Development patterns in two hemlock–hardwood stands in southern New England

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Two forest stands, composed primarily of northern red oak (*Quercus rubra* L.), red maple (*Acer rubrum* L.), and eastern hemlock (*Tsuga canadensis* (L.) Carr.), were studied by stand-reconstruction techniques to determine the pattern of development of canopy structure. One stand had originated following clear-cutting 87 years ago; the other, following catastrophic windthrow 44 years ago. Juvenile height growth of the hardwood species was much greater than that of hemlock and a stratified canopy developed by age 30 years, with hardwoods forming an overstory canopy above hemlock. Hemlocks maintained overstory positions only if they were 3 m or more in height immediately following canopy disturbance. In the older stand, hardwood height growth was about twice that of the tallest understory hemlocks during the first 30 years. The hardwood overstory slowed after that and grew at the same rate as the tallest understory hemlocks, which maintained a constant rate of height growth, and a constant to accelerating rate of basal area growth for much of the 87-year measurement period. The height growth of the tallest understory hemlocks was apparently limited in part by breakage of terminal shoots, caused by abrasion against branches of overstory hardwood crowns.

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On a étudié au moyen de procédés de reconstitution deux peuplements forestiers composés principalement de chêne rouge (*Quercus rubra* L.), d'érable rouge (*Acer rubrum* L.) et de pruche de l'Est (*Tsuga canadensis* (L.) Carr.), en vue de déterminer l'allure du développement du couvert forestier. Un des peuplements était issu d'une coupe à blanc appliquée il y a 87 ans, tandis que l'autre provenait d'un chablis voici 44 ans. La croissance juvénile en hauteur des espèces feuillues était supérieure à celle de la pruche et un couvert statifié s'est développé vers l'âge de 30 ans, alors que les feuillus constituaient un étage supérieur dominant la pruche. Les pruches n'ont pu conserver leur état dominant que si elles avaient une hauteur supérieure à 3 m immédiatement aprés la perturbation. Dans le peuplement plus âgé, la croissance en hauteur des espèces feuillues dépassait de deux fois celle des plus grandes pruches du sous-étage durant les 30 premières années. Aprés cette période, le couvert de feuillus déclina et s'est accru au même rythme que les plus grandes pruches du sous-étage, qui maintinrent un rythme constant de croissance en hauteur ainsi qu'un rythme constant ou croissant en surface terrière durant la plus grande partie de la période d'observation de 87 ans. La croissance en hauteur des plus grandes pruches du sous-étage fut apparemment limitée en partie par le bris des pousses terminales provoqué par le frottement contre les branches des houppiers du couvert principal de feuillus.

[Traduit par la revue]

Introduction

Descriptions of forest stand development have traditionally followed one of two conceptual models defined by stand age and canopy structure (Smith 1982). The even-aged, single-canopy model is applied to stands that originate following a single major disturbance that destroys the previous forest canopy. The model consists largely of the idea that trees of approximately the same ages (conventionally a range of 20 years or less) differentiate into various crown classes within the canopy and that this process of differentiation is progessive: upper canopy trees dominate the resources required for growth, such that differences among individual trees in height, stem diameter, and crown size become continually greater with increasing stand age. Crown class designations of dominant, codominant, intermediate, and overtopped are often assigned to trees; these not only describe relative tree size, but also imply a prediction that subsequent development will follow the progressive differentiation pattern, with upper crown classes continuing to dominate and lower classes having slower growth and higher mortality rates.

The uneven-aged model depicts a stand as a collection of small, relatively even-aged aggregations that are spatially intermixed. These aggregations begin following small disturbances that in the smallest extreme consist of the death of a single overstory tree. As disturbance size increases, this model merges with the even-aged model described above. The canopy of such a stand is seen as having an irregular upper surface, with canopy height corresponding to differences in age class. Crown class designations are only applicable to the development process within each even-aged aggregation, not for the stand as a whole.

These two models and the associated crown class designations best fit single-species stands or mixed stands that are composed of species with similar growth characteristics and rates of development. Smith (1982) noted that these models do not adequately describe all of the possible variations in stand-development patterns, especially those occurring in complex species mixtures. Recent studies have identified important departures from these simple models. Certain mixed-species stands have been found to develop stratified canopies in which different species tend to occur at different heights even though all originated following a single canopy disturbance (Oliver 1978; Wierman and Oliver 1979). Other mixed-species stands have been found to contain two distinct age-classes, but have uniform canopy tops, with the upper canopy positions being composed of trees of both ages (Marquis 1981). These stands also result from a single disturbance, but scattered residuals from the previous stand survive to form the older age-class. For these two more complicated kinds of stands, the relationship of canopy position to growth rate and survival does not necessarily correspond to that of the even-aged, single-canopy model

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TABLE 1. Climatic conditions at the Harvard Forest (Murison 1963) and the Great Mountain Forest (Winer 1955)

	Harvard Forest	Great Mountain Forest
Mean annual precipitation (mm)	1120	1260
Growing season (days)[a]	138	123
Temperature (°C)		
Annual mean	7	6
January mean	−6	−7
July mean	19	19

[a]Mean length of time between last spring frost and first autumn frost.

because of differences in age and species-specific growth characteristics among individual trees. Standard crown class designations are sometimes applied to those stands, but they are not really appropriate, because they imply a specific pattern of development.

In the present study, the development of mixtures composed primarily of red oak (*Quercus rubra* L.), red maple (*Acer rubrum* L.), and eastern hemlock (*Tsuga canadensis* (L.) Carr.) that originated following a single major canopy disturbance were examined in relation to these various stand-development models. This forest type is prevalent on upland till soils of southern New England and is of particular interest for this study because of the wide range of characteristics of the component species. Most hardwood species are of low to intermediate shade tolerance and have rapid juvenile height growth, whereas hemlock is highly tolerant of shade and has slow juvenile growth. Development patterns were examined in relation to the even-aged, single-canopy model and its two alternatives described above for stands arising from large-scale disturbances. Specific objectives were (*i*) to determine what age and height structures occur in these hemlock–hardwood mixtures and (*ii*) to reconstruct growth rates of individual trees to examine relative growth rates of overstory and understory trees.

Study sites

Two study stands were selected to have the following characteristics in common: both were of the red oak – red maple – hemlock forest type; were on rolling glaciated uplands with thin till soils that had never been cleared for agricultural use; and had originated from a single, large-scale disturbance that completely (or nearly so) destroyed the previous stand over at least several hectares. One site is on the Harvard Forest in central Massachusetts and one on the Great Mountain Forest in northwest Connecticut, 110 km southwest of the Harvard Forest. Both lie within the transition hardwood – hemlock – white pine forest vegetation zone (Westveld 1956). Climatic conditions of the two sites are given in Table 1.

The 3-ha Harvard Forest site (in compartment 7 of the Slab City Tract) occupies the top and upper west-facing slope of a small hill at 300 m elevation. The soil is classified as well-drained Charlton stony fine sandy loam, derived from till of gneiss and schist origin (Simmons 1940). Bedrock outcrops occur within the study area and depth to bedrock varies from 0 to approximately 200 cm. Slopes on sample plots varied from level to 10%.

The 8-ha Great Mountain Forest site occupies the top and upper north-facing slope of a small hill at 460 m elevation. The soil is well-drained to somewhat excessively drained Hollis extremely rocky fine sandy loam (USDA Soil Conservation Service 1970), is a till soil averaging 40 cm to bedrock, and is derived from gneiss and schist parent materials. Slopes on study plots were level to 10%.

The Harvard Forest site was never cleared for crop or pasture use because of its rocky and uneven terrain, although it borders on old-field stands. Records from the mid-19th century indicate that it was used as a farm woodlot (Raup and Carlson 1941). A forest inventory in 1937 (Harvard Forest, unpublished records) showed that the stand consisted mainly of red oak, red maple, sugar maple (*Acer saccharum* Marsh.), white pine (*Pinus strobus* L.), and hemlock. At that time, ages varied from 20 to 90 years and advance regeneration was described as "dense," consisting of hemlock, red oak, sugar maple, red maple, white ash (*Fraxinus americana* L.), black birch (*Betula lenta* L.), and hickory (*Carya* spp.). In September 1938, hurricane winds destroyed the existing overstory. Harvard Forest records indicate that all overstory trees in this stand were uprooted except for a few white pine, which were broken off 3–9 m above the ground. Scattered intermediate and suppressed trees remained standing, but most smaller trees were broken off or uprooted beneath the fallen overstory trees. The present stand has received no treatment since it began following the hurricane.

The Great Mountain Forest stand is in an area where little agricultural development occurred in the 19th century. Extensive timber cutting began in the mid-19th century, with clear-cutting of hardwoods for charcoal production accompanied by cutting of hemlock for sawlogs and tanbark. Hardwoods were used to a minimum diameter of 5 cm or less and hemlocks were used to a minimum diameter of about 15 cm, resulting in nearly complete clear-cutting (Winer 1955). The stand examined in this study originated following a cutting in 1895 and had received no treatment since that time.

Methods

Sample plots were located at fixed intervals along parallel transect lines in both stands. In the Harvard Forest stand, 10 circular 0.01-ha plots were established and all trees that were at least 1.3 m tall (breast height) were measured. In the Great Mountain Forest stand, 18 variable-radius plots were measured using a prism with a basal area factor of 2.3 m^2/ha. All trees judged borderline by prism measurement were verified with measuring tape. All trees detected by the prism were measured, thus limiting data to trees at least 1.3 m tall.

Total height and diameter at breast height (dbh) were measured for each tree and each was classified as overstory (equivalent to dominant and codominant) or understory (equivalent to intermediate and overtopped). A subsample was drawn for age measurement ($n = 41$ trees for the Harvard Forest stand; $n = 42$ trees for the Great Mountain Forest stand) by choosing individuals systematically according to the order in which they appeared on the data sheet. For each tree in the subsample, age was determined from an increment core taken as near to the ground as possible. All measurements were made in 1982–1983.

Groups of competing trees in the Great Mountain Forest stand were chosen for stem dissections to compare growth rates of overstory and understory trees. Overstory red oak and black cherry (*Prunus serotina* Ehrh.) were selected because red oak was the most common species in the overstory and black cherry, while not as prevalent, was found only in the overstory canopy. The tallest understory hemlocks were chosen for comparison to give the growth rates of overtopped trees affected by overstory hardwood crown competition only and not by other hemlocks. From the 18-plot sample in the Great Mountain Forest stand, six groups of four trees each were chosen in the following way. Because black cherry was the least common of these three species, each cherry in the 18-plot sample was assigned a number and six were chosen using random numbers. Each was accepted as a sample tree if its crown was in contact with that of an oak. If a tree did not meet this criterion, another was selected by the same method. Each group consisted, then, of a black cherry and an adjacent red oak, plus the two tallest understory hemlocks growing beneath the crowns of either of these two overstory trees. These six groups came from six different plots.

Additionally, all overstory hemlocks in the 18-plot sample were assigned numbers and six of these were chosen using random numbers. These six came from five different plots.

Each of these 30 trees was felled and cross sections were cut at stump height (0.5 m), breast height (1.3 m), and at each 1.2-m interval above that. Cross sections were sanded and annual rings counted. For each breast-height cross section, 5-year radial increments were measured along two geometric mean radii, averaged, and converted to basal area increment.

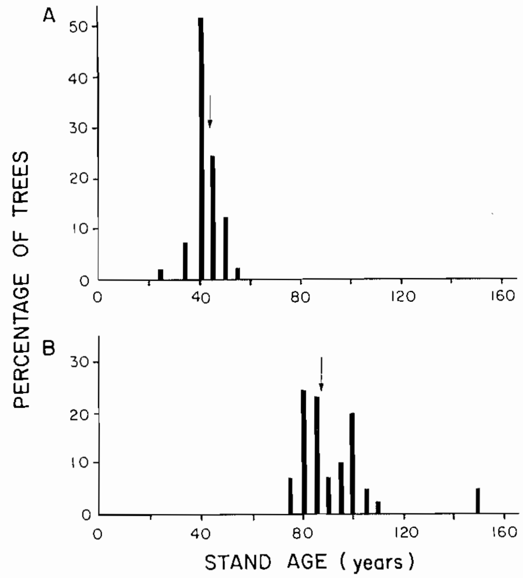

FIG. 1. Age distributions of (A) Harvard Forest stand and (B) Great Mountain Forest stand by 5-year age-class. Arrows denote times of stand-initiating disturbances caused by (A) hurricane 44 years ago and (B) logging 87 years ago.

The upper 5 m of each of the 18 dissected hemlocks (6 overstory, 12 understory) was examined and the occurrence and location of any irregularities in crown form or leader growth pattern were recorded. Seven additional overstory hemlocks felled for a different study within this stand were examined for irregularities in crown form and leader growth, increasing the sample size of overstory hemlocks to 13 for those measurements.

A profile diagram of a single 10 m × 30 m plot in the Great Mountain Forest stand was constructed following the methods developed for tropical forests (Richards 1952; Hallé *et al.* 1978). This plot was subjectively located within the stand to be representative of stand conditions measured in the 18 plots. The positions of all tree stems and crowns on this plot were mapped. Measures of the height, breast-height diameter, height to bottom of living foliage, and position of major forking of stems were made for each tree and used in constructing the diagram.

In the Harvard Forest stand, one overstory hemlock was chosen randomly and a three-tree group was defined consisting of the overstory hemlock, an adjacent overstory red oak, and an understory hemlock growing beneath the oak. These three trees were felled and height growth measurements were made as described above.

Results and discussion

Stand characteristics

Most stems reached stump height (0.5 m) shortly before or after the time of canopy disturbance (Fig. 1). For the Harvard Forest stand, a majority of stems reached 0.5 m during the 5-year period following the 1938 hurricane, with others (mainly hemlocks) being established as advance growth during the 10 years before 1938. Many of the hardwood stems apparently originated as sprouts from damaged advance regeneration, which was abundant at the time of overstory destruction; they showed the rapid initial diameter growth that is associated with such an origin.

In the Great Mountain Forest stand, 48% of the stems sampled had a stump age in the 80- and 85-year classes, including a number of red oak and red maple that originated as multiple sprout clumps. Most others were advance growth up to 25 years old at the time of overstory removal. There were also several residual hemlocks in the 150-year age-class.

TABLE 2. Species composition of the Harvard Forest and Great Mountain Forest stands by stem density and basal area

	Harvard Forest stand		Great Mountain Forest stand	
Species	Density (stems/ha)	Basal area (m^2/ha)	Density (stems/ha)	Basal area (m^2/ha)
Hemlock	2170	21.5	885	20.1
Red oak	610	11.4	176	17.3
Red maple	340	2.7	190	6.0
Black birch	730	5.3	—	—
Paper birch	160	1.4	—	—
Black cherry	—	—	29	2.2
Beech	—	—	164	2.5
Minor species[a]				
Total	4210	43.9	1450	48.4

[a]Minor species include sugar maple, white ash, white pine, yellow birch (*Betula alleghaniensis* Britton), white oak (*Quercus alba* L.), shagbark hickory (*Carya ovata* (Mill.) K. Koch.), chestnut (*Castanea dentata* (Marsh.) Borkh.), and hop hornbeam (*Ostrya virginiana* (Mill.) K. Koch).

Hemlock was the most abundant species in both stands, making up over 50% of stems (Table 2). Both were clearly dominated by hemlock, red oak, and red maple; these three species accounted for 81 and 90% of basal area of the Harvard Forest and Great Mountain Forest stands, respectively. Some species composition differences between stands were due to the effects of insect damage and stand age. Black cherry, which formed a part of the Great Mountain Forest, had been a part of most Harvard Forest posthurricane stands but had been eliminated early in development by forest tent caterpillars (*Malacosoma disstria* Hubner) (Spurr 1956). Paper birch, a relatively short-lived pioneer species, formed a part of the Harvard Forest stand but not the Great Mountain Forest stand (Table 2). Measurements made on two plots within the Great Mountain Forest stand when it was 55 years old (Winer 1955) showed that paper birch had been an important component at that time, making up 17% of the tallest height class.

In the Harvard Forest stand, red oak, red maple, black birch, and paper birch formed the overstory, with the tallest trees having heights of 12–18 m (Fig. 2A). The height distribution of hemlock shows a fairly continuous distribution from 2 to 12 m, with most trees beneath the height of the main canopy. Only 1% of the trees classified as overstory were hemlocks.

In the Great Mountain Forest stand (Fig. 2B), red oak and black cherry formed much of the overstory at heights of 16–21 m; these species were not found with heights less than 15 m. Hemlock formed a bimodal height distribution in the understory. One peak occurred at 13 m; another, at 5 m. In this stand, hemlock made up 18% of the overstory, generally at heights of 16 m or more. Some beech was present, primarily at lower heights, and red maple occupied an intermediate position in the height distribution, with trees in both overstory and understory positions.

The profile (Fig. 3) depicting the Great Mountain Forest stand shows that the hemlocks generally were completely overtopped by hardwoods. The tallest hemlocks reached just to the lower portion of the hardwood crowns. The one exception is the hemlock farthest to the left; although much of its crown was overtopped by portions of several hardwood crowns, the terminal was growing unsuppressed in a small gap between the hardwoods. No hemlocks occupied a clear overstory position in

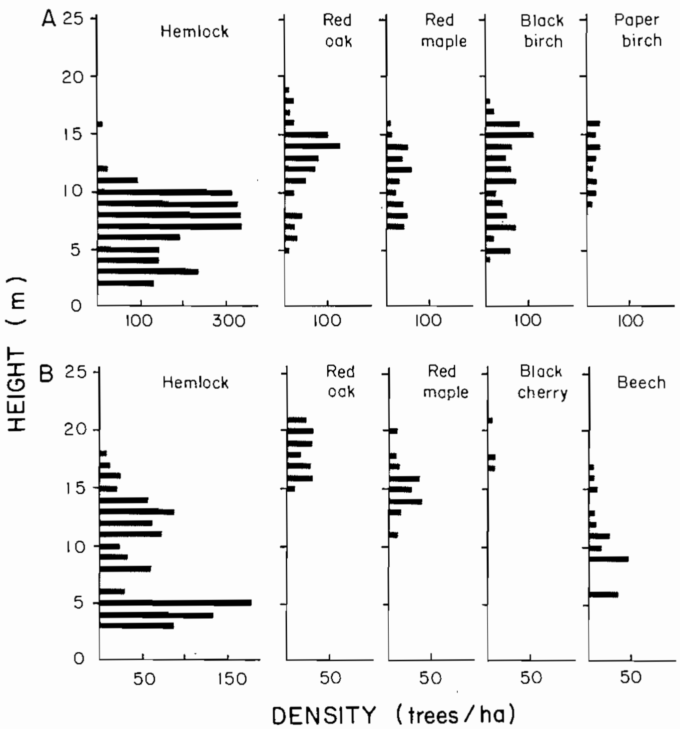

FIG. 2. Tree density distributions by species and 1-m height class for (A) Harvard Forest stand and (B) Great Mountain Forest stand.

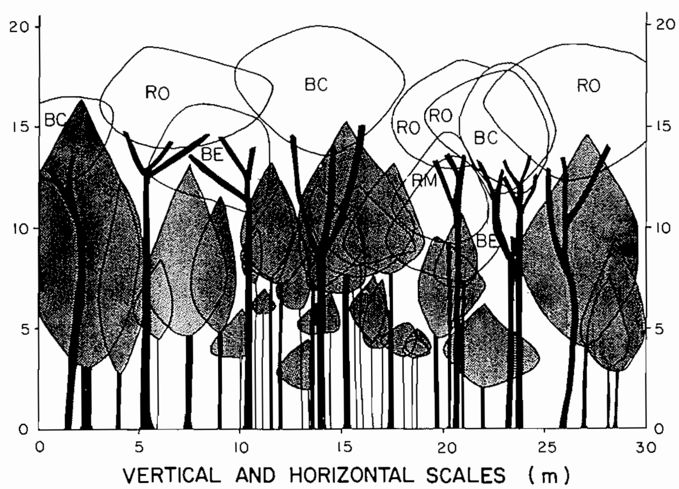

FIG. 3. Profile diagram of a 10 m × 30 m plot in the Great Mountain Forest stand. Tree height, stem diameter, crown dimensions, and position of major branches are drawn to scale, based directly upon measurement. Shaded crowns are hemlock. Hardwood species codes: RO, red oak; RM, red maple; BC, black cherry; BE, beech.

this plot, although they did occur elsewhere in the stand. Where the understory stratum was crowded, as in the center of the plot, an additional set of hemlocks grew beneath the crowns of the taller understory hemlock, red maple, and beech. The presence of this additional layer of hemlocks at about 5 m in height is evident throughout the entire stand (Fig. 2B).

Reconstruction of growth patterns

Reconstructed height growth patterns of overstory red oak and black cherry were compared with that of the tallest understory hemlock for the Great Mountain Forest stand (Fig. 4A). The hardwoods exhibited a two-phase pattern of height growth, with fast initial growth for 30 years followed by a

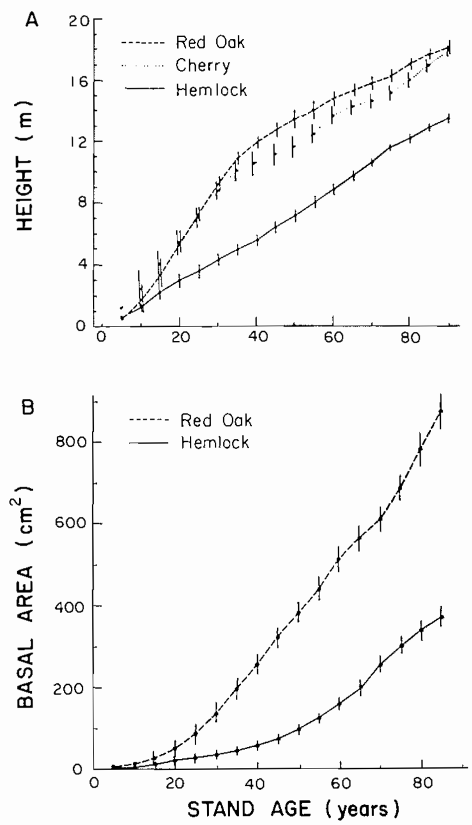

FIG. 4. (A) Average cumulative height growth and (B) basal area growth of trees growing in direct competition in the Great Mountain Forest stand. Results are based on six four-tree plots of overstory red oak (n = 6), overstory black cherry (n = 6), and understory hemlock (n = 12). Black cherry is omitted from Fig. 4B because basal area growth could not be measured because of heartwood decay. A stand age of 0 denotes the year of overstory removal by logging. Vertical lines represent ±1 SE.

slower rate thereafter. Two linear functions were fitted to the average height-growth curves for each of the hardwood species, using 30 years of age as the breaking point between the two phases. For understory hemlocks, a single linear function was fitted to the curve of average height growth. These linear functions fit the average height–age curves well (r^2 = 0.99 or greater in all cases). These correlation coefficients account only for the shape of the average height–age curve, not the total variation in the original data; the total variation is reflected in the standard errors given in Fig. 4A.

The slopes of the regression lines, representing average growth rates in metres per year, were 0.35 and 0.30 for red oak and black cherry from 0 to 30 years and 0.12 and 0.14 from 30 to 87 years, respectively. The slope of the hemlock regression line was 0.16. Thus, during the first 30 years, hardwood height growth was about twice that of the overtopped hemlock. After that time, all three species grew at approximately equal rates; that is, the oak and cherry just maintained the height advantage achieved in the first 30 years, but did not increase this difference.

Basal area growth for these same overstory red oak and understory hemlock followed a different pattern from height growth (Fig. 4B). (Black cherry diameter growth could not be reconstructed because of heartwood decay in many stems.) Following an initial 20-year period of slow growth, oak had a constant to slightly accelerating growth rate, even to 87 years of age. Basal area growth of understory hemlock was initially slow

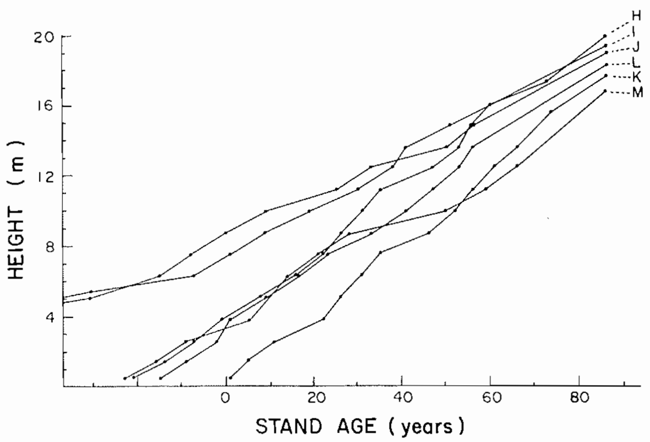

FIG. 5. Cumulative height growth of six overstory hemlocks in the Great Mountain Forest stand. A stand age of 0 denotes the year of overstory removal by logging.

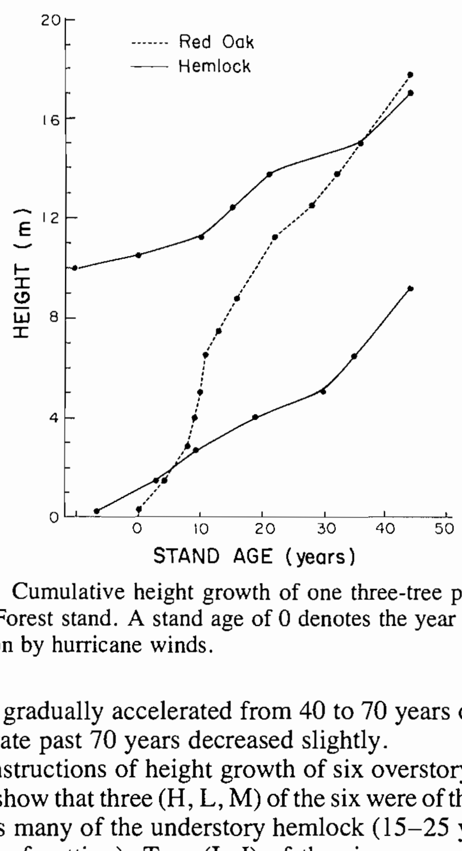

FIG. 6. Cumulative height growth of one three-tree plot from the Harvard Forest stand. A stand age of 0 denotes the year of overstory destruction by hurricane winds.

but then gradually accelerated from 40 to 70 years of age. The growth rate past 70 years decreased slightly.

Reconstructions of height growth of six overstory hemlocks (Fig. 5) show that three (H, L, M) of the six were of the same age cohort as many of the understory hemlock (15–25 years old at the time of cutting). Two (I, J) of the six were considerably older, originating 65 years before the cutting. These five trees were all at least 3 m tall at the time of cutting and the two older trees were above 7 m in height. In contrast, none of the 12 understory hemlock sample trees had been taller than 1.5 m at the time of cutting (Fig. 4A).

One (K) of the six overstory hemlocks, although a small seedling at the time of cutting, was able to reach a height equal to that of the dominant hardwoods. The tree was growing on a rocky seedbed and no hardwood tree or remnants of dead hardwoods were visible. Such a pattern probably represents growth free of hardwood competition.

Only one overstory hemlock fell within the boundaries of a sample plot in the Harvard Forest stand and none fell within the age sample of Fig. 1A. However, a few were present elsewhere in the stand. They were not scattered throughout the area as in the Great Mountain Forest stand but occurred only where protected from the force of the hurricane wind by a small ridge. Increment cores taken from these trees showed that they were 30–80 years old and 5–20 cm in diameter at the time of the hurricane and that diameter growth increased sharply just after that time. These trees are presently as tall as the hardwood overstory.

Height growth was reconstructed for one three-tree set (Fig. 6) consisting of an overstory hemlock, an overstory red oak, and an understory hemlock growing adjacent to one another. As was found for a majority of cases in the older stand, the hemlock that eventually reached the overstory had been present as a tall residual (10 m) following canopy disturbance but did not maintain its height advantage over red oak during early growth. The understory hemlock had developed from a small advance-growth seedling and was quickly surpassed in height growth by the red oak sprout.

Hemlock terminal breakage

Stem dissection revealed that terminal shoots of many of the tallest understory hemlocks had been broken, causing lateral branches to grow vertically and compete for dominance as leaders. The number and height of such terminal breaks and the number of lateral branches competing for dominance after each occurrence were determined for both overstory and understory hemlocks averaging 18 and 14 m in height, respectively. Of 13 overstory trees examined, none showed evidence of terminal breakage. Of 12 understory trees, 11 (92%) had at least one terminal break and 6 (50%) showed multiple instances of breakage. Thus, terminal breakage appears to be a characteristic of trees in the understory position. Among the 12 understory hemlocks sampled, 21 instances of terminal breakage were observed within the upper 4 m of their crowns. The number of new terminals developing from each instance of breakage ranged from 0 (indicating recent terminal death) to 10, with a median of 4.

The leader growth pattern of hemlock has been described by Hibbs (1981). He noted that in both understory and overstory trees 1.5–15 m tall, the leader frequently loses dominance and a lateral takes its place as the terminal shoot. These events occur when the terminal is young (usually the 1st through 3rd year of growth); the original leader may remain alive but take a lateral growth position, or may be killed. Because these occurrences involve small shoots, external evidence of the change in leader dominance is obscured by growth within a few years (Hibbs 1981).

In contrast, the breakage of leaders associated with growth in the understory position observed in the present study has resulted in an enduring change in crown form. Overstory hemlocks exhibited a conical crown form, with a single central stem. Among understory hemlocks, a profusion of lateral branches competing for dominance following leader breakage resulted in flat-topped crowns. In some cases, trees have no identifiable central stem in the upper portion of the crown.

Oliver (1978) observed similar terminal breakage in red maple and black birch growing beneath red oak. He suggested it was caused by direct abrasion of the terminals against the large lower branches of the overstory oak crowns during windstorms, especially if associated with glaze, which makes branches more brittle and prone to breakage. A similar mechanism probably occurs with hemlock, since terminal breakage was confined to understory trees in the present study and these had terminals growing at the levels of the lower parts of the oak and cherry crowns.

General discussion

General developmental patterns

For the most part, the hemlock–hardwood stands studied here are best described as even-aged stratified mixtures as defined by Smith (1962, 1982) and Oliver (1978). Each species tended to occupy a characteristic position within the canopy, even though most trees began growth following a single disturbance. In both stands, hardwood species (predominantly red oak) formed an upper canopy stratum, with hemlock occurring as a dense understory of overtopped trees.

Differentiation into canopy strata was not complete. In both cases, various hardwood species occurred in the understory, although hemlock was most prevalent. Understory hardwoods included smaller members of all the important overstory hardwood species in the Harvard Forest stand, but only the more tolerant red maple and beech remained at understory heights in the older Great Mountain Forest stand. Also, some residual hemlocks that remained following canopy removal maintained overstory positions together with the hardwoods. Where these occurred, the stand can be considered two-aged rather than even-aged, with both age-classes sharing the overstory stratum with a uniform canopy top. Both hurricane blowdown and logging left these hemlock residuals and resulted in essentially the same patterns of canopy structure and development in relation to the position of hemlock within the canopy, although numbers and spatial arrangement of the residuals were different.

Development of the even-aged, stratified component

Superficially, the different canopy strata of the hemlock–hardwood mixtures appear to resemble the different crown positions in a single-species stand. However, the relationship between growth rate and canopy position of individuals is not comparable for the two situations. In pure stands, trees in lower crown classes continually fall further behind upper canopy trees in height and basal area growth (Ward 1964; Bormann 1965; Trimble 1969). Four crown classes are usually distinguished to assess the competitive status of individual trees, but the distinction between two classes appears to be of primary importance in assessing relative growth. Those trees that reach the upper level of the canopy and receive full sunlight, at least at the crown tops, show the highest growth rates; those that survive in lower canopy positions with crowns partially or totally overtopped have lower growth rates and, in some cases, nearly cease growth (Ford 1982; Oliver and Murray 1983).

Similar relationships have been reported in some stratified mixtures. Oliver (1978) found that understory red maple and black birch fell continually further behind overstory red oak in height and basal area growth. Also, Marquis (1981) observed that understory beech and sugar maple essentially ceased height growth, while the growth of overstory black cherry continued.

The growth of hemlocks in the mixed stands of the present study differed from these patterns. Most hemlocks became overtopped by hardwoods in the sapling stage, but once this occurred, the tallest understory hemlocks (those overtopped by hardwoods but not by other hemlocks) did not continue to fall behind in height growth. Once the rapid juvenile phase of hardwood growth ceased at about 30 years of age, the tallest understory hemlocks kept pace in height growth for a 50-year period. Also, while basal area growth of these hemlocks was less than that of overstory oaks, it showed steady acceleration in intermediate years (age 30–70 years), even though no release from competition occurred.

These height and basal area growth rates apply to the set of tallest understory hemlocks that are overtopped only by hardwoods. Smaller hemlocks are shaded by adjacent and overtopping hemlocks as well as by hardwoods and are clearly growing much slower (e.g., note the variation in size of hemlocks in Fig. 3). The high growth rates of the tallest understory hemlocks may depend upon the relatively open crowns of red oak and black cherry, as well as the later date of leaf development in spring for red oak, to allow sufficient sunlight to reach their crowns. Hemlock also frequently grows in mixture with northern hardwood species, predominantly beech and sugar maple, which have denser crowns. Growth rates of hemlock may be slower when it occurs in the understory beneath those species.

For the tallest understory hemlocks, further height growth into the upper canopy layers appeared to be limited in part by physical breakage of terminals as they rubbed against the large lateral branches in the lower portions of the overstory hardwood crowns. Wierman and Oliver (1979) similarly observed that height in understory western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) was limited by abrasion of its terminals against lateral branches of overstory Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), leaving hemlocks with broad, flat-topped crowns. A similar relationship may exist for red maple and black birch growing beneath red oak (Oliver 1978). Their descriptions closely parallel the observations made in this study.

Foresters have long recognized the occurrence of abrasion between crowns of adjacent trees, generally in single-species conifer stands (e.g., Tarbox and Reed 1924; Spurr 1964), which causes breakage of lateral branches. However, the potential role of crown abrasion in interspecific competition suggested by the observations described above has generally not been recognized in ecological literature. For example, in a discussion of mechanisms of plant species interactions, Harper (1977) considered many indirect mechanisms (such as one species sheltering predators of a neighboring species) but did not include crown abrasion or physical competition for crown space.

Development of the overstory hemlock component

Hemlocks generally occurred in the overstory only if left as residuals following disturbance. These consisted of both large advance regeneration and older understory trees from the previous stand. The minimum initial height that allowed development into the overstory was approximately 3 m. This height advantage appears sufficient to prevent them from becoming overtopped during the rapid initial growth of the hardwoods.

These hemlocks occurred as emergents only in the early stages. By 30–40 years of age, red oak and black cherry had caught up in height, even to hemlocks that were 7–10 m tall immediately following canopy disturbance. Thus, the canopy had a fairly even upper surface past that age, so that hemlocks were not obvious as an older component.

This kind of stand structure and development is similar to that found in other mixed stands (Marquis 1981), where residuals were principally beech and sugar maple rather than hemlock. This structure may be rather prevalent in second-growth mixed stands, since logging operations often leave understory residuals of shade-tolerant species. In general, it appears that mixed stands arising from sprouts, new germinants, and advance regeneration with a narrow range in size will tend to become more completely stratified, with shade-tolerant species occurring only in the understory; where older shade-tolerant residuals and large advance regeneration are prevalent, canopy stratification will be less distinct and shade-tolerant species will occur in all strata.

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