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Author(s): Chadwick Dearing Oliver and Earl P. Stephens

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## RECONSTRUCTION OF A MIXED-SPECIES FOREST IN CENTRAL NEW ENGLAND<sup>1</sup>

CHADWICK DEARING OLIVER

College of Forest Resources, University of Washington, Seattle, Washington 98195 USA

AND

EARL P. STEPHENS

Tuskegee Institute, Tuskegee, Alabama 36088 USA

**Abstract.** A 0.36-ha area in the Harvard Forest, Petersham, Massachusetts, was intensively analyzed to determine its history. Natural and man-caused disturbances of varying magnitudes occurred periodically in the central New England mixed-species stand. Evidence of two hurricanes and a fire prior to 1803 were found. Between 1803 and 1952, 14 natural or man-caused disturbances of various magnitudes occurred in the area. Large disturbances created new age classes, but small disturbances did not. Species arising together after large disturbances formed a distinct vertical stratification, with northern red oak (*Quercus rubra* L.) arising after several decades to the dominant canopy. Smaller disturbances to the overstory allowed understory trees such as black birch (*Betula lenta* L.), red maple (*Acer rubrum* L.), and eastern hemlock (*Tsuga canadensis* L. Carr.) to emerge to the dominant canopy. The composition of this forest was more the result of allogenic influences rather than autogenic development.

**Key words:** Black birch; canopy stratification; climax; deciduous forest; disturbance; eastern hemlock; Massachusetts; New England forest; northern red oak; red maple; succession.

### INTRODUCTION

The temporal and spatial development of an old, mixed-species, deciduous forest in central Massachusetts is investigated in the present study by a detailed reconstruction of a 0.36-ha plot. The pattern of development is determined through the investigation of three hypotheses; these hypotheses are concerned with the stem age distribution, the horizontal pattern of new stem recruitment, and the vertical development of the forest canopies.

The first hypothesis is that allogenic succession has been the major contributor to forest development in the case studied. That is, most trees present in the old-growth forest initiated soon after large disturbances, while small disturbances to the overstory allowed understory trees to respond, but did not produce a major recruitment of new individuals. Alternatively, if the autogenic process were more important, the major tree components of the stand would result from the regular recruitment of new stems of more tolerant species.

The second hypothesis is that a forest subjected to disturbances removing part of the overstory is a mosaic of small ( $\approx 0.05$  ha or larger) stands, each of which began after a disturbance to a given area. The alternative to this is that younger trees initiate throughout a forest rather than in distinct patches.

The third hypothesis is that the dominant canopy of the forest studied is comprised of a broad range of ages. The older trees of the dominant canopy are those individuals and of those species which were suppressed during previous stratification but released by sub-

sequent disturbances; the younger dominant trees are those individuals and of those species (primarily red oaks in this case), which attained the superior canopy positions during stratification without an intervening suppression. The alternative is that the dominant trees are all the oldest in the forest and attained the dominant canopy by slow height growth and hence gradual replacement of the overstory.

### AGE DISTRIBUTION OF TREES

Two patterns of development have been described in forests during secondary succession (Mueller-Dombois and Ellenberg 1974). One involves the recruitment of new stems constantly during a stand's history as the overstory alters the environment to favor the growth of younger, more tolerant individuals. The terms "autogenic succession" (Spurr and Barnes 1973) and "relay floristics" (Egler 1954) have been used with reference to this process. The other pattern has received only limited attention (Mueller-Dombois and Ellenberg 1974). It involves "allogenic succession" (Spurr and Barnes 1973) and "initial floristic composition" (Egler 1954). In this case, new individuals are recruited primarily after disturbances. The species arising after a disturbance then occupy the available growing space and through competition exclude later arrivals. Direct evidence supporting either pattern is minimal, as has been shown by Drury and Nisbet (1973) in their review of the subject.

### *Autogenic succession*

By this explanation, internal changes of the forest environment caused by the trees' growing promotes a steady recruitment of more tolerant trees into the understory (Clements 1916, Oosting 1956, MacArthur

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and Connell 1966, Daubenmire 1968). Most of these die as they get older; however, a few continue to grow and eventually replace the overstory trees, with decreasing numbers of individuals in each successively older age class. The frequency distribution of such a forest by age classes appears as a reverse-J-shape (Raunkiaer 1928). Such a forest is referred to as all-aged, or balanced uneven-aged.

Evidence supporting the autogenic succession explanation has been indirect. Mixed species stands contain a broad range of diameters which, when arranged by diameter classes, may approach a reverse-J-shaped distribution. The explicit or implicit assumption that tree diameter is an indication of tree age has led to the acceptance of a forest with such a diameter distribution as being all-aged (Hough 1932, Meyer and Stevenson 1943, Phillips 1959, Piusi 1966, Daubenmire 1968, Minckler 1974). Mixed stands also often contain a vertical stratification of tree heights by species, which has been interpreted as the shorter trees being younger and later successional species, as will be discussed later.

#### *Allogenic succession*

The role of disturbances—whether natural such as fires, landslides, hurricanes, tornadoes, or floods; or man-created such as forest cuttings—in forest succession is becoming increasingly appreciated. Many parts of the eastern deciduous forest have been subjected to natural and, more recently, man-caused disturbances of various causes and magnitudes at intervals shorter than the potential life of the component species (Lutz 1940, Hough and Forbes 1943, Goodlett 1954, Bormann and Buell 1964, Raup 1964, Loucks 1970, Henry and Swan 1974, Sprugel 1974).

Evidence during the past 20 yr has led many scientists to believe that tree species are more directly competitive than was earlier believed. Consequently, rather than older trees creating favorable environments for "later successional" species, established trees tend to compete for the same soil and light "growing space" as younger ones. The competitive advantage of the previously established trees tends to exclude the initiation of young individuals. By this theory the times when most new trees become established in a forest is when a disturbance releases some of the previously occupied "growing space." By the allogenic theory the age distribution in most eastern deciduous forests should be quite irregular, with each new influx of trees originating after a disturbance. This theory has been advocated by workers at the Harvard Forest (Stephens 1956, Raup 1964, Henry and Swan 1974) and others (Johnson 1972, Smith 1973, Drury and Nisbet 1973, Oliver 1977).

#### *Spatial distribution of ages in a forest*

The spatial distribution of trees initiating in a forest has received only limited attention. The autogenic

succession theory implies that the later successional species initiate throughout the forest. With more appreciation of the role of disturbances, the "gap phase" concept has developed whereby new individuals initiate in the openings created by the death of the older trees (Bray 1956, Bormann and Buell 1964). This implies that a forest is a mosaic of post-disturbance stands, the individuals in each having originated after the same disturbance (Johnson 1972). The size of each area would depend on the size of the initiating disturbance.

#### *Vertical development of a forest*

Within a single stand tree heights vary considerably, with smaller individuals existing beneath and between the canopies of the taller trees. Often segregation by species occurs, with certain species occupying the upper canopy stratum, and different ones occupying lower strata (Oliver 1977). It has frequently been assumed that these smaller trees are younger, are comprised of shade tolerant species, and will eventually replace the taller ones in the upper canopy strata (Jones 1945, Braun 1950). By this explanation a stand of mixed species is constantly recruiting new trees and the dominant trees are the older, earlier stages of succession.

Alternatively, it has been found on the present study site and in other central New England mixed forests on similar soils that a vertical stratification by species can occur among individuals which initiate together soon after a single disturbance (Oliver 1977). After the third decade and lasting at least through the tenth, northern red oak (*Quercus rubra* L.) was found to occupy the upper canopy. Red maple (*Acer rubrum* L.), black birch (*Betula lenta* L.), sugar maple (*Acer saccharum* Marsh.), and eastern hemlock (*Tsuga canadensis* L. Carr.) were principle components of the understory. Rather than the understory individuals being younger, they were the same age and often had at one time been as large as or larger than the dominating oaks.

#### PROCEDURES

The selected area for the present study was in Compartment VI of the Tom Swamp tract of the Harvard Forest in Petersham, (northcentral) Massachusetts. This was one of the older, least recently disturbed areas on the forest. The upland till soils of granite and schist origin were typical of upland New England and the site was one of the few in the area which had never been plowed for agriculture. There had been cuttings earlier; however, the western exposure protected the forest from complete blowdown by the 1938 hurricane and previous windstorms. The forest appeared to be an old-growth stand with trees of a large number of sizes and many species in the dominant as well as lesser canopies.

Between 1950 and 1955 the second author thoroughly dissected a 0.36-ha sample of this stand

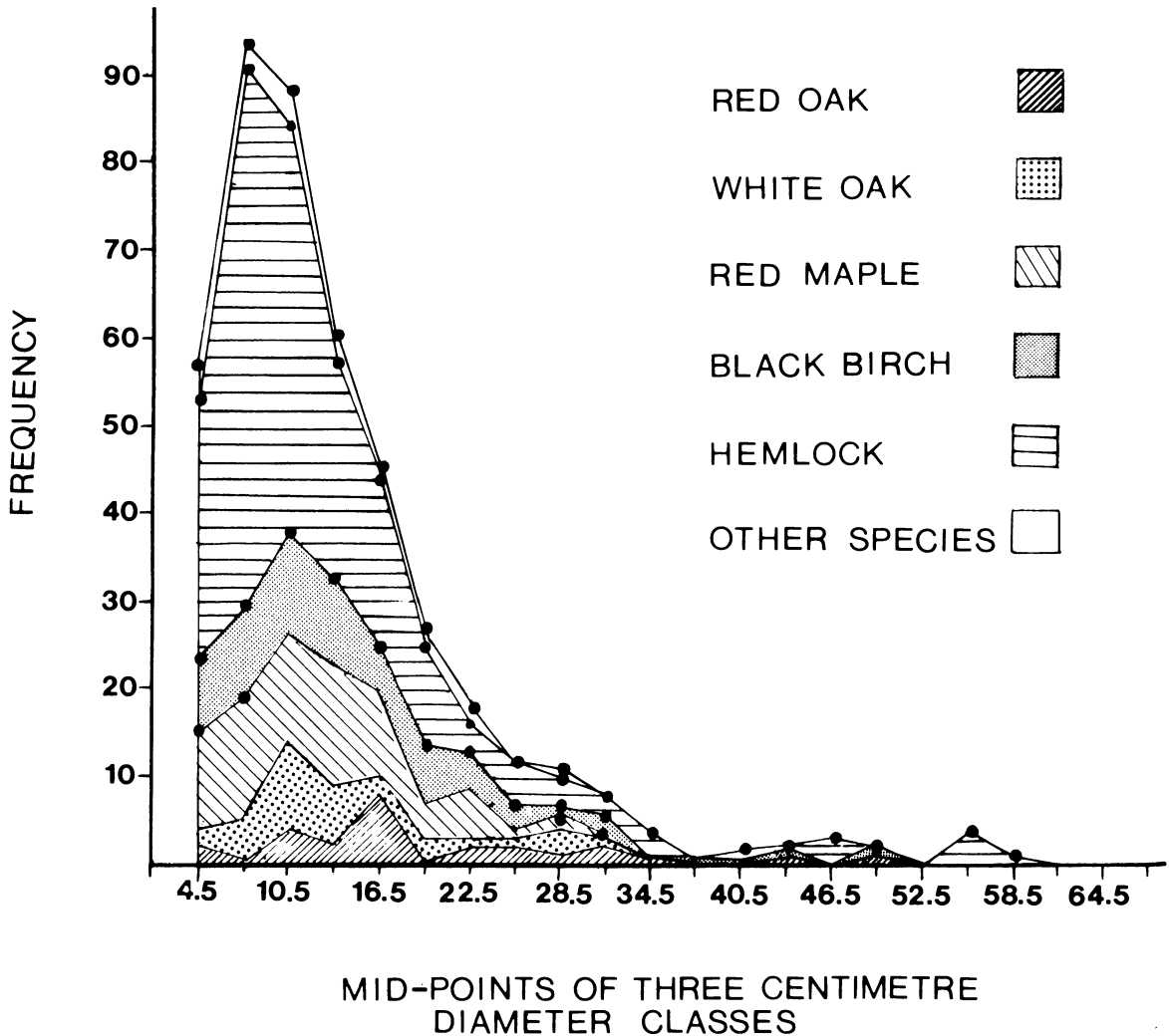


FIG. 1. Distribution of all trees on the Tom Swamp transect in 1952 by diameter and species.

(Stephens 1955, Henry and Swan 1974). A large amount of data was collected and most of them were not analyzed, assimilated, or published. The previously published parts concern the detection of windthrow mounds (Stephens 1956), methodology (Stephens 1955), and tree height growth (Oliver 1977). In 1974 Dr. Stephens gave the first author permission to examine, analyze, and publish an analysis of these data.

Stephens established a transect 25.6 m wide and 140.2 m long, running in an east-west direction (parallel to the slope) from 235 m to 274 m elevation and mapped it for intensive study. Part of the surrounding forest was studied less intensively for additional information.

He made a contour map of the transect on a 15.2-cm interval, located on it and described all trees, dead stems, boulders, stones, and other potentially interesting portions of the forest. In all, 444 living trees

were recorded by species, diameter, canopy position (dominant, codominant, intermediate, suppressed, or leaning), abnormalities in the stem, physiological condition, stem origin (seed, stump sprout, etc.), and location of root collar (on another stump, log, windthrow mound, etc.). All 245 dead stems, stumps, and stump remnants within the transect were similarly described in as much detail as possible.

All of the living and dead trees were felled, their heights measured, and aged at 0 m. Annual diameter growth at the root collar (0 m) was recorded. Three hundred and twenty-two of the living trees were also aged at 1.4 m, and every 1.2 m higher along the stem. All buried stems and stumps beneath other trees were meticulously uncovered, identified, dated, and aged.

The soil was then studied by carefully removing the litter layer. From visual observations and study of the topographic map, 62 mounds and pits were detected of varying degrees of freshness resulting from the uproot-

TABLE 1. Number and estimated age of windthrow mound age groupings

Relative age class groupings	Number of mounds	Estimated date of formation
I	12	1938
II	2	1851
III	8	1815
IV	1	1730-1750
V	15	1635
VI	18	1500 or earlier

ings of trees (Stephens 1956). The direction of tree fall was determined for each. Sixteen of the uprootings were obviously from the 1938 hurricane of 14 yr prior. The 46 others were each excavated along a transect parallel to the direction of tree fall; the profile and gross anatomical features were described. Three other profiles in the stand (but not in the 0.36-ha transect) were also studied because their dates of origin could be determined very closely from the ages of live trees growing on the mounds.

Configuration of sprout growth and time of sprout initiation gave further evidence of patterns of disturbances. Supplemented with historical documents of the area, Stephens reconstructed the forest backward in time by noting years of disturbance, species composition, and changes in age distribution in the present forest. The minimum age of the mounds, the minimum age of charcoal found, and the minimum age of dead trees and stumps were estimated wherever possible by obtaining the age of the oldest trees growing on them.

Using this large quantity for information much can be interpreted about the development of this forest over time.

## RESULTS

### *Forest structure and disturbance patterns*

Stephens' careful documentation and description of the forest on the transect in 1952, at the time of dissection, shows it contained 12 living tree species. There were 5 species in the dominant and codominant canopies: red oak, white oak (*Quercus alba* L.), red maple, black birch, and hemlock. Red maple, birch, and hemlock were the most numerous species in the lower canopies. Other species included sugar maple (*Acer saccharum* Marsh.), paper birch (*Betula papyrifera* Marsh.), American beech (*Fagus grandifolia* Ehrh.), bigtooth aspen (*Populus grandidentata* Michx.), eastern white pine (*Pinus strobus* L.), and American chestnut sprouts (*Castanea dentata* [Marsh.] Borkh.). The diameter distribution as shown in Fig. 1 has the reverse-J-shape common to mixed species forests.

The cross sections of the mounds and pits and the direction of tree fall were compared. The detection

and dating of the windthrow mounds has been described in detail by Stephens (1956). The close relation between profile form and internal structure allowed a grouping of the windthrows into four major relative age classes (Table 1) and two minor ones (Classes II and IV, Table 1). Mounds of each major age class were scattered throughout the forest rather than being grouped. In each age class the directions of tree fall were concentrated in a narrow arc in the northwest and/or southwest quadrants. This group-wise distribution not only substantiated the age class groupings, but also indicated that the windthrows had resulted from storms, probably hurricanes, comparable to the one of 1938.

Ages of all but the oldest windthrow age class were approximated from ages and relative positions of trees having grown on the mounds and pits. A literature survey showed that central Massachusetts was subjected to hurricanes in 1938, 1815, and 1635 (Perley 1891, Brooks 1939, 1945, Tannehill 1944). Their dates of occurrence coincided with the dates of origin calculated from field evidence for age classes I, III, and V, respectively.

The mounds and pits of age class I had resulted from the hurricane of 1938. Perched living trees dated precisely classes II and III as 1851 and 1815, respectively. Age class III was therefore probably caused by the hurricane of 1815. Because of a heavy cutting of the forest just prior to this (as will be discussed later), this hurricane caused the windthrow of relatively few trees. From a 147-yr-old tree growing on a previously eroded mound, the single uprooting of class IV was estimated to have occurred between 1730 and 1750. A reconstruction of the ages of living stems growing on dead stem fragments on some of the mounds dated age class V to the first half of the seventeenth century, possibly the hurricane of 1635. The age of class VI could not be determined directly; however, the minimum ages of the largest previously cut stumps having grown on the mounds indicate it probably originated about 1500 or before.

Bar graphs of basal diameter growths were made for each living tree by plotting date (in sequential years beginning before 1800 and ending in 1952) on the horizontal axis and yearly diameter growth on the vertical axis. Similar bar graphs were also plotted of dead stems where the diameter growth patterns could be detected and where the exact date of death could be determined, such as by the tree sprouting after a cutting. The dendrograms were placed in a vertical column with the dates aligned.

Several developmental trends became apparent such as a coincidence of stems initiating and/or increasing in diameter increment soon after noted times of disturbances. By comparing the bar graph patterns with evidences such as previously cut stumps and windthrow mounds, the histories of other disturbances in the area were reconstructed.

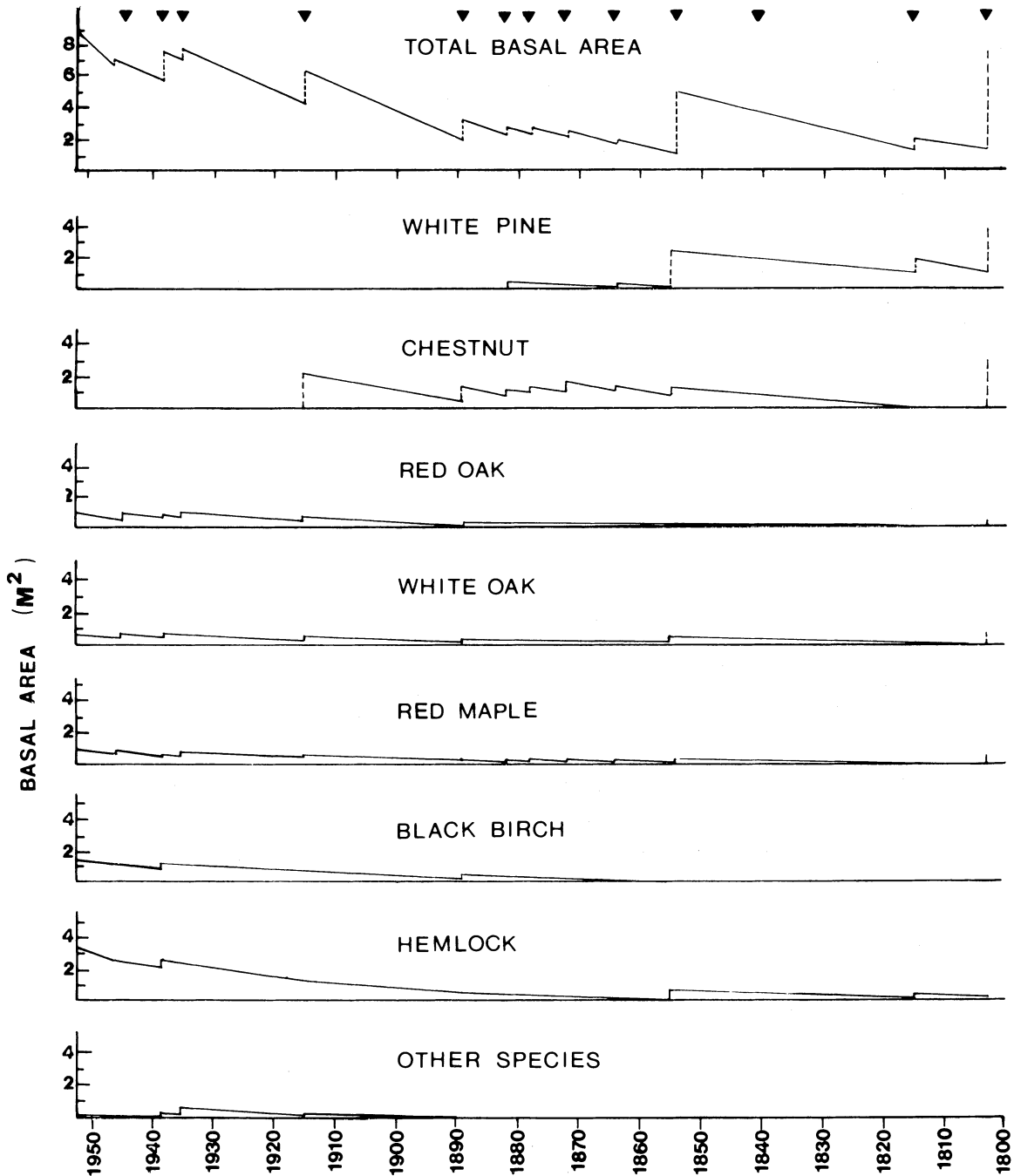


FIG. 2. Change in basal area on the Tom Swamp transect between 1803 and 1952. Triangles at top note times of disturbances. (From Stephens 1955.)

Table 2 lists the detected disturbances and composition changes which occurred on the plot since 1800. A rough estimate of the basal area changes was made similarly by a study of the living and dead stems. This is shown in Fig. 2.

The coincidence between ages, especially of the stump sprouts, and dates of marked increases in radial

growth rates indicated that the plot had been logged several times. The most prominent dates of logging were 1939, 1890, 1864, 1854, and 1803. Several minor operations were indicated between 1864 and 1890, and others in 1841 and 1935.

As discussed previously, hurricanes had caused the overturning of trees in 1938, 1815, and previously.

TABLE 2. History of forest composition since 1800, detected from field evidence such as cut stumps and wind-throw mounds, from coinciding patterns of diameter growth, and from corroborations of these evidences with the literature. See Results section of text

Year	Type of disturbance	Basal area (m <sup>2</sup> )			Main species removed
		Removed	Left	Total	
1803	Logging (clearcut)	7.73	1.56	9.29	white pine ( <i>Pinus strobus</i> ) chestnut ( <i>Castanea dentata</i> )
1815	Hurricane	1.10	1.38	2.48	white pine, hemlock ( <i>Tsuga canadensis</i> )
1841	Minor logging operation		(basal area and species changes not estimated)		
1854	Logging	4.42	1.47	5.89	white pine, chestnut
1864	Fuelwood cutting	.276	2.30	2.58	chestnut
1872	Fuelwood cutting	.644	2.67	3.31	chestnut
1878	Fuelwood cutting	.460	2.94	3.40	chestnut
1882	Logging	.828	2.76	3.59	white pine, chestnut
1889	Logging	1.66	2.30	3.96	chestnut, hemlock
1915	Chestnut salvage	2.76	5.15	7.91	chestnut (dying of blight)
1935	Fuelwood cutting	1.20	8.37	9.57	red oak ( <i>Quercus rubra</i> ), aspen ( <i>Populus</i> ), hemlock
1938	Hurricane	2.21	7.18	9.38	red maple ( <i>Acer rubrum</i> ), black birch ( <i>Betula lenta</i> ), white oak ( <i>Quercus alba</i> ), hemlock
1945	Gypsy moth damage	.276	8.28	8.56	red oak, red maple, black birch
1952	Research cutting	10.40	0	10.40	All trees removed for study

Sudden decreases in radial growth rates during 1944 and 1945, especially in the oaks, suggested the area was subjected to the gypsy moth outbreaks of epidemic proportions in the immediate vicinity in 1944 and 1945 (Bess et al. 1947).

A series of successive growth rate increases between 1908 and 1920, primarily in the understory hemlocks, was probably caused by the chestnut blight which was important in the area between 1911 and about 1918 (Rane 1911, 1912, 1916).

Charcoal was found in the soil at 23 locations. These remnants may have been from Indian or early colonist campfires (Stephens 1955) or forest fires.

Petersham was first settled in 1733, so it is obvious from the analysis that disturbances occurred in the region before and after colonial immigration.

#### *Changes in forest composition*

An estimate of the change in forest composition since 1803 can be made from the living and dead stems. Basal area, calculated from diameter growth patterns, was the best preserved evidence for past tree growth. Because the basal area in a stand is related to the crown size and physiological condition of the trees (Holsoe 1948, Berlyn 1962, Oliver 1977), total basal area by species is used here as the best available index of forest composition.

Figure 2 shows the estimated change in basal area by species on the transect between 1803 and 1952. The change in basal area caused by the logging of about 1841 was not estimated (Fig. 2 and Table 2) because this event was very heavily masked by later events. Most striking is the decline in white pine and chestnut.

The chestnut fell off in 1915 because of the introduced chestnut blight (see Table 1). The white pine was primarily in large old trees and did not become reestablished well on the site after the logging of 1854. It is probable that the pine was established in the first place following some very early fire. This is what Henry and Swan (1974) found in a pine stand which originated after a fire following the 1635 hurricane in southern New Hampshire. Later the 1938 hurricane eliminated most pine and now deciduous species successfully dominate the same area.

#### *Tree age distribution*

The age distribution of all trees living in 1952 (measured at the root collar) is shown in Fig. 3. The accompanying bar graph shows the time of each disturbance to the area between 1803 and 1952 and the intensity as measured by basal area loss. Many trees of the oldest age classes were apparently eliminated in later disturbances; however, the age distribution shows that most of the trees became established soon after the times of disturbances. They did not initiate continually in this stand as would be expected under the autogenic concept of stand development.

Trees can reproduce by both sexual and vegetative means, and the root collar ages of those which exist for long periods as suppressed seedlings living near the forest floor indicate the times of germination—not the times of release. Tree age is commonly dated from the time of stem release (Morris 1948, Sprugel 1974, Oliver 1977). Figure 3 compares the root collar and released ages of a subsample of 322 trees on the transect, using stem age at 1.4 m as an indication of the age from

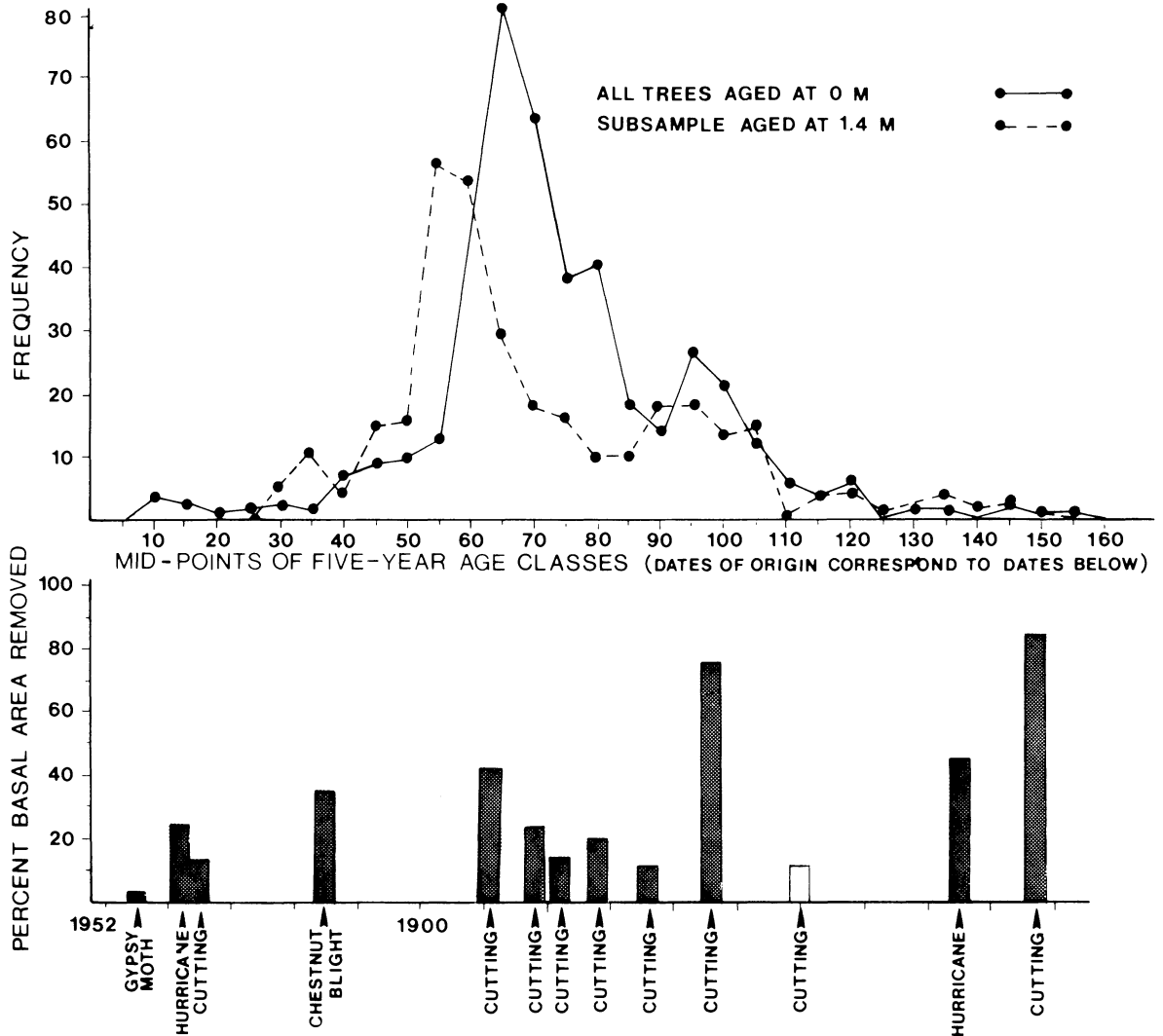


FIG. 3. Distribution of root collar age of all trees in transect and of subsample aged at 1.4 m (upper graph). Corresponding distribution and intensities of disturbances is shown in lower graph.

release. When aged from time of release the response of the trees to the various large disturbances becomes more obvious.

Major disturbances occurred in 1803 and 1854. Because of the frequent cuttings and large proportion (although small absolute amount) of vegetation removed between 1882 and 1889, the effect was the same as a large disturbance. Other small disturbances occurred after 1889 although little recruitment of new stems occurred. The existing trees apparently usurped the growing space provided by the new disturbances, thus excluding younger trees. The age distribution within the forest was irregular, and the potential of small disturbances to create a more uniform age distribution was not realized. New trees began after rather large disturbances, not after the smaller ones. In 1915 it had been 25 yr since a notable disturbance; removal of 35%

of the basal area did not create a major recruitment of new individuals. Similarly, removal of 24% by the 1938 hurricane did not initiate new individuals.

#### *Spatial distribution of trees*

From Stephens' data a large map was made noting the age of each living stem at its root collar position. Starting from the most recent disturbance and working backwards, systematic attempts were made to circumscribe any irregularly or regularly shaped areas containing trees which had initiated from a particular disturbance. Although the attempted circumscriptions were as small as 6 m minimum diameter, single-age patches could not be found. Contrary to the hypothesis, the stand was not composed of mosaics of small stands in which all individuals arose after the same disturbance. Instead, trees initiating after each distur-



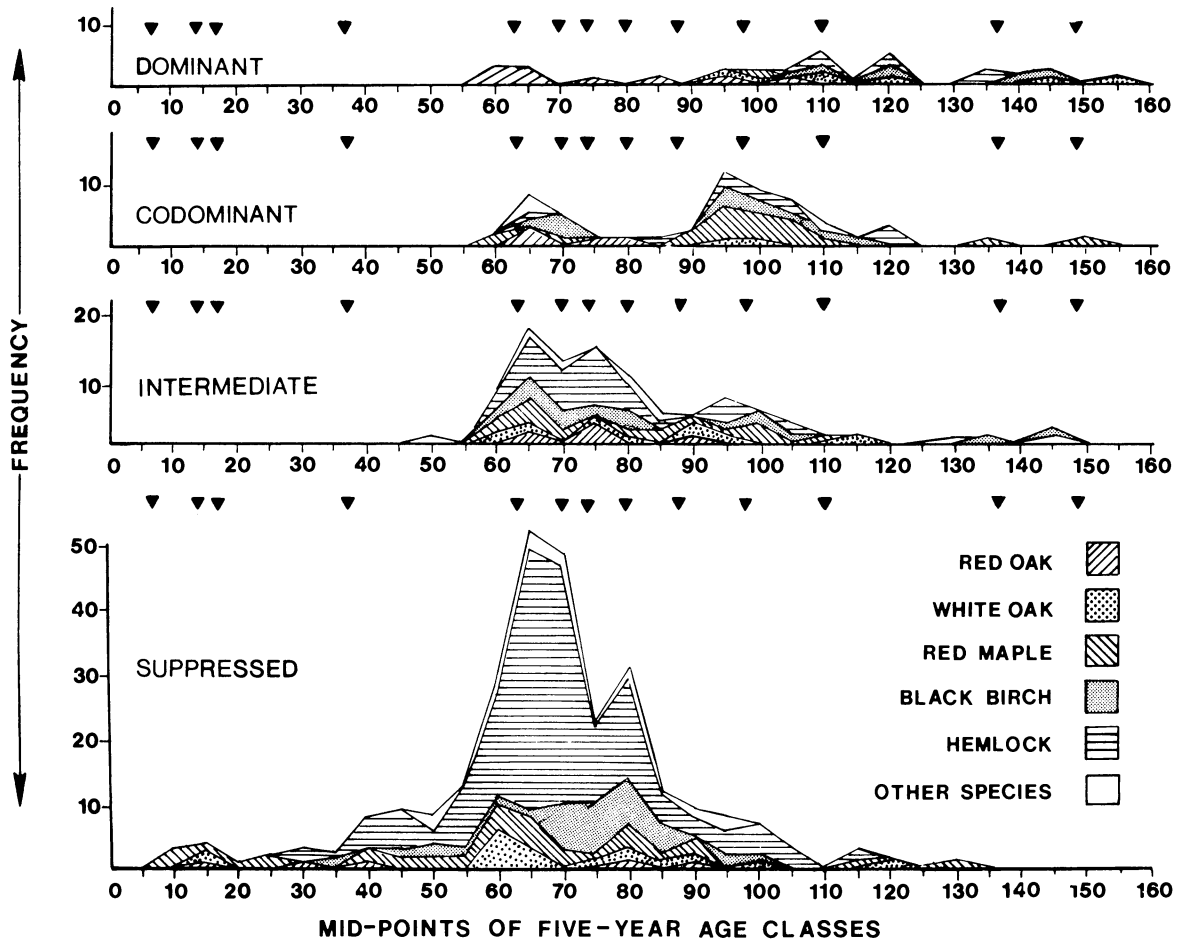


FIG. 4. Distribution of species by age and crown class. Triangles note times of disturbances.

bance were relatively uniformly distributed throughout the area. Henry and Swan (1974) found similar results when reconstructing a stand in southern New Hampshire.

#### *Canopy positions and growth patterns*

Figure 4 shows the distribution of species by age and canopy position. The dominant and codominant red maples, black birches, and hemlocks were highly significantly older (1%-level; Wilcoxon's Rank Sum Test) than the red oak dominants and codominants. The older oaks were probably not present because they were cut; however, the cause of exclusion of the younger birches, maples, and hemlocks from the upper crown classes is not as obvious. Certain species, especially northern red oak, were rarely present in the lower crown classes. To determine the growth patterns of individual trees which when taken together defined stand development pattern, the recorded diameter growths of stems at the root collar were examined. Two patterns were observed: a constant, steady, or slightly decelerating diameter growth pat-

tern indicating a tree whose canopy position was not frequently and abruptly altered; and a step-like pattern indicating a series of crown suppressions and releases.

The diameter growth habit of the 84 dominant and codominant trees on the transect were classified: 38 had steady growth while 46 followed a step-like pattern. The species in each class varied. Two-thirds of the red oaks had steady diameter growth patterns indicating eventually-dominating red oaks generally did not undergo a period of severe suppression and sudden release. Approximately one-half of the black birches, one third of the red maples, and only one-fifth of the hemlocks had steady diameter growth patterns. To varying degrees, these species showed a greater tendency than red oak to recover from suppressions.

Four dominant and codominant trees of each major species with typical diameter growth habits were selected for study of their height growth patterns. Height growth was found to reflect diameter growth: trees with step-like diameter growth had step-like height growth; and steady diameter growth patterns were accompanied by steady height growth patterns.

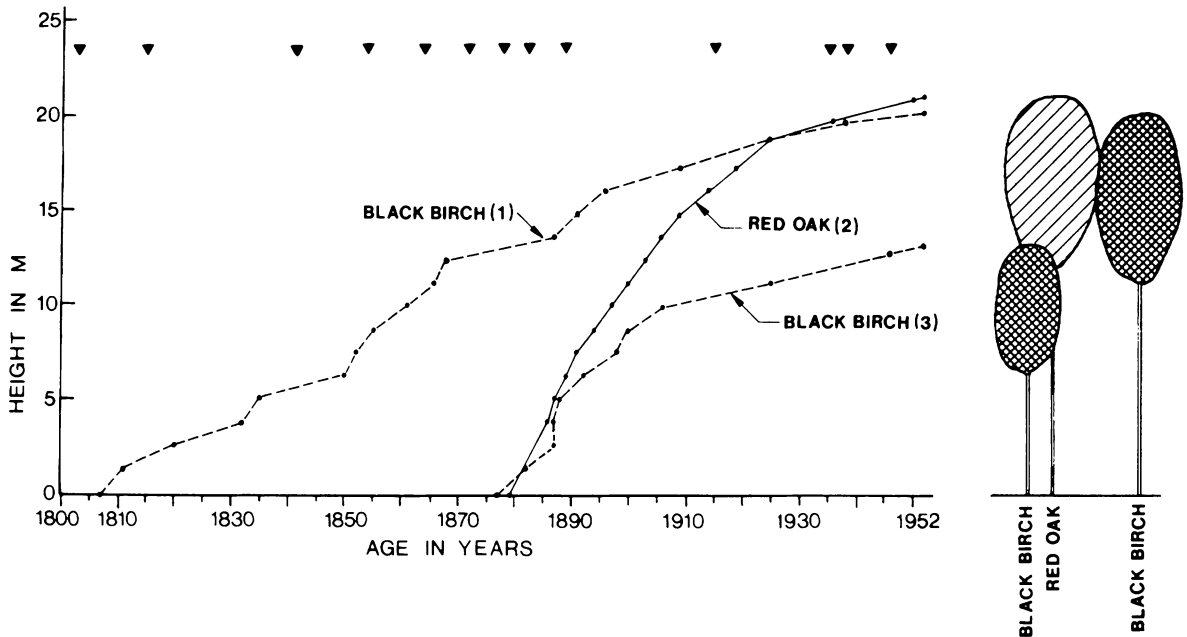


FIG. 5. Growth of selected trees with steady diameter and height growth (red oak #2) and step-like diameter and height growth (black birch #1). Note both trees reached the dominant canopy—the red oak by steady growth, and the black birch (31) by responding to a series of releases. Tree #3 is an example of a black birch which fell behind its contemporary red oak to form a lower strata. Triangles note times of disturbances.

Figure 5 shows height-age curves of two typical dominant trees: black birch #1 with fluctuating height and diameter growth patterns and red oak #2 with steady height and diameter growth patterns. Figure 5 also shows a black birch (#3) which started at the same time as the red oak but soon fell behind to form a lower stratum beneath the contemporary red oak. The stratification pattern of red oak #2 dominating a contemporary black birch (#3) is typical of the red oak stratification and suppression of both black birch and red maple in this stand and elsewhere in New England (Oliver 1977). The early growth of black birch #1 is similar to black birch #3. It is probable that trees with a step-like growth pattern such as black birch #1 grew in the step-like pattern because it was initially suppressed by a contemporary red oak (or perhaps another species such as chestnut) which was removed in a later disturbance, allowing the black birch to respond to release and achieve the upper canopy. The upper canopy is, therefore, composed of two types of trees: those which grew immediately to the overstory after a disturbance; and those which stratified beneath other, probably contemporary, trees and later accelerated again upon removal of the overstory.

#### DISCUSSION

Both natural and man-caused disturbances occurred at frequent intervals in the forest relative to the potential life span of the component trees.

Most trees of the mixed forest on the study area started after discrete disturbances: therefore, the al-

logenic pattern of development was predominant here. The variety of species in the upper canopy was created by disturbances which allowed understory species to grow into the main canopy. Disturbances, therefore, appear to have two effects which are not mutually exclusive: they can create a new age class; and they can alter the relative canopy position of species in the existing forest.

When a disturbance releases light and soil growing space, it can be refilled both by previously existing trees expanding their canopies and roots and by new individuals initiating to occupy it. If the previously existing trees are vigorous enough to expand quickly and/or if the disturbed area is small, the advantage of the preexisting vegetation will exclude newly-initiating stems. Consequently, whether a disturbance creates a new age class (a "large" disturbance) or does not (a "small" disturbance) depends on both the size of the disturbance and the ability of the preexisting vegetation to expand rapidly.

The process of development of the stand studied can be generalized from the evidence as follows: after a large disturbance a stand is initiated and its characteristics are determined by the type of disturbance, species present, soil, light, and meteorological regimes. Thereafter a characteristic pattern of stratification develops which may change in time autogenously, although the recruitment of new individuals is eventually curtailed until another large disturbance occurs. During the intervening period when small disturbances remove dominant trees, the substrata species as well

as surrounding trees in the upper canopy respond by accelerating their height and/or diameter growth.

The apparent process of trees excluding later-arriving ones implies that the recruitment of new individuals in a forest is more allogenic than autogenic. For example, the more tolerant hemlocks are not later invaders to the forest, although their often small height and diameter may lead one to believe they are. They initiated after the large disturbances like the other species, but tended to become more prominent as small disturbances removed their larger, often contemporary competitors. The hemlocks increased in basal area, but not in numbers, markedly between 1890 and 1952, a period characterized by small disturbances (Figs. 2 and 3). As evidenced by the periodic hurricanes disturbing the study area, both large and small disturbances occur at intervals more frequent than the life span of most trees present. Therefore, rather than use the term "climax" to refer to such species as hemlock (Daubenmire 1968, Graham 1941), it may be more accurate to describe such species as tolerant ones which increase in prominence with small disturbances.

Allogenic succession does not necessarily produce obvious, very small mosaics of contemporary individuals within the forest, perhaps because the root and shade influences of a tree extend well beyond a vertical projection of its canopy. Removal of a tree, therefore, would alter the soil and light regimes in a large area and beyond the immediately neighboring trees that remain.

#### CONCLUSIONS

Large- and small-scale disturbances of natural and man-created origin were basic to the structure of the central New England forest studied. The allogenic pattern of succession predominated here rather than the autogenic pattern. When a large disturbance removed a high proportion of the trees on an area it initiated new trees within the forest; when a smaller disturbance removed fewer trees it generally did not allow recruitment of new trees but rather allowed accelerated growth of the remaining trees. The resulting forest was not composed of obvious, small mosaics of post-disturbance stands; but trees of different age classes were each created by a large disturbance and were intermingled.

Species arising together after a large disturbance formed a distinct vertical stratification, with certain species occupying each crown layer. Smaller disturbances to the overstory trees allowed species that would otherwise be relegated to the understory to emerge as dominants—creating a forest with a mixed upper canopy.

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