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FORTY YEARS OF FOREST SUCCESSION IN CENTRAL NEW ENGLAND¹

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Abstract. The first 40 yr of forest succession on permanent plots at the Harvard Forest in central New England followed the initial floristic composition model of forest succession. After the 1938 hurricane removed the previous white pine (*Pinus strobus*) canopy, species regenerated within 4-6 yr by sprouts, buried seed, and wind-blown seed, with no method of regeneration uniformly contributing more to species success than another. Hemlock (*Tsuga canadensis*) was the only species successfully regenerating after 1948. Pin cherry (*Prunus pennsylvanica*) was the early dominant in size and numbers (5000 stems/ha). At year 10, pin cherry, red maple (*Acer rubrum*), white ash (*Fraxinus americana*), and red oak (*Quercus rubra*) were dominant. Species diversity had reached a maximum. By year 40, red oak and paper birch (*Betula papyrifera*) showed strong canopy dominance, making up only 7.5 and 4.9%, respectively, of total density but 37.5 and 12.5%, respectively, of the size-dominant stems. Red maple and white pine were also codominant in 1978. Some evidence for an intermediate stage dominated by red maple and gray birch (*B. populifolia*) was found. On one previously hardwood plot, the same species were present, and similar trends in species composition and dominance were followed, but there was more surviving hemlock advance regeneration and a lower density of some shade-intolerant early dominant species. The canopy structure was loosely multilayered, and at any given point in succession, species tended to be found in characteristic layers, although these relative positions could change with time.

Key words: *Acer rubrum*; forest succession; forest structure; New England; *Pinus strobus*; *Prunus pennsylvanica*; *Quercus rubra*; transition hardwood forest.

INTRODUCTION

The study of forest succession is made difficult by the time scale involved, so only rarely (e.g., Christensen 1977, Peet and Christensen 1980, Stephens and Waggoner 1980) have studies followed vegetation change on the same area for more than a few years. Most studies have been of general changes over large areas (Cooper 1939, Stearns 1949, Lawrence 1958, Waggoner and Stephens 1970). Various methods have been employed to deal with the time-scale problem. Studies tend to be of similar sites of different successional age (a chronosequence, e.g., Cowles 1899, Crocker and Major 1955, Viereck 1966, Reiners et al. 1971, Sprugel 1974, Christensen and Peet 1981), the vegetative history of a small area found through historic reconstruction (Stephens 1955, Henry and Swan 1974, Oliver and Stephens 1977), or models of long-term succession (Leak 1970, Botkin et al. 1972, Horn 1975). In addition, much emphasis has been placed on succession immediately following agricultural abandonment (Oosting 1942, Keever 1950, Odum 1960), which involves only species reproducing primarily by seed.

From these and many other studies have come several attempts to generalize the process of succession

(Clements 1916, Egler 1954, Odum 1971, Connell and Slatyer 1977) as well as critiques of these attempts (e.g., Drury and Nisbet 1973). Three themes found in many of these generalizations are: (1) succession is a process of sequential colonization and dominance (relay floristics as defined by Egler [1954]), (2) the smaller trees in the forest are younger and will comprise the next dominant stage of the sere, and (3) primarily as a consequence of (1) and (2) above, increase in diversity with succession continues for many years.

These statements are undoubtedly true for many successional systems. It seems likely, however, that the following alternatives to these three statements are more generally applicable to temperate forest secondary succession: (1) succession is primarily a sequence in dominance by species that colonized more or less simultaneously following the initiating disturbance (initial floristic composition model), (2) younger forests (<≈50 yr in central New England) are essentially even aged, and some species found in the lower canopy are characteristic of this position, by virtue of species-specific differences in rate of height growth (Oliver 1978), and (3) diversity peaks during the early phase of "stand initiation" (Oliver 1981) or "reorganization" (Bormann and Likens 1979) and then decreases gradually for many years. An important exception to this diversity trend may be Douglas-fir forests (Franklin et al. 1981).

In a recent study of forest succession in the Piedmont of North Carolina, Peet and Christensen (1980) observed that "establishment and mortality directly determine changes in community composition and

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structure." To this should also be added the effect of differing rates of height growth among the component species. Oliver (1978) showed that in mixed hardwood stands in southern New England, red maple (*Acer rubrum*) is taller than red oak (*Quercus rubra*) at age 20, but because the rate of height growth of red maple decreases faster than that of red oak, the relative canopy positions are reversed by age 40 (see also Hibbs 1982a). A fourth generalization to be considered, then, is that forest structure is regulated by establishment, mortality, and species-specific growth rates and concomitantly, that a community has a predictable, though changing with time, vertical canopy structure with individual species found in characteristic strata.

The study reported here tests these alternative hypotheses through a 40-yr study of succession on permanent plots following canopy removal by the 1938 hurricane. The use of permanent plots in this study allows a detailed analysis of individual species survival and growth through the most dynamic period of forest development. It also provides insight into the role or position in the canopy that a species has at one stage of succession and how this role changes with time.

PROCEDURES

Study area and previous work

The forests of central New England have been variously described as (1) a transition between the Appalachian oak and the northern hardwood forest (Kuchler 1964), (2) the white oak–black oak–northern red oak type (Society of American Foresters 1980), and (3) the transition hardwood zone (Braun 1950).

Several forest types have been common in the area since pre-colonial times, including white pine (*Pinus strobus*), mixed hardwood/softwood (white pine and hemlock [*Tsuga canadensis*]), and hardwood (Cline and Lockard 1925, Cline and Spurr 1942). The hardwood type with a large oak component and some late-emerging white pine was probably predominant (Cline and Lockard 1925, Goodlett 1954, Raup 1966).

In 1938, a hurricane passed through central New England, destroying 253 000 ha of forest (Baldwin 1942). This event created the conditions for a broad-scale study of forest succession (Spurr 1956) and emphasized the importance of wind disturbance in the forest dynamics of New England. Little work had been done on forest dynamics in New England prior to 1938 because of the long colonial history of land use of the region and the resulting lack of study areas relatively free from the prolonged influence of humans. The hurricane of 1938 coincided with the restoration of forest cover over much of New England following farm abandonment in the mid-19th century.

Spurr (1956) summarized the initial regeneration on disturbed sites immediately after the 1938 hurricane. He found more or less abundant regeneration 2–3 yr after the hurricane on all but the driest soils and found

species differences over the range of soil types encountered. He also reported on vegetation change on permanent plots over 10 yr, following the hurricane at the Harvard Forest, Petersham, Massachusetts. He found little additional colonization after the 3rd or 4th yr, but did find a difference in species composition between stands on well-drained glacial till and glacial outwash. He predicted that forest stands on glacial till would eventually be dominated by red oak and red maple, while stands on glacial outwash would be dominated by white pine. White pine regeneration, while plentiful on till soils, was suppressed under the faster-growing hardwood canopy. Spurr predicted that it would not survive long in the shade of these stands.

Spurr's 1956 study included 14 permanent plots scattered throughout the Harvard Forest in forest stands from which the canopy was removed by the 1938 hurricane. Prior to 1938, 10 of the 11 plots examined in this paper had supported unmanaged, mature (50+ yr) white pine originating on abandoned agricultural land, primarily pasture, that had been farmed for periods ranging from 30 to 70 yr. These pine stands did include considerable hardwood regeneration (Spurr 1956). The 11th plot previously supported hardwoods. The remaining three plots supported immature or managed pine or had been burned since 1938 and are not considered here.

The soils of the Harvard Forest are glacial till and glacial outwash of varying depths. Five of the originally pine plots and the previously hardwood plot are on glacial till (medium soils), which tend to support red oak, red maple, paper birch (*Betula papyrifera*), and white pine. The other five plots are on glacial outwash (light soils), which support white pine with red oak, black oak (*Quercus velutina*), red maple, and paper birch (Goodlett 1960).

METHODS

The plots established in 1940 were relocated using the original field notes and maps. The 11 plots were square and either 0.01 (3 plots) or 0.04 ha (8 plots) in area. Following the old sampling scheme, the larger plots were divided into eight rectangles of equal area, four of which were sampled (50% sample). Sampling consisted of recording diameters at 1.3 cm above the ground (diameter at breast height, dbh), crown position, and stem origin (single or multiple stem) of all stems over 1.3 m dbh. Crown position classes used were dominant (the crown extends slightly above the level of the main canopy), codominant (forms the main canopy), intermediate (shorter than above but in lower levels of the upper canopy), and overtopped (below upper canopy) (Smith 1962). Regeneration, the number of woody stems <1.3 cm dbh, was counted by species in 1-m² subplots located in each corner of the 11 primary plots. The presence of all nonwoody plants in each primary plot was also recorded.

Analysis of variance was done based on the 1948

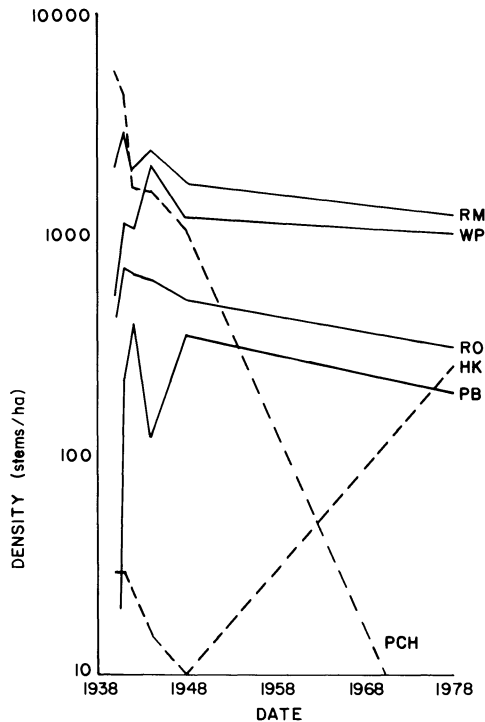


FIG. 1. Change in density of major species since 1938 on previously pine-dominated plots. RM = red maple, WP = white pine, HK = hemlock, PB = paper birch, RO = red oak, PCH = pin cherry.

and 1978 survey results for the 10 previously pine plots. Densities of overstory species were compared on the two soil groups (19 species, 5 plots per soil group) to determine if a significant difference existed in vegetation composition between the two soil groups at each measurement period.

Species richness was calculated as the number of species present. Diversity was calculated as:

$$H' = -\sum_i p_i \log p_i \quad (1)$$

$$D = -\log \sum_i p_i^2 \quad (2)$$

Information covering the period 1940 to 1948 is derived from a reexamination of the original field notes, which remain on file at the Harvard Forest. Nomenclature follows Little (1979).

RESULTS

The 10 previously pine plots

Analysis of variance indicates that, although there was a significant difference in vegetation composition between the two soil types in 1948, there was none in 1978 ($P < .05$). This might be the result of vegetation convergence, small sample size, or unknown factors, but because of it, all 10 plots were grouped and considered together in the following analysis.

In 1948, 10 yr after the hurricane, 19 tree species were present on the plots. Among them, examples of almost every method of regeneration could be found. Most species displayed more than one method (Table 1). White ash (*Fraxinus americana*), red oak, and red maple regenerated primarily by sprout growth, although by 1978 these species were represented almost entirely by single stems. Sprout growth took three forms: stump sprouts, root sprouts, and, most frequently, seedling sprouts. "Seedling sprout" is an expression used to describe advance regeneration that has a root collar <5 cm in diameter and older than the stem (Society of American Foresters 1950). These are small plants that have died back, sometimes repeat-

TABLE 1. 1948 stand composition and origin of trees. The first two columns contain relative values among species (only 10 of 19 shown), while the remaining six columns give, within a species, the commonness of three methods of reproduction and the percent of stems free to grow* within each method. Average total density equals 8831 stems/ha.

	Stand composition All species		Reproductive method					
			Seedlings†		Seedling sprouts†		Stump sprouts†	
	All stems (%)	F.T.G. stems* (%)	All stems (%)	F.T.G. stems (%)	All stems (%)	F.T.G. stems (%)	All stems (%)	F.T.G. stems (%)
<i>Acer rubrum</i>	18.4	15.2	15.1	0.0	78.4	3.2	6.5	56.8
<i>Fraxinus americana</i>	15.4	13.4	30.1	0.0	67.8	8.0	2.1	50.0
<i>Prunus pennsylvanica</i>	11.2	32.5	88.2	24.5	11.8	0.0	0.0	0.0
<i>Betula populifolia</i>	11.1	5.4	100.0	3.6	0.0	0.0	0.0	0.0
<i>P. serotina</i>	10.9	3.2	91.6	1.9	8.4	5.9	0.0	0.0
<i>Pinus strobus</i>	10.8	3.2	100.0	2.2	0.0	0.0	0.0	0.0
<i>Quercus rubra</i>	5.3	10.1	26.5	3.8	70.9	15.1	2.5	100.0
<i>B. papyrifera</i>	3.8	1.8	99.3	3.5	0.7	0.0	0.0	0.0
<i>B. lenta</i>	1.8	1.8	68.1	4.3	11.6	0.0	20.3	21.4
<i>Tsuga canadensis</i>	0.1	0.0	100.0	0.0	0.0	0.0	0.0	0.0
Total	88.8	86.6						

* Free to grow (F.T.G.): an old forestry term denoting those trees with a 90° or greater unobstructed view of the sky.

† Seedlings: stems originating from seed primarily after disturbance; seedling sprouts: small advance regeneration, root older than stem; stump sprouts: stems originating as sprouts from the stump of a tree (see Results for details).

edly, to ground level and then resprouted (Merz and Boyce 1956). They may have resprouted following damage from the hurricane. Seedlings may include some individuals present before 1938, although these individuals comprise a small minority (except in the case of hemlock). Seedlings of the birches, red maple, pin cherry (*Prunus pennsylvanica*), white pine, and the aspens (*Populus*) were all of post disturbance origin. White pine, hemlock, the birches, and the cherries regenerated primarily or only by seed, the pin cherry from buried seed (Marks 1974).

Although many species were numerous in 1948, pin cherry comprised the largest portion of the dominant stems, followed at a distance by red maple, white ash, and red oak (Table 1: column 2). Dominance was indicated by the expression "free-to-grow" (used in the plot measurements of 1940–1948), which denoted a stem with a 90° or greater unobstructed view of the sky. Pin cherry and red oak show strong dominance relative to their density, while gray birch (*Betula populifolia*), black cherry (*Prunus serotina*), and white pine expressed relatively poor dominance.

Among species utilizing several methods of reproduction, sprouts were more dominant than stems arising as seedlings (Table 1). Stump sprouts of black birch (*B. lenta*) were particularly successful as were stump and seedling sprouts of red maple, red oak, and white ash.

In addition to canopy dominance (Table 1), pin cherry achieved early numerical dominance with over 5000 stems/ha in 1940, but had already declined to 1000 stems/ha in 1948 (Fig. 1). In 1978, only a few standing dead stems remained. Other pioneer species, including aspens (*Populus tremuloides* and *P. grandidentata*), birches, white pine, and black cherry, colonized the sites more slowly, reaching peak densities in 1944 or 1948 and declining from this peak by 1978.

In 1940, pin cherry was the numerical dominant. In 1948, numerical dominance was shared among many species, but pin cherry, red maple, white ash, and red oak, in that order, comprised the upper canopy layer of the stands (Table 1).

Between 1948 and 1978 there was considerable change in stand structure related to differences in life histories. Some species had completed their life cycles by 1978, while others had only just begun to reproduce. Pin cherry had died out, although seeds presumably remain (Marks 1974), and gray birch is rapidly declining, as 40 yr is near its normal life span (Elias 1980). Hemlock, on the other hand, after having dropped in density between 1940 and 1948, increased from 10 to 250 stems/ha between 1948 and 1978.

In 1978, red maple and white pine comprised over 50% of the stems (Table 2), with 16 species making up the remainder. Canopy dominance was shared among only five species. Red oak and paper birch held a disproportionately large number of dominant canopy positions and comprised a disproportionately large

TABLE 2. Forest structure in 1978, 9 of 18 species shown. Average total density equals 4057 stems/ha.

Species*	Forest composition (% of stems)	Dominant† stems (%)	Codominant† stems (%)	Basal area (%)
<i>Acer rubrum</i>	30.5	16.7	18.3	9.6
<i>Pinus strobus</i>	23.3	0.0	33.1	34.3
<i>Betula populifolia</i>	9.3	25.0	11.3	8.1
<i>Quercus rubra</i>	7.5	37.5	19.0	15.5
<i>Tsuga canadensis</i>	6.5	8.3	2.1	7.1
<i>Fraxinus americana</i>	5.5	0.0	0.0	2.6
<i>B. papyrifera</i>	4.9	12.5	15.6	11.2
<i>B. lenta</i>	3.0	0.0	0.4	2.6
<i>Prunus serotina</i>	3.0	0.0	0.0	2.5
Total	93.5	100.0	99.8	93.5

* Nomenclature after Little (1979).

† Dominant trees stand slightly above the main canopy. Codominant trees form the main canopy.

amount of the basal area. Red maple exhibited an opposite tendency. White pine was found in a third of the codominant canopy positions but in no dominant ones. Black cherry and white ash had decreased dramatically in relative density and dominance.

Following the hurricane, species richness and diversity increased rapidly for ≈5 yr, after which they increased slowly to about year 10 (Table 3). By year 40, all values except total number of tree species had dropped.

The hardwood plot

Red maple was the early numerical dominant, with paper and black birch increasing in relative density over the 40 yr (Table 4). Pin cherry never achieved high densities, and along with red oak and gray birch, it has not survived. The populations of white pine and white oak have remained relatively stable.

TABLE 3. Species richness and diversity following the 1938 hurricane. The surveys of 1942 and 1944 appear to be incomplete; the presence and density of nontimber-producing species were only sketchily recorded. Values in parentheses, therefore, are low.

Date	No. of tree species	No. of tree spp. with freq. >10%	No. of woody species	Total no. of species	Tree diversity* H'	Tree diversity* D
1940	16	16	39	72	0.691	0.498
1941	19	17	46	72	0.841	0.710
1942	(16)	(14)	(33)	(48)	(0.963)	(0.895)
1944	(17)	(16)	(29)	(34)	(0.928)	(0.857)
1948	19	19	51	81	0.973	0.905
1978	18	15	36	53	0.911	0.772

* $H' = -\sum_i p_i \log p_i$, $D = -\log \sum_i p_i^2$, after Pielou (1977).

TABLE 4. Succession following the hardwood forest type; 9 of 15 species found are shown. Data from one 0.04-ha plot. Dominance here refers to crown position classes (see Methods).

Species	Relative density (%)				1978 (% of class)	
	1940	1944	1948	1978	Dominant	Codominant
<i>Acer rubrum</i>	33.2	11.2	12.3	26.05	0.0	46.6
<i>Betula lenta</i>	6.6	3.1	10.2	14.3	0.0	20.0
<i>B. papyrifera</i>	0.0	0.9	12.8	20.4	50.0	26.7
<i>B. populifolia</i>	0.0	21.5	12.8	0.0	0.0	0.0
<i>Pinus strobus</i>	5.7	22.4	16.2	14.3	0.0	0.0
<i>Prunus pennsylvanica</i>	13.3	5.8	4.3	0.0	0.0	0.0
<i>Quercus alba</i>	3.8	4.0	1.7	2.0	25.0	0.0
<i>Q. rubra</i>	7.6	5.8	2.1	0.0	0.0	0.0
<i>Tsuga canadensis</i>	7.1	2.2	1.9	10.2	25.0	6.7
Other	22.7	23.1	25.7	12.3	0.0	0.0
Density (no. stems/ha)	10 428	11 021	11 614	2422		

In 1978, paper birch showed strong dominance. Two hemlocks and one white oak of 40.6, 35.7, and 27.9 cm dbh, respectively, comprised the dominant and codominant individuals of these species. Their size was considerably larger than that of other trees on the plot, so it appears that they were remnants of the previous stand. The codominant portion of the canopy was primarily composed of red maple and paper and black birch.

DISCUSSION

Colonization

Following complete canopy destruction at the Harvard Forest by the hurricane of 1938, regeneration occurred by almost all possible methods, some individual species utilizing as many as three methods. Among species, there appears to be no generalization possible about the relationship between early and late successional (early and late dominant) species and method of reproduction. Examples from each group reproduced by seed or sprouts. In addition, among the species employing several methods of reproduction, one method did not uniformly produce more dominant stems than another.

Change in composition

Most species present in the first 40 yr of succession, including those presently dominant, arrived before or almost immediately after the disturbance. Stump and seedling sprouts and buried seed responded quickly, and species with wind-blown seed came in soon after, within 6–10 yr. From this point on, succession was a sorting process determined by species life spans and relative growth rates. The observed changes were only changes in numerical or canopy dominance. The only species to colonize after year 10 was hemlock. The above changes, with the exception of hemlock, follow the initial floristic composition model of vegetation change (Egler 1954).

None of the successional models proposed by Connell and Slatyer (1977) completely describes the type

of vegetation change observed here, in part because these models are designed to encompass the whole successional sequence. Because hemlock requires partial shade for establishment (United States Forest Service 1965) and is a late colonizer, it fits the facilitation or relay floristic model. However, most other species do colonize immediately after the disturbance. The tolerance model, an initial floristic composition model, is the alternative choice.

Change in structure

Canopy structure should be envisioned not as one layer of mixed and overlapping tree crowns but as a structure with horizontal variation and a moderate degree of vertical order. At any one time in succession, a given species tends to have a characteristic canopy position, but this position may change relative to other species with time because of differential mortality and changing growth rates.

Three stages in 40 yr of canopy development can be identified. The first is typified by the 1948 stand structure and probably covers the first 15 yr of succession. A high proportion of dominant pin cherry is characteristic of this stage. The third stage begins about year 40 or 50 and continues, in the absence of major disturbance, for up to 100 yr. This stage is typified by a canopy of red oak, paper birch, red maple, and white pine, with birch and maple dominance decreasing over time.

The second stage falls between these two and was not directly observed in this study. However, Oliver's work (1978) indicates that some time between years 15 and 40, with the continuing loss of pin cherry, red maple was at least partially dominant over red oak. Table 1, however, does also show some red oaks as being early dominants. Grey birch also appears to have been more dominant in this stage. It is a short-lived pioneer species that showed a surprising degree of dominance in 1978, considering its age and poor physical condition; it seems likely that this dominance is a carry-over from the recent past.

Dominance of canopy position can come about in

one of two ways. A tree can simply grow taller than its neighbors; red oak and paper birch are the two most obvious examples of this. In the 1978 survey, they were not numerous but comprised a disproportionately large number of the dominant trees. Alternatively, a tree colonizing a more sparsely inhabited area may be dominant only by virtue of its presence. Red maple may be thought of in this way. It comprised 30.5% of the tree stems in 1978 but only 16.7% of the dominant stems (Table 2). In effect, it flooded the forest with regeneration, and the few that found uncontested sites have flourished.

With the exception of hemlock, no evidence was found in this study to support the idea that the smaller understory trees represent a coming seral stage. Rather, support has been given to the generality of a loosely multilayered canopy model and the idea that species can have characteristic, although changing with time, positions in this canopy in temperate forests (Hill 1977, Oliver 1980).

Connell (1978) observed that "plants in general have not specialized along the food niche axis." However, the canopy structure and change in structure with succession observed in this study may indicate the existence of both vertical and temporal divisions of the light resource by these woody plant species. This temporal division supports Pickett's (1976) view of succession as species arrayed along a time gradient.

Study of the stratification of canopies in other forest types is only beginning (Oliver 1980). The silvicultural implications of the phenomenon are great.

Diversity

The observed changes in species richness and diversity are better described by the early stages of the model by Bormann and Likens (1979) in which diversity increases rapidly in the earliest stage of succession and then drops gradually after year 10 or 15. The observed changes bear little resemblance to the more traditional models of a gradual increase with time (Margalef 1963, Loucks 1970, Odum 1971), as seen in post-agricultural succession.

Previous canopy type

In general, there were few differences in the vegetation change observed following the different canopy types. The set of species involved was nearly the same. The trends in numerical and canopy dominance were the same except that red oak regeneration did not survive.

The remnants of the previous forest found on the plot may have been left because of the partially sheltered nature of the plot, a gentle west-facing slope, or simply because of the generally greater resistance to wind disturbance of New England hardwood forest types (Rowlands 1941). The presence of these remnants and the shade they cast may account for some of the differences observed. On the previously pine

plots, initial hemlock mortality was high. The partial shade on this plot may have been sufficient to reduce the mortality of advance-regeneration hemlock. The shade may also have played a role in the exclusion of red oak, a shade-intolerant species, and the inclusion of black birch (*Betula lenta*), a moderately shade-tolerant species (United States Forest Service 1965). On the other hand, the shade was not so great as to affect the successful colonization by several other shade-intolerant species.

Forest succession

The forests of pre-colonial central New England were primarily hardwood with a smaller white pine and hemlock component (Cline and Lockard 1925, Cline and Spurr 1942) and were subject to disturbance by wind, fire, insects, and disease (Henry and Swan 1974, Oliver and Stephens 1977). There was considerable regional variation in disturbance agent and frequency, with wind being the most common agent in the vicinity of the Harvard Forest.

Succession following a large wind disturbance in the pre-colonial forest of central New England was probably similar to that found in this study. Much growth would have been from advance regeneration, and the only obvious major difference in composition would be a greater hemlock presence from the understory of the previous stand. This conclusion is also supported by the findings of Henry and Swan (1974) in southwest New Hampshire following the blowdown of a 250-yr-old pine/hemlock forest. Surviving understory hemlock was joined by red maple and black birch, which reproduced from wind-blown seed. Because of its low rate of height growth, this hemlock would rarely become dominant in 40 yr and so would have little effect on the early trends in canopy structure described here. Through succession, the forest composition and structure would continue to simplify as shorter-lived species dropped out and as differences in height growth rates amplified differences in tree height. This process would continue until a disturbance opened canopy gaps large enough to regenerate species other than hemlock or until the stand was destroyed and the cycle reinitiated.

The 1938 hurricane interrupted a long post-agricultural successional sequence from field to pine to mixed hardwoods. Had the hurricane not occurred, time and small disturbances would have slowly removed the old-field pine and led to replacement by hardwoods. The hurricane hastened this replacement. In doing so, it produced an even-aged forest that regenerated in open, high-light conditions.

The type of vegetation structure and dynamics observed on a site, then, is a function of the kind and intensity of disturbance (its effect on environmental conditions, the characteristics of species available for colonization, and when in succession the disturbance occurs [the effect of previous canopy type]). In central

New England where large- and small-scale wind disturbance is common (Smith 1946, Ludlum 1963), only two types of natural dynamics and their associated structure and composition are common: (1) large-scale disturbance on more exposed sites, producing succession similar to that described in this paper and (2) gap dynamics on more sheltered sites, leading to a forest similar to that described by Oliver and Stephens (1977). Following a large-scale wind disturbance, many short-lived, shade-intolerant species can be found regenerating along with the more shade-tolerant species that eventually will comprise the mature forest. The age and type of the previous canopy may affect the type and quantity of advance regeneration, but otherwise, species response is dependent on species availability, light, moisture, seed bed conditions, etc., and generally independent of previous canopy type. When regeneration is regulated by gap dynamics, most mature forest species are found to reproduce successfully, and the short-lived, shade-intolerant species are missing (Oliver and Stephens 1977, Hibbs 1982b). With time, forests regenerating from large- and small-scale disturbances might be expected to converge in structure and composition.

CONCLUSIONS

Following the removal of the white pine canopy by the 1938 hurricane, sites at the Harvard Forest regenerated by a variety of mechanisms. All tree species present in the first 40 yr of succession, with the exception of hemlock, colonized within the first 10 yr. Hence, diversity peaked early in the sere.

Large changes were observed in both canopy and numerical dominance. Evidence was found for three stages in canopy composition and structure. Natural mortality due to limits to longevity and species-specific patterns of rates of height growth appeared to be the driving forces behind this succession. These growth patterns cause species to characterize different layers in the canopy loosely.

The described trends apply primarily to forests that previously supported white pine. In general, these trends probably also apply to post-hardwood succession with the addition of some hemlock advance regeneration and, perhaps, a small decrease in the importance of shade-intolerant species in the early seral stages.

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