewhat subjective, it proved surprisingly easy and apparently fairly precise.

Five soil moisture conditions were recognized, these five conditions being set up as a result of the study of the local soils and site qualities. The base of the classification was the Harvard Forest soils map (Simmons 1939-1941), modified where necessary by field reconnaissance. Generally but not always, Merrimac, Hinckley and Jaffrey soils were considered very well drained; Gloucester, Charlton, and Brookfield soils were considered well drained; Acton and Sutton soils were considered imperfectly drained; Whitman soils were considered poorly drained; and peat and muck deposits were considered very poorly drained.

When all the stands were sorted according to the above criteria, it was found that each class thus set up was characterized by a distinctive stand composition. This sorting, therefore, was used as the basis for the presentation of information on the present-day forest associates. All frequency values are based upon the percentage of the mapped stands in which a given species was listed on the type maps as an overstory species.

IMPORTANT SPECIES

Many writers have stressed the variability of the composition of the transition hardwood region in general and the Harvard Forest in particular. Indeed, a great many tree species do occur. Jack (1911) has listed 10 commercially important softwoods and about 24 commercially important hardwoods, in addition to a long list of non-commercial woody plants.

One of the most pronounced facts to come out of the present study, however, is that relatively few tree species predominate as primary components of the local forest associations. Table 4 gives the number of stands in which each species occurs as a major or as a minor component in the 235 stands studied, together with the total occurrence reduced to a frequency percentage basis. Only two species, red maple and red oak, occur in more than 40% of the stands—red maple in 86% and red oak in 75%. These two species may be said to characterize the region. Only

TABLE 4. Frequency of occurrence of tree species in the Harvard Forest, 1947.

Common name	Scientific name*	Number of Stands in Which Species Occurs			Frequency Percent
		Major Component	Minor Component	Total	
Red maple......	*Acer rubrum*	154	48	202	86.0
Red oak†.......	*Quercus rubra*	140	36	176	74.9
Hemlock........	*Tsuga canadensis*	52	34	86	36.6
White pine......	*Pinus strobus*	48	29	77	32.8
Paper birch.....	*Betula papyrifera*	19	46	65	27.7
Yellow birch.....	*B. alleghaniensis*	14	36	50	21.2
Black birch......	*B. lenta*	9	34	43	18.3
White oak.......	*Q. alba*	14	24	38	16.2
White ash.......	*Fraxinus americana*	11	24	35	14.9
Gray birch......	*B. populifolia*	9	16	25	10.6
Black cherry....	*Prunus serotina*	2	13	15	6.4
Hickory.........	*Carya* spp.	9	5	14	6.0
Sugar maple.....	*A. saccharum*	2	11	13	5.5
Beech..........	*Fagus grandifolia*	2	10	12	5.1
Elm............	*Ulmus americana*	4	5	9	3.8
Aspen..........	*Populus tremuloides* & *P. grandidentata*	3	3	6	2.6
Black spruce....	*Picea mariana*	3	2	5	2.1
Black gum......	*Nyssa sylvatica*	2	2	4	1.7
Red spruce......	*P. rubens*	2	1	3	1.3
Tamarack.......	*Larix laricina*	1	2	3	1.3

Based upon a total of 235 stands, 25 feet or over in height, 30 percent or better stocking, naturally restocked, and 1.0 acre or more in area.
*Little, Elbert L., Jr. 1953. Check list of native and naturalized trees of the United States (including Alaska). U. S. Dept. Agric. Agric. Handbook 41. 472 pp.
†Probably includes scattered black oak (*Quercus velutina*).

two additional species, hemlock and white pine, occur as major components in more than 10% of the stands. These four species—red oak, red maple, hemlock, and white pine—and only these four species, may be said to constitute the major components of the local forest stands.

Six other species—the four native birches, white oak, and white ash—are locally abundant, occurring in more than 10% of the stands, usually as minor components. Finally, 10 other species occur in more than 1 but less than 10% of the stands. Black oak (*Quercus velutina* Lam.) is present but not listed, as the distinction between black and red oak on the stand maps is not trustworthy. Its ecological position in the locality is treated by Bess, Spurr & Littlefield (1947).

The local forest, therefore, appears to be relatively homogeneous despite the patchwork impression that the stands present on the stand maps. Of 20 significant tree species, only 4 are of primary importance in that they are both abundant and widely distributed throughout the forest.

It still remains, however, to isolate and discuss the individual forest associations. This may best be done by treating separately the pioneer types, the transitional types, and the late successional types.

PIONEER TYPES

Some 46 stands were classified as pioneer associations, 28 occurring on old field sites and 18 on cut-over sites. The sample was insufficient to permit further segregation into soil moisture classes, although the composition trends associated with soil moisture are apparently closely comparable with those described later for the transitional and late successional types.

The composition of the pioneer types is summarized in Table 5, which gives the percent frequency with which each species occurs as a major and as a minor stand component. On old fields the well-known white pine type emerges. White pine occurs as a major component in all but one stand, frequently forming a pure pine type. Red maple and red oak are the other two primary species, both occurring in two-thirds of the stands. Red maple occurs as a major species in slightly more than one-half of the stands, and red oak in slightly more than one-third. Of the minor species, paper birch, gray birch, black cherry, and white ash occur in 18 to 21% of the stands. The old-field white pine pioneer association may, therefore, be characterized as a white pine association with red maple, black cherry, gray birch, paper birch, white ash, and red oak occurring in greater or lesser numbers.

The largest and oldest of these old-field white pine stands covers about 13 A. Remeasurement of a quarter-acre permanent sample plot in 1949 located in the best part of the stand gave a total height of 91 ft, basal area of 189 sq ft per A, 140 stems of white pine and 20 stems of hemlock over 6 in. in diameter per A, and a total volume of 7,600 cu ft per A.

TABLE 5. Frequency of occurrence of species: Pioneer types. 1947. Percent of stands in which species occurs as a major or minor component.

	OLD FIELD SITES			CUT-OVER SITES		
	Major	Minor	Total	Major	Minor	Total
White pine.....	96	4	100	..	6	6
Red maple......	54	14	68	89	11	100
Red oak........	36	32	68	72	11	83
Gray birch.....	4	18	21	45	33	78
Black cherry....	..	18	18	6	33	39
White ash......	..	18	18	6	6	11
Paper birch.....	11	7	18	..	..	..
White oak......	4	7	11	6	6	11
Aspen..........	..	7	7	17	6	22
Hickory........	7	..	7	11	..	11
Black birch.....	..	7	7	..	..	..
Hemlock.......	4	..	4	..	6	6

Based upon 28 stands on old field sites and 18 on cut-over sites.

In the young pioneer stands on cut-over and similar sites, red maple and red oak again appear as primary species, with gray birch being nearly as frequent. Minor components listed in order of frequency include black cherry, aspen, hickory, white ash, and white oak. Of the two aspen species in the forest, the trembling aspen is considerably more abundant than the large-toothed aspen.

The pioneer association on cut-over land is similar in many respects to the natural restocking on hurricane blowdown areas (Spurr 1956a). McKinnon, Hyde & Cline (1935) reported similar stand composition in a regional study of the composition and stocking of volunteer hardwood stands following the clear-cutting of old field white pine.

TRANSITIONAL TYPES

A total of 139 stands on the 1946-47 maps met the requirements of size, height and density of the present analysis and were classified as transitional types. These represented all sites, but nearly half of the stands occurred on well drained sites.

The frequency of occurrence of various species in the transitional types is presented in Table 6. Grouping all sites together, red maple and red oak appear as the two characteristic species, both occurring as major components in approximately three-quarters of the stands. The chief minor species is paper birch with an overall frequency of 30%. Six species are grouped with frequencies between 19 and 25%. These include in order of decreasing importance: hemlock, yellow birch, white oak, white ash, white pine, and black birch. Of these, hemlock occurs chiefly as an understory tree, presaging late successional stages characterized by that species, while the others occur in between 5 and 10% of the stands as major components and in a somewhat greater number of stands as minor components. The overall transitional type, then, is predominantly red maple and red oak association with the understanding that a number of other species occur in varying amounts. A typical transition hardwood stand is pictured in Fig. 8.

A check on the overall composition of the transition hardwoods is provided by the records of 17 permanent sample plots in the Prospect Hill tract. These were established in 1944 by the author and C. T. Brown, Jr. and consist of a series of plots, mostly one-quarter acre in size, located in practically all the natural stands of timber in this largest of the Harvard Forest blocks. In the larger stands, more than one plot was established. Most of the plots were located in protected areas, as the stands on the more exposed sites had suffered greatly from hurricane blowdown and cutting. Therefore, the average site was somewhat better than would normally be the case.

The average basal area per A by species of the 17 plots in the transition hardwood stands is given in Table 7. Red oak and red maple are the characteristic species as in the preceding analysis. Of the

TABLE 6. Frequency of occurrences of species: Transitional types. 1947. Percent of stands in which species occurs as a major or minor component.*

	VERY WELL DRAINED			WELL DRAINED			IMPERFECTLY DRAINED			POORLY DRAINED			VERY POORLY DRAINED			ALL SITES		
	Maj.	Min.	Sum	Maj.	Min.	Sum	Maj.	Min.	Sum	Maj.	Min.	Sum	Maj.	Min.	Sum	Maj.	Min.	All
Red maple...	..	83	83	61	21	82	81	13	94	100	..	100	100	..	100	74	16	90
Red oak.....	67	17	83	95	3	98	81	13	94	42	25	67	20	..	20	73	10	83
Paper birch..	..	33	33	14	26	40	9	19	28	8	13	21	..	7	7	10	20	30
Hemlock....	..	33	33	3	27	30	..	12	12	4	29	33	..	13	13	2	23	25
Yellow birch.	..	..	..	..	13	13	12	22	34	17	25	42	..	13	13	6	16	22
White oak...	33	17	50	13	18	31	6	3	9	..	4	4	..	..	..	9	10	19
White ash...	..	..	..	3	13	16	19	28	47	8	..	8	..	..	..	7	12	19
White pine..	50	33	83	6	15	21	..	9	9	4	13	17	..	7	7	6	13	19
Black birch..	..	..	..	5	26	31	3	6	9	4	8	12	13	..	13	5	14	19
Sugar maple.	..	..	..	2	10	11	3	9	12	..	..	..	..	7	7	1	7	9
Hickory.....	..	..	..	6	6	13	3	3	6	..	..	..	..	..	..	4	4	7
Elm........	..	..	..	..	..	..	3	3	6	..	4	4	13	..	13	2	1	4
Beech.......	..	..	..	..	8	8	..	..	..	..	..	..	..	..	..	..	4	4
No. of stands	6			62			32			24			15			139		

*Apparent inconsistencies in sums are due to rounding-off.

FIG. 8. Transitional hardwood stand on glacial till. Red oak, red maple and paper birch are the characteristic overstory species. Hemlock is prominent in the understory.

secondary species, sugar maple has the largest basal area, primarily because two of the sample plots were arbitrarily placed in small stands characterized by this species. Otherwise, the relative importance of species is much the same as for the frequency study of the entire forest; yellow birch, white ash, paper birch, white pine and hemlock each making up a minor proportion of the forest.

The transitional types, however, vary greatly according to the moisture relationships of the soil. The contrast in the distribution of red oak and red maple is especially well marked. Both occur on all sites. Red maple, however, occurs only as a minor constituent on the very well drained sites and becomes increasingly important with increasing soil moisture,

TABLE 7. Prospect Hill transition hardwood stands (17 plots).

	Free trees*	Overtopped trees†	All trees
	Basal area per acre (sq. ft.)		
Major components			
Red oak	22.7	1.5	24.2
Red maple	18.9	4.0	22.9
Minor components			
Sugar maple	4.4	1.2	5.6
Yellow birch	3.5	0.7	4.2
White ash	2.8	0.3	3.1
Paper birch	2.9	0.1	3.0
White pine	2.5	0.4	2.9
Hemlock	1.1	1.0	2.1
Black birch	1.5	0.2	1.7
White oak	1.2	0.4	1.6
Black cherry	1.3	0.2	1.5
Others‡	1.2	0.4	1.6
Total	64.0	10.4	74.4

*Overstory trees in dominant or codominant crown position.
†Intermediate and suppressed trees.
‡Gray birch, beech, basswood.

being of major importance in all the stands on poorly drained and very poorly drained sites. Red oak has diametrically opposite habits. It is of minor importance on the very poorly drained sites, becomes increasingly important with decreasing soil moisture, and is of major importance on well drained and very well drained sites.

The other species exhibit just as pronounced adaptation to site although none are as abundant as red maple and red oak. Only hemlock appears to be about equally frequent on all sites. White pine is a major species only on very well drained soils, and apparently decreases in importance with increasing soil moisture. Paper birch has much the same distribution except that it is most important on well drained sites. White oak is important only on the very well drained sites, decreases with increasing soil moisture and is not found on the very wettest sites. Since only these species are found on the very well drained sites, the transitional forest on these dry soils may be described as being a red oak and white pine association with white oak and red maple being characteristic minor components.

In contrast, the transitional forest on the well drained sites is considerably more complex. Twelve species have frequencies of 8% or greater on these sites. Beech, hickory, and sugar maple are apparently confined to well drained and imperfectly drained soils. The transitional forest on well drained sites is basically composed of red oak and red maple with lesser numbers of paper birch, white oak and black birch. Hemlock occurs primarily as an understory tree, again foreshadowing late-successional stages. White pine, white ash, hickory, and sugar maple also occur more or less frequently as major components.

On the imperfectly drained soils, red oak and red maple are of equal importance. White ash is the third most frequent species, being very largely confined to these soils. Considering the minor components, the transitional forest on imperfectly drained sites may be summarized as a red oak and red maple association with white ash, yellow birch and paper birch also being characteristic species.

On the poorly drained sites, fewer species are found, and the stand structure is somewhat simpler. Red maple is by all odds the characteristic species with red oak being clearly second in importance. Yellow birch is more abundant on these sites than on any others, while all the other species show a general decline in abundance from the imperfectly drained soils. The association on poorly drained soils, then, may be generalized as composed of red maple and red oak with yellow birch.

As in the previous cases, hemlock occurs primarily as an understory tree. White pine, paper birch, black birch, and white ash are locally of some importance. Fig. 6 shows a red maple swamp directly behind the headquarters building. This stand has been thinned once.

Finally, on the very poorly drained soils, red maple is the only tree that occurs in more than 20% of the stands, and it occurs on all of the fifteen sites. Chief among the minor components are red oak, American elm, and black birch, with yellow birch and hemlock being nearly as frequent but occurring only as minor components. The transitional type on very poorly drained soils is basically red maple with lesser amounts of red oak, black birch, and elm.

From the above discussion, it can readily be seen that the transitional types are highly interrelated and form a continuous and gradual gradational series from the driest to the wettest types. The transitional associations are characterized by red oak and red maple, the relative importance of each being determined almost perfectly by soil drainage. All the other components occur less frequently, and serve to indicate soil moisture conditions. Thus, white pine in the transitional associations is prominent on very well drained or well drained sites; black birch on the well drained to very poorly drained soils; paper birch on the well drained and imperfectly drained soils; white ash on the imperfectly drained soils; yellow birch on the imperfectly drained and poorly drained soils; and finally elm only on the very poorly drained soils. The actual range of each species is, of course, somewhat greater than that indicated above, but their characteristic range is largely as stated.

Late Successional Types

Fifty stands were classified as belonging to the more maturely developed or late successional stages. None of these stands approach the nature of the theoretical climax association as few are apparently stable in composition and all show clearly the effect of past land use and management practices. Relative to the transitional stages, however, they do represent a later stage in forest succession.

Hemlock is the characteristic species of late successional associations, occurring as a major stand component in 96% of the stands (Table 8). Red maple and red oak are the other two species with frequencies greater than 50%. Of the other species, only white pine and three of the birches occur in more than 15% of the stands. The overall late successional association may be characterized as a hemlock-red maple-red oak association with minor representation of white pine, yellow birch, paper birch, and black birch.

Considering variations in composition with relation to variation in soil moisture, both red oak and red maple behave much as they do in the transitional types, the former species tending to predominate on the drier soils and the latter on the wetter soils. The only reason that red maple occurs more frequently than red oak in the late successional stands appears to be that a higher percentage of the stands on the more poorly drained sites reach this stage of development, as these sites are generally more protected from wind and fire.

An insight into the average composition of late successional stands is given by the average basal area values from 6 permanent sample plots in the Prospect Hill Block established and measured in 1944 (Table 9). Hemlock makes up nearly 70% of the basal area of these stands, with red maple and red oak being the other species contributing appreciably to the basal area. White pine and the three longer-lived birches are the other chief components.

On the very well drained sites, white pine is a major species. Black birch, white oak, and paper birch occur frequently as minor stand components. The late successional forest on the very well drained sites consists primarily of hemlock, white pine and red oak with red maple, white oak, and black birch. This association differs from the comparable transitional association in that hemlock is a major species and that white pine has become somewhat more prominent.

TABLE 8. Frequency of occurrence of species: Late successional types. 1947. Percent of stands in which species occurs as a major or minor component.*

	Very Well Drained			Well Drained			Imperfectly Drained			Poorly Drained			Very Poorly Drained			All Sites		
	Maj.	Min.	Sum	Maj.	Min.	Sum	Maj.	Min.	Sum	Maj.	Min.	Sum	Maj.	Min.	Sum	Maj.	Min.	All
Hemlock	100	..	100	100	..	100	88	12	100	100	..	100	91	..	91	96	2	98
Red maple	..	44	44	29	47	76	75	25	100	40	40	80	64	36	100	40	40	80
Red oak	33	44	77	47	41	88	38	..	38	20	20	40	..	..	..	30	24	54
White pine	67	22	89	24	..	24	..	50	50	20	20	40	18	18	36	26	18	44
Paper birch	11	11	22	6	47	53	..	62	62	..	40	40	..	..	..	4	32	36
Yellow birch	..	11	11	18	12	29	12	38	50	40	40	80	..	27	27	12	22	34
Black birch	..	33	33	..	53	53	..	..	..	40	..	40	..	..	..	4	24	28
Spruce	..	..	..	..	..	..	..	..	..	..	..	..	36	27	64	8	6	14
Beech	..	11	11	..	18	18	25	..	25	..	20	20	..	..	..	4	10	14
White oak	..	33	33	..	18	18	..	..	..	..	..	..	..	9	9	..	14	14
Elm	..	..	..	..	..	..	..	..	..	..	40	40	9	..	9	2	4	6
Tamarack	..	..	..	..	..	..	..	..	..	..	..	..	9	18	27	2	4	6
Black gum	..	..	..	..	..	..	..	..	..	..	..	..	9	9	18	2	2	4
No. of stands	9			17			8			5			11			50		

*Apparent inconsistencies in sums are due to rounding-off.

TABLE 9. Prospect Hill hemlock stands (6 plots).

	Free trees*	Overtopped trees†	All trees
	Basal area per acre (sq. ft.)		
Major components			
Hemlock	60.8	8.6	69.4
Red maple	12.6	0.8	13.4
Red oak	9.0	0.7	9.7
Minor components			
White pine	3.2	0.3	3.5
Black birch	3.0	0.1	3.1
Yellow birch	2.6	0.3	2.9
Paper birch	2.4	0.1	2.5
Others‡	2.5	0.8	3.3
Total	96.1	11.7	107.8

*Overstory trees in dominant or codominant crown position.
†Intermediate and suppressed trees.
‡Red spruce, beech, white ash, black cherry.

On the well drained sites, white pine is less important than on very well drained sites, and various hardwoods are more frequent. The average composition obtained from the frequency study is similar to that obtained from the basal area study of the Prospect Hill sample plots in Table 9. Hemlock, red oak and red maple are the key species, while white pine, yellow birch, paper birch and black birch are also common constituents. White oak and beech are also important constitutents locally. Again, in contrast to the comparable transitional type, this late successional association is distinguished by the predominance of hemlock and the greater importance of white pine and yellow birch.

A similar late-successional association is found in the eight stands growing on imperfectly drained sites. Hemlock and red maple are the chief species with yellow birch, paper birch, white pine, and red oak. As in the corresponding transitional type, red maple is more common and red oak less common than on the drier sites. Hemlock and white pine are again more important than in the related transitional types. Beech also occurs as a somewhat less frequent stand component than the other species.

On the poorly drained sites, hemlock is still the most frequently occurring species, followed closely by red maple and yellow birch. The sample is too small to permit accurate analysis of the minor species, but black birch, red oak and white pine are the only ones occurring as major stand components. Elm and paper birch, however, occur as minor stand components in 2 out of the 5 stands. Tentatively, the stand may be described as a hemlock-red maple-yellow birch association with minor components of black birch, red oak and white pine.

Finally, on the very poorly drained sites, hemlock and red maple are again the characteristic species. Here, however, spruce (red on the Prospect Hill Tract and presumably black on the Tom Swamp Tract) are prominent, along with white pine, tamarack, black gum, and yellow birch. We are, therefore, dealing with the softwood swamp type. Two plots in the Prospect Hill peat bog give basal area data typical of the large bog, but not of the smaller bogs or the Tom Swamp bog (Table 10). In these values, red spruce has the greatest basal area and is also the most abundant tree, followed by hemlock and red maple, with the other species only making up a total of 5 sq ft of basal area per A. The late successional association on very poorly drained soils varies widely from spot to spot, but may be generalized as usually containing hemlock, red maple and spruce with occasional white pine, tamarack, yellow birch, and black gum.

TABLE 10. Prospect Hill peat bogs (2 plots).

	Free trees*	Overtopped trees†	All trees
	Basal area per acre (sq. ft.)		
Red spruce	30.4	5.0	35.4
Hemlock	25.0	1.1	26.1
Red maple	12.8	1.1	13.9
Others‡	4.9	0.3	5.2
Total	73.1	7.5	80.6

*Overstory trees in dominant or codominant crown position.
†Intermediate and suppressed trees.
‡Black birch, gray birch, white pine, black gum.

All in all, the late successional associations bear a strong resemblance to the corresponding transitional associations. The most striking differences are the predominance of hemlock and the greater importance of white pine in the former stands. Hemlock arrives at its position by coming up through the understory, while pine does not increase in numbers over the years, but rather maintains itself by the persistence of those few stems which managed to survive early hardwood competition and thereby reaches a position of dominance over the rest of the stand.

As with the other associations described, red oak and red maple are usually present, the former being more frequent on the drier and the latter on the wetter sites. White ash does not occur noticeably in the late successional stands, but whether this is due to its inherent inability to meet long-term competition, or merely to the inadequate sampling of this study cannot be specified at this time.

DISCUSSION

Apparently, then, the associations in the Harvard Forest, far from being made up of a hodge-podge of species scattered indeterminately over the area, constitute a regular series of interrelated types, composed predominantly of surprisingly few species, and closely correlated to successional stage and site as expressed in terms of soil drainage. The species characterizing each of the three successional stages and the five soil drainage classes are summarized in Table 11.

TABLE 11. Tree species characterizing associations in the Harvard Forest.*

Site	Pioneer Associations	Transitional Associations	Late Successional Associations
Very well drained	WHITE PINE GRAY BIRCH Red maple Paper birch Red oak Black cherry	RED OAK WHITE PINE *White oak* Red maple	HEMLOCK WHITE PINE RED OAK Red maple White oak
Well drained	WHITE PINE (old fields) RED MAPLE RED OAK *Gray birch* *Black cherry* White ash Paper birch	RED OAK RED MAPLE *Paper birch* *White oak* Black birch	HEMLOCK RED OAK RED MAPLE *White pine* *Yellow birch* Paper birch Black birch
Imperfectly drained	Insufficient data Red maple, white ash, and birches predominate.	RED OAK RED MAPLE *White ash* *Yellow birch* Paper birch	HEMLOCK RED MAPLE *Red oak* Yellow birch
Poorly drained	Insufficient data Red maple and birches predominate	RED MAPLE *Red oak* *Yellow birch*	HEMLOCK RED MAPLE *Yellow birch*
Very poorly drained	Insufficient data	RED MAPLE *Red oak* *Black birch* *Elm*	HEMLOCK RED MAPLE *Spruce* White pine Tamarack Yellow birch Black gum

*Relative importance is indicated by capitals, followed by italics, followed by ower case.

Two species are practically omnipresent. Red oak and red maple are equally prominent in all successional stages and one or the other is prominent on all sites. As stated previously, however, both exhibit marked relationship to soil moisture, red oak being most frequent on the drier and red maple on the wetter sites.

White pine appears to be both less important than assumed by earlier white pine enthusiasts and more important than assumed by later hardwood enthusiasts. It is, of course, the characteristic old-field tree. Furthermore, as has previously been well established by many investigators, it is the characteristic tree of very well drained sites in all successional stages. Regionally, it occurs on somewhat better sites than those frequented by pitch pine and on slightly better sites than those where red pine is found, chiefly to the north of the Petersham area. On the typical Merrimac and Hinckley soils as well as on the dry ridges of the Pisgah Tract (Cline & Spurr 1942) and similar sites in the Harvard Forest, white pine is a tree of major importance in all successional stages.

The present data further indicate, however, that scattered white pines persist into the transitional stages on all sites, and make up an increasing percentage of the stand volume in the late successional stages as a few trees reach the overstory and become dominant over the rest of the stand. The higher frequency of white pine in the late successional stages as compared to transitional stages may be due to the fact that most of the present late successional stands originated in the mid-nineteenth century when extensive land clearing and woodland grazing created sod conditions favoring the establishment of the species. White pine thus appears to be a minor but important and characteristic component of late successional stages on all sites from the wettest to the driest.

Hemlock occurs in more or less equal numbers in late successional stands on all sites. It occurs but infrequently in pioneer and transitional associations, but is the characteristic species of late successional stands. As the period since farm abandonment increases in length and as clearcutting is supplanted by partial cutting, hemlock is becoming increasingly important. Already one of the most frequent species of the forest, it should become more abundant as partial cutting is practiced in the future.

Of the other species, the various birches are the most important. Paper birch is best adapted to the drier sites, black birch to the average well drained sites, and yellow birch to the wetter sites. White ash is locally important on the imperfectly drained soils, but shows little persistence into late successional stages. White oak is important in all successional stages on the drier soils, while hickories are somewhat less xerophytic, being found on the well drained as well as on the very well drained sites. Beech and sugar maple are occasionally found on the intermediate sites; while red and black spruce, tamarack, elm, and black gum are found on the wettest sites.

Everything considered, all the forest associations found in the Harvard Forest seem to represent a continuous gradational series correlated with successional stage and soil moisture (Table 11). Thus, the old-field white pine and the pioneer hardwood types are pioneer associations which vary in composition according to the site where they occur. Among the transitional types, the white pine-hardwoods type on the driest sites grades into the transitional hardwoods type on the intermediate sites which in turn grades into the swamp hardwoods types on the wettest sites. Among the late successional types, the white pine-hemlock-hardwoods type on the driest sites grades into the softwood swamp type on the wettest sites. A similar gradational series is found on each site as between the different successional stages. In general, the pioneer hardwood associations (but not pioneer white pine) are less than 30 years old, the transitional associations from about 30 to 60 years old, while the late successional associations are older.

It may be mentioned that the associations here described bear little resemblance to the standardized forest cover types as described by the Society of American Foresters (1954). The Harvard Forest associations have been deduced from a study of actual composition of all the forest stands of a given area, while the Society's cover types are based more on economic rather than upon ecological considerations, and relate primarily to broad regionally types rather than to what actually may occur in a specific locality.

It has already been noted that few if any of the stands described approach the condition of a theoretical climax in that their present composition and structure would persist unchanged indefinitely in the absence of disturbance or climatic change. None the less, it is of interest to project the successional trends noted. The regional climax as described by Nichols (1935) is a hemlock-white pine-northern hardwoods association; beech, sugar maple, and yellow birch being the prevalent hardwood species. On the basis of the present study, the local climax might well be a hemlock-white pine-hardwood forest. White pine, however, would be a prominent member of the association only on the drier sites. The hardwoods would be quite different from those named by Nichols, being chiefly red oak and red maple. Certain of the other hardwoods, particularly yellow and black birch, would apparently be constituents of any climax community. There is, however, no evidence in the present study of any trend toward greater numbers of the northern hardwood species. The physiographic climax on the drier sites is basically a hemlock-white pine-red oak association; the climatic climax on the intermediate sites is a hemlock-red oak-red maple association; and the physiographic climax in the swamps, a hemlock-red maple-spruce association. Together with the key species listed above, white pine, yellow birch, and black birch would occur in lesser numbers on a variety of sites. Such an ensemble of climax associations would not only be in accord with the successional trends here described, but would also agree with the conclusions reached in the study of the virgin upland forest of central New England (Cline & Spurr 1942).

SUMMARY

1. Forty years of recorded forest history in the Harvard Forest, Petersham, Massachusetts, provide an opportunity to evaluate the influence of site and successional development on the composition of forest associations. Changes in composition are recorded by stand maps covering 1852 A and prepared at intervals from 1907 through 1947.

2. The virgin forests of central New England were made up of the same species that are common today, and were highly variable due to variations in site and catastrophic history. White pine was apparently abundant only on sandy and gravelly soils and on exposed ridgetops, although it occurred either singly or in groups throughout the forest. Oaks, chestnut, and hickories formed the upland forests for the most part. The distribution of hemlock was possibly restricted to ravines and other protected sites by precolonial fires.

3. The pre-colonial forests were almost completely cut before the end of the eighteenth century, and much of the area cleared for farming. Following widespread land abandonment in the mid nineteenth century, much of the farm and pasture land seeded in to white pine. Logging of the white pine early in the twentieth century resulted in the establishment of second-growth hardwood forests.

4. Repeated mapping of the Harvard Forest from 1912 to 1946 indicates a decrease in the acreage of white pine from 26 to 2% of the 1852 A; an increase in the acreage of hardwoods from 44 to 56%, and an increase in the acreage of hemlock-hardwoods mixture from 5 to 12%. Open land has been reduced from 12 to 3% while 18% of the total land area has been planted.

5. The present-day associations constitute a regular series of interrelated types, composed predominantly of surprisingly few species, and closely related to successional stage and to site as expressed in terms of soil drainage. The characteristic species of the three successional stages recognized on the five sites are summarized in Table 11.

6. Two species are practically omnipresent. Red oak and red maple are prominent in all successional stages and sites. Red oak is the most frequent on the drier and red maple on the wetter sites.

7. White pine is the characteristic old-field tree and is also frequent on very well drained sites. On all sites, however, scattered white pine persist into the successional stage and become increasingly important in the late successional stage as a few trees reach the overstory and become dominant.

8. Hemlock has increased markedly in abundance over the past 40 years and is now the third most frequent species in the Forest. It exhibits little preference for site, but is largely restricted on areas long removed from agricultural use or clearcutting.

9. The present forest associations are apparently complex, but turn out to be fairly simple in their broad aspects, being closely related to soil drainage and to successional stage. A well defined series of gradational stages relate white pine on very well drained sites to spruce on very poorly drained ones. On well drained sites, short-lived species such as gray birch, cherries, and aspen characterize pioneer associations, with white pine as the principal old-field species. The transitional association is basically a red oak-red maple type, with other hardwoods making up minor proportions of the stand. In late successional stages, hemlock and occasional white pine join with red oak to make up the basic association.

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