ABSTRACT

THE DEVELOPMENT AND PRODUCTIVITY OF HEMLOCK-HARDWOOD FORESTS IN SOUTHERN NEW ENGLAND

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1984

Forest stands composed primarily of northern red oak (Quercus rubra), red maple (Acer rubrum), black birch (Betula lenta), and hemlock (Tsuga canadensis) were studied. These had regenerated following a single canopy disturbance caused by logging or windstorms. The development of these stands follows the "initial floristic composition" model of succession--they maintained an even-aged character, even 87 years following disturbance.

Juvenile height growth of the hardwood species was much greater than that of hemlock, and a stratified canopy developed early in stand growth, with hardwoods forming an overstory canopy above hemlock. Hemlocks grew into overstory positions only when present as large advance regeneration (3 m or more in height) at the time of canopy disturbance. The crowns of the larger understory hemlocks reached a short distance into the lower portions of the hardwood crowns, and their height growth was limited in part by breakage of terminal shoots from abrasion against branches of overstory hardwood crowns. These larger understory hemlocks maintained a constant rate of height growth, and a constant to accelerating rate of basal area growth for much of their lives. This vigor contrasts with growth patterns of many tree species in suppressed canopy positions.

Hemlock-hardwood stands of ages 44 and 87 years were found to have greater basal area and aboveground biomass than adjacent hardwood stands of the same age, site conditions, and disturbance histories, but which lacked hemlock. Comparisons with published data showed that the basal area and biomass of pure hemlock stands of similar age and site conditions were also exceeded by that of hemlock-hardwood mixtures. Thus, the mixed stands with two-layered canopies produced greater yields than stands of either the overstory or understory component alone.

The Development and Productivity of Hemlock-Hardwood Forests in Southern New England

A Dissertation

Presented to the Faculty of the Graduate School

of

Yale University

in Candidacy for the Degree of

Doctor of Philosophy

by

Matthew John Kelty

May 1984

PREFACE

Owners and staffs of several forestry establishments generously supplied funding, research and living facilities, access to forest land, and other assistance that made this study possible. The author wishes to thank:

--Mr. Edward C. Childs, the Great Mountain Forest Corporation of Norfolk, Connecticut, and the forestry staff of the Corporation;

--The White Memorial Conservation Center, Inc., of Litchfield, Connecticut, and Mr. Gene F. Marra, Executive Director;

--the faculty and staff of the Harvard Forest, Petersham, Massachusetts, and Dr. Ernest M. Gould, Jr., Acting Director; the author completed the study while in residence at the Harvard Forest, and is grateful for being given full use of office and laboratory facilities during that time.

Financial support throughout graduate studies was provided through a Yale Graduate Fellowship, with additional funding from the Romill Foundation. This support is greatly appreciated.

The author is especially grateful for the continued advice and encouragement of his dissertation advisor, Dr. David M. Smith of Yale University. Other members of the dissertation committee were of great assistance. Dr. Thomas G. Siccama, also of Yale, helped particularly with the study of Catlin Wood, and Dr. Ralph D. Nyland of the the State University of New York at Syracuse provided important critical review of early drafts of the dissertation.

The author also wishes to thank D'Ann Sauer Kelty for preparation of graphics and editorial review of the manuscript, and for intelligent consideration and advice on topics outside her professional field.

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CHAPTER 1

Introduction

OBJECTIVES

Forests on upland sites in southern New England are comprised of stands with great diversity in tree species composition. Consequently, the developmental and successional patterns of these forests are highly complex. The component species, dominated by northern red oak[1], red maple, and in some cases hemlock, exhibit a wide array of growth patterns. Knowledge of each of these patterns, and of their interactions when species grow in direct competition, is required to accurately describe overall stand development and form reliable predictions concerning forest growth.

Considerable research over the past several decades has focused upon the process of regeneration and early stand development in these and similar complex, mixed stands in eastern North America. However, long-term developmental patterns are poorly understood. The structure and growth of these stands appears to differ from that of single-canopied, even-aged stands, typified by plantation monocultures. Lacking appropriate developmental models, the behavior of these stands may appear to be chaotic.

The main hypothesis of this study is that predictable patterns of growth and development do occur in even-aged hemlock-hardwood stands,

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[1]hereafter referred to as "red oak". Common names of plant species are used throughout; scientific names are listed in Appendix 1.

and that these can be explained by the model of the even-aged, stratified mixture as described by Smith (1962, 1982) and Oliver (1981). According to this model, differences among species in height-growth regime and degree of shade tolerance result in stands comprised of separate canopy strata, even though all trees began growth at approximately the same time. This stratification does not remain static. Instead, competitive relationships among species may change with stand age, as different species come to dominate various canopy strata at different times in a rotation. A similar description of the development of canopy structure has been proposed by Halle et al. (1978) in their model of "sylvigenesis" for complex species mixtures in tropical forests.

While previous descriptions (e.g., Braun 1950) of mixed-species forests of eastern North America have incorporated the concept of separate canopy layers composed of different species, few studies have examined the development of canopy structure or the growth and form of individual trees forming these strata. Oliver's (1978) work with red oak in mixed-hardwood stands in southern New England has included these aspects, and forms a basis for the present work.

The nature of biomass production in species mixtures also proves to be more complicated than in single-species stands. Variations in species composition can affect overall stand production, both because of differences in the inherent assimilation efficiencies of the various species, and because of variations in canopy structure that accompany compositional differences. Certain species combinations may prove to be highly productive because differences in growth patterns among the species may decrease competition and allow stands of high density to develop (Assmann 1970, Harper 1977). However, so many combinations of species are possible in these stands that few investigations have been attempted.

Knowledge of the natural processes of forest growth is a necessary basis for the effective silvicultural manipulation of any stand. Silvicultural practice consists of encouraging, limiting, or otherwise controlling the natural course of development. Decisions must be made concerning the kinds of stands that are most productive for defined objectives, and the kinds of treatments that will create these stands. For complex species mixtures, these decisions have often been extrapolated from knowledge of how forest stands of simple composition develop, and are adapted to mixed forests with little knowledge of how well the projections apply.

The study reported herein investigated certain aspects of the natural course of stand development and production in hemlock-hardwood mixtures which originated following large-scale natural or artificial canopy disturbance, but which had received no subsequent treatment. Objectives included:

1. assessment of the composition and canopy structure of such stands of various ages (Chapters 2, 3, and 4);
2. reconstruction of growth rates of individual hemlock, red oak, and black cherry growing in direct competition within one of these stands (Chapter 2);
3. comparison of the productivity of hemlock-hardwood mixtures with that of stands composed of either the hardwood or hemlock component alone (Chapter 5).

A general review of literature concerning composition, development, and production in hemlock-hardwood and related forest stands is contained in this chapter. Additional information from pertinent literature can be found in the introductions of Chapters 2 and 5.

LITERATURE REVIEW

Forest type. The forests that are the focus of this study have been classified as part of the "transition hardwoods-white pine-hemlock" zone (Westveld 1956). These transition stands include species found in both the northern hardwood zone to the north and the central hardwoods to the south, and thus are quite diverse. However, forests on moist, well-drained sites tend to be dominated by two species--red oak and red maple (Spurr 1950, Oliver 1978). Other important species include black birch, paper birch, black cherry, pin cherry, white oak, black oak, white ash, sugar maple, and beech. Additional hardwood species may also be present, but usually in rather small numbers.

The two coniferous species occur sporadically throughout these forests. White pine reaches high densities only on dry, sandy soils or on former agricultural land. Otherwise, it is usually present in small numbers scattered among the hardwoods (Cline and Lockard 1925, Spurr 1950).

Hemlock is completely absent from many of these stands. Studies of old-growth remnants in southern New England (Nichols 1913, Lutz 1928, Bromley 1935, Winer 1955) indicate that hemlock formed a major component of stands on upland sites in the presettlement forest, in mixture with hardwood species and small amounts of white pine. This hemlock-hardwood type is greatly reduced in second- and third-growth forests. For example, on the Yale Forest in northeastern Connecticut, only about 10% of forest area is in hemlock-hardwoods (Meyer and Plusnin 1945); on the Harvard Forest in central Massachusetts, 12% is of this forest type (Spurr 1950). This reduction occurred because hemlock is highly susceptible to damage from fire, and is also slow to become reestablished following elimination by fire or other severe disturbance such as plowing. Thus, it tends to be limited to sites on which the forest may have been cut, even repeatedly, but which had escaped these other disturbances associated with human settlement Raup and Carlson 1941, Winer 1955, Rogers 1978). Additionally, even on sites where other conditions are suitable for hemlock establishment, regeneration can be limited by deer browsing (Behrend et al. 1970, Rogers 1978).

The term "hemlock-hardwood" as used in this study describes stands composed of mixed hardwood species dominated by red oak and red maple, plus an important component of hemlock; these stands may or may not contain white pine as a minor component.

Stand initiation. The composition of a young stand developing after major canopy disturbance depends greatly upon whether advance regeneration had previously developed in the understory and had survived the disturbance (Smith 1982, Halle et al. 1978). In forests of the central New England region, most natural disturbances result from wind during hurricanes and other storms (Henry and Swan 1974, Oliver and Stephens 1977). These tend to destroy the overstory but have little effect upon understory vegetation, although fires that kill understory growth are sometimes associated with large-scale forest blowdown (Henry and Swan 1974). Timber harvesting has generally produced similar effects. Both kinds of disturbance favor species which can survive as advance growth, rather than those that can become established only on exposed sites following fire.

Following overstory destruction, young stands are made up of sprouts from seedlings and stumps, as well as true seedlings of advance-growth species. Those capable of developing from advance regeneration include shade-tolerant species such as hemlock, sugar maple, and beech, which often occur in large numbers in understories. However, even many species of intermediate to rather low shade tolerance can develop effectively from advance regeneration. These include the upland oak species (McKinnon et al. 1935, Sander and Clark 1971), black cherry and red maple (Marquis et al. 1975), and white ash and yellow birch (Richards and Farnsworth 1971, McKinnon et al. 1935).

The species of these forests that often become established on exposed sites following disturbance include black, paper, and gray birch, aspen, black cherry, and pin cherry (McKinnon et al. 1935, Spurr 1956). White pine becomes established on certain seedbeds on exposed sites, as it frequently does on old farm fields, but it can also develop as advance growth.

The size of canopy disturbance can prove important in influencing the number of species that can survive and respond vigorously. Studies of the single-tree selection system, where isolated, mature trees were harvested, have shown that few shade-intolerant species become established in these small gaps, and those that do soon fall behind the growth of more shade-tolerant species (Eyre and Zillgitt 1953, Leak and

Wilson 1958, Bramble and Fix 1980). However, other evidence indicates that the minimum gap size which allows even the most shade-intolerant species to become established and grow vigorously is actually rather small. D. Smith (1973) concluded, based in part upon studies of red oak-red maple-hemlock stands, that openings which are 1 to 2 times the height of the surrounding trees in the smallest dimension are sufficient to allow regeneration and vigorous growth of even the most intolerant species. H. Smith (1977) similarly found that canopy gaps only 45 m in diameter had regeneration density, species composition, and height development similar to that of large clearcuts. When openings are of this size or greater, and advance regeneration is present, a wide variety of species can occur in mixture.

Stand development. The development of mixed-species stands following canopy disturbance has been described by the "initial floristic composition" model of secondary succession (Egler 1954, Connell and Slatyer 1977, Smith 1982). That is, successional changes in vegetation result from different species, all initially present on the site at or soon after the time of disturbance, growing to dominance at different times. This model was proposed as an alternative to that of "relay floristics", in which groups of species are successively replaced by others newly arrived on the site. The latter model appears to be more important following severe disturbances, where the site is significantly altered, or at least where advance regeneration as well as overstory trees are destroyed.

An important facet of the initial floristics model is that the vegetation which develops soon after disturbance dominates the site and makes conditions unsuitable for further invasion by new species (Egler 1954, Connell and Slatyer 1977). Thus the stand remains even-aged for an extended period, if age is measured from time of the initiating disturbance. It is in this "stem exclusion" stage (Oliver 1981) that a characteristic forest structure develops.

Certain kinds of stands that follow the initial floristics successional pattern have been described by Smith (1962, 1982) as even-aged, stratified mixtures. The concept of stratification of the forest canopy has previously been employed by ecologists to explain the physiognomy of extremely species-rich tropical stands (Richards 1952, Halle et al. 1978). The main thesis of these descriptions is that the crowns of various species or groups of species occupy different layers in the forest canopy. (See Appendix 10 for further definition of "stratification"). Halle et al. noted that there is often a tendency to exaggerate the stability of such strata, viewing the vertical arrangement of species as fixed through time. They suggested that much important information lies in the study of the changes in canopy structure during stand development. In tropical areas, this must be done primarily from repeated, direct observations of the growth of young stands. In temperate regions, it is also possible to use growth-ring analysis to determine tree age and to reconstruct past growth patterns. Thus, the concept of the even-aged, stratified mixture can serve not just as a structural description, but as a model of development for certain types of forest stands.

Research has supported the occurrence of this pattern of development in some New England forests, where establishment of regeneration was confined to a short period following canopy disturbance. Stands which regenerated following hurricane blowdown of the overstory developed from advance growth, plus pioneer species (primarily pin cherry and black, paper, and gray birch) which became established in the first 3 years after the hurricane (Spurr 1956). Germination after that time did not result in successful establishment. Similar patterns were observed for regeneration which followed clearcutting of old-field white pine stands (McKinnon et al. 1935); these stands reached high density by 5 years of age, creating conditions unsuitable for further seedling establishment. Similar results were obtained in northern hardwood stands which followed clearcutting (Bormann and Likens 1979), and shelterwood cutting (Kelty and Nyland 1981).

In general, rapid juvenile growth occurs in pioneer species, but these generally have a relatively short lifespan. Thus, species such as pin cherry and gray birch may form an upper stratum early in the life of a stand, but slow in height growth and die long before other species (McKinnon et al. 1935, Bormann and Likens 1979). This mortality of pioneer species triggers much of the change in canopy structure during development.

Some species may dominate the upper canopy layer early and maintain that height dominance for long periods. This is true in the interaction between black cherry, beech, and sugar maple in northern hardwood stands in northwest Pennsylvania. When these species arise from clearcutting which leaves only small advance regeneration, black cherry grows most rapidly and develops height dominance over maple and beech in the first years (Marquis 1979). By age 35, the cherry has formed a nearly pure upper canopy with the other two species growing in a separate understory stratum (Marquis 1981). This stratification will likely be maintained as long as the black cherry survives, which can exceed 100 years.

In other species mixtures, the pattern of canopy stratification can change, even without any of the species dying. The change results from an alteration in species height growth rates. For example, Oliver (1978) found that red oak grew in height at rates equal to or somewhat lower than red maple or black birch during the first 20 years following overstory removal. After that point, oak continued rapid height growth, while birch and maple slowed and lapsed into an understory stratum. By reconstructing crown development, Oliver found that as oak grew into the dominant canopy position, lateral crown expansion resulted in the formation of a horizontally continuous canopy stratum above the crowns of the shorter species.

These detailed studies of the development of red oak and its associates did not include hemlock. However, general observations indicate that hemlock characteristically forms an understory layer when growing in mixture with hardwood species (Lutz 1928, Spurr 1950). It is tolerant of shade, and in these forests can exist in the understory for long periods and still respond to release. Most hemlocks which exist today in overstories seem to have initially survived beneath a hardwood canopy, and been released by selective cutting or by small natural canopy disturbances (Merrill and Hawley 1924, Marshall 1927, Oliver and Stephens 1977).

Species composition and stand productivity. Tree species show considerable variation in efficiency of biomass production per unit of land area. Thus, variations in stand composition can have great effects on production. This can most readily be seen in comparison of pure stands of different species, growing on similar sites (Ovington and Pearsall 1956, Assmann 1970). These generally indicate that higher production efficiencies are found in species of greater shade tolerance, although only a few studies have been designed to make this kind of comparison.

If all species in a mixture occupy the same horizontal canopy stratum, the biomass production of the mixture would most likely be less than that of a pure stand of the most efficient species. However, mixed stands with stratified canopies may show different results. Smith (1962) and Assmann (1970) suggested that production in a mixture of a shade-intolerant overstory species plus a shade-tolerant understory species would likely exceed that of a stand of the understory species alone, because the light passing through the overstory foliage would be used in photosynthesis in the understory. Similarly, for New England hemlock-hardwood stands, Lutz (1928) considered that vertical layering in the canopy (and possibly in the rooting stratum as well) would cause reduced competition and increased production over that of hardwood stands alone. On the other hand, the characteristics of shade-tolerant species of maintaining dense canopies and intercepting a high proportion of incoming sunlight indicates that production in pure stands of such species may exceed that of mixtures. However, few data exist to test these hypotheses concerning production in mixed stands compared to pure stands.

CHAPTER 2

Canopy structure and development of even-aged hemlock-hardwood stands

INTRODUCTION

From observations in both plantations and natural stands, a model of development has been established to describe growth patterns in even-aged, single-species stands (Smith 1962, Assmann 1970). Competition is incorporated as the primary factor which controls variation in height growth, crown expansion, basal area growth, and survivorship among individual trees within a stand. As a stand develops, one set of trees gains a dominant position in the canopy, and develops wide, deep crowns, while other trees lapse into subordinate crown positions. As the stand matures, shorter trees with smaller crowns decline progressively in vigor, and lapse further behind in growth compared to trees in upper crown positions. This process is referred to as "differentiation into crown classes"--these classes being qualitative estimates of crown size and relative height.

Ford (1975) described this differentiation process as the formation of a "hierarchy of exploitation," stressing the fact that position in the canopy controls the overall rate of resource utilization and tree growth. Numerous studies have shown that in pure, even-aged stands, a strong relation exists between crown class and stem diameter growth. Thus, as trees differentiate into various crown classes, differences in stem size also progressively increase. In many of these studies, four or more crown classes are recognized (e.g., Ward 1964, Trimble 1969). However, Ford (1975, 1982) observed that bimodal distributions in stem size, measured as either diameter or basal area, were formed in pure Sitka spruce stands, and related this pattern to the development of two classes of trees--those with crowns that reached the upper level of the canopy and received full sunlight from above, and those that survived below that level. Even when more classes are recognized, this basic distinction in tree vigor appears to be of primary importance. For example, Oliver and Murray (1983) found that in young Douglas-fir stands, dominant and codominant trees grew well, whereas trees of intermediate and suppressed crown classes had nearly ceased growth at the size achieved before they had become relegated to the lower crown classes.

The extent to which mixed-species stands develop according to this model is not clearly understood. In the central New England stands studied by Oliver (1978), red oak was consistently found in a dominant canopy position, with red maple and black birch in subordinate positions. Red oak also grew in diameter at greater rates, and the differences among species in height and diameter increased as the stand matured. Thus, the development of these mixed-species stands appears to conform to the model for pure stands described above, but with the important distinction that each species tended to occupy a particular position within the crown canopy.

In this same forest type, hemlock is an important component of some stands, together with the hardwood species discussed above. As a shade-tolerant evergreen conifer, hemlock differs greatly from associated species in growth characteristics. This chapter focuses upon the canopy structure and development of these hemlock-hardwood mixtures. Of particular interest is whether these stands depart from the developmental model commonly used to describe single-species stands, regarding the relationships among crown position, height growth, and basal area growth of individual trees. Two hemlock-hardwood stands of different ages were examined to assess canopy structure and stem diameter distributions. The older one was then studied more intensively through stem dissection techniques to reconstruct the development of small groups of competing survivor trees.

STUDY SITES

One study site was located on the Great Mountain Forest in northwestern Connecticut, and one on the Harvard Forest in central Massachusetts (see Appendix 2 for locations). These stands were selected to have the following characteristics in common: they were both of the red oak-red maple-hemlock forest type, were on 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.

Climate and soils. Climatic conditions of the two sites are similar, as summarized below:

VARIABLE	HARVARD FOREST	GREAT MTN. FOREST
Precipitation (yearly mean--mm)	1120	1260
Number of frost-free days	138	123
Temperature (C)		
yearly mean	7	6
January mean	-6	-7
July mean	19	19
	(Murison 1963)	(Winer 1955)

The site at the Harvard Forest is at 300 m elevation, and has soil classified as Charlton stony fine sandy loam, derived from till of gneiss and schist origin (Simmons 1940). Charlton soils are well-drained, and develop in deep till. Since bedrock outcrops occur within the study stand, it is likely that the general depth to bedrock is less than usual for Charlton soils. Slopes on sample plots varied from level to 10%.

The Great Mountain Forest site is at 460 m elevation. The soil is Hollis extremely rocky, fine sandy loam (U.S. Dept. Agric., Soil Cons. Serv. 1970), a till soil averaging 40 cm to bedrock, also derived from gneiss and schist parent materials. Hollis soils are somewhat excessively drained. Slopes on study plots were level to 10%.

Stand histories. The Harvard Forest site, because of its rocky and uneven terrain, was never cleared for crop or pasture use. Records from the mid-nineteenth 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, white pine, and hemlock. Ages varied from 20 to 90 years, and the presence of stumps testified to its former use as a woodlot. At that time, advance regeneration consisted of hemlock, red oak, sugar maple, white ash, and black birch, in that order of abundance. In September 1938, a hurricane completely destroyed the existing stand. Most timber was salvaged in early 1939; horses were used to extract the logs when there was a light snow cover, so litle additional disturbance was done to the soil surface beyond hurricane effects. Remnants of unsalvaged oak and chestnut logs are still present in the stand, and make it possible to define the limits of the woodlot, since the adjacent, former pasture land contained primarily white pine at the time of the hurricane. The present stand had not received any treatment since its formation.

The Great Mountain Forest stand is in an area where little agricultural development occurred in the nineteenth century. Extensive timber cutting began in the mid-nineteenth century, with clearcutting 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 to a minimum diameter of about 15 cm, resulting in nearly complete clearcutting. The particular stand studied was purchased for charcoal production by the Barnum Richardson Co., an iron company, sometime before 1865, and was sold in 1910 (Winer 1955). Evidence from tree-growth patterns of the present stand suggest that it received some kind of partial cut in the 1870's and was then clearcut in 1895 (this evidence will be discussed below). It has received no treatment since the time of clearcutting.

METHODS

Stand measurements. In both stands, plots were established along a grid system. Eighteen plots were measured in the Great Mountain Forest stand and 10 in the Harvard Forest stand. Because of the differences in stem-size distribution between the stands, different plot measurement methods were used. In the younger (Harvard Forest) stand, circular 0.01 ha plots were established and all trees were measured which were at least 1.3 m in height (breast height). In the older stand, the variable-radius-plot method was employed, using a prism with a basal area factor of 2.3 m^2/ha. All trees that were judged borderline by prism measurement were verified by measuring distance to the tree. All trees detected by the prism were measured, thus limiting data to trees at least 1.3 m tall. In neither stand were there important numbers of trees or shrubs less than 1.3 m in height.

Measurements of diameter at breast height, total height, and height to bottom of living crown were made of all trees on the plots. A subsample was drawn for age measurement by choosing individuals systematically, according to the order in which they appeared on the data sheet. For each tree in the subsample, an increment core was taken as near to the ground as possible, and annual rings were counted to the pith.

Individual-tree growth measurement. From the 18-plot sample in the older stand, 6 groups of 4 trees each were chosen for stem dissection, with each consisting of one dominant red oak, one dominant black cherry, and two understory hemlocks. The six groups were chosen in the following way. Since black cherry was 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, an adjacent red oak, and the two tallest understory hemlocks growing beneath the crowns of either of these two overstory trees.

Additionally, all dominant and codominant hemlocks in the 18-point sample were assigned numbers and 6 of these were chosen using random numbers.

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 2 radii, averaged, and converted to basal area increment. The two radii chosen were geometric mean radii (the square root of the product of maximum and minimum radii of the cross-section).

The upper 5 m of each of the 18 dissected hemlocks was examined, and the occurrence and location of any irregularities in crown form or leader growth pattern were recorded. Seven dominant or codominant hemlocks were felled for other purposes in a nearby stand while this study was being made. Irregularities in crown form and leader growth were also noted for those seven.

Height growth was analysed for all dissected trees according to the methods used in site index studies (Carmean 1972), with one important exception. Data for individual trees were plotted as height versus calendar year rather than height versus tree age. The graphs thus reflect the simultaneous relative heights of groups of competing trees over the life of the stand. See Appendix 3 for further discussion.

A profile diagram of a single 10m x 30m plot in the older stand was constructed following the methods described by Halle *et al*. (1978). The positions of all stems and crowns on this plot were mapped, and height, breast-height diameter, height to bottom of living foliage, and position of major forking of stems were measured for each tree. This information was combined into a vertical profile diagram and crown map.

RESULTS

Stand characteristics. Age distributions of both stands show that most stems reached stump height (0.5 m) shortly before or after the time of canopy disturbance (Figure 1). For the Harvard Forest stand, the hurricane is well documented as having occurred in September 1938. A majority of stems reached 0.5 m during the 5-year period following disturbance, 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 small advance regeneration, which was abundant at the time of overstory destruction--they showed the rapid initial diameter growth which is associated with such an origin.

The time of clearcutting in the Great Mountain Forest stand is not known precisely from historical records. Forty-eight per cent of the stems sampled had a stump age in the 80- and 85-year classes, suggesting that cutting took place shortly before 1900. These included

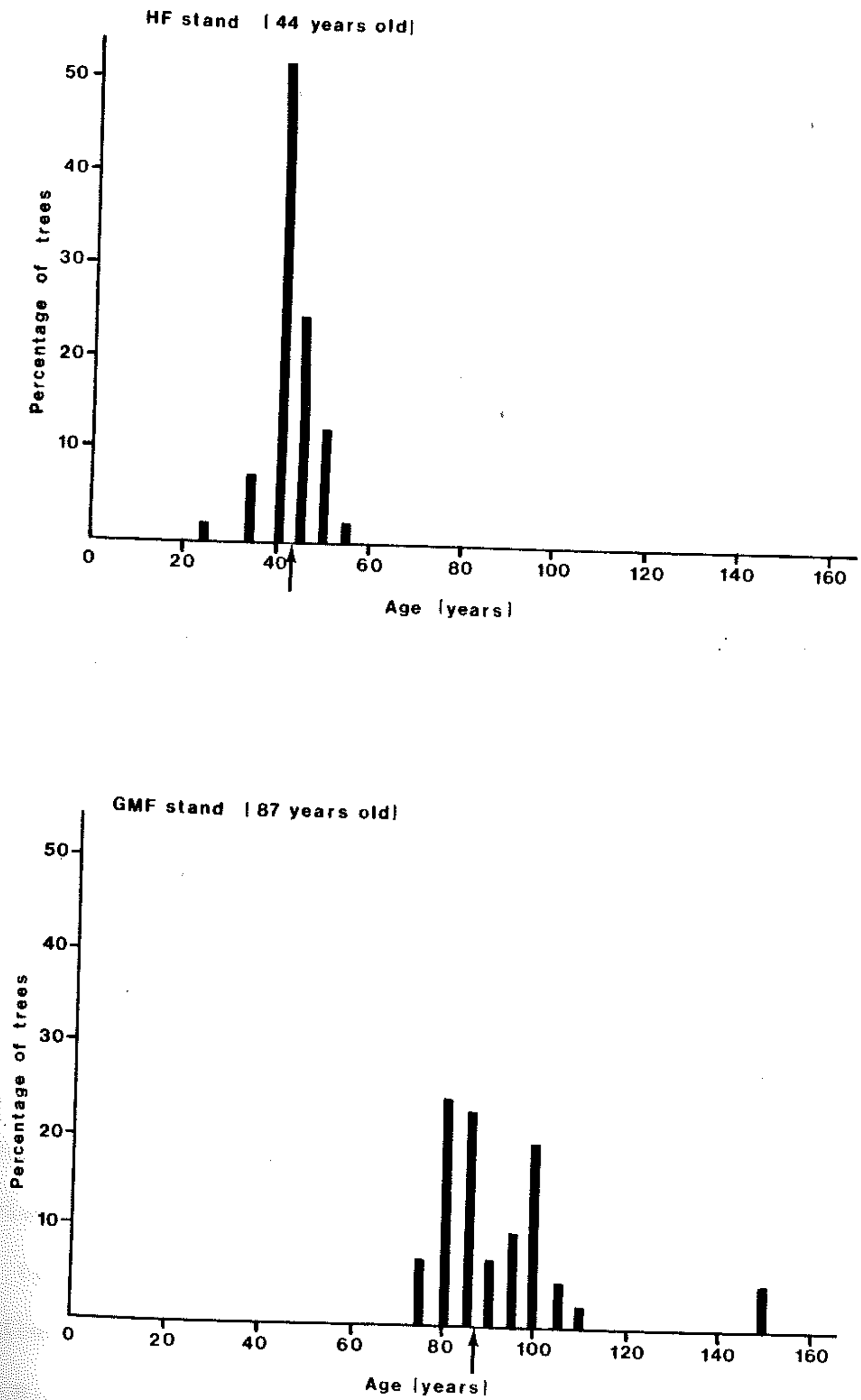


Figure 1. Distribution of ages of sampled trees in Harvard Forest (HF) and Great Mountain Forest (GMF) stands, by 5-year age classes. Arrows denote times of stand-initiating disturbances.

a number of red oak and red maple which originated as multiple sprout clumps. Most others apparently were advance growth and now occur in the 90-, 95-, and 100-year age classes. Diameter growth in these stems increased in 1895, suggesting a release from competition just prior to that time. That date, then, is the probable time of clearcutting. A partial cutting or other minor disturbance may have occurred 15-20 years prior to 1895, allowing establishment of the advance growth. Also present in this stand was a small number of scattered residual hemlocks in the 150-year age class.

No important numbers of trees became established more than 10 years after the disturbances in either stand. Thus, both are considered even-aged, recognizing that some older residual hemlocks occurred in the Great Mountain Forest stand.

Tree density and basal area for each species are shown in Table 1. Hemlock is most numerous in both stands, comprising over 50% of stems. Both are clearly dominated by hemlock, red oak, and red maple; these three species comprise 81% and 90% of basal area of the younger and older stands, respectively.

Height distributions of both stands are shown in Figure 2. In the younger stand, red oak, red maple, black birch, and paper birch occupied the overstory with tallest trees having heights of 12 to 18 m. Fewer trees of these species occurred at lower heights. 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.

In the older stand, red oak and black cherry formed much of the overstory at heights of 16 to 21 m; these species were not found with heights less than 15 m. Hemlock formed a bimodal height distribution

Table 1. Tree density distribution by species and breast-height diameter class in hemlock-hardwood stands; also, distribution of basal area by species. Totals include minor species not listed separately in the tables.

HARVARD FOREST HEMLOCK-HARDWOOD STAND (44 years old)

Diameter class	Hemlock	Red oak	Red maple	Paper birch	Black birch	Total
(cm)	Trees per hectare					
0	80				20	100
5	600	90	90	20	280	1180
10	830	130	180	100	300	1580
15	480	170	60	40	120	930
20	170	180	10		10	370
25	10	40				50
Total	2170	610	340	160	730	4210
Basal area (m^2/ha)	21.5	11.4	2.7	1.4	5.3	43.9

GREAT MOUNTAIN FOREST HEMLOCK-HARDWOOD STAND (87 years old)

Diameter class	Hemlock	Red oak	Red maple	Black cherry	Beech	Total
(cm)	Trees per hectare					
0						0
5	283				64	347
10	127		12		13	153
15	168		88		62	317
20	159	14	40		17	231
25	81	25	27	14	5	153
30	39	36	15	8		100
35	14	38	4	1		57
40	8	34	3	3	1	50
45	5	23		2	1	30
50	3	3		1		7
55	2	2				4
60		1				1
Total	885	176	190	29	164	1450
Basal area (m^2/ha)	20.1	17.3	6.0	2.2	2.5	48.4

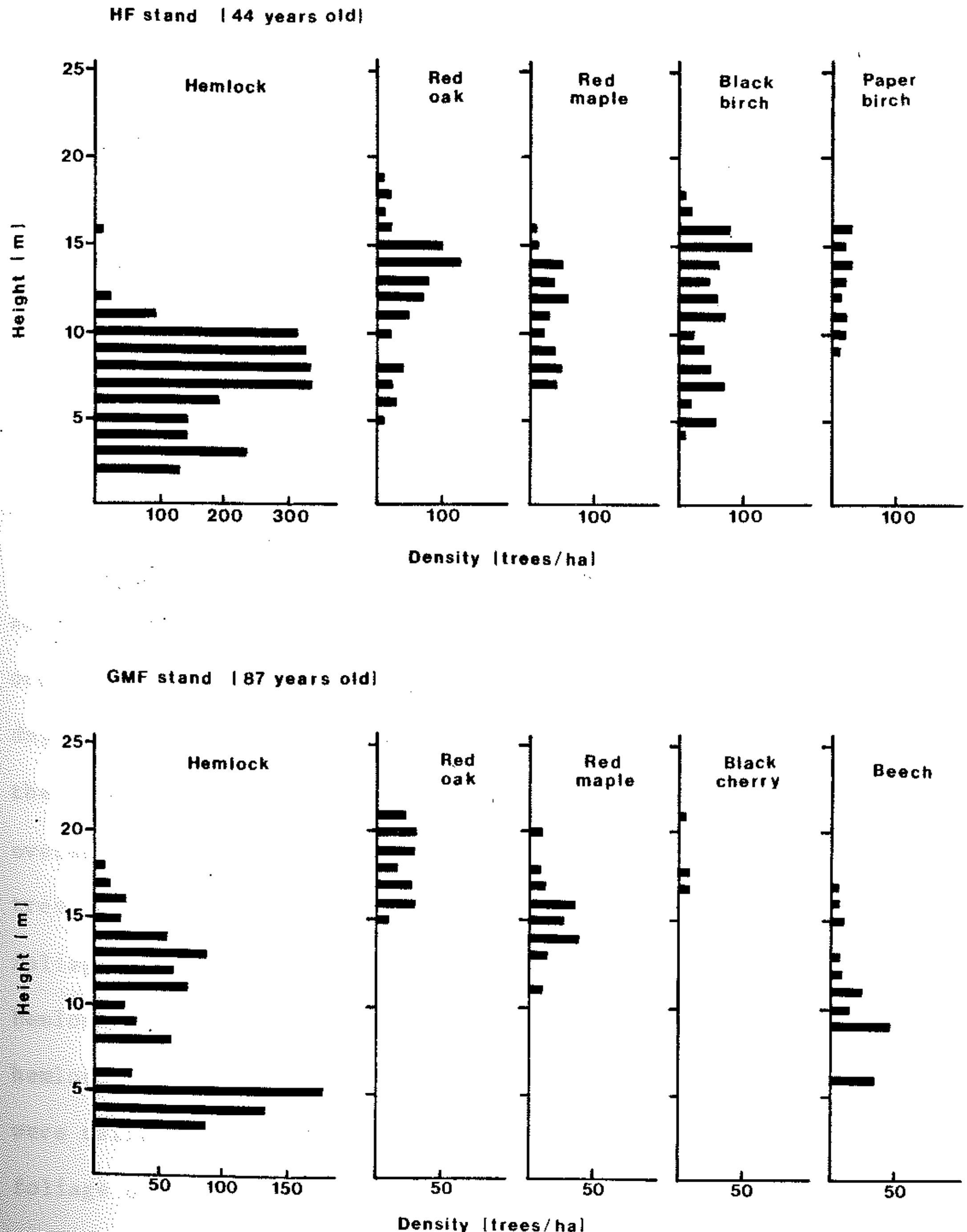


Figure 2. Tree density distributions in Harvard Forest (HF) and Great Mountain Forest (GMF) stands, by species and one-meter height class.

in the understory. One peak occurred from 11 to 14 m and another at 5 m. In this stand, a number of hemlocks occurred in the overstory stratum at heights of 16 m and taller. Some beech was present, primarily at lower heights, and most red maple occupied an intermediate position in the height distribution, although some occurred in the upper stratum with oak and cherry.

Table 2 summarizes the difference between these two stands with regard to representation of hemlock in the overstory stratum. In the younger stand, only about 1% of the overstory was made up of hemlock, whereas the older stand overstory included 18% by number and 20% by basal area of hemlock.

These data indicate that, in terms of total tree height, different species tended to occur more frequently in specific canopy strata. In order to better assess how foliage was vertically distributed, the depth of foliage of each tree crown was measured. Figure 3 compares the height to the bottom of living foliage for red oak, the major overstory species, to the top of foliage for hemlocks (i.e., the total tree height of hemlock). In both stands, the bottom of overstory oak foliage is overlapped by the upper crowns of hemlock. So, while most hemlocks were shorter than the oaks, the tallest of the understory hemlock reached at least to the bottom the red oak crowns, and some were taller than the lower portions of the oak crowns. Thus, the foliage of the two species tended to occupy two distinct strata, but with a transition zone of several meters where the crowns of the two species overlap.

With some exceptions, stem diameters reflected the canopy positions of the various species (Table 1). In the younger stand, red

Table 2. Proportion of overstory stratum composed of hemlock in Harvard Forest and Great Mountain Forest stands.

	Density #/ha	Basal area m^2/ha
HARVARD FOREST (44 years old)		
Total overstory	940	16.3
Hemlock in overstory	10	$<$ 0.1
Percent of overstory composed of hemlock	1%	$<$ 1%
GREAT MOUNTAIN FOREST (87 years old)		
Total overstory	276	24.2
Hemlock in overstory	50	4.8
Percent of overstory composed of hemlock	18%	20%

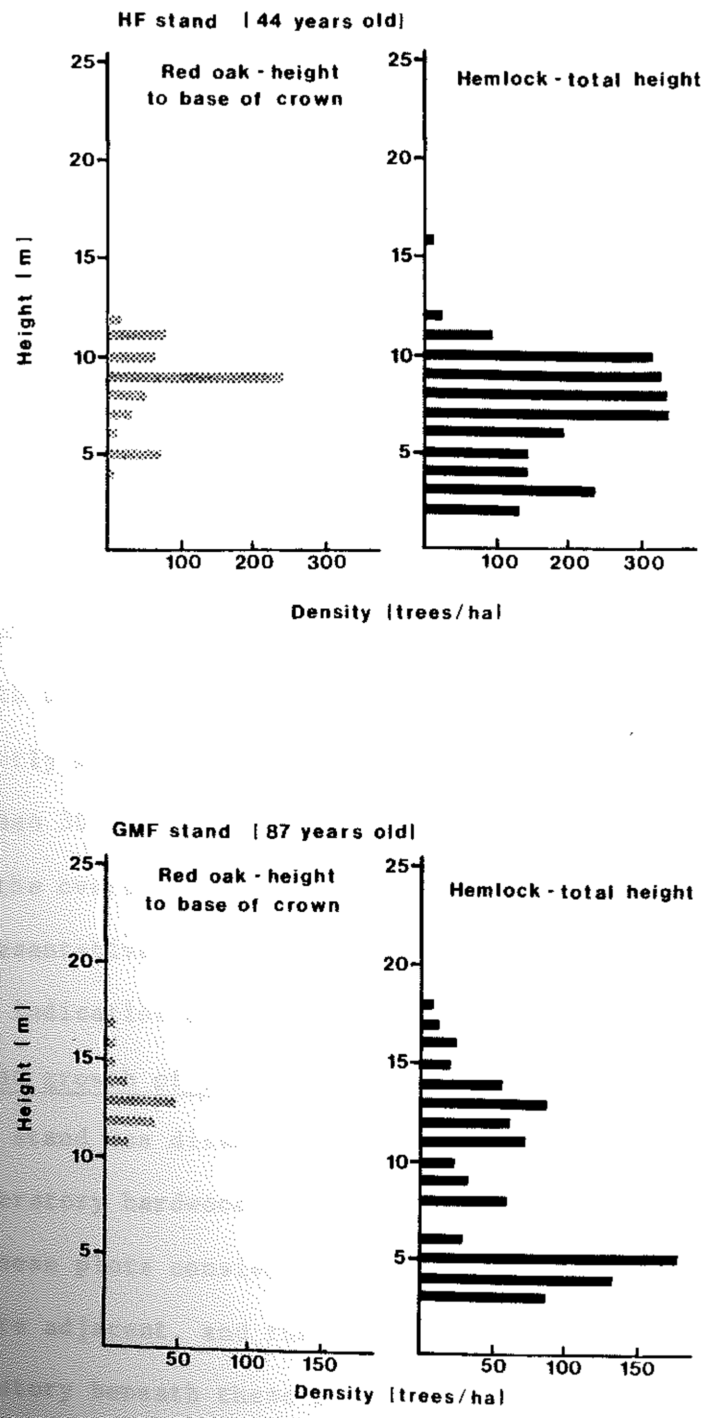


Figure 3. Tree density distributions of height to bottom of red oak crowns, compared to total height of hemlocks, in Harvard (HF) and Great Mountain Forest (GMF) stands, by one-meter height classes.

oak occurred in the larger diameter classes, disproportionate to its total numbers; it comprised only 14% of all stems, but 52% of all stems 20 cm and larger. Most other stems of this size were hemlock, although 92% of all hemlocks were less than 20 cm diameter. Although many paper birch, black birch, and red maple occupied the upper canopy with red oak, few had grown into the larger diameter classes. Most of these species were in the 5-15 cm diameter classes together with the majority of hemlock.

In the older stand, red oak again occurred primarily in the larger diameter classes, comprising 49% of all stems 30 cm and larger, but only 12% of total stem numbers. Most hemlock occurred at smaller sizes, with 65% of hemlocks still only 5 to 15 cm in diameter. The predominantly middle-stratum red maple and beech also had few trees greater than 30 cm in diameter. However, 48% of black cherry, which occupied the overstory with red oak, was at least 30 cm dbh.

Representative views of the two stands are shown in Figure 4, giving an indication of stand density and stem sizes.

Height growth of individual trees. Each of 4 trees on 6 plots in the older stand was dissected to reconstruct the relative height growth of the overstory hardwood species compared to the hemlock understory. Each of these plots consisted of a red oak and black cherry whose crowns were adjacent, and the two tallest of the overtopped hemlocks in the understory beneath these trees. The results of stem dissections for one of these plots is given in Figure 5, to show the range of growth patterns that occurred. In this plot, the oak originated as a sprout soon after cutting. One of the understory hemlocks apparently was a young seedling at this time. The second hemlock and the black

Figure 4. Views of the two study stands. Clipboard (23 x 30 cm) for scale.

a. Harvard Forest 44-year-old stand. Arrow indicates overstory red oak. Other species present in foreground include hemlock, paper birch, black birch, and red maple. An oak blown down by the 1938 hurricane is visible in right foreground.

b. Great Mountain Forest 87-year-old stand. Arrows indicate two overstory red oaks. All other trees in foreground are understory hemlocks which are overtopped by these two red oak.

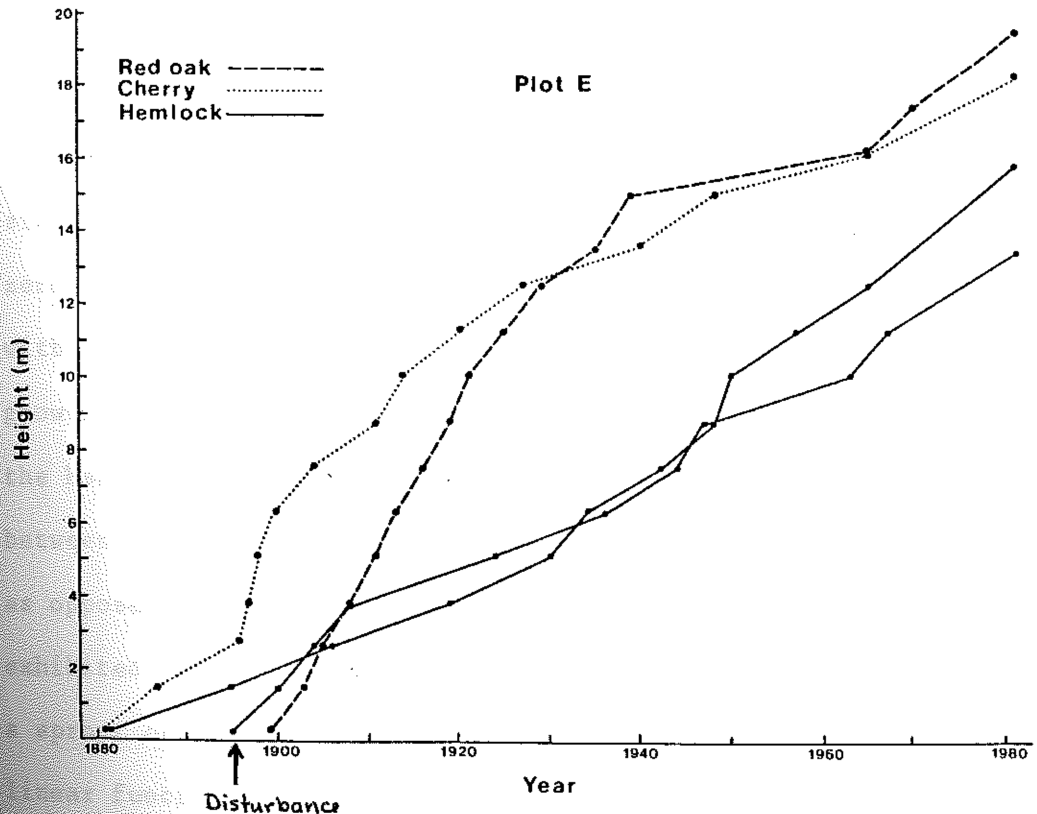


Figure 5. Cumulative height growth of a single four-tree plot of overstory red oak and black cherry and understory hemlock in 87-year-old Great Mountain Forest stand. Arrow denotes time of stand-initiating disturbance.

cherry were saplings at the time of cutting, having originated shortly before 1880. The black cherry clearly shows a height growth response to the 1895 cutting. Regardless of these differences in size at the time of disturbance, both hardwoods soon had crowns within the overstory canopy layer and were of comparable height from 1930 on. Both hemlocks grew more slowly, and lapsed into understory positions. Results from each of the six plots are shown in Appendix 4.

Figure 6 shows the graphs of average height over stand age for the six plots combined, beginning in 1895 (considered as stand age of zero). The hardwoods exhibit a two-phase pattern of height growth, with fast initial growth for 30 years, followed by a slower height growth rate thereafter. Two linear functions were fitted to each of the hardwood species growth curves, using age 30 as the breaking point between the two phases. The linear pattern of juvenile height growth, as opposed to the initial phase of the kind of sigmoidal curve exhibited by many species, is commonly observed in oaks, and indicates a sprout origin (Carmean 1972). For the understory hemlock, a single linear function was fit 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), but this accounts only for the shape of the average height-age curve, not the variation in the original data (see Appendix 3 for explanation of calculations). The total variation is reflected in the estimates of standard error given in Figure 6.

The slopes of the regression lines are given below, representing average growth rates in meters per year.

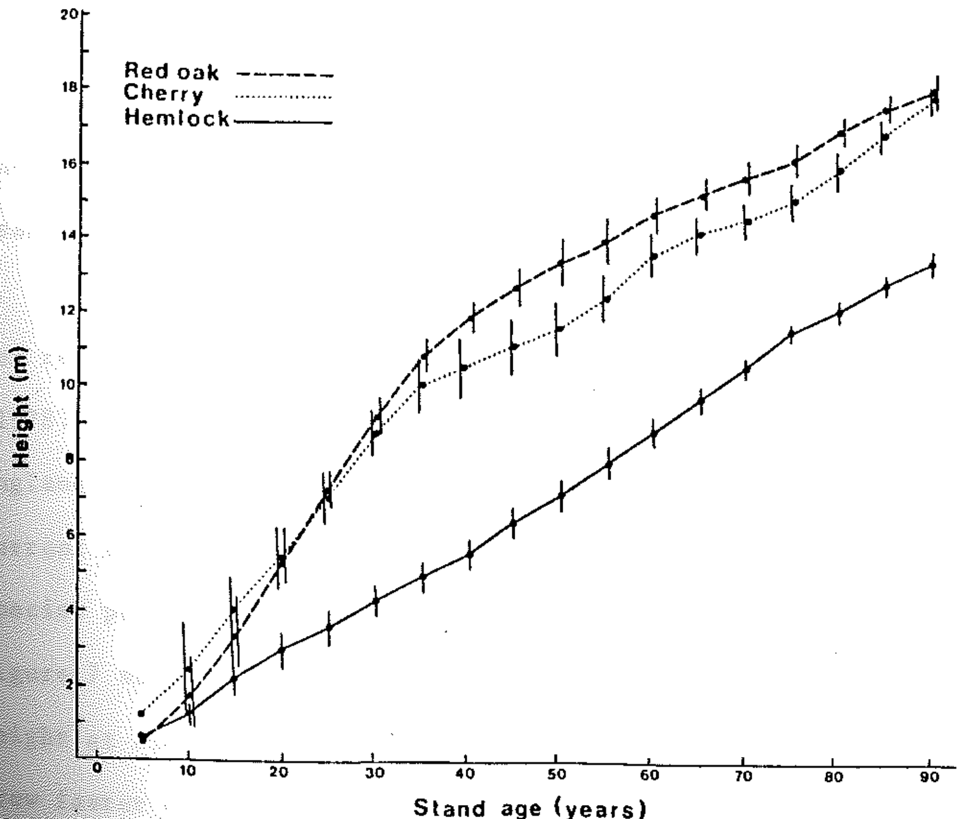


Figure 6. Average cumulative height growth of trees growing in direct competition--from six four-tree plots of overstory red oak and black cherry and understory hemlock in 87-year-old Great Mountain Forest stand. Vertical lines show ±1 standard error.

Species	Stand age (years)	
	(0-30)	(31-87)
Red oak	.35	.12
Black cherry	.30	.14
Hemlock	------.16-------	

During the first 30 years of stand growth, 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.

For purposes of comparison, Figure 7 shows average height growth for red oak, black birch, and red maple, taken from the study of Oliver (1978) of certain mixed-hardwood stands also growing in central New England. These sample trees were selected in the same way as for the current study--the birch and maple were the tallest individuals of each species present that were growing in the understory beneath the oaks. Figure 7 shows that, in this interaction, all three species grew in height at similar rates for about 15 years. Oak and black birch then grew faster than maple until about age 25, when height growth of birch slowed. The height advantage of oak over both species progressively increased thereafter.

Basal area growth of individual trees. Figure 8 shows the average basal area growth for the dissected overstory red oak and understory hemlock from the Great Mountain Forest stand. Similarly, in Figure 9, average basal area growth of overstory red oak and understory black birch and red maple is shown, calculated from data reported by Oliver (1978).

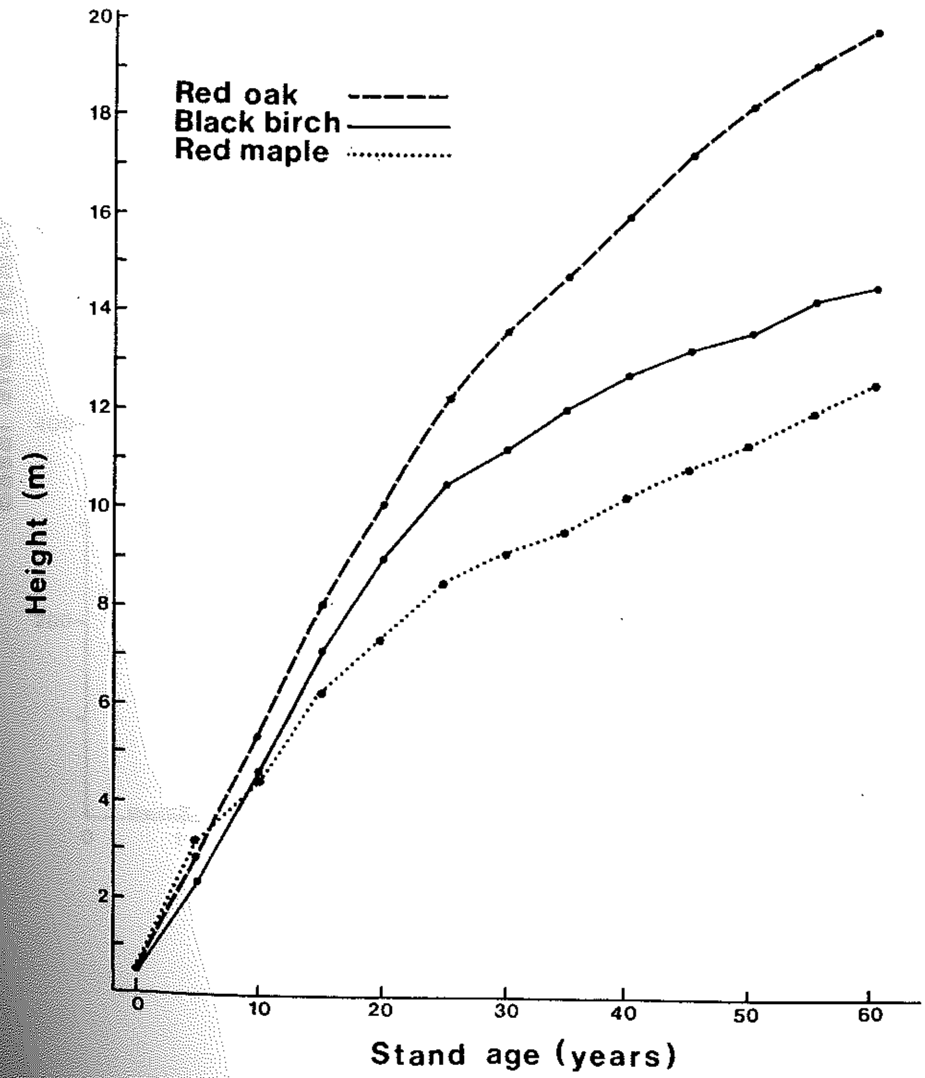


Figure 7. Average cumulative height growth of trees growing in direct competition--overstory red oak and understory black birch and red maple from 60-year-old mixed hardwood stands, from Oliver (1978).

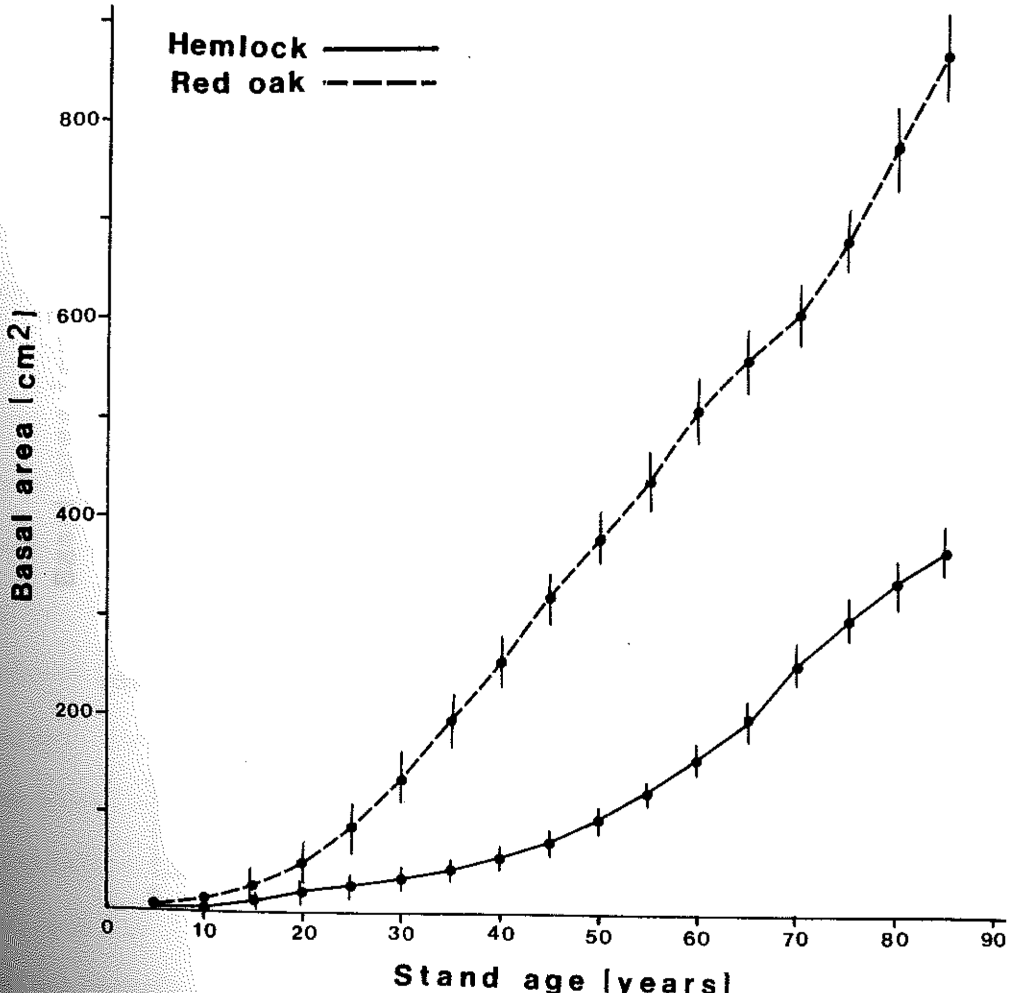


Figure 8. Average cumulative basal area growth of individual trees growing in direct competition--overstory red oak and understory hemlock from 87-year-old Great Mountain Forest stand. Vertical lines show ± 1 standard error unit.

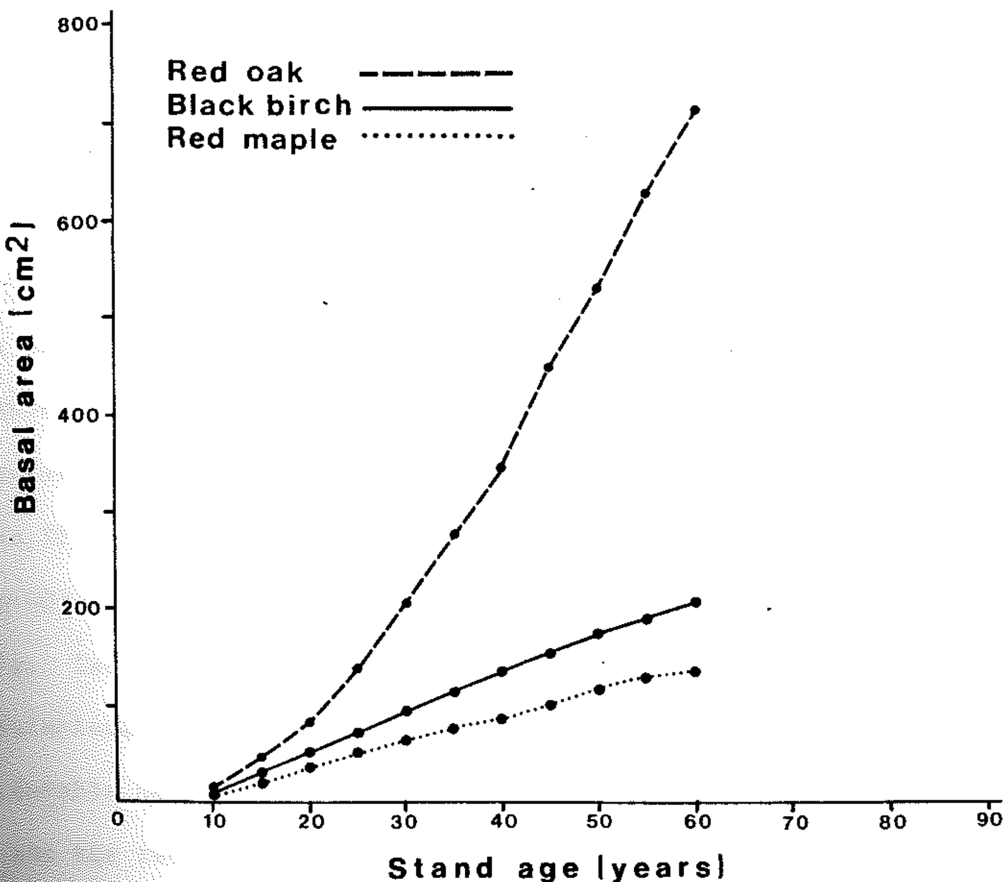


Figure 9. Average cumulative basal area growth of individual trees growing in direct competition--overstory red oak and understory black birch and red maple from 60-year-old mixed-hardwood stands, from data of Oliver (1978).

In both kinds of stands, overstory oak showed no sign of approaching an asymptote in basal area growth. Following an initial 20-year period of slow growth, oak had a constant to slightly accelerating growth rate, even to age 85 in the hemlock-hardwood stand. In Figure 9, the overtopped red maple and black birch both showed a constant, low rate of basal area increase throughout the 60 years of growth. In contrast, basal area growth of understory hemlock started slowly, but then gradually accelerated from age 40 to 70 years. The growth rate past that age showed only a slight decrease.

Growth of overstory hemlock. Height distributions from the entire Great Mountain Forest stand indicated that 18% of the trees in the overstory were hemlock (Table 2). Six of these overstory hemlocks were dissected, and reconstructions of their height growth are given in Figure 10. Three (H, L, M) of these six were of the same age cohort (1870-80) as many of the understory hemlock and some of the oak and cherry. Two (I, J) of the six were much older, dating from 1830. A characteristic that these five trees had in common was that all were of considerable height at the time of the 1895 disturbance; all were above 3 m, and the two older trees were above 7 m in height. None of the hemlock sample trees that eventually lapsed into the understory had been taller than 1.5 m at the time of cutting.

One (K) of the six overstory hemlocks was a small advance-growth seedling in 1895. The growth of this tree indicates that it was possible for a hemlock to reach overstory height (a height equivalent to that of the dominant hardwoods) though starting as a small seedling at the time of disturbance. This tree was growing in an area where the seedbed was very rocky, and no hardwood tree or remnants of dead

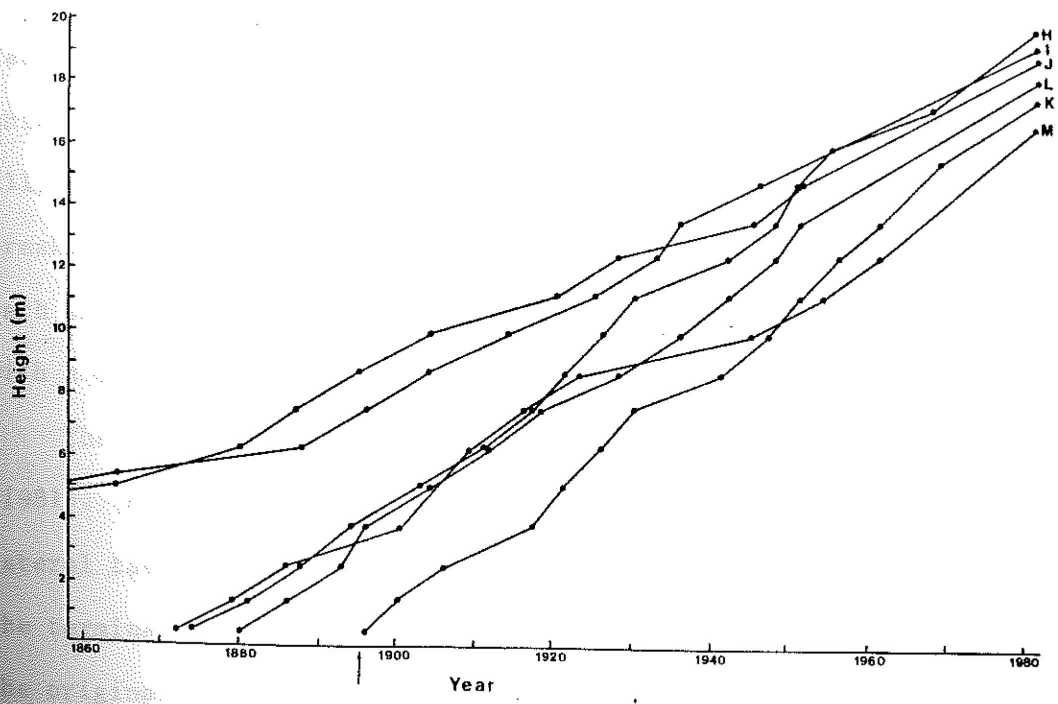


Figure 10. Cumulative height growth of six overstory hemlocks in 87-year-old Great Mountain Forest stand. Arrow denotes time of stand-initiating disturbance.

hardwoods were visible. Such a pattern of height growth probably represents that of a hemlock developing free of hardwood competition.

Hemlock crown abrasion. During stem dissections, it was observed that terminal shoots of many 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. Table 3 shows the frequency of occurrence. These data suggest that this phenomenon was unique to trees in the understory position. In all, among the 12 understory hemlocks sampled, 21 instances of terminal breakage were observed, with numbers of laterals growing vertically in each instance ranging 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 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 first through third year of growth); the original leader may remain alive but take a lateral growth position, or may be killed. Since these occurrences involve fine twigs, 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 in the stand studied here has resulted in an enduring change in crown growth. Overstory hemlocks exhibited a conical crown form, with a single central stem. Among understory hemlocks, a profusion of lateral branches competing for dominance

Table 3. Frequency of terminal shoot breakage in hemlocks in 87-year-old Great Mountain Forest stand. Overstory hemlocks averaged 18 m in total height; understory hemlocks averaged 14 m. Understory hemlocks were overtopped by crowns of red oak or black cherry, but not by other hemlocks.

	Overstory hemlocks	Understory hemlocks
Number of trees in sample	13	12
Number with at least one break in terminal	0 (0%)	11 (92%)
Number with more than one break in terminal	0 (0%)	6 (50%)

following leader breakage resulted in flat-topped crowns, in some cases leaving trees with no identifiable central stem in the upper portions of the crown (Figure 11). The broken terminals of these trees are shown in Figure 12.

Development of canopy structure. In order to depict the structural development of the 87-year-old hemlock-hardwood stand, the height growth patterns of the individual plots have been translated into a composite forest profile (Figure 13), following methods of Oliver (1978). The 1895 profile shows the heights of residual stems left after cutting. Stems not shown for 1895 were those that sprouted from stumps or had been seedlings less than 0.5 m at that time. The 1905 profile for plots A to F show that, after 10 years of growth, no clear pattern of height differentiation among species had occurred for trees that survived to 1982. Some hemlocks were taller than associated hardwoods, and there was considerable variation in height among hardwoods. This mainly reflected the size of advance growth in 1895. However, because of their fast initial growth, hardwoods were in tallest positions by 1935, and hemlocks in plots A-F had fallen far behind, some being less than one-half the height of competing hardwoods. The 1981 profile shows that during the next 46 years, the understory hemlocks kept pace with overstory height growth. The terminals of many of these hemlocks grew into the bottoms of the umbrella-shaped layer of foliage of the oak and cherry trees.

In 1895, the hemlocks left as larger residuals during cutting (plots H-M) were as tall or taller than advance-growth hardwoods (plots A-F). By 1935 the hardwoods had caught up with these hemlocks, and

Figure 11. Upper sections of four hemlock trees from 87-year-old Great Mountain Forest stand. Foliage has been removed to reveal branch structure. Scale pole is marked at one-half-meter intervals.

a & b. Overstory hemlocks, with conical crown form and single central stem.

c & d. Understory hemlocks, with flat-topped crowns, and in c., with no identifiable central stem. Numbered arrows point out terminal and lateral breakage shown in enlargements in Figure 12.

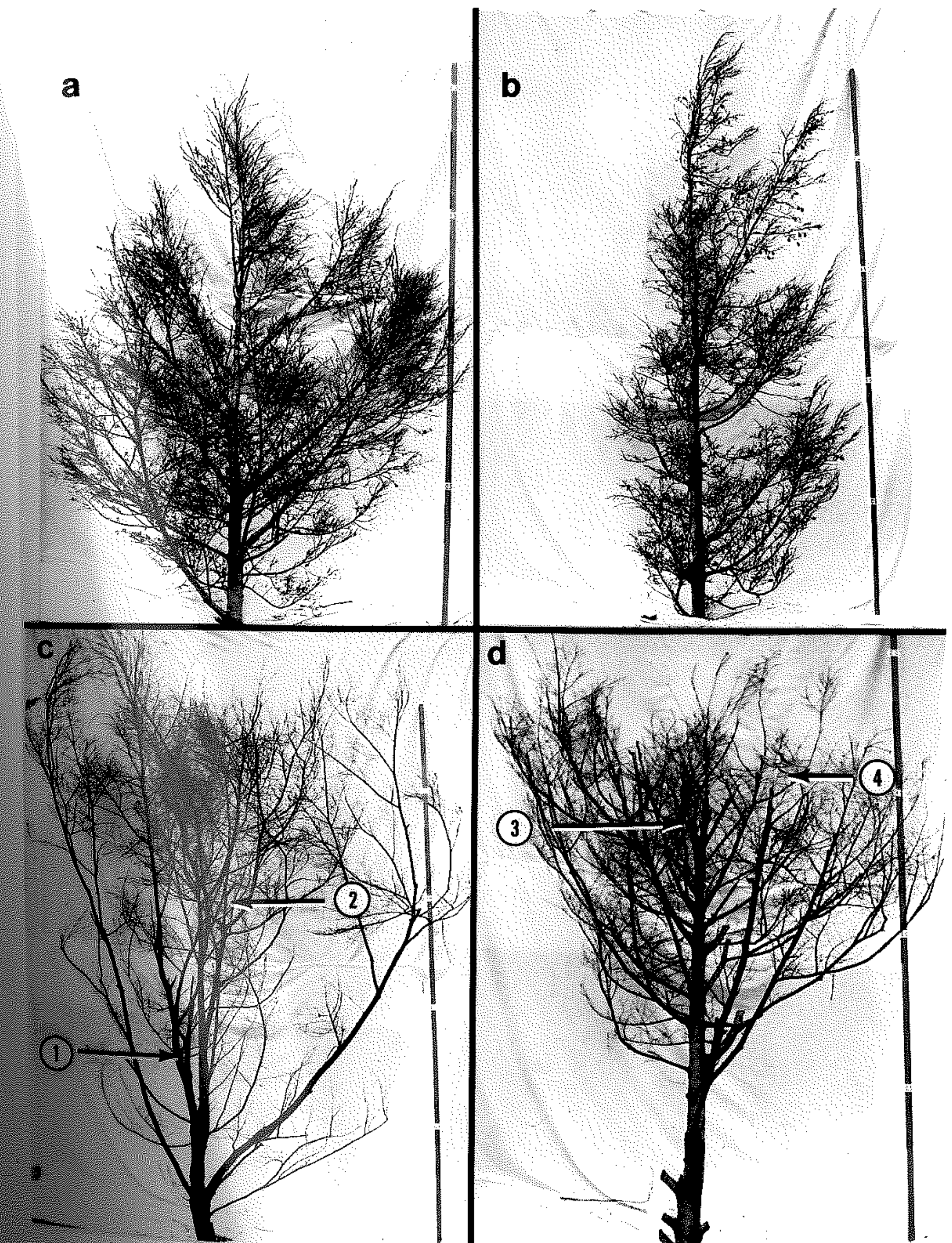


Figure 12. Stem breakage in the understory hemlocks shown in Figure 11c and d. Numbered arrows in this figure correspond to those in Figure 11.

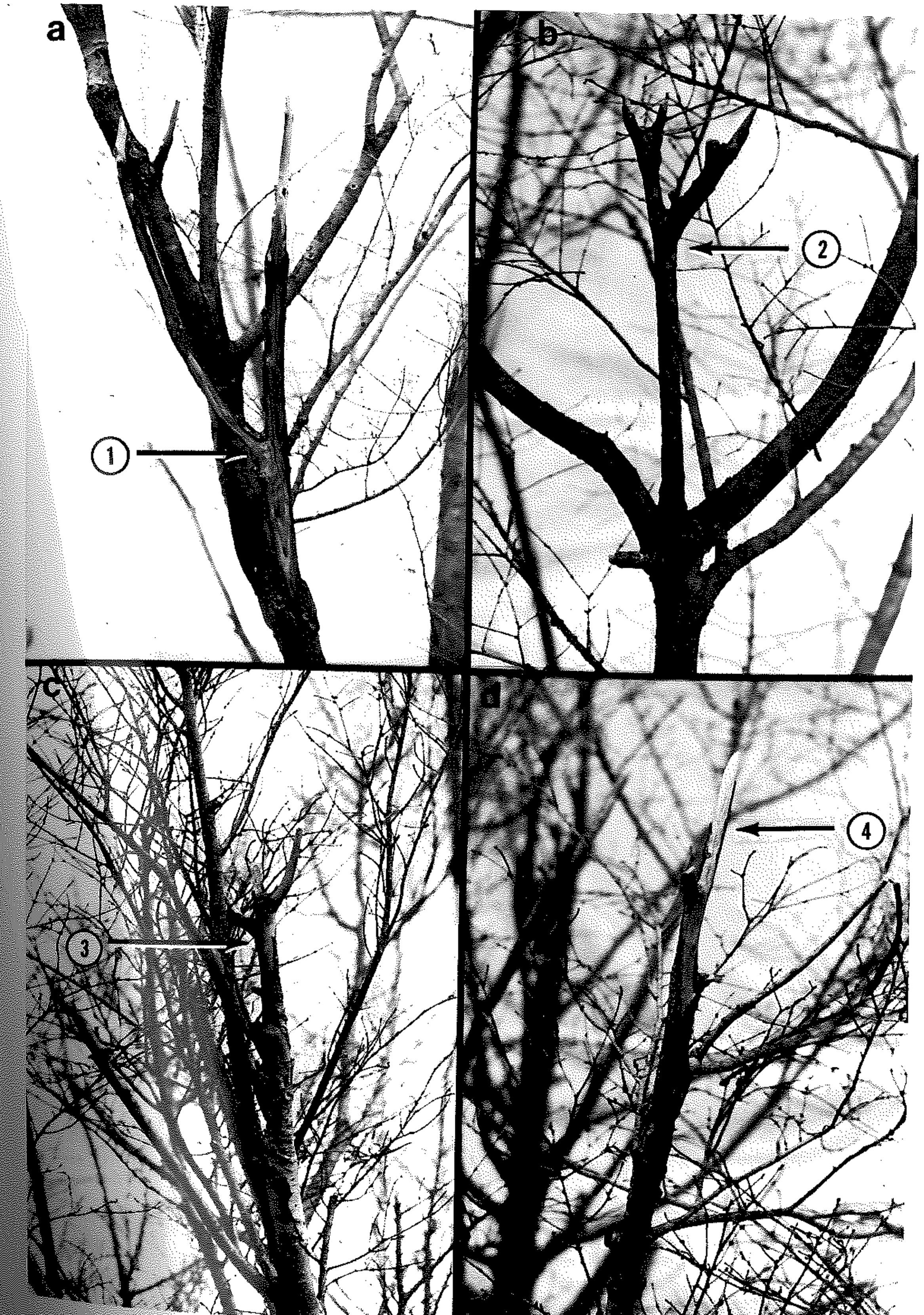
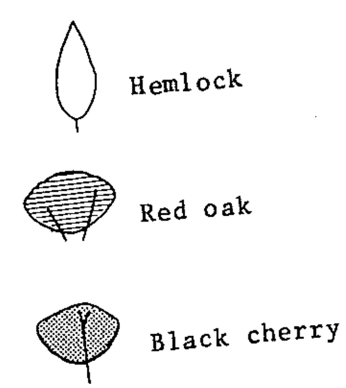
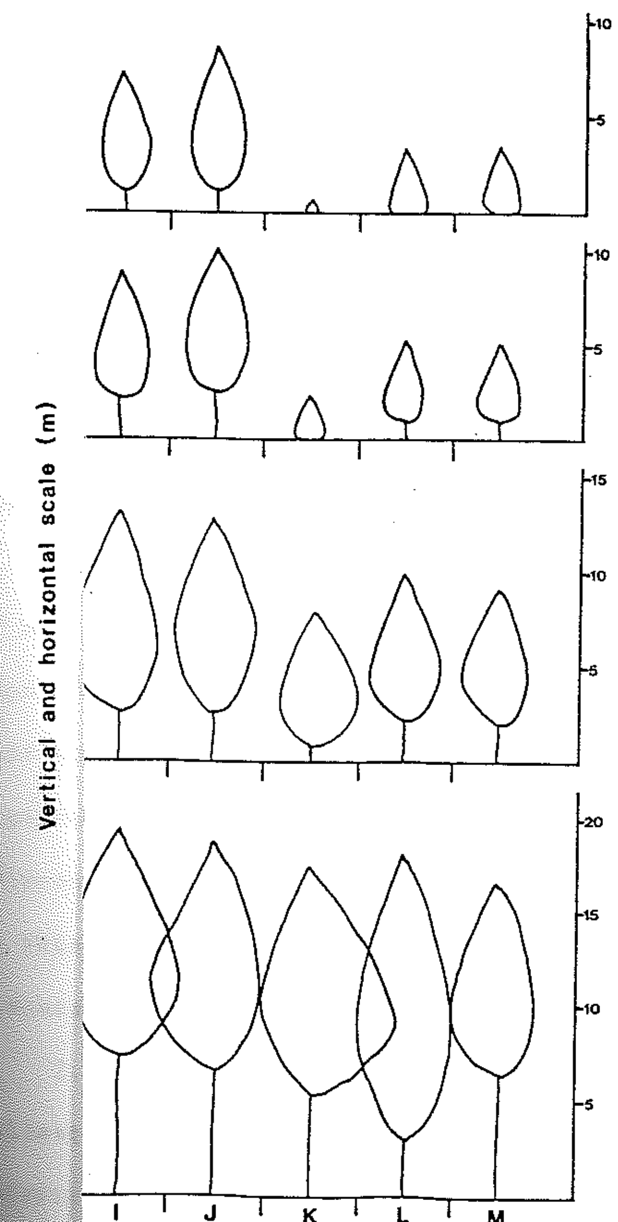


Figure 13. Composite forest profile of twelve plots from 87-year-old Great Mountain Forest stand. Plots A-F each consisted of an overstory red oak, an adjacent overstory black cherry, and the two tallest understory hemlocks growing beneath the oak and cherry. Plots H-M each consisted of a single overstory hemlock. Plots were not adjacent to one another as drawn in the figure, but were intermixed throughout the stand.

In the 1981 profile, the height, crown width, crown depth, branching pattern, and spatial arrangement of trees within each plot are drawn to scale. In other profiles, height is based upon stem-dissection measurements, and crown dimensions are based upon average dimensions of trees of similar ages measured at the Harvard Forest and Great Mountain Forest.





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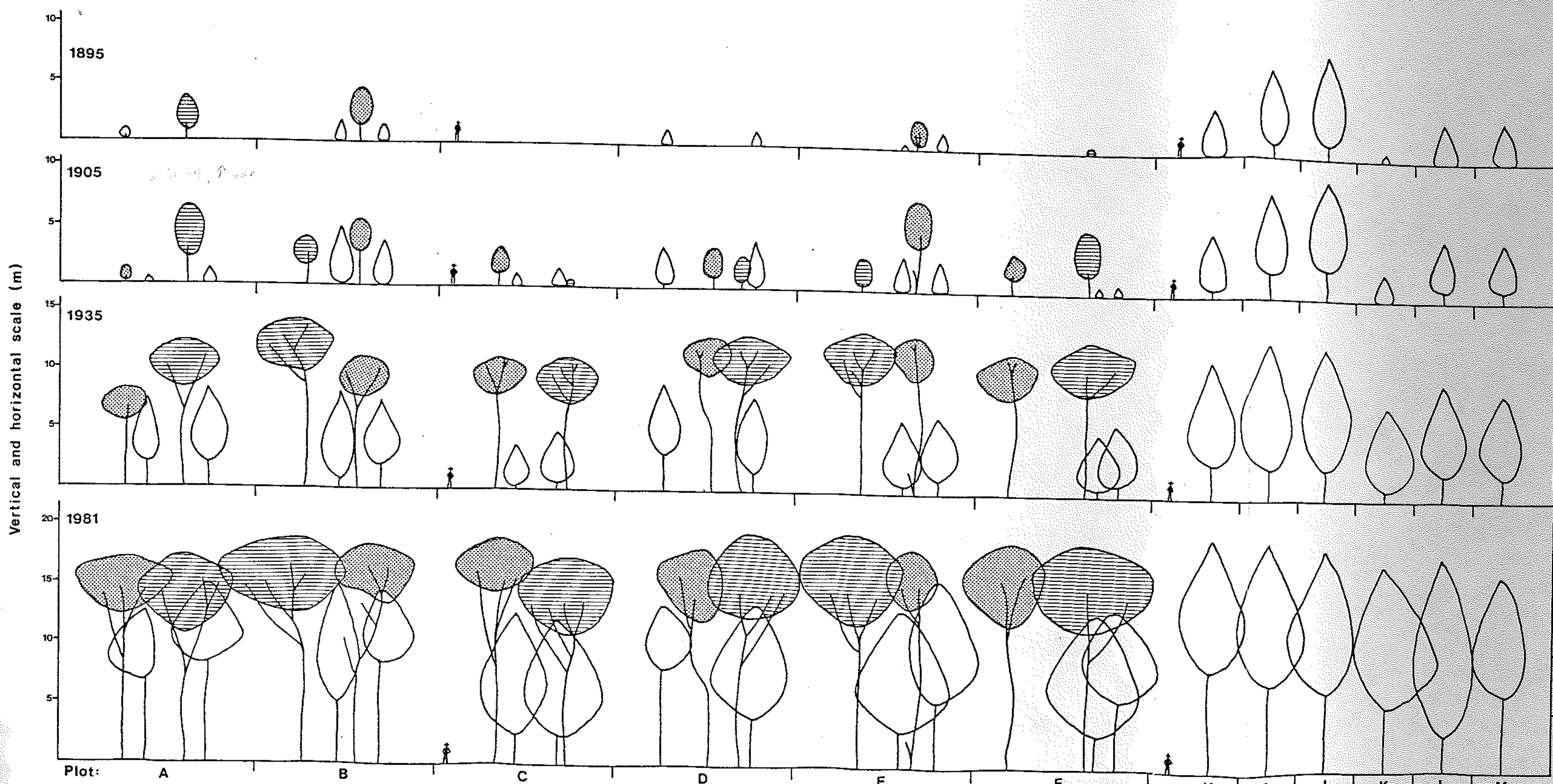

1895
1905
1935
1981
Vertical and horizontal scale (m)
Plot:
A
B
C
D
E
F
H
I
J
K
L
M

subsequently tended to occupy the same canopy position as these isolated overstory hemlocks.

The reconstruction of stand growth in Figure 13 shows only the trees selected for stem dissection; many others were present on these plots as well. In order to depict total canopy structure, a plot profile was constructed following the methods developed to describe tropical forests (Richards 1952, Halle _et al_. 1978). This profile includes all stems within a 10m x 30m plot (an extension of plot D of Figure 13). The profile is diagrammed in Figure 14, as is a map of all stems and crowns. These include all trees living in 1981.

This profile illustrates several aspects of structure described quantitatively by methods presented earlier:

1. The tallest hemlocks reach to the lower portion of the crowns of overstory red oak and black cherry. In this profile, the one exception is the hemlock farthest to the left; although much of the crown of this tree is overtopped by portions of several hardwood crowns (see Figures 14b and c), the terminal is growing unsuppressed in a small gap between the hardwoods. No hemlocks occupied a clear overstory position in this profile, although they did occur elsewhere in the stand, as discussed previously.

2. Red maple also occurs in the understory stratum with the tallest hemlocks. In this profile, one of the two beech present is intermediate between the two strata, although most beech in the stand were also in the understory.

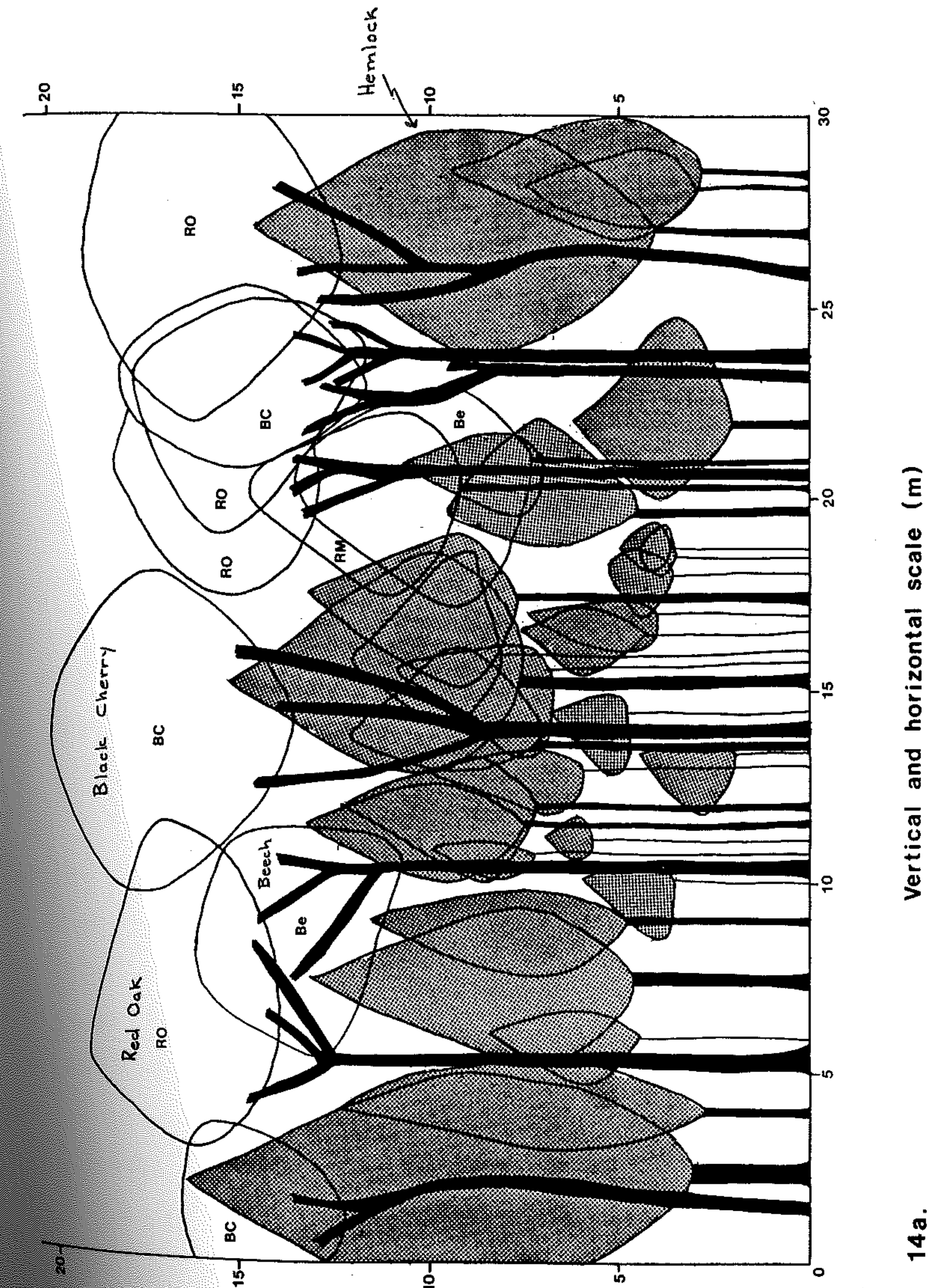
3. Where the understory stratum is crowded, as in the center of the plot, there is an additional set of even shorter hemlocks growing beneath the crowns of the taller hemlock, red maple, and beech. The

Figure 14a. Profile diagram of 10 x 30 m plot in 87-year-old Great Mountain Forest stand. Tree height, stem diameter, crown dimensions, and position of major branches are drawn to scale, based directly upon measurements.

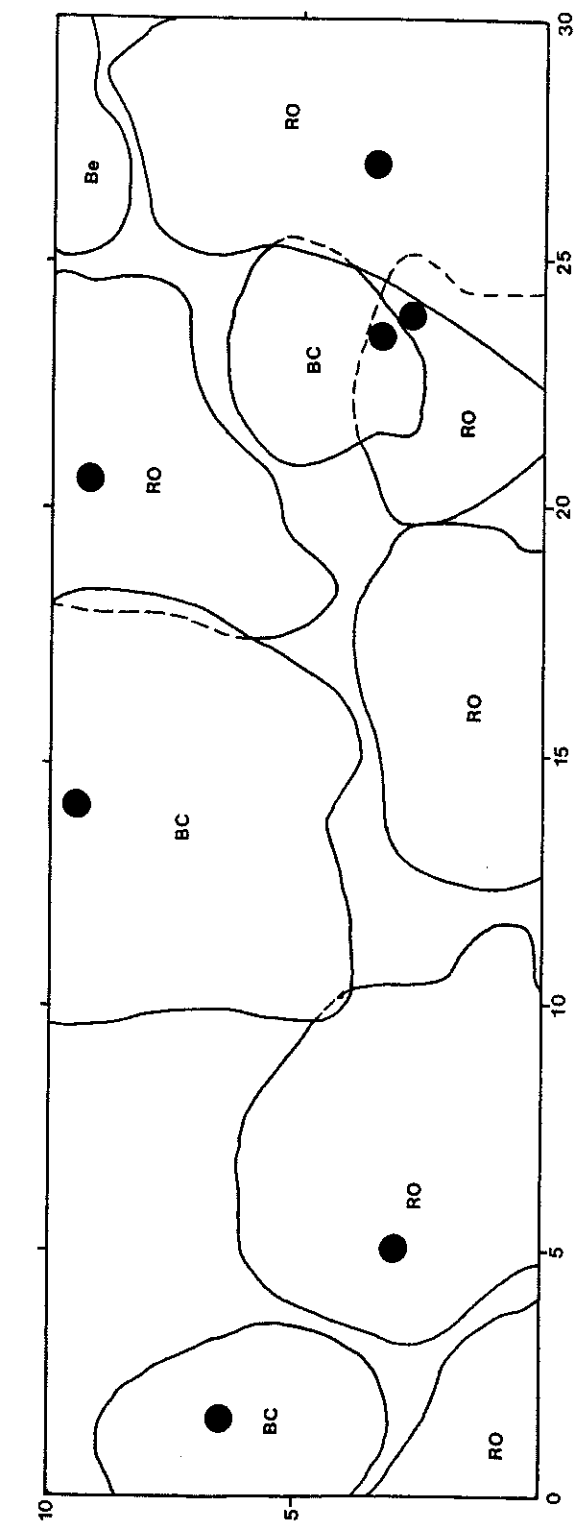
14b. Crown and stem map of overstory stratum.

14c. Crown and stem map of understory stratum.

Two trees in this plot--the left-most hemlock and the left-most beech--are in intermediate crown positions. Crowns of these two are largely, but not entirely, overtopped by adjacent trees. They are included in the understory stratum in 14c. No hemlocks occupied clear overstory positions in this plot, although they did elsewhere in the stand.



14a.



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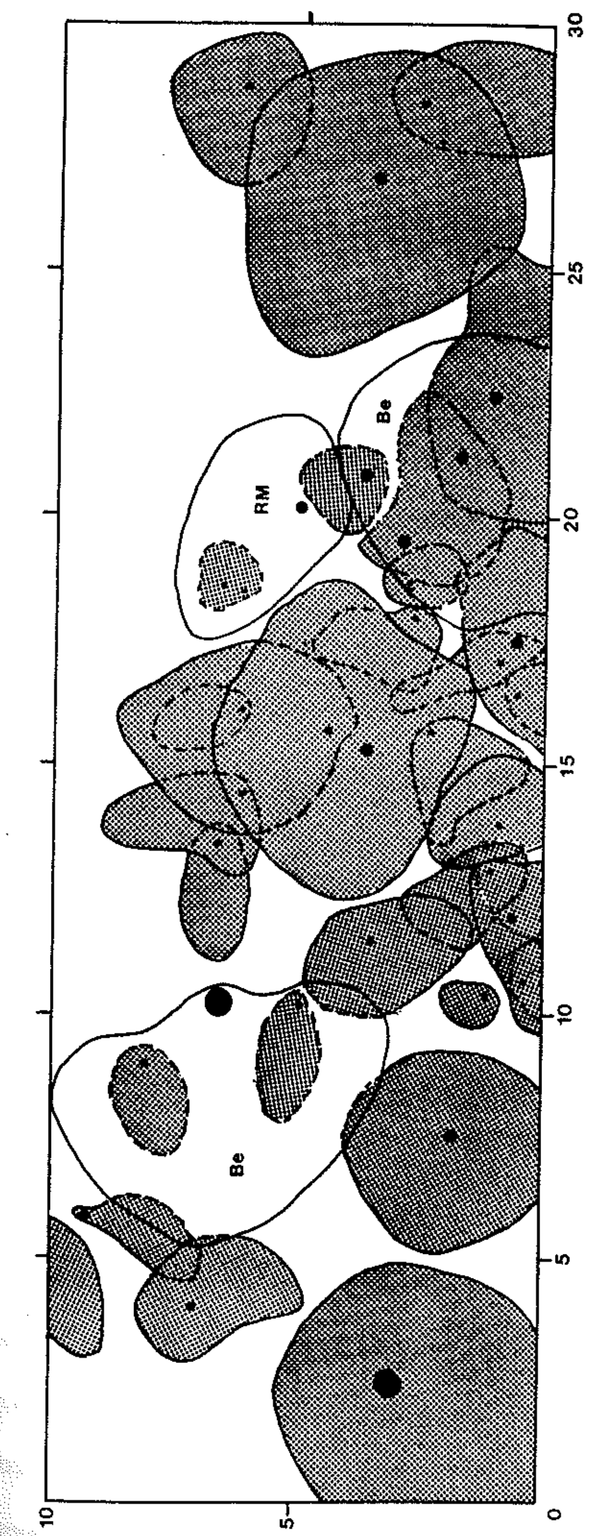


14c.

presence of this additional layer of hemlocks at about 5 m in height is evident throughout the entire stand (see Figure 2).

DISCUSSION

Canopy structure. The hemlock-hardwood stands studied here qualify as even-aged, stratified mixtures as defined by Smith (1962) and Oliver (1978). Various species tend to occupy typical positions within the canopy, even though nearly all trees began growth following a single canopy disturbance. In the 44-year-old stand, red oak forms an upper stratum together with paper birch, black birch, and red maple. In the 87-year-old stand, the upper stratum is comprised predominantly of red oak, with small amounts of black cherry, red maple, and hemlock. Hemlock forms a dense understory of overtopped trees in both stands.

The upper portions of crowns of the tallest understory hemlock reach a short distance into the lower parts of the overstory red oak crowns. Thus, with respect to these species, two separate foliar strata exist, with a zone of overlap between them. Paper birch and black cherry also occur most frequently in the upper stratum, with few stems of lower heights. Red maple and black birch show more variation in height, so that foliage of these species extends into both strata. Thus, canopies of these stands are generally, though not completely, separated into an upper stratum of hardwood foliage and a lower stratum of hemlock foliage.

Stand development patterns. The development of these hemlock-hardwood stands does not appear to conform to the model generally accepted for single-species, even-aged stands, and also differs in several respects from patterns observed in other stratified mixed-species stands. In pure stands, trees in lower canopy positions continually fall farther behind upper canopy trees in height growth. Most researchers measure canopy differentiation in terms of crown class rather than tree height, but in cases where height was measured (e.g., Bormann 1965), the height difference between upper and lower canopy trees increased with age. Similarly, in stratified mixed-hardwood stands in New England, understory black birch and red maple fell continually farther behind red oak in height (Oliver 1978). In other stratified mixtures in which black cherry formed an upper stratum, it was observed that understory sugar maple and beech nearly ceased height growth, while height growth of cherry continued (Marquis 1981).

The growth of hemlock in the mixed stands of the current study differs from these patterns. Most hemlocks lapsed into a subordinate crown position beneath faster growing oak and cherry early in development, but once this occurred, the tallest hemlocks did not continue to fall behind in height growth. Rather, the tallest understory hemlocks kept pace with the overstory hardwoods, as hardwood growth slowed. For these hemlocks, further height growth into the upper canopy layers appeared to be limited in part by physical breakage of terminals as they grew into the bottom of the hardwood overstory crowns. Wierman and Oliver (1979) similarly observed that height in understory western hemlock was limited by abrasion of its terminals against lateral branches of overstory Douglas-fir, leaving hemlocks with broad, flat-topped crowns. Their descriptions closely parallel the observations and photographs presented here.

In pure stands, basal area growth rates of individual trees have been correlated to crown class (Trimble 1969, Ward 1964). This indicates that as stands age and crown-class differentiation proceeds, variation in stem size increases (Gilbert 1965, Bormann 1965). Any number of classes may be distinguished to assess the competitive status of individual trees, but the distinction between two classes is of primary importance. Those trees that reach the upper level of the canopy, and receive full sunlight at least at the crown tops, show highest basal area growth rates; those that survive in lower canopy positions with crowns partially or totally overtopped have slower growth rates, and in some cases nearly cease growth (Ford 1982, Oliver and Murray 1983).

A similar relationship between crown position and basal area growth was observed in mixed-hardwood stands studied by Oliver (1978), where understory black birch and red maple grew at steady, low, basal area growth rates which were much lower than that of overstory oak. A different pattern was observed in the hemlock-hardwood stand studied here. The tallest understory hemlocks initially had low basal area growth rates, but then steadily accelerated in growth, even though their position as understory trees was not altered. From age 65 to 70 the basal area growth rates of oak and hemlock were comparable.

Growth of hemlock into overstory stratum. Data presented here indicate that the majority of hemlocks occurred in subordinate crown positions when growing in mixture with hardwoods in even-aged stands. They tended to achieve upper canopy positions only if they were left as fairly large residuals following the stand-initiating disturbance. In the Great Mountain Forest stand, the minimum initial height allowing eventual development into the overstory appeared to be about 3 m.

Only one overstory hemlock fell within the boundaries of a sample plot in the Harvard Forest stand, and only a few others were present elsewhere in the stand. These were not scattered throughout the stand as were the residuals left after cutting of the Great Mountain Forest stand; rather, they were in a position protected from the force of the hurricane wind by a small ridge. Increment cores taken of these trees showed that they were 30-50 years old and 10-20 cm in diameter in 1938, and that diameter growth increased at the time of the hurricane. These trees are presently as tall as the hardwood overstory. This evidence further suggests that hemlock achieves overstory status primarily by a two-step process. It must first achieve a certain minimum size as advance growth or as an understory member of the previous stand, and then must be freed of overtopping competition when the main canopy is removed or destroyed.

Data gathered in this study also indicate that hemlock can achieve overstory status if it germinates on a seedbed unfavorable to other species in the stand, leaving it free of competition. This happened infrequently in these stands, but may be important on some sites.

Marquis (1981) described another forest type which develops in a similar pattern. Following clearcutting in the Allegheny Mountains, sugar maple and beech both occur primarily in the understory with black cherry as the dominant tree. In that region, these two species seem to attain overstory status only when left as residual saplings during over-story removal or destruction. Saplings of greater size have a greater probability of achieving overstory status. Marquis noted that many intermediate-aged stands in the Allegheny Mountains today have a mixture of cherry, maple, and beech in the overstory, and concluded that these stands probably developed following cutting that removed all trees except small, unmerchantable beech and maple saplings.

Thus, this is similar to the development pattern observed for stands following cuttings for charcoal and tanbark at the Great Mountain Forest, and following hurricane blowdown at the Harvard Forest, although the number and spatial arrangement of large residuals among the advance regeneration differed among these cases. Stands with a greater variation in age or size of advance growth (i.e., those which contained a larger number of residual saplings of shade-tolerant species) tend to have an overstory canopy stratum containing a greater mixture of species. Stands that had a narrow range of age and size at the time of stand initiation developed a more distinctly stratified canopy.

CHAPTER 3

Initial stages of development

INTRODUCTION

Reconstruction of the growth of older stands by stem dissection techniques inevitably omits some aspects of early stand development. Many stems which were present in early stages are missing from these older stands, and some species are entirely absent. Direct observations of young stands are necessary to provide a portrayal of early height growth and canopy development for these species.

Such observations were made in an experiment designed by Professor David M. Smith of Yale University. The objective of this experiment was to compare the height growth of seedlings of a wide variety of tree species growing in mixture, all starting from seed or small advance growth. This was done by clearcutting a strip in a hemlock-hardwood stand, and eliminating most advance regeneration and all subsequent sprouting by herbicide application and cutting. Height measurements were made at stand ages of 2, 7, and 8 years by Smith and others, and at age 14 as part of the current study.

STUDY SITE

The clearcut strip was located on the Great Mountain Forest in northwestern Connecticut, about 500 m from the 87-year-old stand described in Chapter 2. Soil and climatic conditions were similar at the two sites; the soil is classified as Hollis extremely rocky, fine sandy loam (U.S. Dept. Agric., Soil Cons. Serv. 1970). The clearcut strip was situated to incorporate the two main variations that occur within this kind of site. Part of the strip included a shallow swale crossed by an intermittent stream; this part was underlain by relatively deep till. Level areas on either side of this swale, which were on more shallow till, were also included within the cutting area.

METHODS

Experimental treatments. The stand was approximately 70 years old at the time of cutting, and was comprised primarily of red oak, red maple, beech, hemlock, and sugar maple. The strip was clearcut in early autumn of 1967; the removal of felled trees was done in a manner to cause a minimum of disturbance to the litter. The cutting area was 24 m wide in the north-south dimension, and approximately 120 m long in the east-west dimension. This created a spectrum of microsite conditions from complete exposure on the northern edge to dense shade on the southern edge.

Just before cutting, all small woody plants, including tree seedlings, were sprayed with an oil solution of 2,4,5-T. The only plants reserved from this treatment were 1-year-old red oak seedlings averaging about 20 cm in height, and the few small, advance-growth hemlocks which were present; evidence had previously indicated that these species would not reproduce well from seed after clearcutting.

During subsequent years, sprouts from roots and stumps were eliminated by cutting; only root suckers of beech proved too persistent to be eliminated by cutting, but these were not present in large numbers. Thus, except for red oak and small numbers of beech and hemlock, all regeneration was from seed germinating after overstory removal. To supplement the seedfall naturally occurring on the site, seed of hemlock, white pine, red maple, sugar maple, and birch species was sown in the cutting area. The portions of the area where measurements were to be made were fenced to prevent browsing of regeneration by white-tailed deer.

Measurements. Height measurements were made in 1969, 1974, 1975, and 1981, after or near the end of the period of annual height growth. Two different sampling methods were used, necessitated by the changing density of the stand as it developed. Both methods met the objective of sampling the heights of the tallest individuals of each species, by zones progressing from the southern to the northern edge of the strip, as follows:

1. 1969 and 1974: The strip was divided into 8 zones, each of which was 3 meters in width and ran the entire east-west length of the cutting area; both kinds of sites were included within each zone. Within each of the two sites, the heights of the 5 tallest individuals of each species (or as many as available if less than 5) were measured in each zone.

2. 1975 and 1981: Transects were established across the strip in a north-south direction. Each was 2 meters wide and was divided into 1.5 meter segments. Two transects were located on the shallow till site, and one on the deep till. Within each 2 m x 1.5 m plot, the

tallest tree of each species was measured, with the following exception. If a tree immediately adjacent to the plot was taller than any conspecific within it, and was so tall as to influence development within the plot (*i.e.*, directly compete with trees within it), this tree was taken as the sample tree instead.

Data analysis. Objectives of the experiment included comparing tree growth at varying microsites along the north-south axis of the strip, and between the two kinds of sites--deep and shallow till. However, the focus of the current study lay in determining whether species-specific trends in height growth occurred in early stages of development under conditions similar to those of the older stands--where all or most overstory competition had been removed in a single disturbance. Therefore, measurements were analyzed only for trees in the central 12-meter section of the 24-meter-wide strip. The southern edge of the strip was subject to both root competition and shading from the untreated bordering stand. The northern edge received direct sunlight, but also was subject to root competition. Also, measurements from both the shallow and deep till sites were analyzed as a single unit, to encompass the variation found within a single stand.

For each measurement date, heights of the tallest trees of each species, sampled as described above, were averaged, and significant differences among means were determined by Scheffe's procedure (Snedecor and Cochran 1980). Sample sizes (see Table 4) varied among species, since many were not present in each measurement zone.

Table 4. Height (m) of the tallest individuals found on each sample plot, for each species in clearcut strip. Each table gives mean, standard error of mean, sample size, and results of Scheffe's procedure for separation of means for all species with n < 10 (means sharing same letter are not statistically different at P = .05 level).

1969--age 2 years

species	mean	s.e.	n	
Pin cherry	1.18	0.08	40	a
Paper birch	1.04	0.03	40	ab
Gray birch	0.81	0.03	29	bc
Black birch	0.74	0.04	34	c
Black cherry	0.67	0.05	28	c
Red oak	0.63	0.03	40	c
Red maple	0.34	0.03	27	d
Hemlock	0.31	0.02	4	
White pine	0.13	0.01	23	d
Beech	--	--	0	

1974--age 7 years

species	mean	s.e.	n	
Pin cherry	4.68	0.20	28	a
Paper birch	3.93	0.13	37	a
Gray birch	3.20	0.20	21	b
Black birch	3.04	0.18	28	b
Black cherry	2.91	0.20	22	b
Red oak	2.81	0.12	44	b
Beech	1.90	0.06	3	
Red maple	1.82	0.15	24	c
Hemlock	1.45	0.32	5	
White pine	1.13	0.10	18	c

Table 4. (continued)

1975--age 8 years

species	mean	s.e.	n	
Pin cherry	5.36	0.41	16	a
Paper birch	4.63	0.18	27	a
Black birch	4.30	0.34	17	a
Black cherry	3.35	0.75	8	
Gray birch	3.17	0.18	7	
Red oak	2.74	0.25	24	b
Beech	2.10	0.22	11	bc
Red maple	1.68	0.24	15	bc
Hemlock	1.65	0.28	3	
White pine	0.85	0.16	11	c

1981--age 14 years

species	mean	s.e.	n	
Pin cherry	9.02	0.44	12	a
Black birch	8.38	0.73	13	a
Paper birch	7.86	0.28	25	a
Black cherry	7.32	1.17	7	
Gray birch	6.80	0.45	6	
Red oak	4.57	0.48	22	b
Beech	3.05	0.35	11	b
Hemlock	2.68	0.62	3	
Red maple	2.65	0.43	8	
White pine	1.25	0.41	5	

RESULTS

General observations. The most striking result was the important effect that deer browsing had upon vegetation in the clearcut strip. Woody plants were nearly absent from areas outside fences, with hay-scented fern dominating the vegetation in these areas; within fenced areas, tree seedlings were dense. These conditions persisted at all sampling dates.

Initially, hay-scented fern was also abundant on the deep till site within the fenced area, as were blackberry and raspberry throughout the cutting area. However, many tree seedlings outgrew these species and overtopped them by the second year.

Although overall tree density was not measured quantitatively, several important differences were evident for relative density among species. Of the species originally important in the mature stand, none recolonized the cutting area in large numbers. Regeneration of hemlock and red oak appeared to be restricted to seedlings present prior to cutting. Red oak had been well represented as advance regeneration, but few hemlock had been present. Red and sugar maple, which were eliminated as advance growth, did not germinate in large numbers although they were among the species artificially seeded; few of those that did germinate survived to age 14. Beech also became established in only limited numbers. The shade-intolerant cherry and birch species, in contrast, germinated at high densities.

Comparative height growth of tree species. Table 4 shows the average height attained by the tallest of each tree species, at the four sampling dates. Results are graphed in Figure 15. Scheffe's test

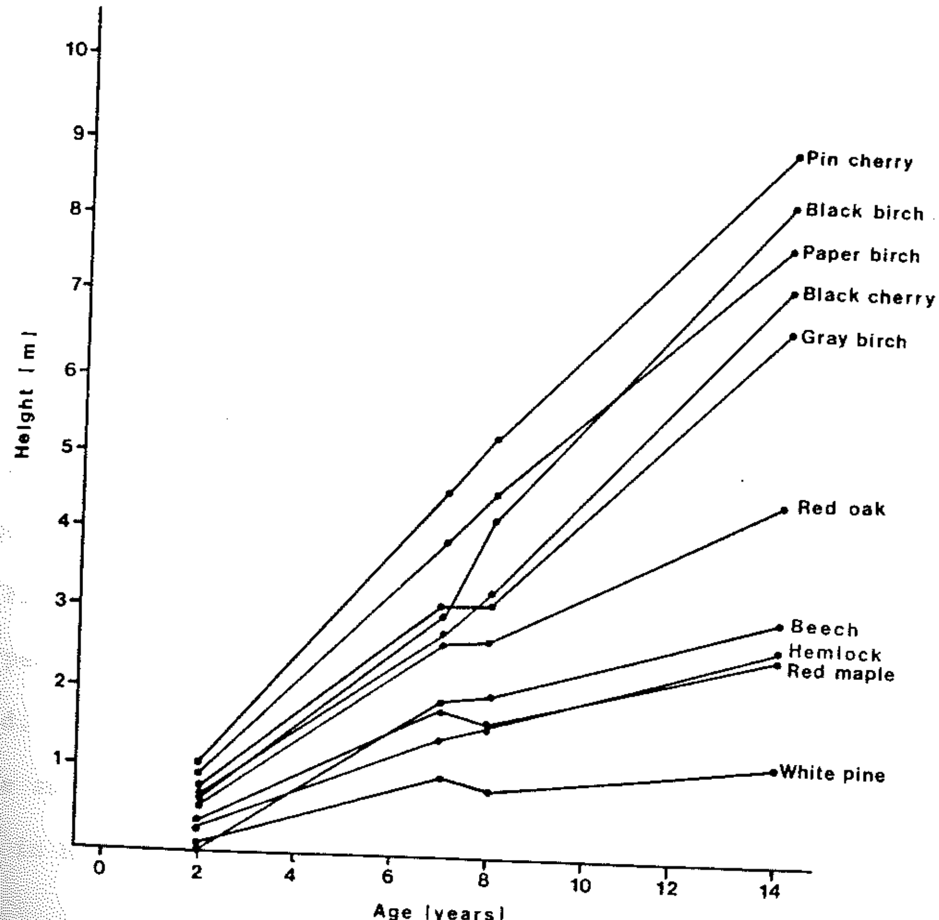


Figure 15. Average cumulative height growth of the tallest individuals found on each sample plot, for each species in clearcut strip.

for separation of means was used for all species with sample sizes greater than 10; results are shown in Table 4. Means and standard errors for other species are also listed in Table 4, but were not included in statistical tests.

These results show that, beginning at the earliest measurement, pin cherry and paper birch were significantly taller than red oak and red maple, with other cherry and birch species being intermediate between these groups. This relative ranking in height persisted to age 7, with pin cherry and paper birch (plus black birch at age 8), having significantly greater heights than all other species tested. By age 14, two distinct strata were discernible, with cherry and birch species taller than all other species. Red oak had the greatest height of the shorter set of species, but averaged only one-half the mean height of pin cherry.

Figure 15 shows that, for the most part, the relative rankings of the species in height remained constant throughout the measurement period. Only black birch changed importantly in position; it was one of the shorter of the less tolerant species at age 7, but was nearly equal in height to pin cherry by age 14.

DISCUSSION

These results are most valuable when compared with those of two earlier regeneration studies in which no special treatment of advance growth or vegetative sprouts had occurred. In one of these, McKinnon *et al.* (1935) made an extensive study of regeneration following clearcutting of old-field white pine stands in the vicinity of the Harvard Forest. In the other case, Spurr (1956) and Hibbs (1983) traced stand development on 14 permanent sample plots at the Harvard Forest. These plots were located in areas where the overstory had been destroyed by hurricane winds; most of these had been dominated by white pine at the time of the hurricane. In both of these studies, data concerning relative tree heights were collected by dividing trees into two crown classes: overtopped and free-to-grow. Stem origins were also noted, distinguishing seedlings, seedlings sprouts, and stump sprouts.

In these stands, the less shade-tolerant birch and cherry made up a large part of the upper canopy (free-to-grow) stratum during the first 10 to 15 years of growth, with pin cherry being the most numerous in this stratum. Many red oak and red maple grew in overtopped positions beneath pin cherry and birch species, as also occurred in the clearcut strip of the present study. However, stump and seedling sprouts of red oak and red maple, many in multiple-sprout clumps, also occurred in upper canopy positions. In post-hurricane plots, sprouts of these two species made up approximately 25% of the free-to-grow stems at age 10 (Hibbs 1983). In clearcut stands, red maple multiple-sprout clumps occurred as free-to-grow stems in 100% of the 15-year-old stands examined by McKinnon and coworkers, and red oak occurred in this condition in 50% of stands. Thus, no clear pattern of vertical stratification existed in these stands. The differences seen between these stands and the regeneration in the clearcut strip of the current study demonstrate the importance of vigorous sprouting by red oak and red maple in early canopy development. Where sprouting had been suppressed, and regeneration developed only from seed or small advance-growth seedlings, distinct stratification occurred, with red oak and red maple growing only in subordinate canopy layers.

In addition to sprouting, differences in size of advance regeneration can also decrease the consistency with which species become arranged in particular canopy strata. This can be especially important in the case of hemlock, which does not sprout and has slow juvenile height growth. For example, Hibbs (1983) reported that the one post-hurricane plot located in a former hardwood stand contained hemlock as an upper canopy component at age 40. Some hemlocks had occurred in upper canopy positions in this plot even at age 10 (Spurr 1956), simply because they had existed as large advance regeneration at the time of overstory removal.

It is probable that the older stands described in Chapter 2 contained the kind of unstratified canopy in early development that was observed in the studies of Spurr and McKinnon and coworkers. Those stands, which became established following overstory removal of previous hemlock-hardwood mixtures, would have differed from the regeneration that followed white pine in that they would likely have contained more hemlock advance growth and more hardwood stump sprouts. Both of these factors would serve to increase the proportion of red oak, red maple, and hemlock in the upper stratum, and thus decrease early canopy differentiation into distinct species layers.

CHAPTER 4

A late stage in stand development--Catlin Wood

INTRODUCTION

Although the transition hardwood-white pine-hemlock mixture is the prevalent forest type throughout much of southern New England, few old stands of this type exist for comparison with younger stands described in previous chapters. This is particularly true of sites with moderate slopes and favorable soil-moisture characteristics. Most land even marginally suitable for agricultural use was cleared at some time, so that much of the present forest is now in the first or second generation following the cessation of agricultural use; few of these stands are more than 100 years old. On land not suitable for agriculture, forests were cut heavily for charcoal or fuelwood, continuing through the early years of the present century. For the most part, only where steep, rocky slopes or ravines limited human access have small areas remained which escaped human disturbance for long periods.

One transition hardwood-white pine-hemlock stand of considerable age, known as Catlin Wood, exists in the northwestern Connecticut town of Litchfield, and represents one of the oldest examples of this forest type on a relatively good site (Smith 1956). Smith hypothesized, from the limited evidence provided by stumps of seven windthrown hemlocks, that the stand arose following a series of disturbances occurring in 1806, 1822, and 1833, consisting probably of both cutting and windthrow. Little further study has been done concerning the origin of this stand.

The present investigations were carried out primarily to compare the structure of this older stand to the younger examples of the hemlock-hardwood type as described in Chapter 2. Research into the land-use history of the area was first carried out, since disturbances in this stand were not documented as they had been for the younger stands. Besides determining the date and type of disturbance that led to the establishment of the present stand, it was of interest to determine why the area had not been used for agriculture.

STUDY SITE

Catlin Wood, comprising about 12 ha, is located on the lands of the White Memorial Foundation, and has been reserved as a natural area since 1913. At 280 m elevation, it is somewhat lower than the sites of the younger stands described earlier. It is also farther south and closer to Long Island Sound; thus, it has a slightly warmer climate than the other two study sites (see Appendix 2 for locations). Climatic conditions (U.S. Dept. Agric., Soil Cons. Serv. 1970) measured in Cornwall, a town adjacent to Litchfield, are summarized below:

Precipitation (yearly mean--mm)	1138
Number of frost-free days	165
Temperature (C)	
yearly mean	9
January mean	-4
July mean	21

A map of Catlin Wood and surrounding area is shown in Figure 16.

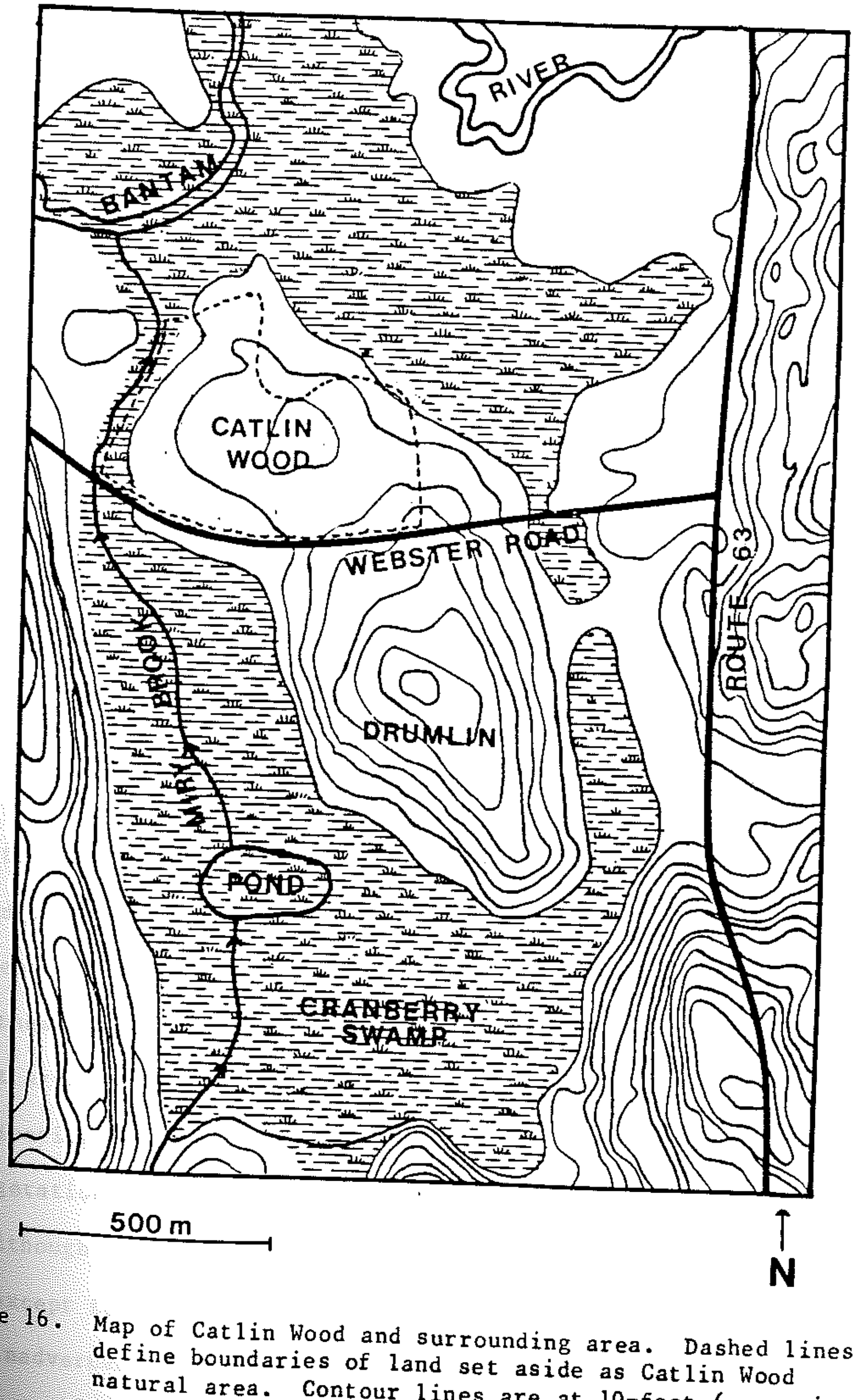


Figure 16. Map of Catlin Wood and surrounding area. Dashed lines define boundaries of land set aside as Catlin Wood natural area. Contour lines are at 10-foot (approximately 3-meter) intervals. Top contour line of drumlin is at 970 feet (295 m).

Immediately to the south is a drumlin, which extends into the southeastern part of Catlin Wood; this adjacent drumlin area remains in agricultural use as of 1982. The drumlin and adjoining Catlin Wood area are nearly surrounded by wetlands.

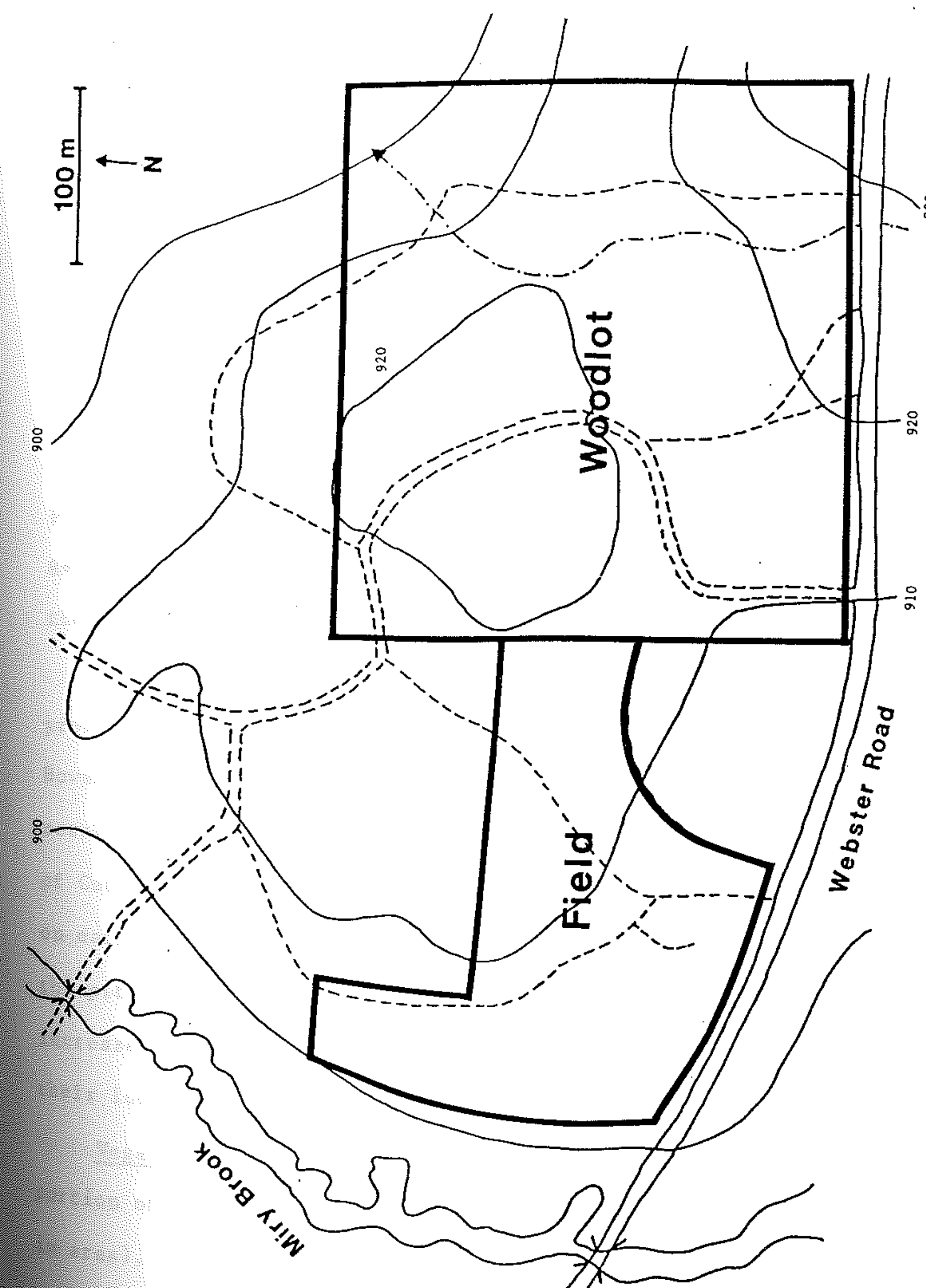
Soils on the drumlin are of the Paxton series. Because of a perched water table, this soil is among the best in the region for forest or crop growth. The Paxton and bordering Charlton till soils occur in the southeastern part of Catlin Wood (see Appendix 5). The remaining area of Catlin Wood has primarily Windsor and Deerfield soils formed in stratified sands deposited by glacial meltwater. This includes an area in the southeastern part containing an intermittent stream that drains part of the drumlin. There are also several wet areas with AuGres and peat soils.

Catlin Wood is not homogenous in past land use or present vegetation. Studies by Siccama (1983) have defined the outlines of a former plowed field that lies within its boundaries (Figure 17). Land ownership studies, to be discussed in detail below, showed that the eastern portion of Catlin Wood was maintained as a farm woodlot during the nineteenth century, and probably had been continuously forested before that; these boundaries are also delineated in Figure 17. This eastern woodlot area, underlain partly by till soils, fits the criteria used for selecting other stands in this study, and was used as a study site for vegetation measurements.

Although the stand has been reserved from timber harvesting since 1913, except for salvage of dead trees, some selective cutting took place inadvertently within the boundaries of the stand in 1972. While this is unfortunate for many scientific purposes, it provided an

Figure 17. Map of Catlin Wood, showing boundaries of abandoned farm field and former farm woodlot.

- Improved road
- Major bridle trail
- Minor trail
- Intermittent stream
- 10-ft. contour lines



opportunity for accurately aging the stand, which would not otherwise have been possible. The only other partial cutting involved the removal of chestnut during or shortly before the time that the lethal chestnut blight disease reached the area (Smith 1956).

METHODS

Land ownership. The land transfer records on file in the Litchfield Town Clerk's Office were examined to trace the ownership of Catlin Wood and adjacent property from the time of settlement to the present. Other deeds not pertaining directly to Catlin Wood, but which gave information about the occupations of its owners, were included in the search.

Age structure. Determination of tree ages from increment cores proved difficult for trees of the size present in Catlin Wood. However, evidence of stand age structure was provided by stumps resulting from the 1972 logging. A survey was made of the entire area of Catlin Wood to identify all such stumps. A clean surface was planed on each of these, and annual growth rings were counted to as near to the pith as possible. Records were also made of dates where ring width increased suddenly in size. Thirty-eight stumps were located and aged; their locations are shown in Appendix 5.

Vegetation structure and composition. The eastern "woodlot" portion of Catlin Wood was gridded with 25-meter-square plots (.0625 ha in area). From these plots, a subsample was chosen which had not been recently disturbed by wind, logging, or other agents. Twelve such plots were located, and on these, total height and breast-height diameter were measured for all trees 10 cm and greater in diameter. The biomass of each tree was calculated, using the regression equations of Monteith (1979). These relate aboveground dry weight of individual trees to total height and breast-height diameter. The equations are listed in Appendix 6.

RESULTS

Land ownership. Reconstruction of land ownership records are summarized in a series of maps in Figure 18. A more detailed account of the land ownership changes, including deed citations, is included in Appendix 5. Each map shows the road that is now called Route 63; this road was present at the time of initial land division in 1723, and was then known as Woodbury Road. Webster Road is not shown until it was initially surveyed for construction in 1823.

The initial settlement of Litchfield followed the general pattern of most New England towns of the seventeenth and eighteenth centuries. The process consisted of dividing the land by a lottery system among the individuals ("proprietors") settling there. The first rounds of land division consisted of assigning house "lots" within the designated village area. Larger areas were then divided; these were known as "pitches" rather than "lots". In every round, each proprietor received an equal share, with one share each being set aside for the church, the minister, and the school.

On the first 60-acre pitch of the property division of Litchfield

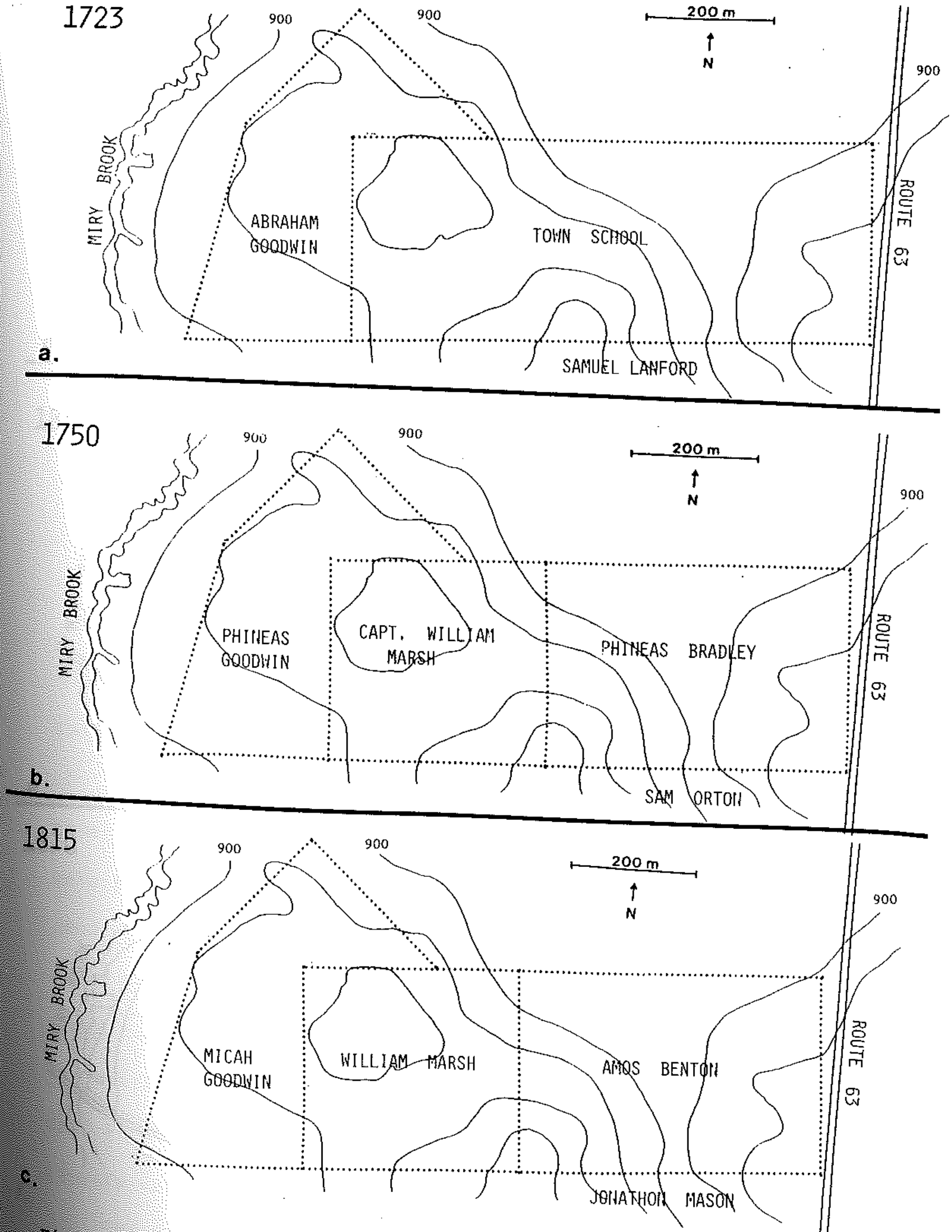


Figure 18. Series of maps tracing ownership history of Catlin Wood and adjacent land. See text for description of land transactions.

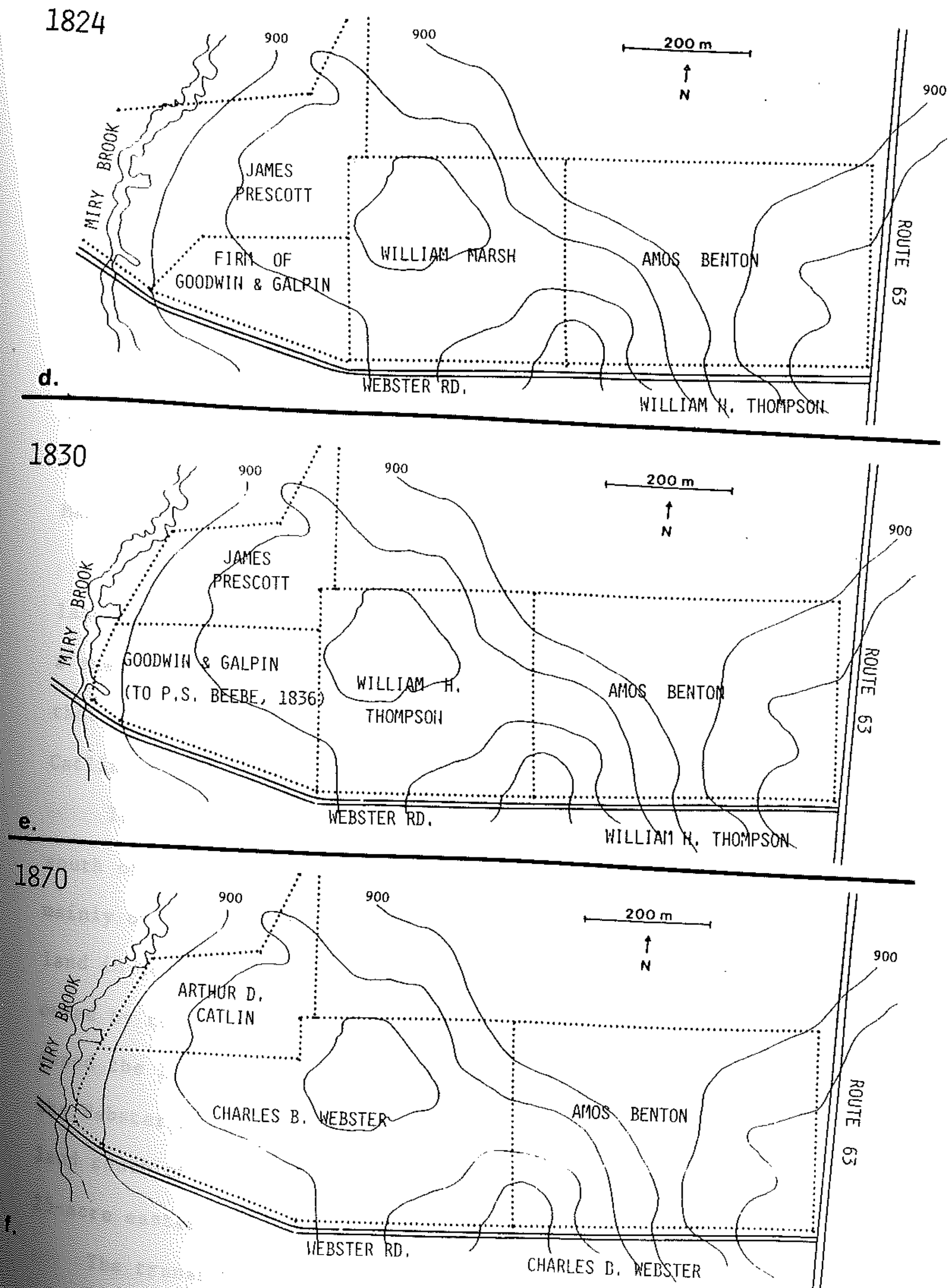


Figure 18. (continued)

in 1723, the town school was assigned a block which now contains the eastern half of Catlin Wood (Figure 18a). Adjacent to the west, on the second round of 60-acre pitches in 1724, Abraham Goodwin was assigned land. To the south, Samuel Lanford (Sanford?) received the pitch containing the drumlin.

The Goodwin land remained in the ownership of that family for nearly a century, until 1817 (Figure 18b,c). The "school-right" land was sold soon after division to raise funds for the new school, and the 25-acre portion which now encompasses the eastern half of Catlin Wood was acquired by Captain William Marsh in 1749. It remained in the Marsh family until 1827.

The early deeds documenting these transfers give no description of land use. However, other deeds indicate that the Goodwin family owned a sawmill and gristmill about one mile from their Catlin Wood land, and that the Marsh family owned a mill of some sort about 2 miles from Catlin Wood.

In 1822, William Thompson began acquiring parcels of land to the south of Catlin Wood to form a farm (Figure 18d); these consisted mainly of the original Lanford land. He purchased the adjoining Marsh land in 1827. This was the first time that a part of Catlin Wood was owned by the same individual who farmed the adjacent land. Thompson owned the land until his death in 1868, whereupon his heirs sold it to the Webster family (Figure 18e,f). Deeds of this sale state that the land south of the road was supporting a crop of rye, and describe the 25-acre eastern portion of Catlin Wood as a woodlot.

The transfer of ownership of the western portion of Catlin Wood (the Goodwin land) in the early nineteenth century was exceedingly complex. The land was repeatedly divided and subdivided, and was used as collateral for loans. Portions were held by the firm of Goodwin and Galpin for speculative purposes, apparently because the construction of an access road (now Webster Road) was proposed in 1823; the right-of-way was surveyed and purchase was begun in that year. However, this road was apparently not actually completed until sometime after 1836. An 1824 deed for a part of the Goodwin and Galpin land does describe the southern boundary as a highway, but a deed dated 1836 which transferred the Goodwin and Galpin land to P.S. Beebe states that the southern boundary is the land of Julius Deming, but is "subject to a public highway across the south border", implying that the road did not yet exist.

In 1869, the year after he acquired the eastern half of Catlin Wood from Thompson, Webster purchased most of the western portion and consolidated the ownership of the drumlin farmland and the major part of Catlin Wood. It was from the Webster family that Alain and May White purchased Catlin Wood as part of the formation of the White Memorial Foundation in 1913.

Conclusions pertaining to land-use. The pattern of ownership documented here suggests reasons why the land of Catlin Wood was not subjected to the uses of surrounding land of similar quality--clearing for agriculture, possibly followed by use as unimproved pasture and eventual abandonment. The land of Catlin Wood is naturally isolated from the north, west, and southwest by "flooded land" as described in the original deed of 1723, and would logically be considered for development as a part of the good drumlin farmland to the south (see

Figure 16). Indeed, the original settlers apparently viewed this land as a unit, calling it "South Pine Island". However, a property boundary was drawn between these two areas in the original land division, so that the ownership of Catlin Wood was separate from that of the drumlin during the time of initial land clearing for crop and pasture use. The two families who owned the land of Catlin Wood in the eighteenth century had businesses other than farming; both owned mills 1 to 2 miles from their Catlin Wood land. Furthermore, there was no improved access road to the land at least until 1823, and possibly until after 1836.

When William Thompson purchased the drumlin farmland in the early 1820's, there apparently was sufficient land available that had already been cleared. After he added the eastern portion of Catlin Wood to his holdings, he maintained it as a woodlot. Portions of the borders of the Thompson woodlot remain discernible in 1982. The southern border lies along Webster Road, and along the eastern border and the southern part of the western borders are trees which lean away from the woodlot, with open-grown crowns on the side away from the woodlot. These grew as border trees next to cleared land, which now contains old-field stands of white pine and mixed hardwood species.

Age structure. Figure 19 shows the date of diameter growth response for 38 trees for which ages were determined from stumps. These were all from the woodlot portion of Catlin Wood. They ranged in diameter from 28 to 90 cm at stump height, and included 14 hemlock, 18 red oak, 2 white oak, 1 white ash, 1 black birch, and 2 white pine. The date shown in this graph is the point at which there was a sudden increase in diameter growth from the initially slow growth achieved as

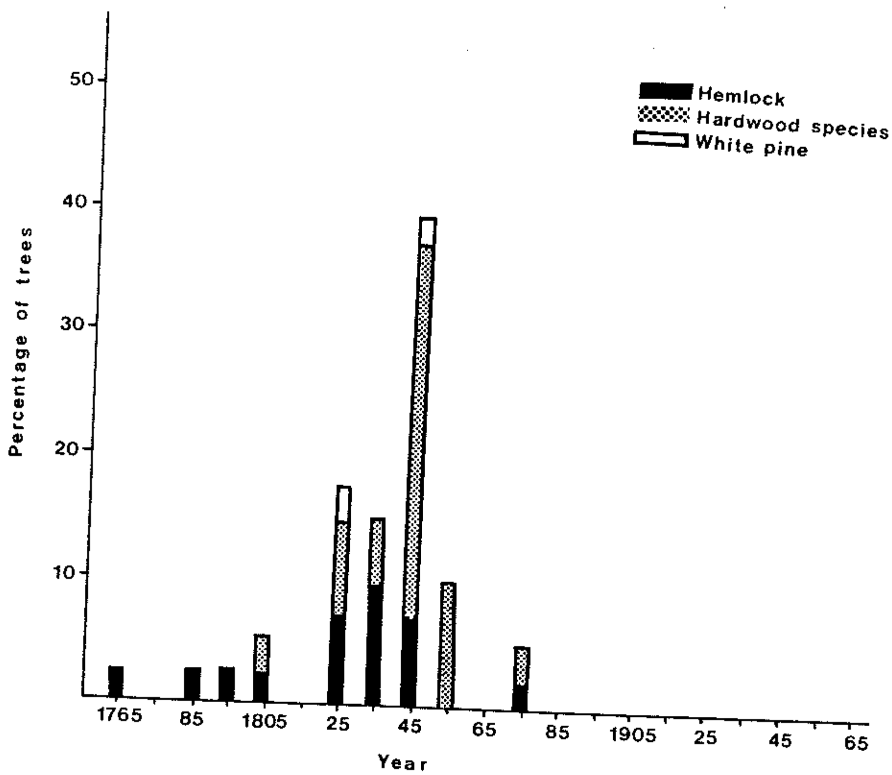


Figure 19. Age distribution of trees sampled in Catlin Wood "woodlot" area. Age given is that of time of release from suppression as advance growth.

advance regeneration. This date could be accurately determined, whereas the time prior to rapid growth response often could only be estimated due to the difficulty of counting the narrow rings of the center core. For most of the trees, this initial period of slow growth lasted about 10 years, although in a few cases it lasted at least 50 years. The date of increased growth rate gives the time when a disturbance likely occurred, allowing the regeneration to grow more freely, and thus represents an important indicator of stand age.

Figure 19 shows that the majority of stems began a period of rapid diameter growth in the decades 1820 to 1850, with others responding in the 50 years before that. These results generally support the estimates of Smith (1956), that the years 1806, 1822, and 1834 were dates of disturbances that had released advance regeneration. In the present study, increases in diameter growth were found to have occurred on or near those dates. However, the sample in this study has shown that the decade of 1840 (and probably the specific year 1846) was the date of the last major disturbance that released advance regeneraton of hemlock, white pine, oak, and other hardwood species. The present stand is thus considered to be 135 years old. This disturbance was almost certainly a cutting, since property deeds indicate that the stand was being maintained as a woodlot by the owner of adjacent farmland at that time. It is also likely that the cutting was heavy, since species of low shade-tolerance, including red oak, white ash, white pine and yellow-poplar, formed a large part of the new stand. The advance regeneration released by the cutting was mostly rather small in diameter; the central core of suppressed growth in most stumps contained about 10 years of growth and was 2-5 cm in diameter in 1846.

However, the new stand also contained some larger trees which had been released by disturbances during the previous 30 years, plus a few much older residuals, most of which were hemlock.

One of the hemlocks dating to 1822 was situated on a windthrow mound, and had grown in a suppressed condition for its entire life, measuring 33 cm in diameter at stump height at age 152. This indicates that it germinated in a rather small windthrow area, which may be attributable to a hurricane which moved through the region in September 1821 (Smith 1956). However, the fact that half or possibly all of Catlin Wood was held by owners of sawmills in the early nineteenth century suggests that partial cutting may have been the cause of some of the disturbances which allowed advance regeneration to form within the stand before the heavy cutting of 1846.

All but one of the oak stumps sampled showed a central core of slow growth, indicative of their origin as advance regeneration. This suggests that the earlier cuttings were indeed partial, and not the complete removal cuttings associated with harvesting for fuelwood. Had there been repeated fuelwood cuttings, the majority of oaks in the present stand would likely have shown rapid diameter growth from the first year, indicating trees of sprout origin.

Prior to these major disturbances, 4 hemlocks and 1 red oak in the sample showed signs of release from suppression in the years 1765, 1799, 1802, and 1805. These endured subsequent periods of suppression, followed by releases coincident with the 1820-1846 disturbances. Two of these hemlocks, germinating in about 1755 and 1778, were located on windthrow mounds, indicating that disturbances caused by wind accounted for at least some of the earlier regeneration. The presence of tree stumps and windthrow mounds that date to the eighteenth century indicates that a sequence of agricultural clearing and field abandonment prior to use as a woodlot was highly unlikely for this stand.

Present vegetation composition and structure. Table 5 shows the present stem density by species and diameter class for the 12 undisturbed plots measured in Catlin Wood. The species composition is largely the same as in the 87-year-old Great Mountain Forest hemlock-hardwood stand (see Chapter 2), except that some species represented by only a few stems in that stand occur in important numbers in Catlin Wood. These include white pine, white oak, and beech. The other major species--hemlock, red oak, and red maple--are important components of all three stands.

Diameter distributions shown in Table 5 indicate that red oak and white oak occurred primarily in the larger diameter classes, with red maple, beech and birch species present at smaller sizes. White pine was found almost exclusively in the largest diameters (60- and 75-cm classes). Hemlock had by far the greatest stem density, comprising one-half of the total number of trees. While most of these were of relatively small diameter, hemlock occurred in such great numbers throughout the diameter distribution that it dominated all classes except the largest (75 cm).

Table 5 also shows the distribution by species of basal area and aboveground biomass. Hemlock dominated the stand by both of these measures, as well. Although they were represented by relatively few stems, oak and pine made up much of the balance of basal area and biomass, because of the large sizes of most individuals of these

Table 5. Density distribution of trees 10 cm and greater in breast-height diameter, by species and diameter class, from 12 undisturbed plots in Catlin Wood woodlot area. Also, basal area and aboveground biomass by species for these plots. Standard error of mean given in parentheses for stand totals.

Diameter class (cm)	Hemlock	Red oak	White oak	White pine	Red maple	Beech	Birch[a]	Total[b]
	Trees per hectare							
15	72		1		15	12	16	132
30	77	12	7	1	23	15	31	175
45	56	8	5		4	12	7	93
60	24	13	4	8		1		51
75	4	4		7				15
Total	233	37	17	16	41	40	53	465 (38)
Basal area (m^2/ha)	23.5	7.3	2.2	5.4	2.4	3.4	3.4	48.7 (4.2)

[a]includes black, paper and yellow birch

[b]includes minor species not listed separately in table

species.

Considerable variation existed among plots in species composition and stand density. Density on three plots notably exceeded the averages presented in Table 5; these had a basal area of 60 to 82 m^2/ha, and aboveground biomass of 420 to 520 t/ha. Since the plot size of this study was rather large (1/16 hectare), these high figures were not simply the result of 2 or 3 large trees occurring in a clump on a sample plot. Each of these three plots contained 11 to 18 large overstory trees (over 20 m in height).

The height distribution of the important species on the 12 plots is shown in Figure 20. For many species, the pattern is similar to that found in the 87-year-old hemlock-hardwood stand discussed in Chapter 2. As in that stand, oak was found mainly in the overstory canopy. Hemlock occurred over the range of heights, but was most commonly found in lower height classes. Also, red maple, beech, and other hardwood species occurred in understory and intermediate crown positions with hemlock. An important difference in the Catlin Wood stand was the presence of white pine, occurring at heights greater than that of oak and hemlock. These were not plentiful enough to form a horizontally continuous canopy layer, and thus occurred as emergents above the main overstory stratum. Representative views of the sampled plots are shown in Figure 21.

<u>Pre-settlement vegetation</u>. Surveyors of the original land division of Litchfield in 1723 used witness trees to specify boundary corners. This record provides a small sample of the species present in the pre-settlement forest; locations and species of 7 witness trees in

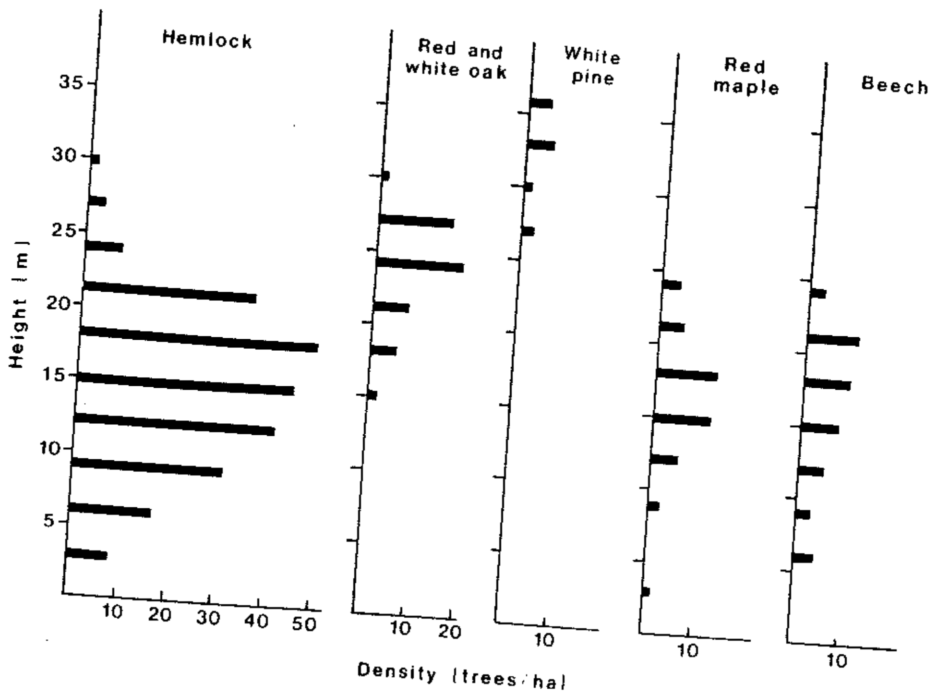


Figure 20. Tree density distribution by species and 3-meter height class in undisturbed plots in Catlin Wood "woodlot" area.

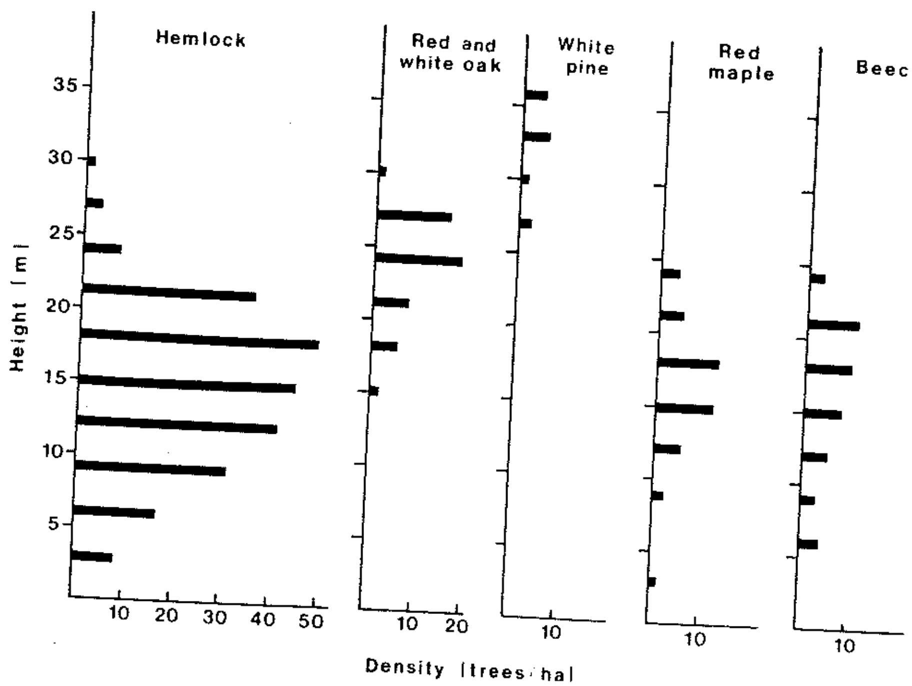


Figure 20. Tree density distribution by species and 3-meter height class in undisturbed plots in Catlin Wood "woodlot" area.

Figure 21. Views of portions of Catlin Wood free of recent disturbances.

a. Author stands next to white pine which is 32 meters tall and emerges above level of main canopy. All other stems in foreground are hemlock.

b. Red oak in foreground is 28 meters tall and forms a part of the main overstory canopy. Other stems in view are white pine, hemlock, and red oak.

the area of Catlin Wood are given in Figure 22.

A sample of 7 trees clearly is too small to indicate any details of forest composition, but it does suggest certain things:

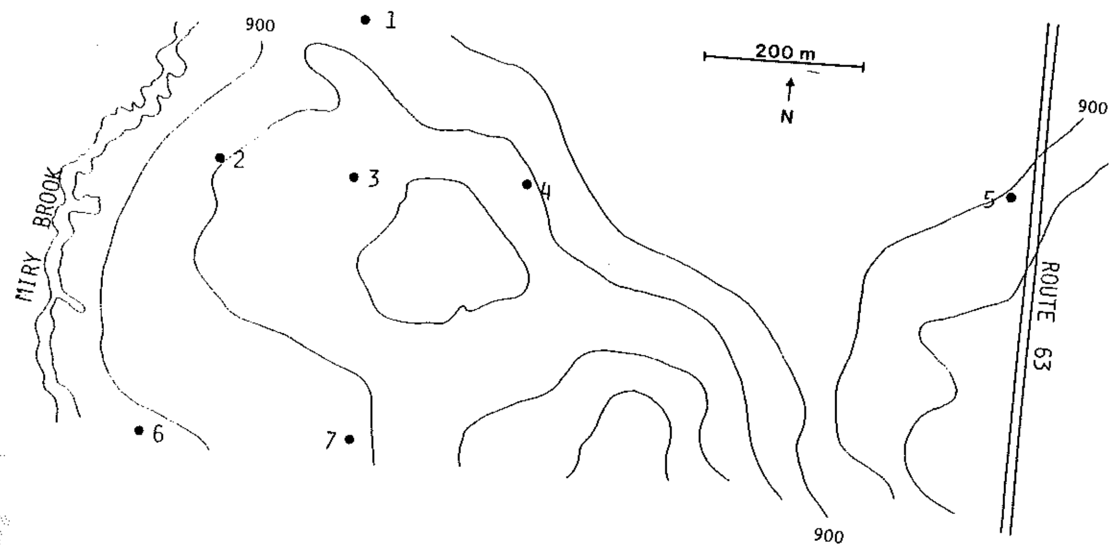
1. Pre-settlement vegetation was not composed solely of shade-tolerant species, as would be expected if the stand had been free of major disturbances for an extended period.

2. The stand contained white pine and hardwood species, as it does at present, although the presence or absence of hemlock in the forest of 1723 is not clear. The absence of any particular species from such a small sample does not indicate its absence from the stand as a whole.

3. The pre-settlement forest may have had a structure similar to that of the present stand, with white pines towering above a hardwood canopy layer. This is suggested by the fact that the area was referred to as "Pine Island" by early settlers, although there apparently were hardwood species prevalent in the stand. The pines seem to have been the most noticeable trees in 1723.

DISCUSSION

Catlin Wood is of particular ecological interest because it is one of the oldest examples of the hardwood-white pine-hemlock forest type growing on a good site in central New England. Its location and site characteristics would have made it a likely area for the kind of agricultural development that occurred on surrounding land of similar quality. This apparently did not occur simply because original land divisions separated the ownership of Catlin Wood from the adjacent drumlin farmland, and divided Catlin Wood itself into two ownerships. The development potential was further limited by the lack of an access road until the early 1800's. Not until after the major period of land clearing had passed was one portion of the land purchased by farmers of



1. "Great" white pine
2. white pine
3. chestnut "stadle" (small tree)
4. white pine
5. white oak
6. white pine
7. white oak

Figure 22. Map of Catlin Wood and adjacent land, showing location of seven witness trees used to define boundaries of original land division in 1723. Witness tree locations correspond to boundary corners in 1723 ownership map shown in Figure 18a.

the adjacent land, and it was then used as a farm woodlot. This woodlot area was the study site for the present work.

Development of the present Catlin Wood stand on this former woodlot seems to parallel the general pattern observed in the younger Harvard Forest and Great Mountain Forest stands. Although it did not appear to arise from a single disturbance as did the younger stands, a series of disturbances during a fairly brief interval (about 30 years) gave the stand a basically even-aged character.

The last major disturbance was a cutting in about 1846 which removed most of the overstory, releasing small advance growth--mostly less than 5 cm in stem diameter. Some larger understory trees, mostly hemlock, were also left during the cutting. This would likely have occurred because these hemlock were too small to be of use as sawtimber, whereas hardwoods were useful as fuelwood even to a very small diameter. A similar stand-initiation pattern was observed in the 87-year-old hemlock-hardwood stand described in Chapter 2, where cutting for charcoal left scattered understory hemlocks as residuals to develop along with the smaller advance growth.

Measures made in portions of the stand free from recent disturbance showed that although trees in the 135-year-old Catlin Wood stand were larger, stand structure was similar to that of the 87-year-old hemlock-hardwood stand. An oak-dominated upper stratum grew above a hemlock-dominated lower stratum of similar age in both woodlands. In Catlin Wood, the main canoy included both red oak and white oak, with small numbers of other hardwood species including white ash, shagbark hickory, and yellow-poplar. The lower stratum in both stands was comprised primarily of hemlock, with lesser amounts of red maple, black birch, yellow birch, and beech. Some hemlocks, presumably the larger residuals left in the 1846 cutting, shared the upper stratum with red and white oak.

A major difference between the stands was that in Catlin Wood, an emergent stratum of white pine occurred above the main oak canopy. This species was entirely absent from the 87-year-old stand. Age measurements from 2 white pine stumps and 1 living white pine in Catlin Wood showed that these originated following the 1820-1846 disturbances, and are thus the same age as the majority of other species. White pine has been shown on some sites to have equal or slower height growth than most associated hardwood species when young, but later continue to grow and emerge above the hardwood canopy (Hibbs 1982).

For three plots in the eastern part of Catlin Wood, total basal area reached 60-82 m^2/ha and aboveground biomass was calculated at 420-520 t/ha. These plots represent one of the highest levels of biomass accumulation reported for hardwood-white pine-hemlock forests of New England.

Interesting parallels exist between the structure and dimensions of these portions of Catlin Wood and those of stands in the western Great Lakes region described by Goff and Zedler (1968). They found that the greatest basal area development of any of the wide range of stands sampled was in multi-storied, old-growth stands of hemlock, white pine, and hardwoods. These had as much as 70 m^2/ha--similar to the maximum observed in Catlin Wood. The diameter distribution they reported was also similar. White pine had the greatest diameters, and the smaller classes were mostly made up of hemlock and red maple, but with sugar maple instead of oaks having the greatest diameters among hardwood species. In these stands, the tallest white pines reached 42 m, with the hardwood and hemlock canopy beneath. Crow (1978) estimated the aboveground biomass at approximately 600 t/ha. These authors hypothesized that such stands contain the greatest biomass attainable in the forest region.

In his sampling of forests in the Great Smoky Mountains, Whittaker (1966) also found that the greatest stand dimensions occurred in a mixture of hemlock, sugar maple, and beech. Basal area of this stand was 64 m^2/ha, with aboveground biomass of 610 t/ha. These measures exceeded those of even the two cove hardwood stands in the sample, which had basal area of 53-54 m^2/ha and biomass of 500 t/ha. Greater basal area was found in various pure conifer stands in these studies, but these were much shorter, and clearly contained less biomass (Whittaker 1966, Goff and Zedler 1968, Crow 1978). Although such studies provide only fragmentary data, they suggest that mixed stands of hemlock and hardwood, with or without white pine, may have the greatest aboveground biomass in the eastern "deciduous" forest.

It is important to note that the descriptions of structure and dimensions of Catlin Wood in this chapter apply only to undisturbed portions of the former woodlot area. In many areas, natural disturbances caused by wind, lightning, and disease have created gaps in the canopy, and some selective logging has occurred as well. Some of these gaps are small, and tree-growth response appears to be confined to the establishment of advance regeneration of shade-tolerant species, and probably some increase in the growth of adjacent overstory trees. Other gaps have been caused by several adjacent trees falling, and are quite large. Regeneration in these larger gaps includes species of lower shade-tolerance such as yellow-poplar, black birch, and yellow birch, which dominate in number and height, as well as red maple, hemlock, and oak.

Thus, the stand has begun to lose the overall synchrony imposed by logging during the mid-nineteenth century. Some areas have become spatially discrete patches containing new age classes, and repeated minor disturbances may continue to create a mosaic of such patches. However, disturbances may result in the establishment of regeneration throughout the stand rather than in discrete patches, and in the release of the prevalent hemlock understory, as observed at another location by Oliver and Stephens (1977) in a similar hemlock-hardwood stand subject to repeated windstorms and selective logging.

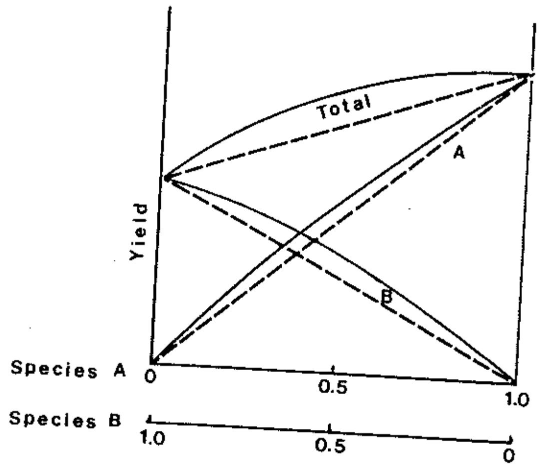
CHAPTER 5

Effect of variation in species composition on stand productivity

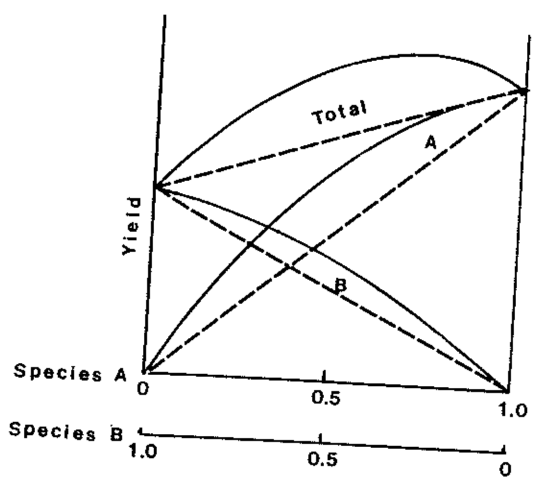
INTRODUCTION

Many studies have been made of the productivity of stands composed of mixtures of species. These studies, reviewed by Trenbath (1974) and Harper (1977), have compared the production of monocultures of different herbaceous species with mixtures of these same species. A standardized experimental design includes a series of plots (a "replacement series") all sown at the same total plant density, but with varying proportions of two constituent species. Resulting biomass yields of each stand are then measured by harvesting, usually after one growing season.

In these experiments, a baseline yield can be established for each constituent species and for the total stand. This assumes that density-dependent interactions between individuals of different species are equivalent to those among conspecifics. This baseline yield is calculated from knowledge of the yield of each species in monoculture: the expected yield of each mixture is simply the sum of the appropriate proportions (as initially sown) of each of the two monoculture yields (see Figure 23). Comparisons of actual yields with this baseline indicate the nature of interactions between the two plant species. For example, Figures 23a and 23b both show situations where the total yields of mixtures exceed that expected if intra- and inter-specific interactions were equivalent. This could result from a symbiotic or



a.



b.

Figure 23. Yield results of hypothetical replacement series experiments. Dashed lines represent expected yield if intra- and inter-specific interactions are equivalent; for example, expected total yield of mixtures of 0.5 A and 0.5 B would be 0.5(yield of monoculture of A) + 0.5(yield of monoculture of B). Solid lines represent experimental yields. Figure a shows the condition in which mixed stands do not produce more than a pure stand of the most productive species; Figure b, the condition in which they do.

commensalistic relationship in which one species actually benefits from the presence of the other. However, such a relationship is not necessary; this situation could also occur simply because competitive interactions among individuals of two species are less severe than those among conspecifics (*i.e.*, the species occupy somewhat different niches).

Some aspects of niche differentiation that have been suggested for sets of species in replacement series studies are:

1. differences in timing of foliage production and duration of photosynthetic activity during the growing season;
2. differences in height, form, and photosynthetic efficiency of foliage; and
3. differences in depth of rooting.

All of these appear important in reducing competitive interference in experiments with various herbaceous species, resulting in yield totals of mixtures exceeding those predicted from monoculture yields (Ellern *et al*. 1970, Trenbath and Harper 1973, Hill and Shimamato 1973). However, such results do not necessarily indicate that maximum yields are obtained from mixtures. For example, in Figure 23a, even though competition was reduced in mixed stands of species A and B, the inherently lower production of species B prevented the mixtures from yielding more than species A alone. Results of the majority of replacement series studies have followed this pattern (Trenbath 1974, Harper 1977). In relatively few cases is competitive interference reduced to the extent that mixtures have greater yields than the more productive monoculture, as shown in Figure 23b. Harper noted that most studies have involved agricultural crop species, and concluded:

> perhaps it is not unexpected that any pair of species or cultivars, bred by man for their high performance in pure stands, will seldom exceed this performance when grown in mixtures; yet it is on these that experiments have been concentrated. A search for 'ecological combining ability' is most likely to be successful in species or varieties that have been specifically bred for or evolved naturally towards some degree of niche separation (Harper 1977, p. 265).

While researchers in forest production and yield have parallel interests, few similar studies have been conducted in forest stands because of the length of time required. In a recent review, Whitehead (1982) concluded, "There is no evidence to confirm that rates of production in a single species tree crop are lower than those in mixed crops." However, some evidence concerning this question in forest stands does exist. In his book on forest yield, Assmann (1970) discussed theoretical considerations of mixed-stand production, and included results from a number of plantation experiments initiated in the nineteenth century. A recent study by Poleno (1981) also addresses this question. These will be considered later in this chapter, together with the results of the present study.

The focus of the current study is the productivity of even-aged, unthinned forest stands in central New England, which are composed of species that naturally occur together in mixture. A comparison is made between stands of mixed hardwood species and adjacent stands of similar composition but which also contain an important component of hemlock. Productivity estimates for pure hemlock stands are taken from published literature. The comparison is thus not between two species and their mixtures, but between a species on one hand, and a group of species on the other--distinguished because of differing basic growth characteristics. Hemlock is a shade-tolerant, evergreen species, while the important hardwood species in these stands--red oak, red maple, black birch, paper birch, and black cherry--are deciduous species of intermediate to low shade tolerance, with much greater juvenile rates of height growth than that of hemlock.

This experiment is possible because of the regeneration characteristics of the important species. Hemlock, red oak, red maple, black birch, and black cherry frequently occur as seedlings beneath the canopies of older stands and seem to require such advance-growth status to successfully regenerate following disturbance. Hemlock seedlings often occur beneath canopies in a patchy distribution. Seedling establishment appears to be restricted to limited areas surrounding hemlock that act as seed sources (Harvard Forest records 1940, Winer 1955). The patchiness may be further enhanced because hemlock usually occurs in a subordinate canopy position, but produces seed only when in an overstory position. Thus, when the overstory is removed, new stands are composed predominantly of hardwood species, but contain an irregular distribution of hemlock which is correlated not to site, but to the presence of overstory hemlocks in the previous canopy.

This situation allows a comparison of adjacent hardwood and hemlock-hardwood stands of the same age and site. Stand yields cannot be compared according to varying proportions of hemlock and hardwood as in replacement series studies, since initial regeneration density of each species is not known. Rather, comparisons are made simply between pure hardwood stands and mixed stands. Also, the total initial density of regeneration is not known, but minor variations among plots should have little effect on final stand yield. Higher mortality rates in stands of greater initial density cause differences among stands to disappear quickly (Harper 1977, Curtis and Reukema 1970).

In this study, two sets of stands were compared. Each set consisted of a hardwood stand and an adjacent hemlock-hardwood mixture. All grow on thin till soils. One set was 44 years old, and the other 87. A further direct comparison of the growth of mixed stands with that of pure hemlock was not possible because hemlock rarely occurs in that form. However, an indirect comparison was made using yield tables developed by Merrill and Hawley (1924) from measurements of occasional groups or small stands of pure hemlock on sites similar to those used for this study.

STUDY SITES

The two sets of stands examined in this study were on the Harvard Forest and the Great Mountain Forest. The Harvard Forest stands were 44 years old, resulting from overstory destruction from hurricane winds in 1938. The Great Mountain Forest stands, age 87, resulted from clearcutting in 1895. The present stands had not received any silvicultural treatment, and all sampled parts had grown as fully stocked stands. In each case, areas of the hardwood and hemlock-hardwood stands were distributed across a slope in an irregular pattern, within a single soil type. The two hemlock-hardwood stands were described in Chapter 2, and the adjacent hardwood stands differed only in lacking hemlock. The climate, soil, and disturbance histories of the mixed stands were described in that chapter and apply to the adjacent hardwood stands as well.

METHODS

Stand measurements. In each set of stands, a series of plots was located along a systematic grid. Plots were aggregated into stands according to the presence or absence of hemlock. Plots with only sparse hemlock (three stems or less on a plot) were included in hardwood stands. If a plot clearly fell in a borderline situation, where part contained dense hemlock and part lacked hemlock entirely, it was omitted from either category. Twenty plots were measured in the Harvard Forest stands and 32 at the Great Mountain Forest.

Different plot measurement techniques were used for the two sites. In the younger stands, circular 0.01 ha plots were established and all living trees at least 1.3 m in height were measured. In the older stands, the variable-radius-plot method was employed, using a prism with basal-area factor of 2.3 m /ha. All living trees detected with the prism were measured, thus limiting the data to those at least 1.3 m in height. There were no important numbers of tree seedlings or shrubs below 1.3 m in height in any stands. Diameter at breast height and total tree height were measured for all trees within the plots.

A subsample of trees was chosen randomly for age measurement. For these, an increment core was taken as near to the ground as possible (about 30 cm above ground level.) A second subsample was selected for measurement of basal area growth, apportioned among species according to the relative basal area importance of each. For each tree, two increment cores oriented at right angles to one another were extracted, each containing at least the last 10 years of growth.

Measurements were made in these stands in 1982. During 1980 and 1981 the stands had been severely defoliated gypsy moths. Since the purpose of these observations was to determine the production of fully foliated stands in which no canopy gaps developed, the measurements took defoliation into account in two ways. First, several dominant oak trees had recently died, due apparently to defoliation; these were counted as living trees. Second, present diameter growth rates could not be estimated by averaging the most recent five years of growth, since growth rings during the last two years were severely reduced in width due to defoliation. Instead, the growth from 1975 through 1979 was used, these being the last 5 years unaffected by defoliation. Thus, estimates of stand parameters reflect growth unaffected by defoliation.

Data analysis. Biomass calculations, estimating total aboveground dry weight of individual trees including foliage, were made using regression equations developed by Monteith (1979). These equations were constructed using weighted linear regression analysis with breast-height diameter and height as independent variables. They were developed by felling and weighing entire trees, sampled from locations throughout New York State. The equations are given in Appendix 6. All trees 1.3 m and taller were included in the biomass estimates.

Similarly, the wood volume of individual trees was estimated using non-linear regression equations developed by Scott (1981). These equations, also given in Appendix 6, use breast-height diameter and stem length from the top of a 30.5-cm stump to an upper limit of 10 cm outside-bark stem diameter as the two independent variables, and give estimates of total cubic-meter wood volume (excluding bark) within that length of stem. Only trees 12.7 cm and greater in diameter were included in volume calculations. Data for the equations were collected as part of the Northeast Forest Survey of the U.S. Forest Service, including measurements from 14 northeastern states.

Basal-area-growth equations were developed for each important tree species in the stands. Average annual diameter growth, measured for the period 1975-1979 from the two increment cores of each subsampled tree, served as an estimate of current diameter growth rate. This was converted to current basal area growth for each of these trees. Their annual basal area growth was then related to their 1982 basal area by linear regression, following logarithmic transformation of both variables. The current annual basal area growth for each tree in the full sample was then predicted using these equations; regression test statistics are given in Appendix 7. The growth of species that occurred in only small numbers in these stands was calculated from the most appropriate of these equations, based upon 2-10 sample trees for each of these minor species.

Current annual basal area increment for each stand was then calculated by the following steps:

1. for each tree in the sample plots, inside-bark basal area was calculated using the equations in Appendix 8;
2. inside-bark basal area was increased by the annual increment calculated using the equations derived from the subsample of current growth rates, as described above;
3. new outside-bark basal area was calculated using equations in Appendix 8;

4. original (measured) basal area was subtracted from new outside-bark basal area for each tree, and this basal area increment was summed for all trees in sample plots of each stand.

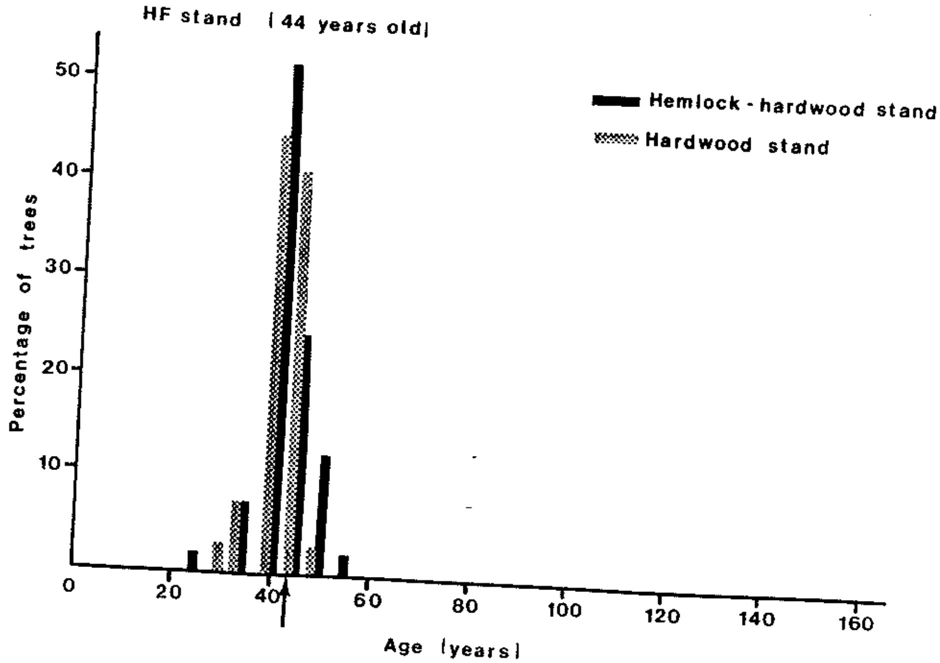
Estimates of basal area increment for each stand thus include growth of both wood and bark. They do not included losses due to mortality.

Current annual increment of volume for each stand was estimated by calculating the volume of each tree in sample plots after current annual basal area increment was added, and subtracting the original volume. Similar calculations were made for biomass. This method of calculation includes estimates of plant material only in relatively permanent tissues--annual fruit and foliage production are not considered. For this reason, biomass increment as discussed in this chapter is not equivalent to net primary production.

In all statistical analyses, standard error calculations reflect the variance among plots within each stand, not that introduced by use of regression equations.

RESULTS

Stand characteristics. Age distributions of all four stands are shown in Figure 24. No important differences existed between the ages of hardwood and hemlock-hardwood stands in either set. Nearly all stems began growth shortly before or after the time of the initiating disturbance. Many of the stems occurred as advance growth, 10 to 20 years old at the time of disturbance. Many stems of the age class just following disturbance were hardwoods which had also been advance



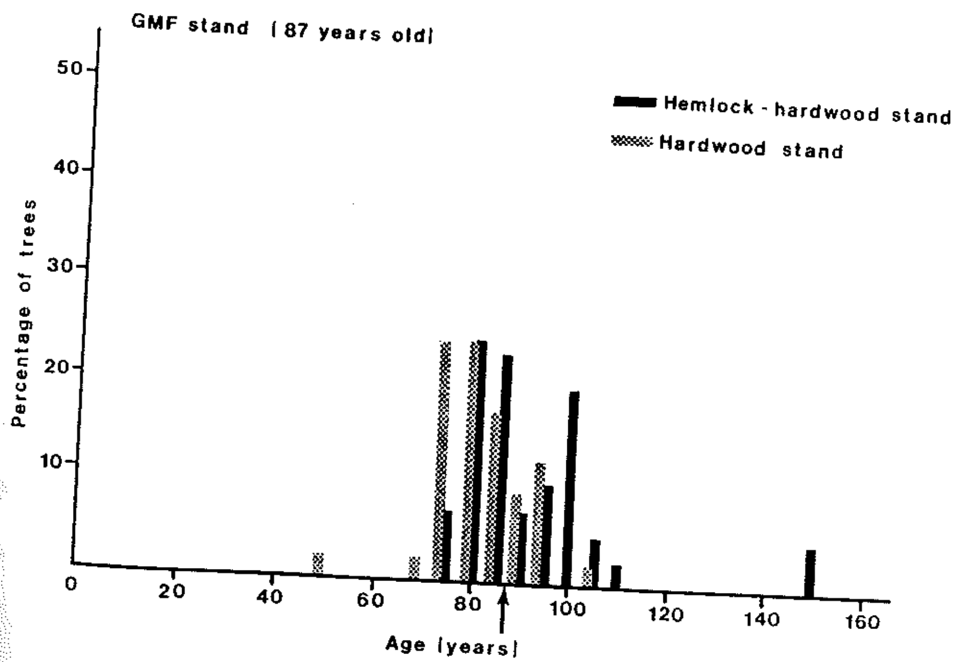


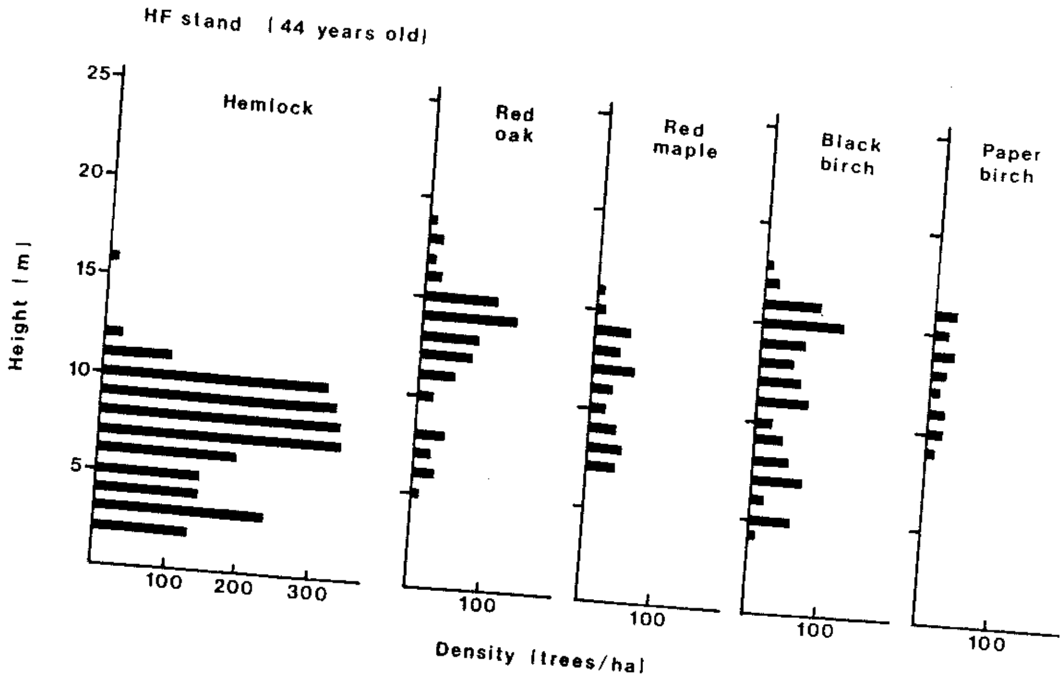
Figure 24. Distribution of ages of sampled trees in Harvard Forest (HF) and Great Mountain Forest (GMF) stands, by 5-year age classes. Arrows denote times of stand-initiating disturbances.

growth, but which had sprouted after being damaged during overstory removal.

Height distributions in the hemlock-hardwood stands (Figures 25 and 26) show that hemlock occurred almost exclusively at heights of 12 m and less in the younger stand and primarily less than 15 m in the older one, although a number of hemlocks did occur in the overstory canopy of the older stand at heights of 15-18 m. Red oak, paper birch, and black birch dominated the upper stratum in the younger hemlock-hardwood stand, as did red oak and black cherry in the older stand. With the exception of hemlock, height distributions in the hardwood stands were similar to those in adjacent hemlock-hardwood mixtures. In the hardwood stands, no species occupied the understory position in numbers comparable to those of hemlock.

Only minor differences existed in densities of hardwood species between adjacent hardwood and hemlock-hardwood stands (Table 6). However, because of the large number of hemlocks, the mixed stands had much greater total stem density than adjacent hardwood stands. Hardwood stands contained only 67% and 58% as many stems/ha as the mixed stands in the younger and older comparisons, respectively. Most hemlocks were in the smaller diameter classes--5 to 10 cm at age 44 and 5 to 15 cm at age 87. Among hardwoods, more red oak occurred in larger diameter classes than did other species; even paper birch and black cherry, which generally occurred in the upper canopy with oak, had smaller diameters.

Yield. Figure 27 shows comparisons of basal area yield between adjacent stands of both ages. Among hardwood species, only beech in the older stands showed a significant difference (greater in the hard-



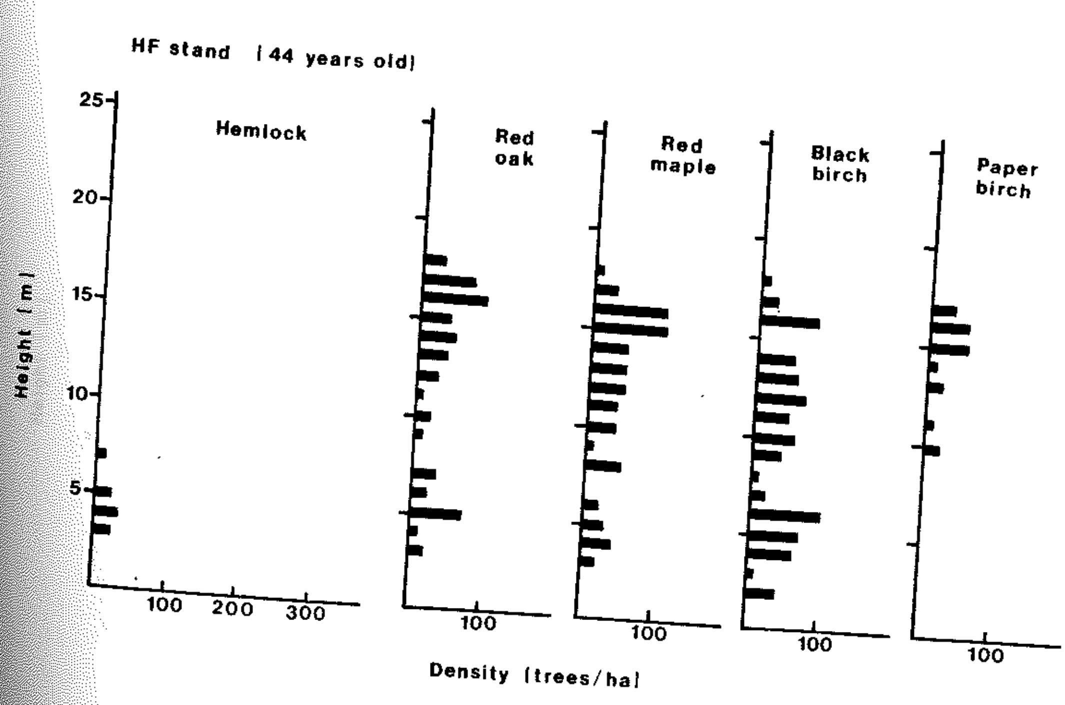


Figure 25. Tree density distributions of Harvard Forest stands, by species and one-meter height class. Hemlock-hardwood stand above, hardwood stand below.

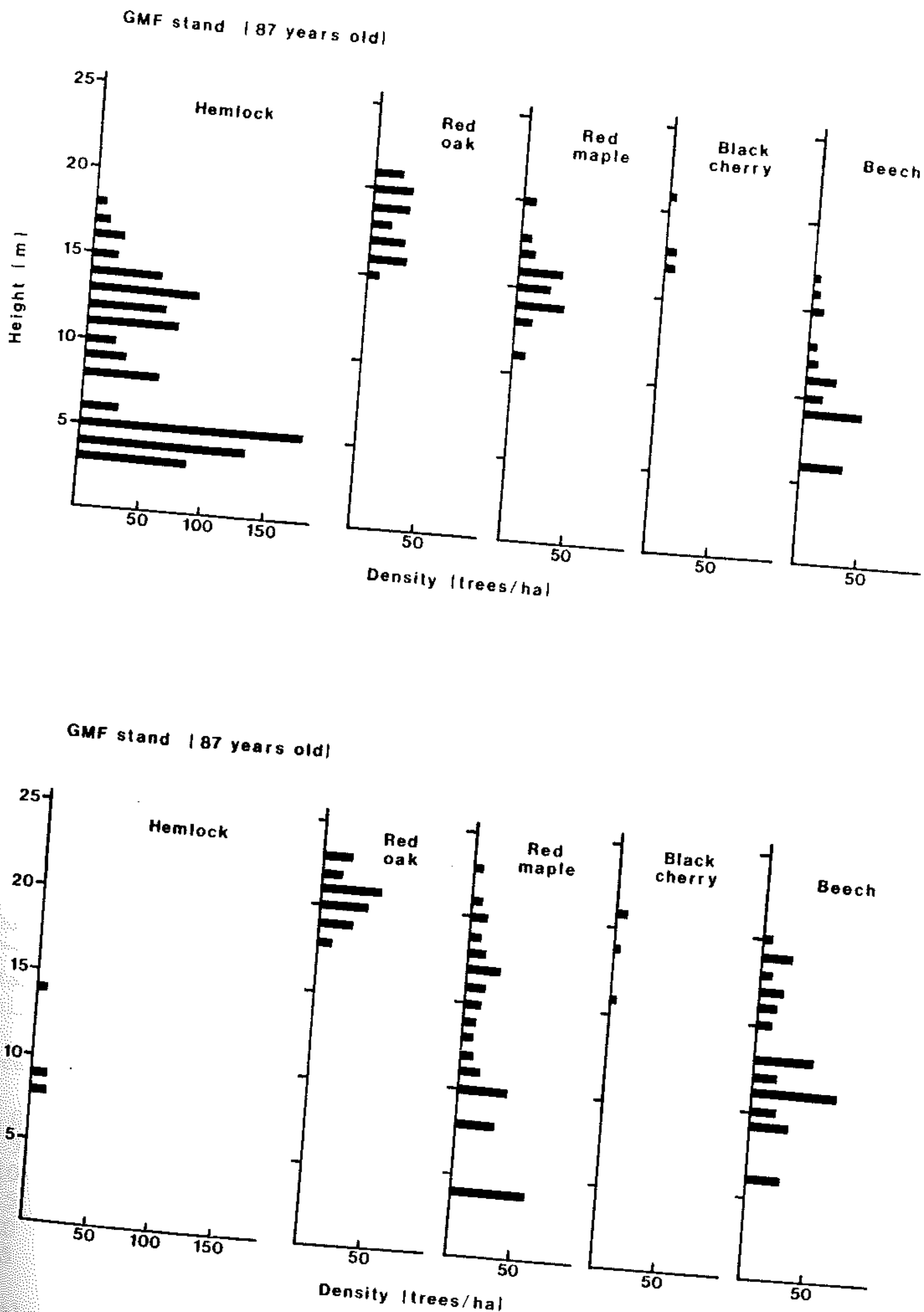


Figure 26. Tree density distributions of Great Mountain Forest stands, by species and one-meter height class. Hemlock-hardwood stand above, hardwood stand below.

Table 6. Tree density distribution by species and breast-height diameter class in hardwood and hemlock-hardwood stands; totals include minor species not listed separately in the tables.

HARVARD FOREST HEMLOCK-HARDWOOD STAND (44 years old)

Diameter class (cm)	Hemlock	Red oak	Red maple	Paper birch	Black birch	Total
	Trees per hectare					
0	80				20	100
5	600	90	90	20	280	1180
10	830	130	180	100	300	1580
15	480	170	60	40	120	930
20	170	180	10		10	370
25	10	40				50
Total	2170	610	340	160	730	4210

HARVARD FOREST HARDWOOD STAND (44 years old)

Diameter class (cm)	Hemlock	Red oak	Red maple	Paper birch	Black birch	Total
	Trees per hectare					
0			20		20	80
5	50	150	150		340	1020
10	30	80	290	50	280	940
15		120	110	130	100	480
20		150	70	10	10	240
25		40				40
Total	80	540	640	190	750	2800

Table 6. (continued)

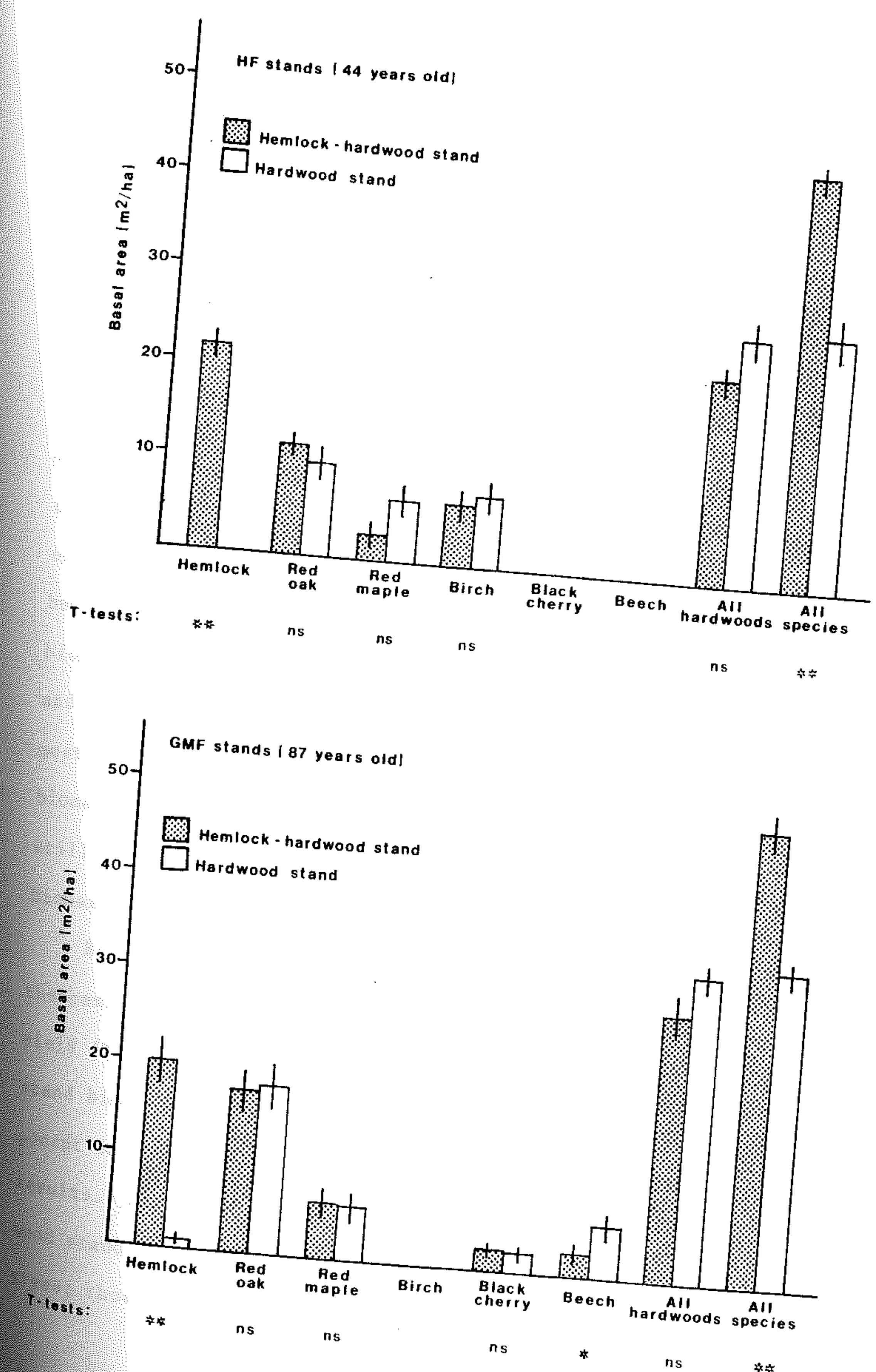
GREAT MOUNTAIN FOREST HEMLOCK-HARDWOOD STAND (87 years old)

Diameter class (cm)	Hemlock	Red oak	Red maple	Black cherry	Beech	Total
	-----	-----	Trees per hectare	-----	-----	-----
0						0
5	283				64	347
10	127		12		13	153
15	168		88		62	317
20	159	14	40		17	231
25	81	25	27	14	5	153
30	39	36	15	8		100
35	14	38	4	1		57
40	8	34	3	3	1	50
45	5	23		2	1	30
50	3	3		1		7
55	2	2				4
60		1				1
Total	885	176	190	29	164	1450

GREAT MOUNTAIN FOREST HARDWOOD STAND (87 years old)

Diameter class (cm)	Hemlock	Red oak	Red maple	Black cherry	Beech	Total
	-----	-----	Trees per hectare	-----	-----	-----
0						0
5			58			58
10			81		197	296
15	22	7	32		19	88
20	4		62	4	61	137
25		19	21	6	10	60
30		30	12	3	12	62
35		37	3	7	3	50
40		45	3		3	51
45		15		2		18
50		9		3		12
55		3				3
60	1	1				2
65						0
70	1					1
Total	27	167	273	25	306	838

Figure 27. Basal area yields of Harvard Forest (HF) stands and Great Mountain Forest (GMF) stands. Vertical lines show ± 1 standard error unit. T-test results are from comparisons between hemlock-hardwood and hardwood stands by each species or species group: ns = no significant difference, * = significant difference at P = .05 level, ** = significant difference at P = .01 level. Values for birch include both paper birch and black birch.



wood stand) between adjacent stands, and this was small compared to total stand basal area. At both ages, the total basal area of the hardwood component in the mixed stand was somewhat less than that of the total hardwood stand, but these differences were not statistically significant. Stand comparisons including all species show that the mixed stands produced 64% and 43% greater basal area yield than adjacent hardwood stands in the 44- and 87-year old stands, respectively.

For the younger stands, results were similar in terms of stemwood volume and total aboveground biomass yield (Tables 7 and 8). The contribution of hemlock to total stand yield was less in terms of volume or biomass than of basal area for three reasons: 1. the wood of hemlock is considerably less dense than that of hardwoods, reducing biomass per unit basal area; 2. many hemlock were below 12.7 cm dbh, and trees of this size were not included in volume calculations; and 3. most hemlocks were shorter than hardwoods, again reducing volume or biomass per unit of basal area. However, the hemlock-hardwood mixture still produced significantly higher yields--29% in volume and 27% in biomass--compared to the hardwood stand (see Tables 7 and 8).

Results from the older stands showed a 19% greater volume yield in the hemlock-hardwood mixture (Table 7), but only an 11% greater biomass yield (Table 8). Also, unlike other stand comparisons, the hardwood stand biomass was significantly greater than that of the hardwood component of the mixture. Two factors apparently produced these different results. First, beech had a significantly higher biomass in the hardwood stand than in the mixed stand, largely in the form of understory trees; thus, the additional hardwood production was in part the result

Table 7. Stemwood volume[a] (m^3/ha) of hemlock-hardwood mixed stands and hardwood stands. Each table gives mean, standard error of mean, and results of t-tests comparing mixed stand with hardwood stand by species or species group: ns = not significantly different, ** = significantly different at P = .05 level, ** = significantly different at P = .01 level. Data for "all species" and "all hardwoods" include minor species not listed separately in table.

Harvard Forest stands -- 44 years old

	Mixed stand		Hardwood stand		
	mean	(s.e.)	mean	(s.e.)	
Hemlock	58.2	(3.9)	0.0	--	**
Red oak	61.9	(5.3)	59.9	(9.4)	ns
Red maple	7.7	(6.3)	27.1	(8.6)	ns
Birch[b]	22.2	(4.5)	30.3	(7.8)	ns
All hardwoods	95.4	(11.0)	120.8	(10.7)	ns
All species	155.6	(9.6)	120.8	(10.7)	*

Great Mountain Forest stands -- 87 years old

	Mixed stand		Hardwood stand		
	mean	(s.e.)	mean	(s.e.)	
Hemlock	99.4	(14.1)	6.1	(3.0)	**
Red oak	134.6	(15.6)	149.6	(19.3)	ns
Red maple	39.3	(9.8)	39.8	(9.9)	ns
Black cherry	18.3	(5.3)	19.7	(6.2)	ns
Beech	12.7	(4.6)	36.4	(9.9)	*
All hardwoods	206.6	(15.4)	251.9	(11.3)	*
All species	306.6	(11.3)	258.0	(12.1)	**

[a] includes wood in trees 12.7 cm dbh, from top of 30.5 cm stump to an upper limit of 10 cm outside-bark stem diameter.

[b] includes both paper birch and black birch.

Table 8. Aboveground biomass (t/ha) of hemlock-hardwood mixed stands and hardwood stands. See legend for Table 7.

Harvard Forest stands -- 44 years old

	Mixed stand		Hardwood stand		
	mean	(s.e.)	mean	(s.e.)	
Hemlock	63.4	(4.1)	0.9	(0.5)	**
Red oak	65.1	(5.8)	60.3	(9.6)	ns
Red maple	10.6	(5.3)	29.3	(8.1)	ns
Birch	36.8	(8.3)	41.9	(9.2)	ns
All hardwoods	117.8	(7.2)	141.8	(11.1)	ns
All species	182.4	(5.3)	143.6	(11.4)	**

Great Mountain Forest stands -- 87 years old

	Mixed stand		Hardwood stand		
	mean	(s.e.)	mean	(s.e.)	
Hemlock	74.2	(8.8)	4.4	(2.2)	**
Red oak	124.9	(14.5)	137.7	(17.8)	ns
Red maple	29.9	(7.3)	31.0	(7.5)	ns
Black cherry	14.6	(4.2)	15.7	(5.0)	ns
Beech	13.5	(4.8)	36.2	(8.7)	*
All hardwoods	184.3	(13.9)	228.2	(10.6)	*
All species	258.5	(11.0)	232.6	(10.8)	ns

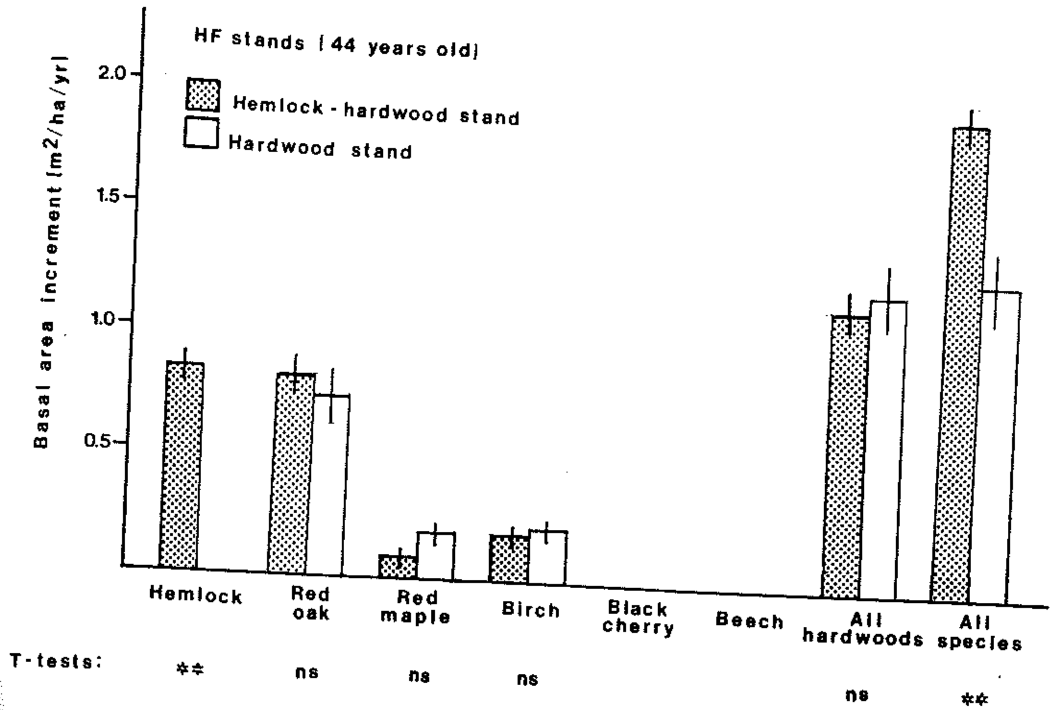
of a species partially replacing the hemlock understory, rather than higher production in the overstory hardwood stratum. Second, a portion of the overstory of the older hemlock-hardwood stand was composed of hemlock (18% by number and 20% by basal area). This partial hemlock overstory would affect the biomass of the stand without affecting basal area or volume, because of the difference in wood density. Measures made in this stand showed that red oak and hemlock in overstory positions had approximately the same horizontal crown area per unit of basal area; however, the biomass of an individual hemlock is only about 60% of that of an oak of similar basal area and height (Monteith 1979). To test if this had an important influence on total biomass yield, the biomass of overstory hemlocks was calculated as if they were red oak. With this adjustment, the hemlock-hardwood mixture would have a 13% greater biomass yield (270 t/ha compared to 234 t/ha), which would be a statistically significant difference.

These calculations represent a conservative estimate of potential biomass in the 87-year-old mixed stand if no overstory hemlocks were present, and instead a complete upper story of hardwoods had developed as in the younger mixed stand. The estimate is conservative because most overstory hardwoods had one or more hemlocks growing beneath them, occupying the same ground space, whereas over-story hemlocks had deep crowns extending close to the ground, with no understory trees beneath them. The potential production of these extra understory hemlocks is not considered in these calculations.

Current increment. The higher yields of hemlock-hardwood stands could have developed in two ways. First, the mixed stands could have greater annual production than hardwood stands throughout the life of the stands, and so contain greater volume or biomass at any given time. Alternatively, both kinds of stands could have produced biomass at approximately equal rates, with hemlock-hardwood mixtures having a greater yield at any time because of differential rates of survivorship among species. This was considered a possibility because hemlock can survive at low light levels with little growth, for much longer periods than associated hardwood species. Hemlock may add little to annual production in any year, but may increase yield simply because it survives for long periods and is present to be measured or recovered.

To assess the relative importance of these two alternative explanations, current production levels were assessed. Basal area growth rates were measured for all important species across the range of stem sizes present. Regression equations relating current basal area growth to basal area were developed for each species and used to estimate present growth for each tree in the sample plots, as described previously.

Figure 28 shows current annual basal area increment for all stands. Basal area increment in hemlock-hardwood mixtures was greater by 52% in the younger stands and by 38% in the older stands than adjacent hardwoods; these relationships are similar to values for basal area yield. As in yield comparisons, increment within the hardwood component of the mixed stands was slightly lower than that of the total hardwood stand, but the difference was not significant. Thus, the contribution of hemlock to current increment in the mixed stand was considerable, and yield differences were not due simply to hemlock's low mortality rate.



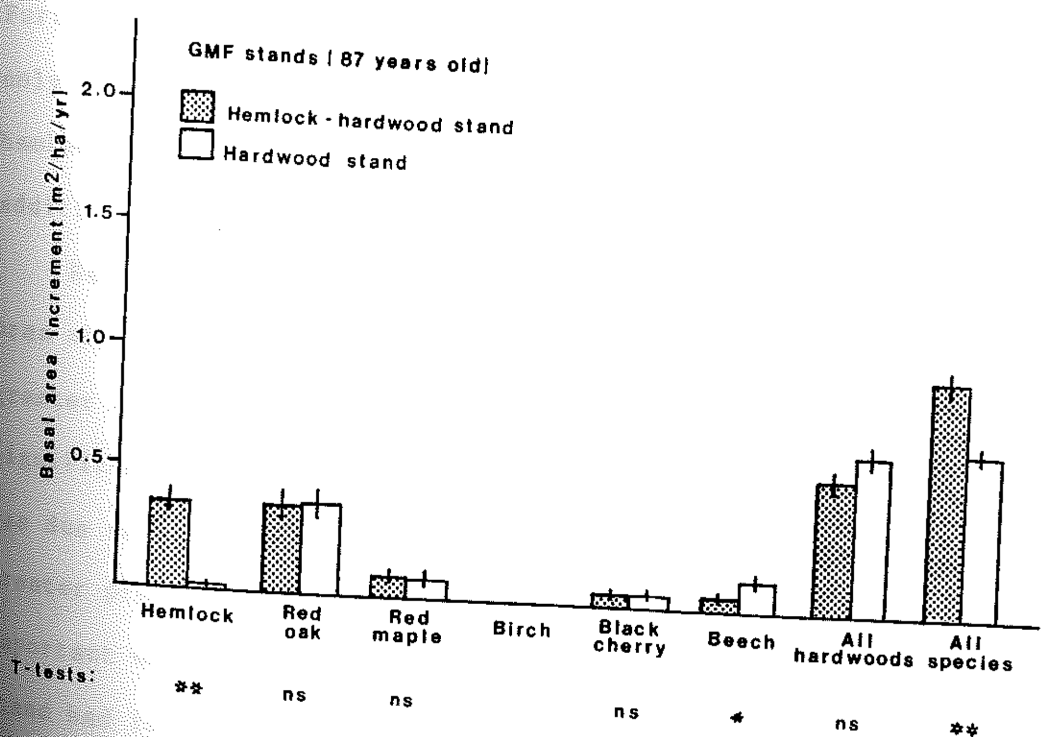


Figure 28. Current annual basal area increment for Harvard Forest (HF) stands and Great Mountain Forest (GMF) stands. See legend for Figure 27.

When current increment was assessed in terms of volume and biomass, similar patterns became apparent (Tables 9 and 10), although the importance of hemlock was less for reasons described above concerning yields. Greater variability in estimates of production resulted in total stand differences falling below the level of statistical significance in most cases.

DISCUSSION

Yield comparisons. In the 44-year-old stands, the hemlock-hardwood mixture had greater basal area, volume, and biomass than the adjacent hardwood stand growing under the same site conditions. Furthermore, the yield of the hardwood component of the mixed stand was only slightly less than that of the adjacent hardwood stand. Thus, the hemlock yield can be considered largely, though not entirely, as additive to that of the hardwoods.

Results were similar in the 87-year-old stands, in terms of basal area and volume yield, but not of biomass--hardwood stand biomass was greater than that of the hardwood component of the mixture, and was not significantly different from the total biomass of the mixture. This was due in part not to greater yield in upper canopy hardwoods, but to greater presence of a beech understory in the hardwood stand. Also important was the fact that the cutting which initiated the older mixed stand had left some residual hemlocks that eventually came to occupy space in the overstory canopy. Data show that for a given amount of crown space in the overstory canopy, oak had more biomass than hemlock.

Table 9. Current annual increment of stemwood volume ($m^3/ha/yr$) of hemlock-hardwood mixed stands and hardwood stands. See legend for Table 7.

Harvard Forest stands -- 44 years old

	Mixed stand		Hardwood stand		
	mean	(s.e.)	mean	(s.e.)	
Hemlock	1.7	(0.1)	0.0	--	**
Red oak	4.6	(0.4)	4.5	(0.7)	ns
Red maple	0.2	(0.2)	0.7	(0.2)	ns
Birch	0.6	(0.1)	0.8	(0.2)	ns
All hardwoods	5.7	(0.6)	6.2	(0.7)	ns
All species	7.4	(0.5)	6.2	(0.7)	ns

Great Mountain Forest stands -- 87 years old

	Mixed stand		Hardwood stand		
	mean	(s.e.)	mean	(s.e.)	
Hemlock	1.7	(0.2)	0.1	(0.1)	**
Red oak	2.8	(0.3)	3.0	(0.4)	ns
Red maple	0.6	(0.1)	0.6	(0.1)	ns
Black cherry	0.3	(0.1)	0.3	(0.1)	ns
Beech	0.3	(0.1)	0.8	(0.2)	*
All hardwoods	4.0	(0.3)	4.9	(0.3)	ns
All species	5.7	(0.3)	5.0	(0.3)	*

Table 10. Current annual increment of aboveground biomass (t/ha/yr) of hemlock-hardwood mixed stands and hardwood stands. See legend for Table 7.

Harvard Forest stands -- 44 years old

	Mixed stand		Hardwood stand		
	mean	(s.e.)	mean	(s.e.)	
Hemlock	2.2	(0.1)	0.0	--	**
Red oak	5.1	(0.5)	4.8	(0.8)	ns
Red maple	0.4	(0.2)	0.8	(0.2)	ns
Birch	1.1	(0.3)	1.2	(0.3)	ns
All hardwoods	6.9	(0.4)	7.4	(0.8)	ns
All species	9.1	(0.3)	7.5	(0.9)	ns

Great Mountain Forest stands -- 87 years old

	Mixed stand		Hardwood stand		
	mean	(s.e.)	mean	(s.e.)	
Hemlock	1.3	(0.2)	0.1	(0.04)	**
Red oak	2.6	(0.3)	2.8	(0.4)	ns
Red maple	0.4	(0.1)	0.4	(0.1)	ns
Black cherry	0.2	(0.1)	0.3	(0.1)	ns
Beech	0.3	(0.1)	0.8	(0.2)	*
All hardwoods	3.6	(0.3)	4.4	(0.3)	*
All species	4.8	(0.2)	4.5	(0.3)	ns

Thus, presence of hemlock in an overstory position resulted in reduced overstory hardwood production in the mixed stand. These two factors appear to account for the difference in results between the study sites.

A direct comparison of mixed stands with pure hemlock stands was not possible because hemlock rarely occurs in the region as even-aged, pure stands, and was not present in that form on the study sites. However, a yield study of hemlock in southern New England (Merrill and Hawley 1924), based upon the growth of occasional small stands of pure hemlock, enables an indirect comparison.

Basal area and volume yield of pure hemlock stands of the same age and site-quality class (based upon height growth of dominant trees) can be taken directly from the Merrill and Hawley yield tables. Details of the interpretation of the yield tables are given in Appendix 9. Basal area estimates are directly comparable to those of the current study. Volume estimates in the hemlock yield tables include wood in the stump and to the top of the stem, and so are somewhat higher for a tree of given dimensions than estimates for the current study, which exclude both the stump and stemwood less than 10 cm diameter.

Estimates of biomass yield for pure hemlock can be derived from the yield tables using the "mean-tree" approach (Madgwick 1970, Parde 1980). In this method, the biomass of the tree of mean basal area (which approximates the tree of mean biomass in even-aged, single-species stands) is determined, and is multiplied by tree density to estimate total stand biomass. For this study, the biomass of the tree of mean basal area, as derived from the yield tables, was calculated using the equations of Monteith (1979).

Estimates of basal area, volume, and biomass yield for pure hemlock stands are given in Table 11, together with the results for stands in the current study. These suggest that the basal area of pure hemlock stands would exceed that of hardwood stands of similar age, but would be less than that of mixed stands. For volume, hemlock stands and mixtures are comparable (recognizing the slight difference in volume estimation methods between studies), and both exceed the volume yield of the hardwood stands. In biomass, hemlock stands appear to have lower yields than either hardwood or mixed stands.

To test the sensitivity of this method of estimating hemlock yield to determination of site-quality class, similar calculations were made for hemlock stands of the next higher site class (see Appendix 9). In this comparison, although the height of hemlock dominants reported from the yield tables considerably exceeds that found in the mixed stands, estimates of biomass yields for pure hemlock stands (142 t/ha at age 44, 246 t/ha at age 87) still do not exceed those of the mixed stands measured in the current study.

Niche separation in mixed stands. When results similar to these have been obtained in replacement series experiments with herbaceous species, reduction in competitive interference among species has been related primarily to vertical separation of foliage and roots, and to variations in timing and duration of growing season. Several of these aspects of niche separation also occur in the mixed forest stands of this study. Probably most important are the differences in height of foliage among species. Measures of total tree height (Figures 25 and 26) show that a high proportion of hemlock occurred in the lower canopy layers beneath a hardwood overstory. In Chapter 2, it was shown that

Table 11. Summary of basal area, stemwood volume, and aboveground biomass yields of stands of different species composition. Data for hardwood and hemlock-hardwood stands are from current study; data for pure hemlock stands are from Merrill and Hawley (1924).

	Basal area (m^2/ha)	Volume (m^3/ha)	Biomass (t/ha)
44-year-old stands			
Hardwood	27	121	144
Hemlock-hardwood	44	156	182
Hemlock	30	159	102
87-year-old stands			
Hardwood	34	258	233
Hemlock-hardwood	48	306	259
Hemlock	44	320	189

[a]Volume estimates for hardwood and hemlock-hardwood stands include wood in stem from top of 30.5 cm stump to an upper limit of 10 cm stem diameter; estimates for hemlock stands include wood in stump and to top of stem, and so are somewhat higher for a tree of given dimensions. Both include only trees 12.7 cm and greater in breast-height diameter.

the hardwoods, primarily red oak, grew into overstory positions early in the development of the mixed stands, and later, the tops of the tallest hemlocks reached into the lower layers of hardwood foliage. Thus, the bulk of hemlock foliage occurred in a lower stratum, with only limited vertical overlap with the foliage of the taller hardwoods. In contrast, hardwood stands tended to lack a comparable understory stratum of foliage. Thus, differences in vertical stratification of the canopy provides a reasonable explanation for differences in production between mixtures and hardwood stands. Because of slow juvenile height growth and high degree of shade tolerance, hemlock will survive beneath the hardwoods and capture the light not intercepted by oak, maple, and other hardwood species of the overstory. Thus, the growth of hemlock is an addition to stand production which does not greatly reduce the production of the other species. In Harper's terms, the production of the lower stratum of trees depends upon "the crumbs from the rich man's table" (Harper 1977, p. 717).

Reasons for the increased production of mixed stands over pure hemlock stands are not as evident. The characteristic of a pure stand of tolerant species of maintaining a dense canopy and intercepting a high proportion of available sunlight may suggest that it would have highest production. However, studies comparing the physiology of sun- and shade-adapted plants, reviewed by Boardman (1977), indicate that a stratified canopy with sun-adapted foliage in the upper stratum and shade-adapted foliage in the lower may achieve higher rates of net photosynthesis than a pure stand of shade-adapted species, even if the total amount of intercepted light is no greater. Foliage of shade-adapted plants reaches the photosynthetic compensation point at low light levels, but it also reaches light saturation under lower light conditions than foliage of sun-adapted species. At high light levels, sun-adapted foliage can achieve higher rates of net photosynthesis. This suggests that hardwood foliage in the upper levels of the hemlock-hardwood canopy uses intercepted light more efficiently than the upper levels of a hemlock canopy, while shorter hemlock foliage in both kinds of stands uses the remaining light with equal efficiency.

Differences in the duration of growing season among species may complement effects of foliage stratification in increasing the production of hemlock-hardwood mixtures. Many evergreen trees show biomass increase during months when deciduous species are not in leaf, as long as temperatures are not too low (Kramer and Kozlowski 1979). Hemlock can probably achieve considerable net photosynthesis during late spring and early autumn, when free of overstory shading. Furthermore, the dominant member of the overstory, red oak, leafs out later in the season than many of the associated hardwood species. At the Harvard Forest, phenology records (Swan 1970) show that leaves of red oak reach full expansion from May 29 to June 13, approximately 7 to 13 days after red maple and black birch growing on the same sites. Thus, with a high proportion of oak in these stands, there will be a longer period each spring when understory hemlock receives little overstory shading, at a time when temperatures would usually not be restrictive to photosynthesis.

Finally, differences in rooting depth may play a role in causing species mixtures to more fully utilize a site by reducing direct competition for nutrient and water absorption. Work by Lyford (1980) has shown that red oak produces a strong taproot and a network of woody lateral roots at soil depths of 20-50 cm, while red maple and other hardwood species produce laterals close to the surface of the mineral soil. Hemlock root systems tend to be quite shallow on some sites, to the extent that it is more vulnerable to windthrow than most associated species; it may thus be comparable to the root system of red maple, indicating that a vertical separation exists between the root systems of the two major species, red oak and hemlock. However, Lyford (1980) found that, although the main lateral roots of oak are rather deep, they produce higher order laterals that grow upward and elaborate networks of non-woody feeder roots in the top layer of mineral soil and in the forest floor. Thus, the importance of differential depth of woody root systems for reducing competitive interference in nutrient and water absorption is not clear.

Results from other mixed forest stands. At various times, mixed stands have been planted experimentally, most often composed of two coniferous species. Many of these attempts at establishing mixed plantations have failed because only one of the planted species survived for long. In some cases, this occurred because one of the species was not suited to the site, or was attacked by a disease or insect. Other causes are more informative concerning mixed stand development, and include two groups:

1. the species which developed into the overstory stratum was planted too densely, so that the understory, even though composed of a shade-tolerant species, could not survive.
2. the mixture was composed of two relatively shade-intolerant species, so that even minor differences in height growth between the species caused high mortality in the slower growing species.

In other cases, both species survived to maturity, but had been planted in groups in checkerboard patterns or alternating multiple rows of each species, so that the opportunity for developing a stratified canopy and reducing intraspecific competition was greatly diminished. For these reasons, limited opportunities remain from these plantation experiments for comparing the productivity of mixtures with that of pure stands.

However, results do exist from a number of German and Swiss studies which address this problem; these have been reviewed by Assmann (1970). Stands in these studies had received repeated, light thinnings. Such practice tends to salvage imminent mortality, but does not leave any significant gaps in the crown canopy. The trees removed in these thinnings were included as part of total yield, thus giving a complete account of stand production. Yield was measured in stemwood volume (including branchwood in some cases), and was converted to oven-dry weight using estimates of average wood density for each species. In most cases, as in the present study, data were available only for the mixed stand and one of the constituent species growing in a pure stand on the same site.

Four of these experiments compared pure stands of the shade-intolerant Scots pine with mixtures of Scots pine and either Norway spruce or European beech as the shade-tolerant component. These showed that the presence of either of the latter species in an understory position decreased the production in both volume and biomass of the pine overstory a small amount, but the understory production more than compensated for this decrease; mixed stands had yields in the range of

50% greater by biomass than pure pine. No direct comparison with the growth of pure spruce or beech stands was made.

Mixtures of a sessile oak overstory with a beech understory gave similar results. Under a regime of light thinning, the mixed stand produced greater yields than pure oak stands. Again, no comparison with a pure beech stand growing on the same site was made.

One experiment cited by Assmann did compare mixed stands with pure stands of the shade-tolerant component species. In this case, production in a mixture of European larch and beech exceeded that from a pure beech stand by 18% in terms of stemwood biomass at age 90. Other yield studies showed that mixtures of larch and various shade-tolerant understory species considerably outproduced pure larch stands, indicating that the mixture had higher yields than either pure stand.

Finally, one experiment included direct comparisons of pure stands of two species--Norway spruce and silver fir--plus their mixture, all growing on similar sites. Although Norway spruce comprises the more shade-tolerant understory component when mixed with Scots pine, it is less shade-tolerant than silver fir and has more rapid juvenile height growth. Mixtures of these two species tend to develop with a spruce overstory above a fir understory. In this experiment, the mixed stands were planted in 3- or 5-row mixtures (3 or 5 rows of spruce alternating with an equal number of fir); however, they were planted quite densely, with trees at spacings of 1.25 x 1.25 m to 1.0 x 1.0 m, and were subsequently thinned, so that development of a two-storied canopy did occur. Results showed that at age 60, Norway spruce and silver fir produced equal amounts of stemwood biomass in pure stands, but mixed stands exceeded that production by 15 to 37%.

A recent Czechoslovakian study (Poleno 1981) also included comparisons of mixed stands with pure stands of both of the constituent species. In this study, comparisons were made of canopy development and basal area yield of stands of Scots pine and Norway spruce of varying age, site quality, and species proportions. In mixed stands, spruce had slower height growth than pine in early years and formed an understory stratum by age 40. At all combinations of age and site quality, mixed stands consistently had greater basal area yield than pure stands of either species, although the difference between mixtures and pure stands of the highest yielding species was only 5% or less in all comparisons.

The evidence provided by these studies, plus the results of the present investigation, show consistency in one type of comparison: mixed stands produced greater yields than stands of the overstory species alone, measured in basal area, volume, or biomass.

The comparison of mixed stand yield with that of the shade-tolerant understory species component is not as clear. The slower juvenile height growth of these species have made them less frequently used in forestry research, so fewer comparisons are possible. However, where direct comparisons were made in the European studies cited above, mixed stands were found to have greater volume and biomass than pure stands of the shade-tolerant species; these studies involved larch-beech and spruce-fir mixtures. For the hemlock-hardwood mixtures of the present study, comparisons with yield tables for pure hemlock suggest that here too the mixtures produce greater biomass yields, although volume yields of the two types of stands would be approximately the same.

These studies do not indicate that every species mixture will outyield pure stands of the component species. Abundant evidence from experiments with herbaceous species show that mixtures involving species with little difference in morphology or phenology do not outproduce monocultures of the higher yielding species (Harper 1977). In all of the forest mixtures discussed above, component species have different growth characteristics such that a stratified canopy is formed, with one or more species of low shade tolerance in an overstory stratum above a shade-tolerant species. Evidence from other forest mixtures which have two species in the same vertical canopy stratum indicates that total stand yield will be decreased by the inclusion of the less productive species, just as was found for herbaceous species. Such evidence is provided by studies of Norway spruce and European beech (Assmann 1970). In pure stands lying adjacent on the same site, spruce outyielded beech in stemwood biomass by 10% to 100%, depending upon site characteristics. Mixtures proved to be more productive than pure spruce stands if beech remained in the understory; however, if spruce was thinned to allow beech to develop into the upper canopy stratum together with spruce, total mixed-stand yield was less than that of pure spruce. Similar results were obtained with oak-beech mixtures, where oak was thinned to increase growth of understory beech.

It is important to note that one silvicultural interest in planting mixed stands is to improve soil conditions in conifer plantations by introducing hardwoods. While this may be important in certain situations, especially in colder climates where the rate of litter decomposition may be an important limiting factor to tree growth, it does not appear to be a necessary factor for increasing stand yields. Mixtures outyielded one or both pure stands in the studies cited above, even where component species were both hardwoods or both conifers.

CHAPTER 6

Conclusions

SUMMARY OF FINDINGS

Focus of study. This study investigated the development and productivity of hemlock-hardwood stands growing on upland till soils in southern New England, on sites which had never been cleared for agriculture. These stands had originated following a single major canopy disturbance caused by logging or windstorms. Additional measurements were made in stands with these same characteristics, but which lacked hemlock.

Age structure. Stands of this kind maintained an essentially even-aged character at 44 and 87 years following canopy destruction. Stands developed from advance-growth seedlings 20 years old or younger, stump and seedling sprouts, and seedlings germinating in the first few years following disturbance. Few trees became established more than 10 years after the stand-initiating disturbance. Some older residuals, primarily hemlock, occurred scattered through the stands.

Canopy structure. The canopies of these stands were generally separated into two strata--an overstory of hardwood foliage above a hemlock understory. The upper foliage of the tallest understory hemlocks reached a short distance into the lower portions of the overstory hardwood crowns, so that a zone of overlap occurred between the strata. In the 44-year-old stand, the upper stratum consisted of red oak, red maple, black birch, and paper birch. In the 87-year-old stand, it was comprised mainly of red oak, with lesser amounts of black cherry, red maple, and hemlock. The presence of hemlock in the overstory made canopy stratification less distinct in the older stand.

Early stages of development. The initial 14 years of stand development were studied in an experimental clearcut strip, where advance growth consisted only of small red oak and hemlock, and sprouting from stumps and roots was suppressed subsequent to overstory removal. Birch and cherry species became established in large numbers, grew rapidly in height, and dominated the upper canopy by age 14. At that age, red oak, red maple, and hemlock occurred only in lower canopy positions beneath those species. Previous studies (McKinnon *et al.* 1935, Spurr 1956, Oliver 1978) have shown that where larger advance growth occurs and sprouts develop from advance growth and stumps, these species can occur in the upper stratum at age 10-15, along with the less shade-tolerant species.

The pattern of stand growth described above for the clearcut strip occurred within fences which excluded deer; regeneration was almost entirely absent outside of fences.

Late stages of development. Observations made in a 135-year-old stand showed that, in areas free of recent canopy disturbances, an overstory of hardwoods (predominantly oak) persisted above a dense understory of hemlock. A number of large hemlocks, which had apparently been present as large advance regeneration or residuals from the previous stand, also occurred in the overstory stratum. Scattered white pine, apparently the same age as the majority of the stand, grew as emergents above the main canopy level. Portions of this stand reached levels of aboveground biomass (420 to 520 t/ha) approaching the highest values reported for forests of eastern North America.

Growth rates of individual trees. Overstory red oak and black cherry exhibited rapid juvenile height growth for 30 years, followed by slower growth. Some of these trees were multiple-stemmed sprout clumps; for many of the single stems, height and diameter growth was rapid even in the first year, indicating a sprout origin from a seedling or small stump. Others developed from suppressed advance growth. Hemlock originating as small advance regeneration had slower juvenile growth, and became overtopped in the sapling stage. Although it remained that way for an extended period, it showed greater vigor than many other species in similar competitive positions. Height growth of the tallest understory hemlocks (those overtopped by hardwoods but not by other hemlocks) remained constant throughout the 87-year period of develoment studied here. After the overstory red oak and black cherry slowed from their rapid juvenile growth phase, hemlock kept pace with them in height growth, with terminals eventually reaching into the lower branches of the overstory crowns. While basal area growth of the largest understory hemlocks was lower than that of overstory oaks, it showed steady acceleration in the intermediate years (age 30-70), even though no release from overstory competition occurred.

In contrast, many other species growing in suppressed positions lapse further behind the overstory trees in height, and show only low rates of basal area growth; in some cases they do little more than survive. Red maple and black birch exhibited these responses to suppression when growing beneath the crowns of red oak (Oliver 1978).

Growth of hemlock into overstory. Hemlock developing from large advance regeneration (at least 3 m tall) or from larger understory residuals grew into the overstory stratum and maintained that canopy position at age 87. Their height growth was slower than that of dominant hardwoods, so they occurred as emergents only in early stages. By about age 40, dominant hardwoods had caught up with these hemlock in height growth.

Hemlock crown abrasion. The height growth of the tallest understory hemlocks was limited in part by breakage of their terminal shoots, apparently caused by abrasion against overstory branches. Such breakage had occurred in 11 of 12 understory trees sampled, but was absent in 13 overstory hemlocks sampled. Crowns of understory hemlocks had flat tops, and some had multiple stems in the upper portions, resulting from the release of lateral branches upon death of terminals.

Canopy structure of stands lacking hemlock. Stands which were located adjacent to the hemlock-hardwood study stands and identified as having similar site and disturbance characteristics were found to have age structure, species composition, and canopy structure similar to that of the hardwood component of the mixed stands, but dense understories were lacking. Only beech in the older stand showed significant increases in basal area, mostly in understory trees. However, no species occupied the understory in numbers comparable to those of hemlock in the mixed stands.

Stand yields. Hemlock-hardwood stands were found to have significantly greater yields, measured in either basal area or stemwood volume, than adjacent hardwood stands of the same age, site conditions, disturbance history, and species composition, except for the absence of hemlock. In the younger stands, the hemlock-hardwood mixture also showed significantly greater aboveground biomass yield than the adjacent hardwood stand. The older stand comparison similarly showed greater biomass in the mixed stand, but the difference was not statistically significant; this smaller difference was due in part to the presence of hemlock in the overstory stratum of the older stand. Hemlock has lower biomass per unit of crown space, so its occurrence in the overstory stratum would reduce stand biomass over that which would occur with a complete hardwood overstory. Also, the hardwood stand had a greater density of beech understory, partly compensating for the absence of hemlock. Comparisons with published data (Merrill and Hawley 1924) suggest that mixed stands would have greater biomass than pure hemlock stands of similar age and site quality, as well.

Analysis of current growth rates showed that in both stands, hemlock contributed to current stand basal area increment in approximately the same proportion as for stand yield. Thus, even at age 87, when most hemlocks had been in overtopped positions for 70 years, that species made up a significant proportion of stand production.

ECOLOGICAL SIGNIFICANCE

Successional patterns. Hemlock-hardwood stands originating after nearly complete canopy destruction develop according to the initial floristic composition model of succession. Red oak, red maple, black cherry, and hemlock develop mainly from advance-growth seedlings, or (for oak and maple) from sprouts arising from advance-growth seedlings or stumps of overstory trees. Cherry and birch species became established in the first years following disturbance. Subsequent changes in vegetation composition and structure result from variations among these species in rates of mortality and growth, not from further establishment of new trees. Stands which were similar in most characteristics but which lacked hemlock were also found to maintain an even-aged structure for extended periods, thus following the initial floristics successional model.

In a related study, Hibbs (1983) analyzed 40 years of records from Harvard Forest permanent sample plots located where old-field white pine stands were blown down by hurricane winds. He concluded similarly that the hardwood component of these stands was even-aged, and thus followed the initial floristics model, but that hemlock followed the relay floristics model, continuing to become established throughout the first 40 years. At the time of the hurricane, these plots had contained little hemlock regeneration, as is characteristic beneath old-field pine stands, but were found to have fairly abundant hemlock at age 40. Examination of these plot records (Harvard Forest records 1940) by this author allowed a more detailed interpretation. These indicate that hemlock establishment generally occurred only on plots where the previous stand had contained some hemlock, and nearby residual hemlocks had survived the hurricane. It is likely that these residuals are important as seed sources. On most plots, little or no hemlock occurred at age 40. This supports the observations of McKinnon et al. (1935), from an extensive examination of stands aged 1 to 45 years in the vicinity of the Harvard Forest, that hemlock is generally absent in stands which follow one generation of old-field white pine.

In summary, stands developing after a single major overstory disturbance generally maintain an even-aged structure (initial floristics model) with the presence of hemlock being dependent upon its occurrence as advance growth. Only in those areas where hemlock advance growth does not exist, but a hemlock seed source is nearby, does hemlock continue to become established after canopy destruction (relay floristics model), thus giving the stand an uneven-aged character.

Development of canopy structure. Results of the present study can be linked with those of earlier work (McKinnon *et al*. 1935, Spurr 1956, Oliver 1978, Hibbs 1983) to describe canopy structure and development in even-aged hemlock-hardwood stands developing from abundant advance growth. In such stands, sites are quickly filled by dense regeneration, comprised of both seedlings and sprouts. Young stands enter into a period of intense competition by age 10. If present, pin cherry, black cherry, and black, gray, and paper birch seedlings grow rapidly during the first few years and form much of the upper canopy stratum (McKinnon *et al*. 1935, Spurr 1956). However, no clear pattern of canopy stratification among hardwoods species is evident in these early stages. Due largely to the vigorous sprouting habit of red oak and red maple, those species keep up with the rapid juvenile height growth of birch and cherry seedlings.

Thus, in the early stages of canopy development, the stand has an undifferentiated upper stratum, composed of many species growing in height at approximately the same rate. The subsequent occurrence of various species in different canopy strata depends upon the interactions of three characteristics of each species: rate of continued height growth, degree of shade tolerance, and inherent longevity.

One set of species can tolerate suppression for only brief periods, so that any individuals not in upper canopy positions soon die. These species, which include pin cherry, gray birch, paper birch, black cherry and (to a lesser extent) red oak, are thus generally found only in the upper stratum of stands past the sapling stage. These species tend to remain in the upper canopy until they reach senescence. Of these species, pin cherry dies first, usually by age 20 to 30; gray birch lives somewhat longer, but by age 40 has disappeared from most stands (McKinnon et al. 1935). Neither of these two species was found living in the 44-year-old stand of the current study, but standing, dead stems of both were present. At this age the upper stratum thus consists of red oak, red maple, black birch, and paper birch. If present, black cherry would also likely occur in the upper canopy at this age, although for the 44-year-old study stand, this species had been eliminated by forest tent caterpillars (Malacosoma disstria) early in development (Spurr 1950).

Paper birch is longer-lived than gray birch and pin cherry, and was present in the overstory in important numbers in the 44-year-old stand, but only an occasional living paper birch was present in the 87-year-old stand. Measurements (Winer 1955) made on two plots in this stand when it was 55 years old showed that paper birch had been an important component, comprising 17% of trees in the tallest height class at that time. Dead, fallen paper birch could be found at age 87.

Red oak and black cherry are even longer-lived, and dominate the upper canopy of the 87-year-old stand. Red oak is also the dominant species of the overstory in the 135-year-old stand. It can withstand shading better than the other species in early years, but generally by age 60 is found only in the upper canopy.

Red maple and black birch also have sufficiently rapid height growth to stay in the overstory in early stages, but they gradually become overtopped when competing with red oak (Oliver 1978). In contrast to the species described above, these two species are sufficiently shade-tolerant to remain in overtopped positions for extended periods. The process of overtopping by red oak may begin at age 20, but many red maple and black birch were in the overstory at age 44 in the current study. By age 87, nearly all red maple were in intermediate to understory canopy positions. Black birch was absent from this stand, although Oliver (1978) found that it too could survive in lower canopy positions to this age.

During this entire period of development, hemlock forms a dense understory layer, being relegated to this position in the sapling stage by its slower juvenile height growth. Hemlock seems to form part of the upper canopy stratum only where it had been present as large advance growth at the time of stand initiation, and so was equal or larger than hardwoods in the early stages of development. If this occurs, then hemlock will remain in the overstory for extended periods, as in the 87- and 135-year-old stands of the current study.

Hemlock can survive for longer periods in overtopped positions than associated species. Thus, it can be found throughout the canopy strata, unlike other species. In later years, the taller overtopped hemlocks form the upper elements of the understory along with red maple and black birch. Other hemlocks occupy even lower canopy positions beneath the level of other overtopped trees. Greater shade tolerance in a species allows a broader segment of the population to survive for long periods; this is reflected in the range of heights and stem diameters of each species. As the most shade-tolerant species, hemlock displays the widest range of diameters and heights at any stage; red maple and black birch are more restricted in range, and other species are rather uniform in size of survivors.

Even-aged and two-aged stands. Stands which may appear one-aged bacause of canopy structure--containing dense, even-topped canopies lacking emergent trees or canopy gaps--may actually contain two age classes, one dating from the major canopy disturbance that destroyed the previous stand, and one consisting of older residuals of shade-tolerant species from the understory of the previous stand. Because of their slower growth, these residuals do not maintain their initial height advantage over the younger less tolerant species, but eventually come to share the main canopy with them, and thus are not obvious as an older component. This situation occurred in the hemlock-hardwood stands of the current study, and was also found in other second-growth forests of the Northeast (LaPlante 1978, Marquis 1981), where residuals were primarily beech and sugar maple. Stands with a narrow range of age and size of advance regeneration tend to become more completely stratified, with shade-tolerant species only in the understory; where large shade-tolerant residuals are more prevalent among advance regeneration, canopy stratification is less distinct.

Competition for crown space. 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). However, the potential role of crown abrasion in interspecific competition has not been recognized in ecological literature. Reduction of limited resources--light, water, and nutrients--is generally considered to be of primary importance in competition between plants. In a discussion of mechanisms of species interactions, Harper (1977, Chapter 11) considered other less direct mechanisms (such as one species sheltering predators of a neighboring species) but did not include crown abrasion or physical competition for crown space.

This mechanism appears to be of some importance for hemlock growing in mixture with hardwoods. In these stands, overstory trees certainly reduce the light available to understory hemlocks, and likely reduce other resource levels as well. However, the height and diameter growth rates of these hemlocks indicate they are able to survive with considerable vigor at the resource levels available to them, but they do not grow into the overstory stratum; even in the 135-year-old stand, many hemlocks had terminals just at the level of the lower oak branches. This suggests that physical abrasion of branches plays a part in limiting their development into an overstory position. Similar evidence of interspecific competition for crown space through branch abrasion has been given for black birch and red maple growing beneath red oak (Oliver 1978), and for western hemlock growing beneath Douglas-fir (Wierman and Oliver 1979).

Productivity of species mixtures. Evidence from studies of herbaceous species (Harper 1977) indicates that mixtures in some cases produce greater biomass yields than monocultures of any of the constituent species, but only if the species involved occupy considerably different niches. In some of these experiments, different varieties of a single species have been used to limit the dimensions of niche separation and isolate certain ones for study. For example, Hill and Shimamato (1973) tested 4 varieties of ryegrass in all possible combinations of two-variety mixtures. They found that only one combination had greater biomass yield than either monoculture. This was composed of an erect, open-canopied variety mixed with a semi-erect, densely canopied variety. This and other such studies indicate that canopy structure can be an important factor of niche separation, decreasing competition and resulting in increased biomass yields.

For forest stands, studies (Assmann 1970, Poleno 1981) consistently show that stands of two species with stratified canopies produce greater biomass yields than pure stands of the overstory species alone. Fewer of these studies provide comparisons of mixtures with the understory species alone, but these too show greater yields for the mixture. In contrast, other comparisons described by Assmann show that for mixtures where two species share the same canopy stratum, the yield of the mixture is less than that of the more productive monoculture.

Evidence from more complex species mixtures in temperate forests is provided by Roach's (1977) study of basal area yields of northern hardwood stands. These stands were composed primarily of sugar maple, beech, black birch, and red maple, but had varying amounts of species of lower shade tolerance--mainly black cherry, but also including small amounts of yellow-poplar and white ash. When present, these less tolerant species tend to occupy an overstory stratum above the other species (Marquis 1981). Roach found that stands containing cherry, ash, or yellow-poplar had greater basal area than those composed of more tolerant species alone, and that basal area was greater with increasing proportion of these overstory species.

These relationships between canopy structure and production were also found in hemlock-hardwood stands of the current study. Dimensions of niche separation cannot be isolated in these forest studies, but canopy structure provides a likely explanation for much of the reduction in competition and increase in productivity.

SILVICULTURAL IMPLICATIONS

This study indicates that, on upland till soils in southern New England, an increase in total wood production can be achieved by favoring the development of hemlock-hardwood stands over ones comprised solely of hardwoods. Such mixtures also yield more biomass than hemlock stands, although in practice this is not an important result, since pure hemlock stands are difficult to create, and produce wood of much lower value than many of the hardwood species. However the greater production of mixtures over hardwood stands may have considerable importance. Southern New England forests on till soils are predominantly hardwood, with hemlock having been greatly reduced from its importance in pre-settlement forests by fire and clearing for agriculture. For example, only 10-20% of second- and third-growth hardwood stands on the Yale and Harvard Forests contain an important hemlock component (Meyer and Plusnin 1945, Spurr 1950). Considerable potential exists for conversion of these stands to hemlock-hardwood mixtures.

Potential advantages of hemlock-hardwood mixtures. In untreated stands, the higher yield from mixtures over hardwood stands comes mainly in the form of small, low-quality material. For example, the largest understory hemlocks in the 87-year-old stand of this study were just greater than the usual minimum diameter limits of merchantibilityfor sawlogs (25-35 cm dbh). In such cases, the added production clearly is important only if a pulpwood market or other fiber use for such wood exists. Since the principal commodity objective of management in these stands is the production of high quality sawtimber from red oak, black cherry, paper birch, and other hardwood species, the greater physical yield of mixtures does not represent a proportional increase in financial yield. However, hemlock-hardwood mixtures may still represent the optimal stand type if forest owners seek to maximize financial returns from timber production, since the growth of hemlock has little effect upon that of hardwoods, and its production can be considered as additive to that of the principal product goal.

Two other factors associated with the presence of a hemlock understory increase the potential merit of mixed stands for timber production. First, the growth of understory hemlock greatly reduces the development of understory vegetation (Lutz 1928) which can interfere with the establishment of advance regeneration of desirable timber species. Where hemlock is absent, mountain-laurel and hay-scented fern in particular can reach high densities beneath hardwood canopies. Second, the dense shade cast by hemlock on the boles of overstory hardwoods may help to improve hardwood timber quality. It probably does not substantially affect tree form in early development, since hemlocks lag far behind the the height growth of hardwoods in early stages. However, it probably has value in suppressing the growth of any epicormic branches that may develop following thinnings. Such branching is important enough to warrant delays of first thinnings or reduction of thinning intensity in oak stands (Carvell 1971). The value of a hemlock understory in improving bole quality of white pine has been previously demonstrated (Tarbox and Reed 1924).

Gypsy moth defoliation has long been an important consideration in the silviculture of southern New England forests. Oaks and gray birch are among the preferred food of young gypsy moth larvae, while foliage of maples, black cherry and other birches is less favored. Hemlock and white pine will not support the younger larvae, but are fed upon by older larvae (McManus 1980). Suggestions for silvicultural control (Behre 1939, Bess et al. 1947) have focused in part upon inhibiting the initial moth population buildup in a stand by reducing the amount of foliage preferred by young larvae. This could be done by entirely replacing oak stands with planted pines or other species, or by favoring mixed stands which contain an important component of less preferred species.

This idea has not been borne out with regard to mixtures of hemlock and red oak. The severe gypsy moth outbreak of 1981 in southern New England brought serious hemlock mortality in some mixed stands, apparently as older larvae dropped down from completely defoliated oaks onto understory hemlocks. Results of the current study suggest that these mixed stands may have been as heavily attacked as pure hardwood stands because they contained comparable amounts of oak foliage. Although foliage amounts were not directly measured in this study, mixed stands were found to contain approximately the same total biomass of oak as in adjacent hardwood stands. It is likely that hemlock must comprise a fairly high proportion of the overstory canopy for the amount of oak foliage to be decreased.

Non-commodity objectives also have considerable importance to forest managers in southern New England. In this region, 66% of forest owners, controlling 63% of commercial forest land, listed recreation or esthetics as the principal benefit derived from their land (Kingsley 1976). Even considering only those owners who harvest timber on their land, these benefits were listed as the most important by 64%. Thus, timber production combined with consideration for such factors as esthetics and wildlife habitat is clearly of importance.

Visual enjoyment of woodlands is enhanced primarily by increasing the diversity of spatial effects seen as one travels through a forested area (Brush 1976). Important aspects include sizes and shapes of visual spaces, intensity of light penetrating the forest canopy, and the distance one can see into a stand. Hemlock can be important in a predominantly hardwood forest, especially in seasons when deciduous species are leafless, because its solid wall of foliage extending near to the ground breaks up and defines visual spaces, increasing sought-after diversity.

In northern climates, provision of winter shelter and browse are important aspects of deer management. Hemlock is an excellent species in southern New England forests for winter yarding of deer, because its low branches and dense foliage affords protection from wind, and its seedlings provide preferred browse within yarding areas (Hosley and Ziebarth 1935). Hemlock also provides important winter shelter habitat for snowshoe hare, rabbits, turkeys, and ruffed grouse (Jordan and Sharp 1967), with young stands of hemlock-hardwoods being the best overall habitat for the latter species.

Regeneration. Considerable evidence has shown that for oak, the size of advance regeneration, and not merely its abundance, is important in determining whether trees will form a part of the main overstory canopy of young stands. Recommendations of 60 to 120 cm minimum height, or 1.2 to 2.5 cm basal stem diameter for advance growth (Sander 1971, Clark and Watt 1971, Ashley 1979) have been made for ensuring successful regeneration. In the current study (Chapter 3), 1-year-old red oak seedlings, approximately 20 cm in height, did not match the height growth of cherry and birch species, and at age 14, tallest oaks were only about one-half the height of the tallest of these competitors, which included long-lived black cherry and black birch. These oaks may or may not eventually grow into main canopy positions. Oliver (1978) noted that, in stands of his study, red oaks which were not in upper canopy positions in the first years of development eventually came to dominate competing hardwood species. However, those oaks, which averaged about 50 cm tall as advance growth, had generally reached heights equal to competing black birch by age 15, unlike the oaks of the current study.

Grisez and Peace (1973) and Marquis (1979) have found that black cherry also develops better if present as advance growth, but that size is not important as for oaks. Seedlings less than 15 cm tall, including 1-year-old seedlings, grew rapidly after canopy removal and occupied dominant positions in young stands. Black cherry can also become established after canopy removal, but the presence of abundant advance growth is important mainly to ensure that some seedlings will survive intense browsing by deer.

Hemlock seedlings are susceptible to dessication in full sunlight (Lutz 1928, Olson et al. 1959), and so have poor survival on exposed seedbeds after overstory removal. Thus, presence as advance growth is also beneficial for hemlock regeneration, and is necessary if hemlock are to grow into overstory positions with hardwoods. Small hemlock advance regeneration consistently ends up in the understory, whereas larger advance growth or residuals from the previous stand can develop into overstory positions. Evidence from this study indicates that the minimum size for eventual overstory status for hemlocks is greater than that for oaks. Seedlings averaging 80 cm (ranging up to 150 cm) were quickly overtopped by hardwoods, while advance growth 3 m and taller successfully developed into overstory positions.

Conversion of hardwood stands to hemlock-hardwood mixtures, then, depends largely upon establishment of hemlock advance growth. In many stands, an important limiting factor appears to be lack of seed source (Merrill and Hawley 1924, Winer 1955). Lack of seed may be a problem even in stands containing abundant understory hemlock, because seed is produced only by overstory trees (Hough 1965). This was evident in the hemlocks felled for measurement in the current study (Chapter 2). Cones were present in the upper portions of crowns of all 13 overstory trees, but were entirely absent on the 12 understory trees.[1]

Natural conversion of hardwood stands takes place slowly, as hemlock advance growth becomes established in the vicinity of seed trees (Merrill and Hawley 1924, Spurr 1950). The best way to speed the process without intensive management is to reserve any hemlocks

[1]This difference can be seen in photographs in Figure 12, although not distinctly, because many of the cones were lost during removal of foliage.

existing in hardwood stands and release them from competiton so that seed may be produced. Lack of seed source can also be overcome by seeding or planting hemlock in hardwood stands. This would not likely be economically justifiable in most situations, but Jordan and Sharp (1967) have suggested its use in areas selected for intensive wildlife management.

The shelterwood regeneration system is well suited to species such as red oak, black cherry, and hemlock, which must occur as vigorous advance regeneration for successful reproduction (Smith 1962, Sander 1979). Advance reproduction may be dense in untreated stands, but may not be large or vigorous enough to outgrow competition upon complete overstory removal. The shelterwood overstory must provide enough shade to allow establishment of desired species, yet not greatly inhibit their height development. Given proper conditions, advance growth populations can build up slowly, since hemlocks can survive for extended periods as seedlings, and oaks can die back and resprout repeatedly. However, optimum residual densities for shelterwood seed cuts are not known for stands dominated by red oak and hemlock.

On some sites, shade-tolerant shrub and tree species may provide severe competition for oaks, and these species often respond vigorously to seed cuts. Control of understory vegetation with burning, mowing, or herbicide application may be necessary to obtain successful oak regeneration (Sander 1979), although the effectiveness of these methods has not been clearly demonstrated. In addition, browsing by large populations of deer is a frequent limitation to regeneration in northeastern forests (Behrend at al. 1970, Marquis 1979), including southern New England (see Chapter 3). Development of large numbers of advance growth seedlings may help to ensure sufficient survivors to form a well-stocked stand, but successful regeneration of stands in these areas likely requires reduction of deer density coupled with the shelterwood system (Marquis 1979, Kelty and Nyland 1981).

Intermediate treatments. Since production of high quality sawtimber or veneer logs is the usual goal of management of oak-dominated stands, intermediate treatments are important for concentrating growth on chosen trees of desired species and form. Abundant evidence shows that if red oak makes up an important part of the upper canopy by age 15, it will come to dominate these stands, even if no cleanings or thinnings are done (Carvell 1971, Oliver 1978, Stephens and Waggoner 1980, Hibbs 1983, Chapter 2 of this study). However, if red oak develops from small advance growth, it will likely be in an intermediate to overtopped position as a sapling. If managers seek to maintain a representation of oak in the overstory, they may have to intervene with cleanings (Carvell 1971), although the long-term fate of such stems, with or without release, is not known.

Even though red oak will dominate the overstory with no silvicultural intervention, thinnings can increase individual-tree growth rates. Red oaks aged 20 to 70 were found to respond to release with increased diameter growth compared to constant growth in unreleased trees (Oliver 1978), or with constant diameter growth compared to slowly declining growth for unreleased controls (Carvell 1971). Thinnings can in large part speed natural stand development by hastening the removal of red maple, black birch, and other species that would eventually lose overstory positions in untreated stands.

Considerable flexibility exists in handling the hemlock component of mixed stands. It can simply be left in a dense understory, and utilized for wood fiber only. Or, if hemlock sawlogs are desired, removal of overstory competition can reduce shading and crown abrasion for the taller understory hemlocks and allow their development into the overstory. Even if thinning of the hardwood canopy is not designed to produce overstory hemlocks, such practice inevitably creates temporary canopy gaps, letting light pass through to the understory hemlock. In hardwood stands, these gaps represent canopy space lost to any timber production. Thus the yield difference between mixed stands and hardwood stands would likely be greater with management than for the unthinned stands of this study.

Yields of hemlock sawtimber could be further increased by lengthening the rotation for hemlock over that for oak and other hardwoods, as with a silvicultural plan of the kind described by Smith (1962). This could be incorporated into shelterwood cuttings, with initial seed cuttings reducing density of all overstory species, and later ones favoring the retention of well-formed hemlocks. Such a scheme would not be justified in other forest types in which the understory is comprised only of small, poorly formed trees of low vigor. However, larger understory hemlocks have considerable size and vigor, as observed in this study, and many would be just reaching minimum size for sawtimber at the end of a 70-90 year rotation for oak and cherry. Observations in southern New England stands indicate that even small hemlocks can respond to release following long periods of suppression (Marshall 1924, Oliver and Stephens 1977). Also, because hemlock is negatively geotrophic, it maintains a straight stem when growing in an overtopped position; this is in marked contrast to phototrophic hardwood species. Two factors concerning regeneration would require attention in this sequential harvesting of the two stand components--sufficient numbers of desirable hardwood species should be retained with the hemlock to act as seed source, and residual hemlocks should not be so dense, nor retained for so long, as to inhibit the establishment and survival of seedlings of the less shade-tolerant specie.

Implications for other forest types. The association of high biomass production with stratified canopy structure in mixed-species stands may have more importance in certain other forest types than the one studied here--particularly where the values of products derived from the component species are more comparable, and where maximizing commodity production is of primary importance. For example, much forestry practice consists of growing single-species plantations of shade-intolerant conifers, even in regions where soil and climatic conditions allow growth of forests of high species diversity. A considerable part of the cost of such practice often involves control of dense understory vegetation which develops in these plantations and inhibits subsequent regeneration efforts. In these situations, the inclusion of a shade-tolerant understory conifer with acceptable wood characteristics may both increase yields and reduce competition from understory hardwood vegetation.

LITERATURE CITED

Ashley, B. S. 1979. Determining adequacy of advance regeneration. In Regenerating oaks in upland hardwood forests, (H. A. Holt and B. C. Fischer, eds.), J. S. Wright For. Conf. Proc., p. 18-22. Purdue Univ., West Lafayette, Ind.

Assmann, E. 1970. The principles of forest yield study. Pergamon Press, Oxford. 506 p.

Baskerville, G. L. 1972. Use of logarithmic regression in the estimation of plant biomass. Can. J. For. Res. 2: 49-53.

Behre, C. E. 1939. The opportunity for forestry practice in the control of gypsy moth in Massachusetts woodlands. J. For. 37: 546-551.

Behrend, D. F., G. F. Mattfeld, W. C. Tierson, and J. E. Wiley. 1970. Deer density control for comprehensive forest management. J. For. 68: 695-700.

Bess, H. A., S. H. Spurr, and E. W. Littlefield. 1947. Forest site conditions and the gypsy moth. Harvard Forest Bull. No. 22. 56 p.

Boardman, N. K. 1977. Comparative photosynthesis of sun and shade plants. Annual Rev. Plant Physiol. 28: 355-377.

Bormann, F. H. 1965. Changes in the growth pattern of white pine undergoing suppression. Ecology 46: 269-277.

Bormann, F. H., and G. E. Likens. 1979. Pattern and process in a forested ecosystem. Springer-Verlag, New York. 253 p.

Bramble, W. C., and W. L. Fix. 1980. Productivity of a managed woodland in the Central States. J. For. 78: 553-556.

Braun, E. L. 1950. Deciduous forests of eastern North America. Blakiston Co., Philadelphia. 596 p.

Bromley, S. W. 1935. The original forest types of southern New England. Ecol. Monogr. 5: 61-89.

Brush, R. O. 1976. Spaces within woods: managing forests for visual enjoyment. J. For. 74: 744-747.

Carmean, W. H. 1972. Site index curves for upland oaks in the Central States. For. Sci. 18: 109-120.

Carvell, K. L. 1971. Silvicultural aspects of intermediate cuttings. In Oak symposium proceedings, p. 60-64. USDA For. Serv., Upper Darby, Penn.

Clark, B. F., and R. F. Watt. 1971. Silvicultural methods for regenerating oaks. In Oak symposium proceedings, p. 37-43. USDA For. Serv., Upper Darby, Penn.

Cline, A. C., and C. R. Lockard. 1925. Mixed white pine and hardwood. Harvard Forest Bull. No. 8. 67 p.

Connell, J. H., and R. O. Slatyer. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. Amer. Naturalist 111: 1119-1144.

Crow, T. R. 1978. Biomass and production in three contiguous forests in northern Wisconsin. Ecology 59: 265-273.

Curtis, R. O. 1964. A stem analysis approach to site index curves. For. Sci. 10: 241-256.

Curtis, R. O., and F. M. Rushmore. 1958. Some effects of stand density and deer browsing on reproduction in an Adirondack hardwood stand. J. For. 56: 116-121.

Curtis, R. O., and D. L. Reukema. 1970. Crown development and site estimates in a Douglas-fir plantation spacing test. For. Sci. 16: 287-301.

Egler, F. E. 1954. Vegetation science concepts: I. Initial floristic composition, a factor in old-field vegetation development. Vegetatio 4: 412-417.

Ellern, S. J., J. L. Harper, and G. R. Sagar. 1970. A comparative study of the distribution of roots of Avena fatua and A. strigosa in mixed stands using a ^{14}C labelling technique. J. Ecol. 58: 865-868.

Eyre, F. H., and W. M. Zillgitt. 1953. Partial cuttings in northern hardwoods of the Lake States. USDA Tech. Bull. No. 1076. 124 p.

Fernald, M. L. 1950. Gray's manual of botany: a handbook of the flowering plants and ferns of the central and northeastern Unites States and Canada. American Book Co., New York. 1632 p.

Ford, E. D. 1975. Competition and stand structure in some even-aged plant monocultures. J. Ecol. 63: 311-333.

Ford, E. D. 1982. High productivity in a polestage Sitka spruce stand and its relation to canopy structure. Forestry 55: 1-17.

Gilbert, A. M. 1965. Stand differentiation ability in northern hardwoods. USDA For. Serv. Res. Pap. NE-37. 34 p.

Goff, F. G., and P. H. Zedler. 1968. Structural gradient analysis of upland forests in the western Great Lakes area. Ecol. Monogr. 38: 65-86.

Grisez, T. J., and M. R. Peace. 1973. Requirements for advance reproduction in Allegheny hardwoods--an interim guide. USDA For. Serv. Res. Note NE-180. 5 p.

Halle, F., R. A. A. Oldemann, and P. B. Tomlinson. 1978. Tropical trees and forests: an architectural analysis. Springer-Verlag, New York. 441 p.

Harper, J. L. 1977. Population biology of plants. Academic Press, New York. 892 p.

Harvard Forest records. 1940. Unpublished records of experiment 40-1: Post-hurricane natural regeneration study. Harvard Forest, Petersham, Mass.

Henry, J. D., and J. M. A. Swan. 1974. Reconstructing forest history from live and dead plant material--an approach to the study of forest succession in southwest New Hampshire. Ecology 55: 772-783.

Hibbs, D. E. 1981. Leader growth and the architecture of three North American hemlocks. Can. J. Bot. 59: 476-480.

Hibbs, D. E. 1982. White pine in the transition hardwood forest. Can. J. Bot. 60: 2046-2053.

Hibbs, D. E. 1983. Forty years of forest succession in central New England. Ecology 64: 1394-1401.

Hill, J., and Y. Shimamato. 1973. Methods of analysing competition with special reference to herbage plants. I. Establishment. J. Agric. Sci. 81: 77-88.

Hosley, N. W., and R. K. Ziebarth. 1935. Some winter relationships of the white-tailed deer to the forests of north-central Massachusetts. Ecology 16: 535-553.

Hough, A. F. 1965. Eastern hemlock (Tsuga canadensis (L.) Carr.). In Silvics of forest trees of the United States, (H. A. Fowells, ed.), p. 703-711. USDA Agric. Handbook No. 271.

Johnson, P. S., and R. D. Jacobs. 1981. Northern red oak regeneration after preherbicided clearcutting and shelterwood removal cutting. USDA For. Serv. Res. Pap. NC-202. 5 p.

Jordan, J. S., and W. M. Sharp. 1967. Seeding and planting hemlock for ruffed grouse cover. USDA For. Serv. Res. Pap. NE-83. 17 p.

Kelty, M. J., and R. D. Nyland. 1981. Regenerating Adirondack northern hardwoods by shelterwood cutting and control of deer density. J. For. 79: 22-26.

Kingsley, N. P. 1976. The forest-land owners of southern New England. U. S. For. Serv. Res. Bull. NE-41. 27 p.

Kramer, P. J., and T. T. Kozlowski. 1979. Physiology of woody plants. Academic Press, New York. 811 p.

LaPlante, J. M. 1978. The prediction of volume in second-growth northern hardwood stands in Upstate New York. M.S. thesis, State Univ. New York, Col. Environ. Sci. and For., Syracuse, N.Y.

Leak, W. B., and R. W. Wilson, Jr. 1958. Regeneration after cutting of old-growth northern hardwoods in New Hampshire. USDA For. Serv. Expt. Sta. Pap. No. 103. 8 p.

Lutz, H. J. 1928. Trends and silvicultural significance of upland forest successions in southern New England. Yale Univ. Sch. of For. Bull. No. 22. 69 p.

Lyford, W. H. 1980. Development of the root system of northern red oak (Quercus rubra L.). Harvard Forest Pap. No. 21. 30 p.

Madgwick, M. A. I. 1970. Biomass and productivity models of forest canopies. In Ecological studies. Volume I. Analysis of temperate forest ecosystems. (D. E. Reichle, ed.), p. 47-54. Chapman and Hall, London; Springer-Verlag, Berlin.

Marquis, D. A. 1979. Shelterwood cutting in Allegheny hardwoods. J. For. 77: 140-144.

Marquis, D. A. 1981. Removal or retention of unmerchantable saplings in Allegheny hardwoods: effect on regeneration after clearcutting. J. For. 79: 280-283.

Marquis, D. A., T. J. Grisez, J. C. Bjorkbom, and B. A. Roach. 1975. Interim guide to regeneration of Allegheny harcwoods. U. S. Dept. Agric. For. Serv. Gen. Tech. Rep. NE-19. 14 p.

Marshall, R. 1927. The growth of hemlock before and after release from suppression. Harvard Forest Bull. No. 11. 43 p.

McKinnon, F. S., G. R. Hyde, and A. C. Cline. 1935. Cut-over old field white pine lands in central New England: A regional study of the composition and stocking of the ensuing volunteer stands. Harvard Forest Bull. No. 18. 80 p.

McManus, M. L. 1980. The gypsy moth. USDA Forest Insect and Disease Leaflet No. 162. 10 p.

Merrill, P. H., and R. C. Hawley. 1924. Hemlock: its place in the silviculture of the southern New England forest. Yale Univ. Sch. of For. Bull. No. 12. 68 p.

Meyer, W. H., and B. A. Plusnin. The Yale Forest in Tolland and Windham Counties, Connecticut. Yale Univ. Sch. of For. Bull. No. 55. 54 p.

Monteith, D. B. 1979. Whole tree weight tables for New York. State Univ. of New York, Appl. For. Res. Inst., Res. Pap. No. 40. 69 p.

Murison, W. F. 1963. Unpublished records of experiment 63-4: Weather summary for 1913-1962. Harvard Forest, Petersham, Mass.

Nichols, G. E. 1913. The vegetation of Connecticut. II. Virgin forests. Torreya 13: 199-215.

Oliver, C. D. 1975. The development of northern red oak (Quercus rubra L.) in mixed species, even-aged stands in central New England. Ph.D. thesis, Yale Univ., New Haven, Conn. 223 p.

Oliver, C. D. 1978. The development of northern red oak in mixed stands in central New England. Yale Univ. Sch. of For. and Environ. Studies, Bull. No. 91. 63 p.

Oliver, C. D. 1981. Forest development in North America following major disturbances. For. Ecol. and Manage. 3: 153-168.

Oliver, C. D., and E. P. Stephens. 1977. Reconstruction of a mixed-species forest in central New England. Ecology 58: 562-572.

Oliver, C. D., and M. D. Murray. 1983. Stand structure, thinning prescriptions, and density indexes in a Douglas-fir thinning study, Western Washington, U. S. A. Can. J. For. Res. 13: 126-136.

Olson, J. S., F. W. Stearn, and H. Nienstadt. 1959. Eastern hemlock--growth cycle and early years. Conn. Agric. Exp. Sta. Circular No. 205. New Haven, Conn. 24 p.

Ovington, J. D., and W. H. Pearsall. 1956. Production ecology. II. Estimates of average production by trees. Oikos 7: 2022-205.

Parde, J. 1980. Forest biomass. For. Abstr. 41: 343-362.

Poleno, Z. 1981. Vyvoj smisenych porostu. [Development of mixed forest stands.] Prace VULHM 59: 179-202.

Raup, H. M., and R. E. Carlson. 1941. The history of land use in the Harvard Forest. Harvard Forest Bull. No. 20. 64 p.

Richards, N. A., and C. E. Farnsworth. 1971. Effects of cutting level on regeneration of northern hardwoods protected from deer. J. For. 69: 230-233.

Richards, P. W. 1952. The tropical rain forest: an ecological study. University Press, Cambridge. 450 p.

Roach, B. A. 1977. A stocking guide for Allegheny hardwoods and its use in controlling intermediate cuttings. USDA For. Serv. Res. Pap. NE-373. 30 p.

Rogers, R. S. 1978. Forests dominated by hemlock (Tsuga canadensis): distribution as related to site and post-settlement history. Can. J. Bot. 56: 843-854.

Sander, I. L. 1971. Height growth of new oak sprouts depends on size of advance reproduction. J. For. 69: 809-811.

Sander, I. L. 1979. Regenerating oaks with the shelterwood system. In Regenerating oaks in upland hardwood forests, (H. A. Holt and B. C. Fischer, eds.), J. S. Wright For. Conf. Proc., p. 54-60. Purdue Univ., West Lafayette, Ind.

Sander, I. L., and F. B. Clark. 1971. Reproduction of upland hardwood forests in the central states. USDA For. Agric. Handbook No. 405. 25 p.

Scott, C. T. 1981. Northeast forest survey revised cubic-foot volume equations. USDA For. Serv. Res. Note NE-304. 3 p.

Siccama, T. G. 1983. Personal communication. (Dr. Siccama is ecologist and lecturer, Yale Univ. Sch. of For. and Environ. Studies.)

Simmons, C. S. 1940. Soil survey of Harvard Forest--Slab City Block. Unpublished report, Harvard Forest, Petersham Mass. 30 p.

Smith, D. M. 1956. Catlin Wood. Bull. Conn. Arboretum 8: 19-24.

Smith, D. M. 1962. The practice of silviculture. Seventh edition. John Wiley and Sons, Inc., New York. 578 p.

Smith, D. M. 1973. Silvicultural practice and stand development in eastern deciduous forests. Paper presented at Symposium on Ecological Impact of Management Practices in Eastern Deciduous Forests, Ecol. Soc. Am., Amherst, Mass. 18 July 1973.

Smith, D. M. 1982. Patterns of development of forest stands. In Forest succession and stand development research in the Northwest, (J. E. Means, ed.), p. 1-4. Northwest Scientific Assoc., Corvallis, Oregon.

Smith, H. C. 1977. Height of tallest saplings in 10-year-old Appalachian hardwood clearcuts. USDA For. Serv. Res. Pap. NE-381. 6 p.

Snedecor, G. W., and W. G. Cochran. 1980. Statistical methods. Seventh edition. The Iowa State Univ. Press, Ames, Iowa. 519 p.

Spurr, S. H. 1950. Stand composition in the Harvard Forest as influenced by site and forest management. Ph.D. thesis. Yale Univ., New Haven, Conn. 294 p.

Spurr, S. H. 1956. Natural restocking of forests following the 1938 hurricane in central New England. Ecology 37: 443-451.

Stephens, G. R., and P. E. Waggoner. 1980. A half-century of natural transitions in mixed hardwood forests. Conn. Agric. Exp. Sta. Bull. No. 783. New Haven, Conn. 42 p.

Swan, J. M. A. 1970. Unpublished records of experiment 70-2: Phenology records. Harvard Forest, Petersham, Mass.

Tarbox, E. E., and P. M. Reed. 1924. Quality and growth of white pine as influenced by density, site, and associated species. Harvard Forest Bull. No. 7. 30 p.

Trenbath, B. R. 1974. Biomass productivity of mixtures. Adv. Agron. 26: 177-210.

Trenbath, B. R., and J. L. Harper. 1973. Neighbour effects in the genus Avena. I. Comparison of crop species. J. Appl. Ecol. 10: 379-400.

Trimble, G. R., Jr. 1969. Diameter growth of individual hardwood trees. USDA For. Serv. Res. Pap. NE-145. 25 p.

Tritton, L. M., and J. W. Hornbeck. 1982. Biomass equations for major tree species in the Northwest. USDA For. Serv. Gen. Tech. Rep. NE-69. 46 p.

U. S. Dept. Agric. Soil Cons. Serv. 1970. Soil survey--Litchfield County, Connecticut. U. S. Govt. Printing Office, Washington, D. C.

Ward, W. W. 1964. Live crown ratio and stand density in young, even-aged, red oak stands. For. Sci. 10: 56-65.

Westveld, M. 1956. Natural forest vegetation zones of New England. J. For. 54: 332-338.

Whitehead, D. 1982. Ecological aspects of natural and plantation forests. For. Abstr. 43: 615-624.

Whittaker, R. H. 1966. Forest dimensions and production in the Great Smoky Mountains. Ecology 47: 103-121.

Wierman, C. A., and C. D. Oliver. 1979. Crown stratification by species in even-aged mixed stands of Douglas-fir--western hemlock. Can. J. For. Res. 9: 1-9.

Winer, H. I. 1955. The history of the Great Mountain Forest. Ph.D. thesis, Yale Univ., New Haven, Conn. 278 p.

APPENDICES

APPENDIX 1.

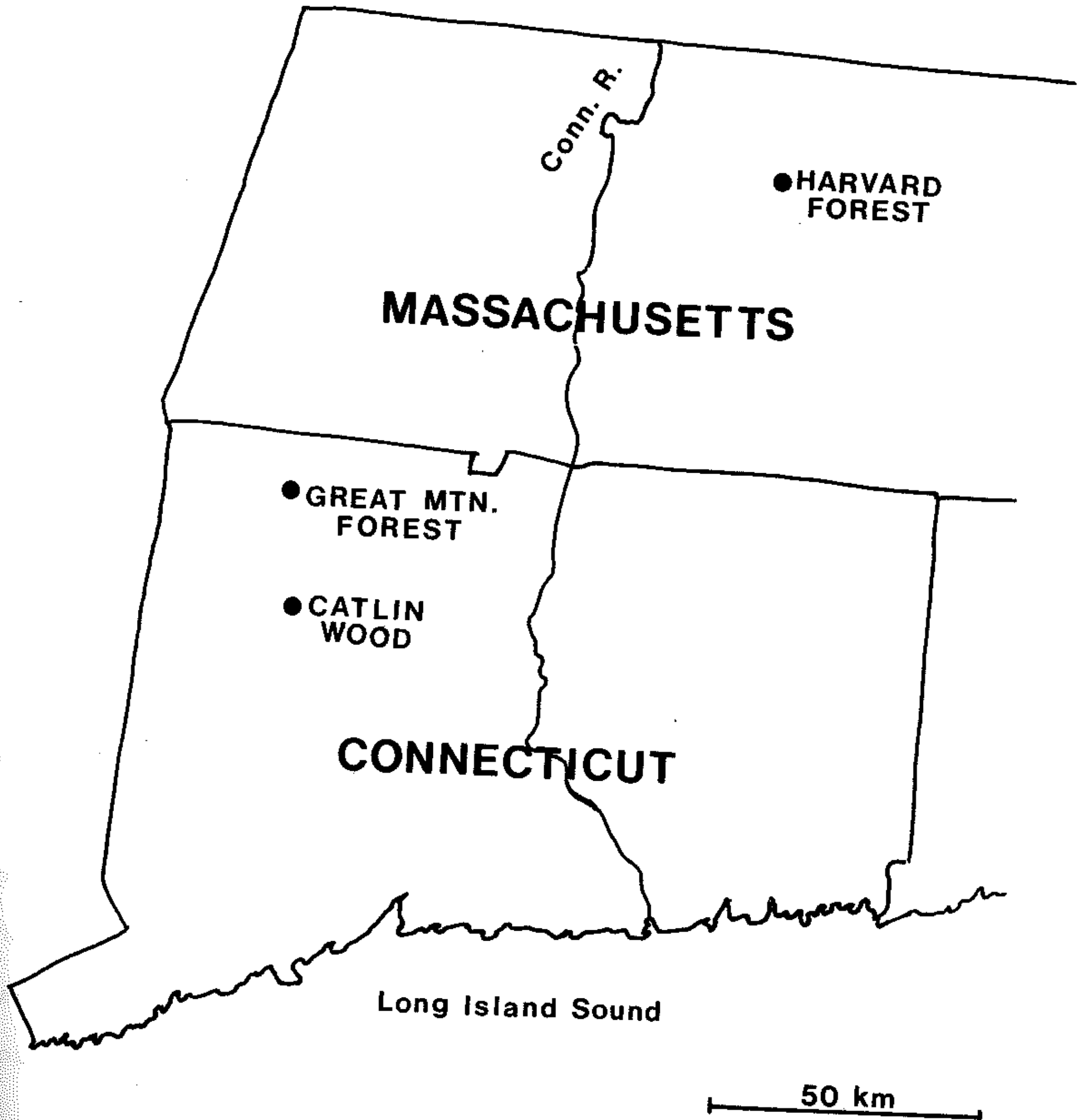
Common and scientific names of plants mentioned in text.

Common name	Scientific name[1]
Ash, white	*Fraxinus americana* L.
Aspen spp.	*Populus* spp.
Beech, American (or simply beech)	*Fagus grandifolia* Ehrh.
Beech, European	*Fagus sylvatica* L.
Birch, black	*Betula lenta* L.
gray	*Betula populifolia* Marsh.
paper	*Betula papyrifera* Marsh.
yellow	*Betula alleghaniensis* Britton
Blackberry	*Rubus* spp.
Cherry, black	*Prunus serotina* Ehrh.
pin	*Prunus pensylvanica* L.f.
Chestnut	*Castanea dentata* (Marsh.) Borkh.
Douglas-fir	*Pseudotsuga menziesii* (Mirb.) Franco
Fern, hay-scented	*Dennstaedtia punctilobula* (Michx.) Moore
Fir, silver (European)	*Abies alba* Mill.
Hemlock, eastern	*Tsuga canadensis* (L.) Carr.
western	*Tsuga heterophylla* (Raf.) Sarg.
Hickory, shagbark	*Carya ovata* (Mill.) K. Koch
Larch, European	*Larix decidua* Mill.
Hop-hornbeam	*Ostrya virginiana* (Mill.) K. Koch
Maple, red	*Acer rubrum* L.
sugar	*Acer saccharum* Marsh.
Mountain-laurel	*Kalmia latifolia* L.
Oak, black	*Quercus velutina* Lam.
northern red (or simply red oak)	*Quercus rubra* L.
sessile	*Quercus sessiliflora*
white	*Quercus alba* L.
Pine, white	*Pinus strobus* L.
Scotch	*Pinus sylvestris* L.
Raspberry	*Rubus* spp.
Ryegrass	*Lolium perenne*
Spruce, Norway	*Picea abies* (L.) Karst.
Sitka	*Picea sitchensis* (Bong.) Carr.
Yellow-poplar	*Liriodendron tulipifera* L.

[1] Based upon Fernald (1950) for North American species.

APPENDIX 2

Location of study sites.



APPENDIX 3.

Analysis of height growth from stem-dissection measurements.

Data collected by stem dissection procedures present difficulty in analysis; the information desired in this case is average height at given age intervals for each species. However, data are in the form of ages measured at given height intervals. This precludes normal regression analysis. The method of analysis frequently used in site-index studies (Curtis 1964, Carmean 1972) is to plot a height-age curve for each tree by linear interpolation between data points. Heights at given time intervals can be read from these individual-tree curves and used to form an average height-age curve for a group of trees.

In site-index studies, regression equations are then fit to these average height-age curves. Resulting squared correlation coefficients in this type of analysis are usually close to 1.00, but these reflect the degree to which the equation describes the average height-age curve, not the variability among the original data. This was the method used for each of the three species analysed in this study.

Variance among the original measurements can be shown in standard error calculations for average height at each time interval (Figure 6). These are only approximations of standard errors, since they are derived from the linearly interpolated curves rather than actual data points.

No such difficulties arise in analysis of growth in diameter or basal area, since data represent actual measures of stem size at given age intervals. Standard error calculations for diameter growth can be made according to usual methods.

APPENDIX 4

Height growth of trees from Great Mountain Forest plots.

Figure 4-1 gives results of reconstruction of height growth of trees in 87-year-old stand; see Chapter 2 for sampling procedures.

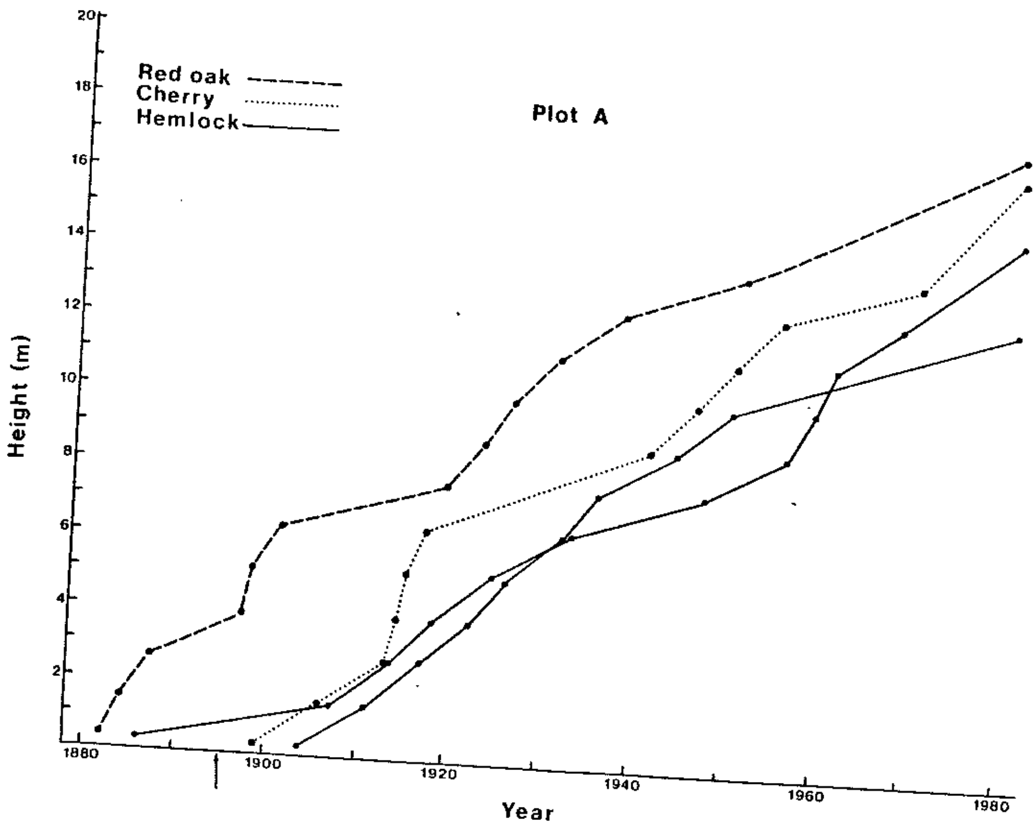


Figure 4-1. Cumulative height growth of trees growing in direct competition, in plots in 87-year-old Great Mountain Forest stand. Each graph gives results of one four-tree plot, consisting of an overstory red oak, an overstory black cherry, and two understory hemlock. Arrow denotes time of stand-initiating disturbance.

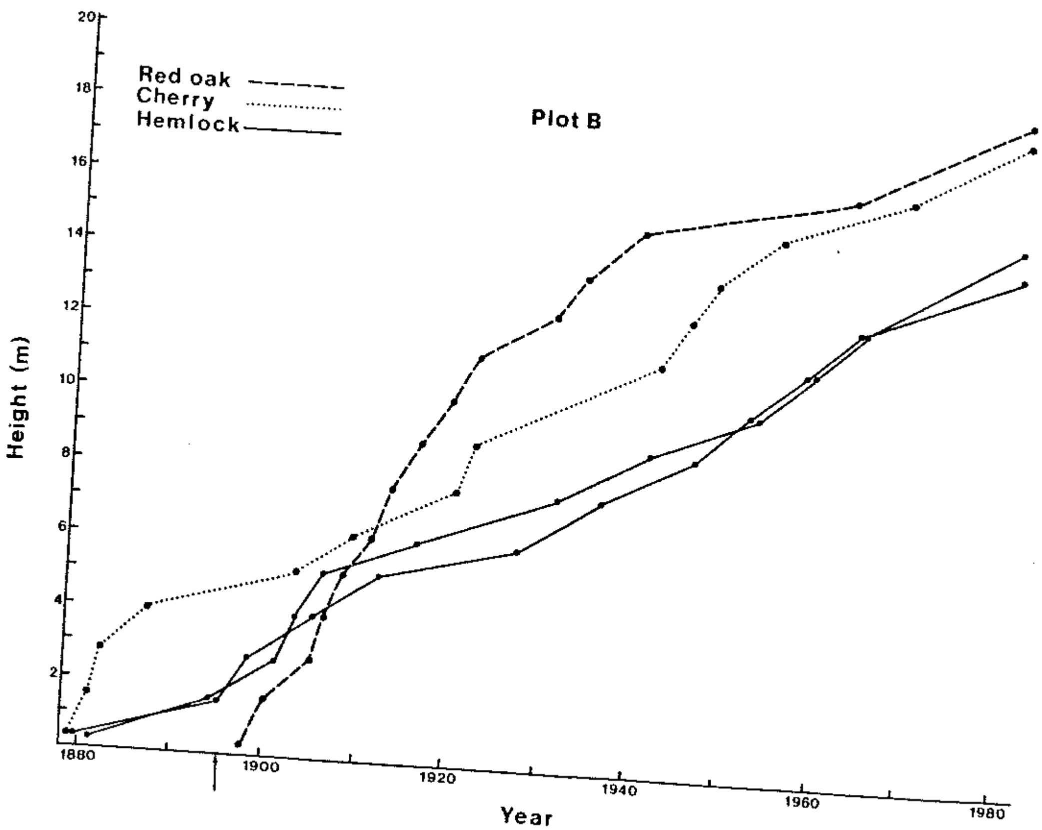


Figure 4-1. (continued)

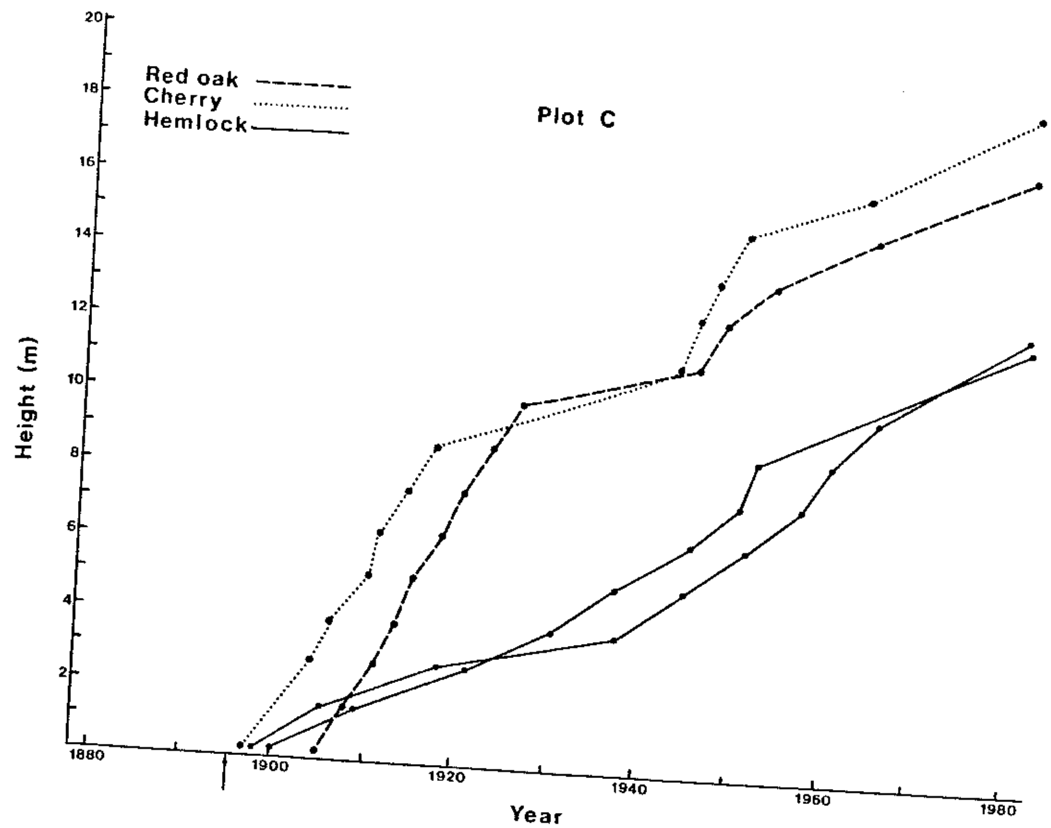


Figure 4-1. (continued)

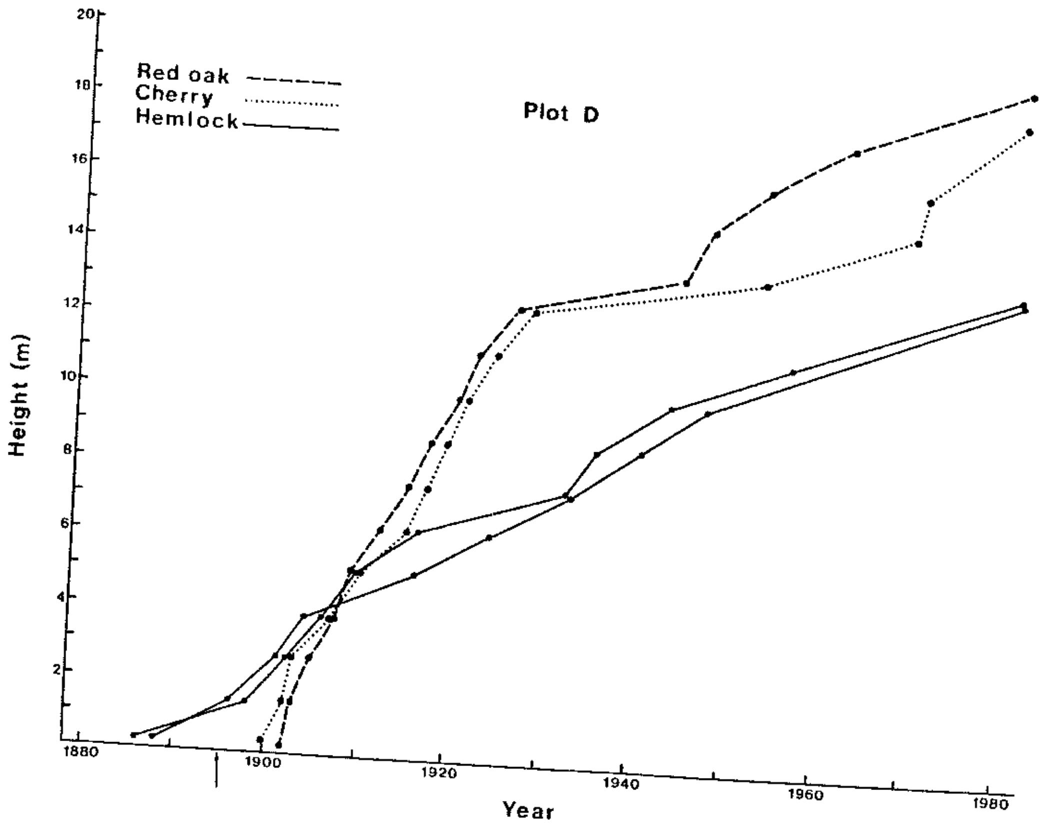


Figure 4-1. (continued)

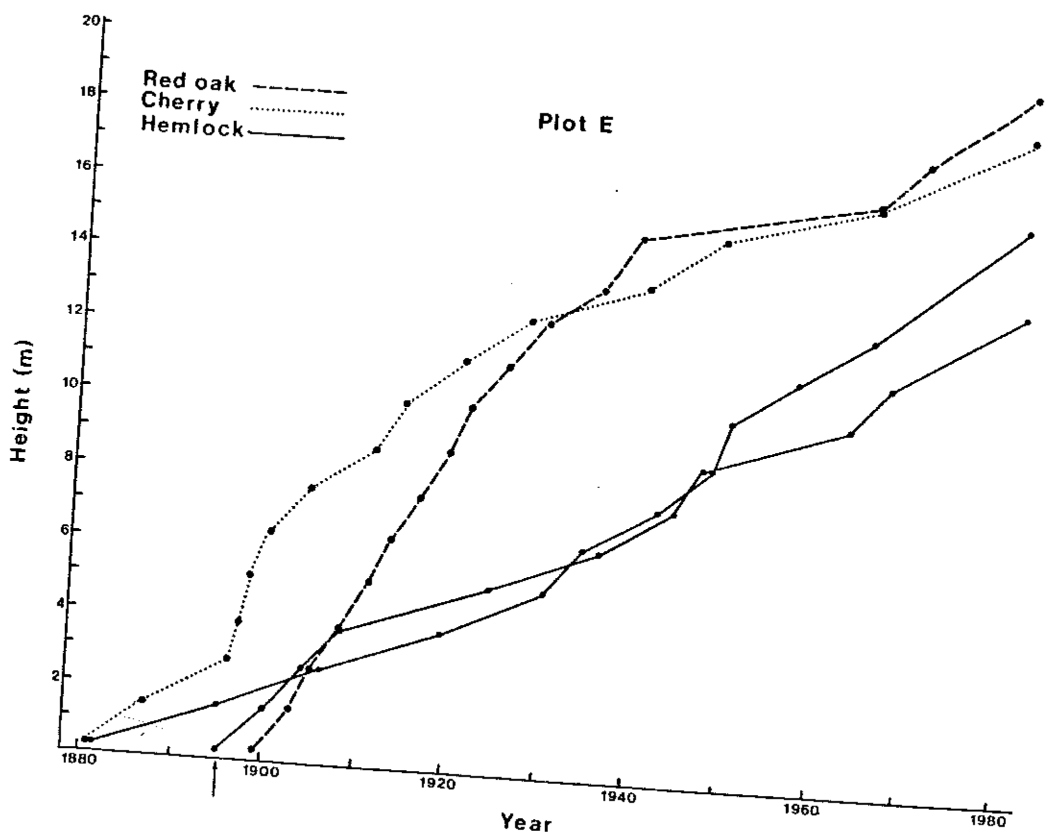


Figure 4-1. (continued)

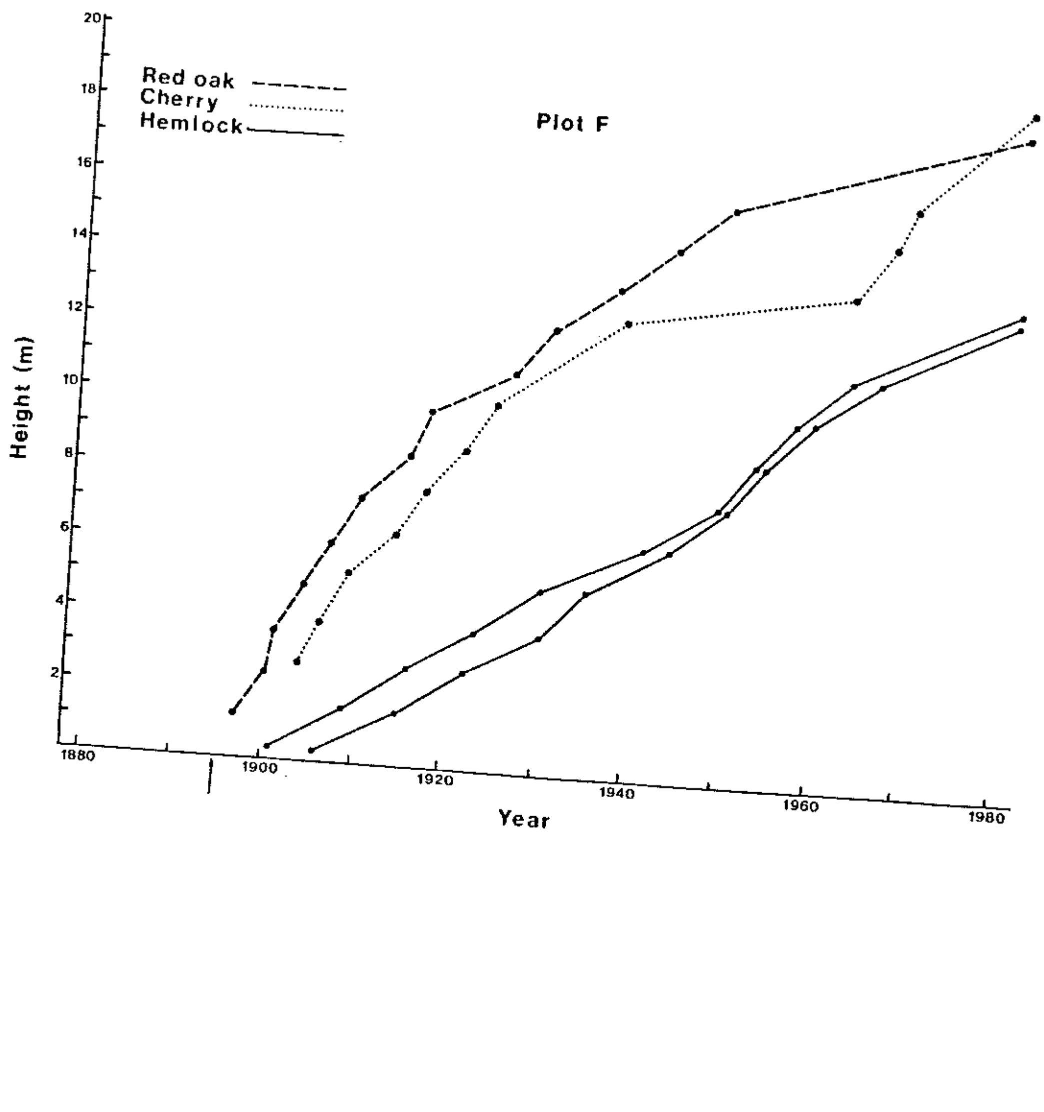


Figure 4-1. (continued)

APPENDIX 5

Catlin Wood.

Soils. Figure 5-1 shows the soil types within Catlin Wood. The area lies in a contact zone between soils derived from glacial till and those derived from stratified outwash sands and gravels. The till soils lie in the southeastern part of Catlin Wood, on parts of the former woodlot where vegetation sample plots were located (compare Figures 5-1 and 5-2.)

Vegetation sample plots. The 12 plots measured in this study were part of a grid of permanent sample plots installed in Catlin Wood in 1981. Location of the sample plot grid is shown in Figure 5-2, as are the plots measured for the present study. Data for these 12 plots are given in Table 5-1. Records of permanent sample plot measurements are kept by the White Memorial Foundation Conservation Center, Litchfield, Connecticut.

Figure 5-2 also shows the areas where selective logging occurred in 1972. The stumps used for stand age determination (see Chapter 4) were located in these areas.

History of land ownership. A description of ownership of Catlin Wood and conclusions pertaining to land use were presented in Chapter 4. The following is a repetition of the ownership history in more detail, citing property deeds by number (all deeds are filed in the Litchfield Town Clerk's Office). The description includes references

Figure 5-1. Soils map of Catlin Wood, from the Soil Survey of Litchfield County (U.S. Dept. Agric., Soil Cons. Serv. 1970) and Siccama (1981).

- Improved road
- Major bridle trail
- Minor trail
- Intermittent stream
- 10-ft. contour lines
- Boundary of soil type

Soils: (symbols are those used in Soil Survey)

Glacial till origin

ChB Charlton stony fine sandy loam; well-drained.

PbB Paxton fine sandy loam; well-drained; internal drainage is restricted by a hardpan layer at a depth of about 60 cm.

Lg Leicester, Ridgebury, and Whitman very stony fine sandy loam; poorly to very poorly drained.

Stratified outwash sands and gravels

Au Au Gres loamy fine sand; poorly drained.

DeA Deerfield loamy fine sand; moderately well-drained.

Sb Saco silt loam; very poorly drained (on flood plains).

WvB Windsor loamy fine sand; excessively drained.

Organic

Pk Peat and muck; water table at or near surface.

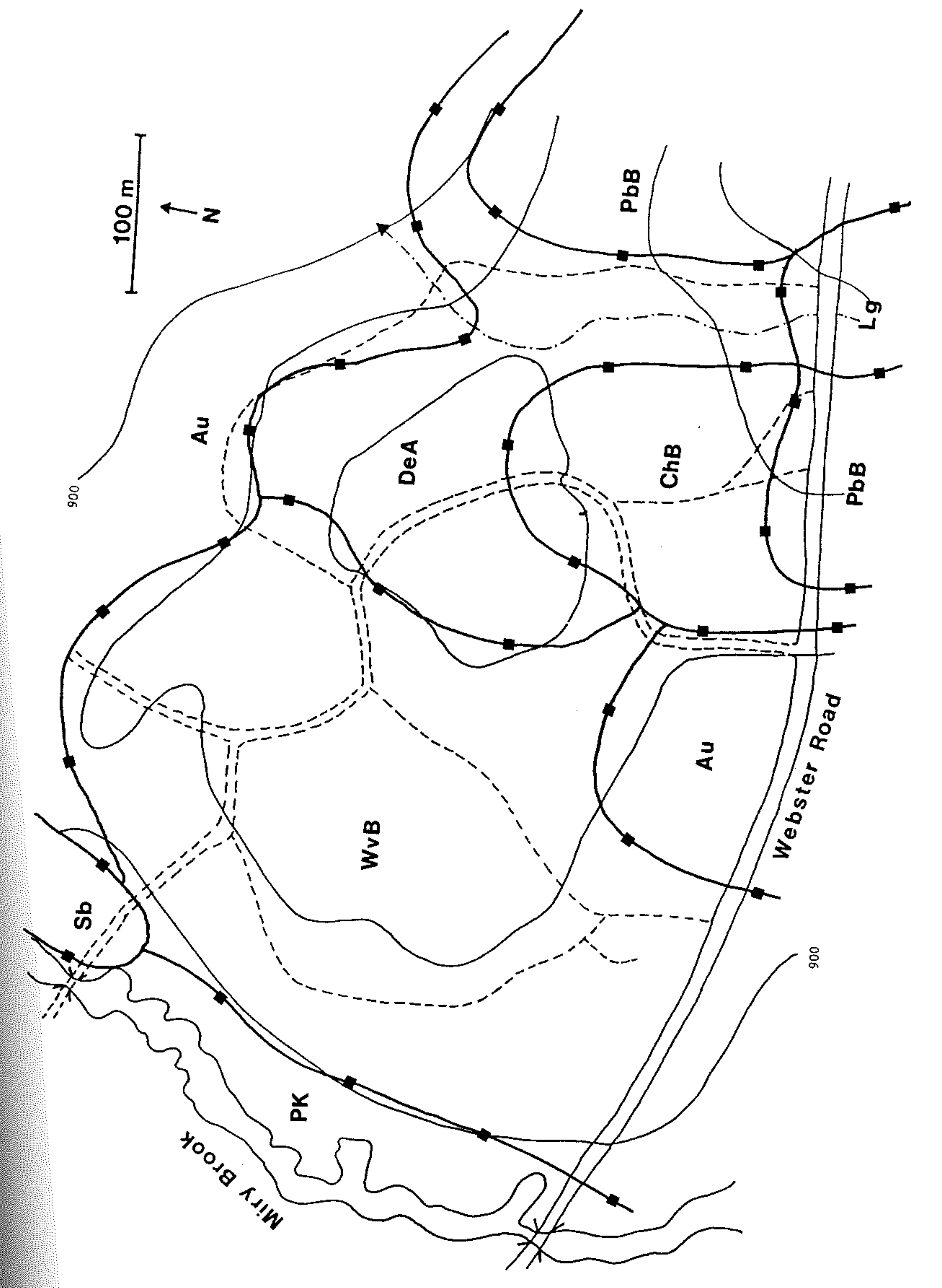


Figure 5-2. Locations of study plots in Catlin Wood.

- Improved road
- Major bridle trail
- Minor trail
- Intermittent stream
- 10-ft. contour lines

Permanent sample plots marked by metal corner posts.

2 Plots measured in the present study.

Locations of stumps from 1972 logging.

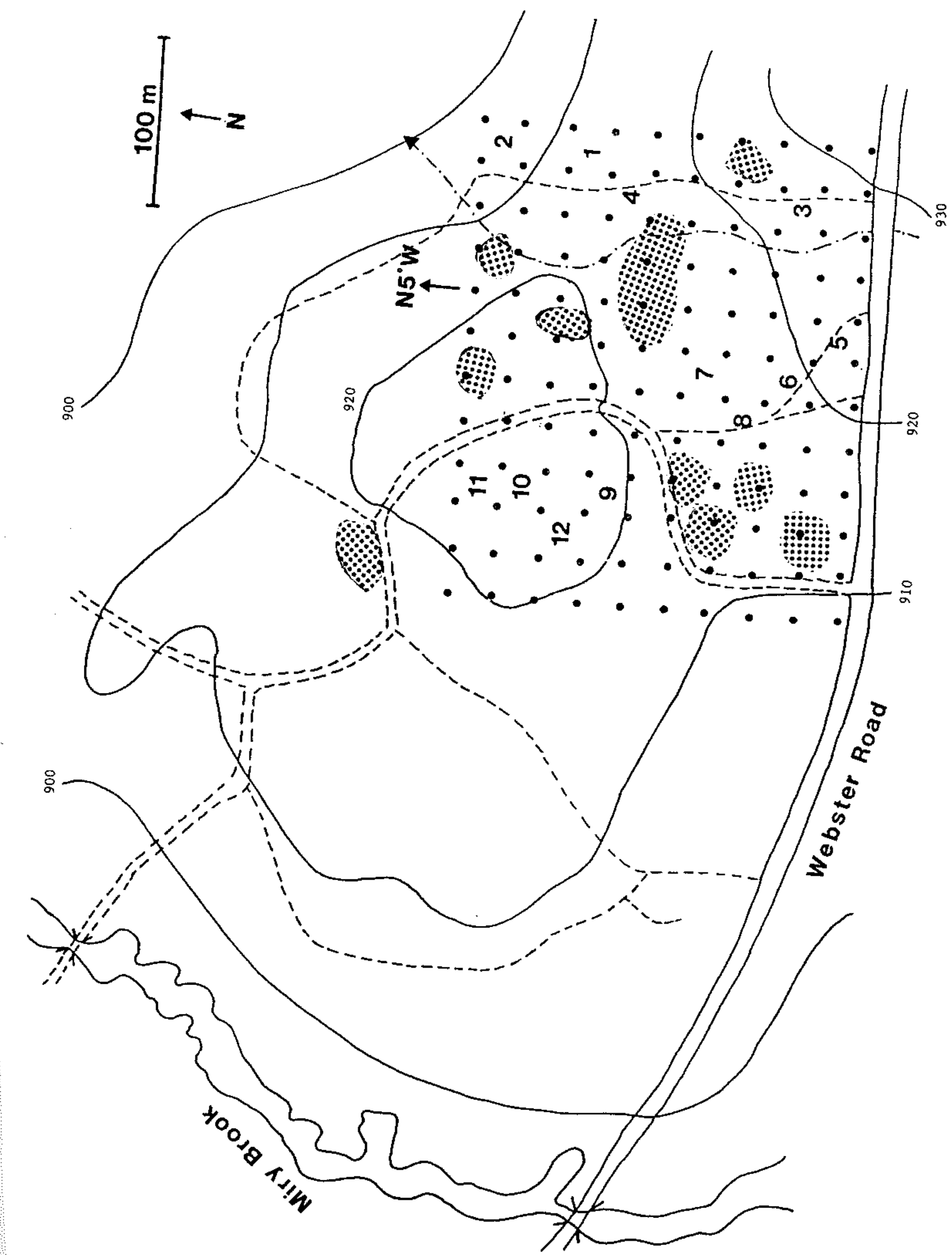


Table 5-1. Data from 12 plots in Catlin Wood woodlot area, for trees 10 cm and greater in breast-height diameter. Plot numbers correspond to those on map in Figure 5-2.

DBH: in centimeters

HT: in 3-meter height classes; midpoints of classes (1.5, 4.5, 7.5 ...) are given

SPP: 1 - hemlock
2 - red oak
3 - red maple
5 - beech
6 -
7 -
9 - white pine
10 - sugar maple
11 - white oak
12 -
13 -

PLOT	SPP	DBH	HT	PLOT	SPP	DBH	HT
1	1	37.8	19.5	3	10	28.8	16.5
1	2	35.3	25.5	3	10	18.4	13.5
1	10	17.3	13.5	3	6	19.5	16.5
1	1	14.5	7.5	3	9	36.7	28.5
1	1	31.1	19.5	3	9	65.7	34.5
1	6	18.5	16.5	3	10	18.1	13.5
1	1	21.3	13.5	3	10	18.3	16.5
1	1	11.1	4.5	3	12	24.1	19.5
1	1	62.4	25.5	3	12	35.7	22.5
1	3	28.7	22.5	3	6	33.2	16.5
1	3	35.0	25.5	3	9	64.7	31.5
1	2	38.3	25.5	3	3	17.9	13.5
1	6	21.0	16.5	3	5	10.7	10.5
1	2	43.6	28.5	3	12	16.1	13.5
1	2	59.3	28.5	3	10	23.5	16.5
1	1	49.4	19.5	3	10	26.1	16.5
1	6	25.9	16.5	3	9	65.9	34.5
1	9	70.4	37.5	3	10	30.0	16.5
1	1	41.3	19.5	3	3	13.1	13.5
1	1	51.3	19.5	3	3	27.1	19.5
1	1	39.8	16.5	3	10	11.0	7.5
1	3	18.2	10.5	3	6	23.9	19.5
1	3	13.6	4.5	3	10	13.3	10.5
1	2	65.1	28.5	3	6	39.8	22.5
1	1	27.8	13.5	3	6	30.4	19.5
2	1	38.4	16.5	4	1	14.6	7.5
2	1	35.0	16.5	4	1	71.3	31.5
2	2	56.7	28.5	4	1	19.2	10.5
2	1	26.6	13.5	4	6	23.1	16.5
2	1	42.9	19.5	4	1	13.7	10.5
2	1	56.2	22.5	4	1	23.0	13.5
2	1	24.2	13.5	4	3	13.9	13.5
2	2	57.8	25.5	4	1	45.8	19.5
2	6	23.1	16.5	4	9	70.2	37.5
2	11	52.8	25.5	4	1	52.6	28.5
2	1	11.2	4.5	4	9	71.2	34.5
2	1	49.5	19.5	4	1	42.5	19.5
2	11	53.6	28.5	4	2	61.6	28.5
2	5	35.6	22.5	4	1	51.4	22.5
2	1	21.4	10.5	4	1	25.4	10.5
2	1	49.9	22.5	4	1	50.0	19.5
2	10	19.1	16.5	4	1	48.1	19.5
2	10	22.3	19.5	4	1	29.2	16.5
2	1	52.6	19.5	4	1	26.3	16.5
2	1	37.4	16.5	4	1	28.0	10.5
2	9	60.5	34.5	4	1	53.1	22.5
2	9	76.6	37.5	4	1	20.5	10.5
2	6	16.6	13.5	4	1	31.2	16.5
2	3	26.8	19.5	4	1	60.1	25.5
2	10	17.0	16.5	4	1	42.0	19.5
2	3	38.4	19.5	4	9	59.4	34.5
2	2	39.4	25.5	4	9	76.2	37.5
2	2	22.8	22.5	4	1	70.1	25.5
2	1	31.9	19.5	4	12	44.0	25.5
2	10	16.9	13.5	4	1	12.4	4.5
2	3	26.7	19.5	4	1	11.9	4.5

Table 5-1. (continued)

PLOT	SPP	DBH	HT	PLOT	SPP	DBH	HT
4	5	36.1	19.5	6	1	23.6	13.5
4	1	19.4	10.5	6	1	19.5	7.5
4	1	10.4	7.5	6	1	53.7	19.5
5	1	40.6	22.5	6	3	20.7	16.5
5	3	51.6	25.5	6	1	47.4	19.5
5	1	33.9	19.5	6	5	50.2	22.5
5	1	60.9	28.5	6	1	18.5	7.5
5	3	41.2	25.5	6	1	27.0	16.5
5	1	28.6	16.5	6	1	42.5	19.5
5	1	20.1	10.5	6	1	18.0	7.5
5	5	31.2	19.5	6	3	25.5	19.5
5	1	40.1	19.5	6	3	27.9	19.5
5	1	28.6	16.5	6	1	22.3	10.5
5	1	29.0	16.5	6	1	30.0	13.5
5	3	23.2	19.5	6	5	22.3	13.5
5	7	36.1	22.5	6	1	35.6	19.5
5	5	19.2	19.5	7	1	40.7	19.5
5	1	17.1	10.5	7	6	16.4	13.5
5	7	29.8	19.5	7	1	16.8	13.5
5	2	33.5	25.5	7	1	18.2	13.5
5	11	41.2	25.5	7	2	43.3	25.5
5	1	11.4	4.5	7	1	20.1	13.5
5	1	35.4	10.5	7	1	36.8	16.5
5	6	17.0	13.5	7	1	27.6	13.5
5	1	33.0	19.5	7	5	33.2	22.5
5	1	18.2	7.5	7	1	22.3	13.5
5	5	23.4	22.5	7	1	33.2	13.5
5	7	35.8	22.5	7	1	20.3	13.5
5	1	21.8	13.5	7	1	16.2	13.5
5	7	27.8	19.5	7	1	33.9	16.5
5	1	14.5	7.5	7	1	37.9	19.5
5	1	44.9	22.5	7	6	24.6	19.5
5	1	66.1	28.5	7	6	29.3	19.5
5	1	33.3	22.5	7	5	43.0	22.5
5	1	36.6	25.5	7	2	69.2	25.5
5	3	24.2	22.5	7	1	13.1	4.5
5	6	23.5	22.5	7	1	27.5	13.5
5	2	71.6	28.5	7	5	39.6	22.5
5	9	55.4	28.5	7	6	29.0	19.5
5	5	38.9	22.5	7	1	38.6	13.5
5	1	35.6	19.5	7	5	40.9	25.5
5	7	34.6	22.5	7	5	18.3	13.5
6	11	39.7	22.5	7	5	12.4	13.5
6	1	12.5	7.5	7	13	20.8	19.5
6	2	69.2	31.5	7	13	30.8	16.5
6	7	44.6	19.5	7	1	42.8	13.5
6	1	30.2	7.5	7	11	31.8	22.5
6	1	15.5	7.5	7	5	19.3	16.5
6	1	43.8	16.5	7	2	47.6	25.5
6	1	10.6	4.5	7	7	30.0	19.5
6	1	38.6	16.5	8	1	27.1	10.5
6	1	38.7	19.5	8	1	26.6	13.5
6	11	64.6	28.5	8	7	38.7	22.5
6	6	26.3	19.5	8	1	45.2	16.5
6	1	13.0	10.5	8	6	23.7	16.5
6	1	16.9	7.5	8	1	25.6	13.5

Table 5-1. (continued)

PLOT	SPP	DBH	HT	PLOT	SPP	DBH	HT
8	1	13.3	10.5	10	1	68.1	22.5
8	1	17.5	13.5	10	11	39.1	22.5
8	1	18.2	16.5	10	3	36.7	22.5
8	1	38.0	19.5	10	7	12.5	13.5
8	6	16.4	16.5	10	7	29.1	19.5
8	1	45.5	19.5	10	1	51.0	22.5
8	1	18.0	13.5	10	2	28.2	25.5
8	1	26.9	19.5	10	3	14.7	10.5
8	1	10.8	4.5	10	3	11.2	13.5
8	1	25.4	13.5	10	5	22.4	19.5
8	3	29.1	19.5	10	1	20.6	13.5
8	1	20.2	16.5	10	1	26.8	13.5
8	1	12.0	10.5	10	1	62.0	19.5
8	1	24.1	16.5	10	1	55.6	19.5
8	1	28.6	16.5	10	1	11.6	7.5
8	11	22.5	19.5	10	1	39.3	13.5
8	1	31.6	16.5	10	3	23.5	19.5
8	1	16.7	10.5	10	11	14.0	16.5
8	1	15.0	10.5	10	2	30.9	22.5
8	1	29.8	19.5	10	7	37.1	16.5
8	1	15.0	10.5	10	2	24.2	22.5
8	1	29.0	19.5	11	1	52.9	19.5
8	11	27.0	22.5	11	11	29.8	19.5
8	3	28.9	19.5	11	7	14.4	13.5
8	1	24.9	16.5	11	5	24.4	16.5
8	1	16.7	10.5	11	7	17.8	16.5
8	1	32.5	16.5	11	1	46.3	22.5
8	1	47.1	19.5	11	1	50.2	22.5
8	2	54.2	25.5	11	1	37.2	16.5
8	1	34.6	19.5	11	1	30.9	16.5
8	1	15.8	13.5	11	1	27.2	16.5
8	1	52.6	22.5	11	5	31.2	16.5
8	1	31.3	13.5	11	1	30.6	16.5
8	6	19.8	13.5	11	1	60.7	22.5
8	1	26.9	13.5	11	1	31.4	22.5
8	1	31.7	16.5	11	1	34.2	22.5
8	3	35.6	19.5	11	5	25.4	16.5
8	1	13.3	7.5	11	3	18.9	16.5
8	1	17.5	13.5	11	3	14.7	16.5
8	1	15.1	10.5	11	5	37.7	19.5
9	2	49.9	28.5	11	2	59.2	25.5
9	11	43.2	28.5	12	3	29.0	16.5
9	5	31.9	22.5	12	7	33.6	19.5
9	1	23.3	13.5	12	1	61.9	22.5
9	1	49.3	22.5	12	1	21.8	13.5
9	1	43.0	22.5	12	7	16.1	13.5
9	1	64.4	22.5	12	1	41.9	25.5
9	1	45.2	16.5	12	5	47.5	25.5
9	7	44.4	22.5	12	7	45.4	22.5
9	1	41.3	16.5	12	5	13.9	13.5
9	5	27.0	19.5	12	5	40.0	19.5
9	5	33.1	19.5	12	3	27.0	16.5
9	2	61.5	28.5	12	5	15.6	10.5
9	11	28.6	16.5	12	1	37.7	16.5
9	1	27.4	10.5	12	1	42.5	16.5
9	1	27.9	10.5	12	5	40.8	22.5
9	5	57.8	22.5	12	7	29.2	19.5
9	1	11.7	7.5	12	2	53.7	28.5
9	3	26.6	16.5	12	1	60.6	16.5
9	1	58.9	19.5	12	3	16.1	13.5
9	6	22.8	19.5	12	2	28.0	25.5
9	2	35.3	19.5	12	2	26.7	25.5
				12	2	66.2	28.5

On the first 60-acre pitch, the town school was assigned a block now in the eastern half of Catlin Wood (Deed 1-70R). Adjacent to the west on the second round of 60-acre pitches, Abraham Goodwin was assigned just over one-half of his pitch (Deed 1-153R). His father Nathaniel was an original proprietor of the town, but in 1723/24 gave his land, both divided and undivided, to Abraham--thus, Abraham received the Catlin Wood pitch directly (see Figure 18a).

Isaac Bissell, also an original proprietor, bought the school-right land (Deed 2-371) and transferred it to his son Isaac Jr., who sold it in 1743 (Deed 4-74) to Phineas Bradley of New Haven. On February 20, 1749/50, Captain William Marsh, son of Captain John Marsh, the founder of the town, purchased the western 25-acre portion of Bradley's land (Deed 4-345); see Figure 18b. This was transferred to Captain Wm. Marsh's son William in 1790 (Deed 18-115).

Meanwhile, on the western edge of Marsh's land, Phineas Goodwin acquired the western half of Catlin Wood from (his father?) Abraham, date unknown. Phineas died as a prisoner of war during the Revolution, and Micah Goodwin acquired the land. This completes transactions to 1815, shown in Figure 18c.

Deeds not pertaining to the land of Catlin Wood indicate that, at least in 1816, Micah Goodwin owned a sawmill and gristmill one mile south of Litchfield on the Bantam River, which would be about one mile from his Catlin Wood land (Deed 29-267). Also, Captain William Marsh owned a mill of some sort, which he transferred to his son William's ownership in 1790 (Deed 18-115). This was on Chestnut Hill, about 2 miles from Catlin Wood. The Marsh house was located at the mill site.

The history of ownership can best be followed separately for the two halves of Catlin Wood from this point. Marsh sold his 25 acres in the eastern half in 1827 (Deed 34-452) to William H. Thompson of Augusta, Georgia, who was acquiring parcels of land just to the south and east to form a farm. Thompson held the land until he died in 1868, and his heirs sold the farm to C. B. Webster. At that time, the land south of Webster Road was supporting a crop of rye, and the 25-acre eastern portion of Catlin Wood was described as a woodlot (Deed 63-498).

The history of ownership of the western (Micah Goodwin) portion is much more complex than the Marsh half, in part because all of the participants seemed to be overextended in their financial dealings. In 1817, Micah Goodwin died, and his land was sold to pay his debts (Deed 29-436,7). Part of the Goodwin land was sold to James Prescott, and part was sold to the firm of Oliver Goodwin and Sylvester Galpin, a firm dealing mainly in the manufacture of musical instruments; see Figure 18d. Goodwin and Galpin's interest in the land apparently was speculation--a road was planned for the frontage of the property. It was surveyed in 1823 (Survey 22-409), but the road was apparently not completed until sometime after 1836. An 1824 deed (Deed 32-383) for a part of the Goodwin and Galpin land does describe the southern boundary as a highway, but a deed dated 1836 (Deed 41-272) states that the southern boundary is the land of Julius Deming, but is "subject to a public highway across the south border," implying that the road did not yet exist.

It seems that Prescott was in debt to Goodwin and Galpin, and mortgaged his land to them in 1825 (Deed 34-68). In 1830, Prescott could not pay his debt, so he signed a quit-claim deed for the southern

4.5 acres (Deed 38-105), and reclaimed the northern 11 acres; see Figure 18e. James Prescott then sold the land to Frederick Prescott in 1832 (Deed 39-125) who mortgaged it to George Prescott, but apparently couldn't pay the mortgage and transferred the land to George P. by quit-claim deed (Deed 46-332) in 1844. Meanwhile, the firm of Goodwin and Galpin had been dissolved, and Galpin sold the land to P. S. Beebe in 1836 (Deed 41-272).

In 1869, C. B. Webster purchased the Beebe land (Deed 63-603). The year before, Webster had purchased the Thompson farm and the eastern half of Catlin Wood, so he apparently was adding adjacent parcels to increase the size of the farm. Thus, most of the land of Catlin Wood was consolidated into a single ownership for the first time in 1869; see Figure 18f.

In 1856 (Deed 557-486), George Prescott sold the northwestern portion to the Litchfield County surveyor Arthur D. Catlin and his wife Elizabeth. It was from the Catlins (Deed 83-241) in 1911, and the Websters (Deed 83-415) in 1913, that Alain and May White acquired Catlin Wood as part of the formation of what is now the White Memorial Foundation property.

APPENDIX 6

Equations for estimation of volume and biomass.

Table 6-1 lists equations used for estimation of individual-tree aboveground biomass. Table 6-2 lists equations for estimation of wood volume in stems from the top of a 30.5 cm stump to a minimum diameter of 10 cm outside bark.

Table 6-1. Biomass equation statistics, from Monteith (1979)[a]. General equation is of the form:

$$W = b_0 + b_1D + b_3H + b_4D^2H$$

where W = weight (kg), D = breast-height diameter (mm), and H = total tree height (m).

Species[b]	b_0	b_1	b_2	b_3	Species[c]
Red maple	1.3785	0.02279	-0.3010	0.0002469	Red maple
Red oak	9.6829	0.4214	-4.1658	0.0002654	Red oak, white oak, shagbark hickory, chestnut, hop-hornbeam
Hemlock	1.4081	0.1824	-1.4563	0.0001842	Hemlock
Sugar maple	0.06116	0.1752	-0.8988	0.0002761	Sugar maple, black birch, paper birch
Beech	0.7833	0.08899	0.5297	0.0002996	Beech
White pine	0.5209	0.07434	-0.5439	0.0001516	White pine
Yellow birch	-4.9178	0.02462	0.5461	0.0002773	Black cherry, yellow birch
White ash	-4.1776	0.2195	0.4421	0.0002038	White ash

[a] Equations also reported in Tritton and Hornbeck (1982).

[b] Species as listed by Monteith (1979).

[c] Species for which each equation was used in this study.

Table 6-2. Stemwood volume equation statistics, from Scott (1981). General equation is of the form:

$$V = b_0 + b_1 D^{b_2} + b_3 D^{b_4} H^{b_5}$$

where V = volume (ft^3), D = breast-height diameter (inches), and H = stem length (ft).

Species[a]	b_0	b_1	b_2	b_3	b_4	b_5	Species[b]
White, red pine	0.11	-0.05977	2.0498	0.04965	2.0198	0.3468	White pine
Hemlock	0.24	-0.05895	2.0362	0.04947	2.0172	0.3366	Hemlock
Soft maple	-0.45	-0.00523	2.2323	0.01338	2.0093	0.6384	Red maple
Black cherry	-0.04	-0.01783	1.8109	0.01358	1.9905	0.6553	Black cherry
Birch species	-0.27	-0.00675	1.9738	0.01327	1.9967	0.6407	Black, yellow, and paper birch
Beech	-0.60	-0.00711	2.2693	0.01399	2.0190	0.6518	Beech
Red oaks	-0.13	-0.00536	1.1972	0.01131	1.9975	0.6549	Red oak
Other hardwoods	0.13	-0.00183	2.3600	0.00944	2.0608	0.6516	Sugar maple, white oak, white ash, shagbark hickory, chestnut hop-hornbeam

[a]Species group as defined by Scott (1981).

[b]Species group for which each equation was used in this study.

APPENDIX 7.

Estimation of basal area growth of individual trees.

To estimate current basal area growth of trees in the full sample of plots, subsamples (sizes given in Table 7-1) were taken for all important species, and current basal area growth was calculated from two increment cores from each tree. When basal area growth was related to basal area in linear regressions, residual variances proved to be heteroscedastic--increasing with increasing value of basal area. Following logarithmic transformation of both variables, residual variances were homoscedastic. The regression equations were of the form:

$$\ln(Y) = \ln(b) + a \ln(X)$$

where Y = basal area growth, X = basal area, and a and b = estimators of regression parameters specific to each species.

Regression statistics are presented in Table 7-1. Squared correlation coefficients (r^2) ranged from 0.60 to 0.94 for all species except red maple and black birch in the younger stands. These were low because these two species had low growth rates regardless of present basal area.

These equations were used to predict the current basal area growth of each tree in the full sample, based upon their present basal area. To do this, the logarithmic regression equations had to be converted back to arithmetic units. This cannot be done directly, simply by

Table 7-1. Basal-area-growth equation statistics. Form of equation is given in text of Appendix 7.

Species	Sample size	r^2	ln(b)	a	s^2(error)
44-year-old stands					
Hemlock	44	.71	-2.9231	0.8540	.2912
Red oak	57	.94	-4.8163	1.3007	.0745
Red maple	19	.20	-1.7870	0.5810	.4277
Black birch	19	.36	-3.0661	0.8358	.2144
87-year-old stands					
Hemlock	46	.81	-4.4460	1.0381	.1789
Red oak	49	.60	-2.7705	0.8237	.0722
Red maple	27	.68	-3.6886	0.8755	.2076
Black cherry	20	.69	-6.0246	1.2592	.1864
Beech	20	.66	-2.6804	0.7753	.1596

determining antilogarithms, since this will give the median rather than the mean Y value for each X, and will result in a consistent underestimate (Baskerville 1972). The unbiased prediction of the mean Y for each X in arithmetic units is of the form:

$$Y = e^{(\ln(b) + a \ln(X) + s^2/2)}$$

where Y = predicted basal-area growth, s^2 = sample variance of regression equation, and others as above.

APPENDIX 8

Relationship of diameter inside bark to diameter outside bark.

Regression equations, from Oliver (1978), were used to calculate diameter inside bark from measured diameter outside bark. Equations were of the form:

$$O = b_1 I^{b_2}$$

where O = outside-bark diameter (mm), I = inside-bark diameter (mm). Regression statistics are given below.

Species[a]	b_1	b_2	Species[b]
Hemlock	1.2594	0.9692	Hemlock
Red oak	1.2821	0.9676	Red oak
Red maple	1.1896	0.9748	Red maple
Black cherry	1.1822	0.9803	Black cherry
Black birch	1.2050	0.9781	Black birch, yellow birch beech, white ash, shagbark hickory
Grey and paper birch	1.2381	0.9689	Paper birch
White pine	1.404	0.9458	White pine
Sugar maple	1.1418	0.9887	Sugar maple
White oak	1.5348	0.9279	White oak, chestnut, hop-hornbeam

[a]Species as listed in Oliver (1978).

[b]Species for which each equation was used in this study.

APPENDIX 9

Estimation of yields of pure hemlock stands.

The yield study of Merrill and Hawley (1924) was used to estimate basal area and volume of pure hemlock stands similar in age and site quality to those measured in the present study. That study incorporated data from 62 plots varying in size from 0.1 to 1.4 acres. Each was pure hemlock; potential plots were eliminated from the study by the presence of any hardwoods, hardwood stumps, or evidence from hemlock growth ring patterns of hardwood competition at early ages. Thus, the data represent hemlock stands which grew free of competition throughout their life. This is similar to the situation for the hardwood and hemlock-hardwood stands measured in this study. The plots of the Merrill and Hawley study were not selected according to a predetermined density criterion for "full-stocking", as in many yield studies. The only criterion was that the ground area was fully occupied by hemlock crowns.

Age measurement of each sample plot was made from increment cores taken at breast height, or some other height. Measurements of seedling growth were made in order to determine the time required for a hemlock to grow from germination to various heights; these showed that it took 9.5 years to attain breast height, and 10 years to reach 1.5 m. Total age of each plot was estimated by adding the appropriate number of years from the seedling study to the age determined from the increment cores.

In the current study, stand age was measured beginning at the time of release by overstory disturbance. Trees of the new stand were already present as advance growth, usually 1 to 2 meters in height, or they sprouted from an established root system and reached a height of 1 to 2 meters in the first year.

In order to equalize results of the two methods of expressing age, 10 years was subtracted from the ages reported in the yield tables. Thus the yields that are compared are those that result from growth during the period that the dominants grew from 1.5 meters in height to their attained height at the time of measurement.

Site-quality class in the hemlock yield tables was based upon the average height of dominants. Comparison of table values with the heights of the few hemlock dominants that occurred in the hemlock-hardwood mixtures of this study showed that the site-quality class designated as "60 feet at age 80" was appropriate. Basal area and volume yields for stands of this site quality at age 44 (table value of age 54) and age 87 (table value of age 97) were determined by linear interpolation between values given for 10-year age classes, as given in Table 9-1.

Yields for stands of the next higher site-quality class "70 feet at age 80" are also given in Table 9-1.

Table 9-1. Yields of pure hemlock stands, from Merrill and Hawley (1924; Table V).

Stand age[a] (years)	Height of dominants[b] (m)	Tree density (#/ha)	Basal area (m^2/ha)	Stemwood volume (m^3/ha)	Biomass (t/ha)
Site-quality class--60 feet at 80 years					
44	13.9	1720	29.8	159	102
87	20.8	664	43.9	320	189
Site quality class--70 feet at 80 years					
44	16.8	1477	38.0	211	142
87	23.8	504	54.2	430	246

[a]This age is 10 years less than that given in Table V of Merrill and Hawley. See text of Appendix for explanation.

[b]In the hemlock-hardwood stands of the present study, height of hemlock dominants averaged 13 m at age 44 and 18 m at age 87.

APPENDIX 10

"Stratification" defined.

Although the term "stratification" had been used as early as 1919 in describing tropical forest canopy structure, the concept was advanced primarily by the work of Richards (1952). Since his work, the term has been used for various purposes, to denote only distinctions among tree, shrub, and herbaceous layers, or among different tree layers where canopy layers are separated by a horizontal gap in which foliage is less dense or absent. However, Richards' original definition simply equated "stratum" with "story" or "layer," as follows:

> By a stratum or story is meant a layer of trees whose crowns vary in height about a mean. In a several-layered forest community each stratum will have a distinctive floristic composition.... The crowns of young trees of a higher stratum and exceptionally tall ones of a lower will also be found between one stratum and the next; if such individuals are numerous, as is often the case, there will be little vertical discontinuity between neighbouring strata and the stratification will be much obscured. (Richards 1952, p. 23)

Smith (1962) used Richards' definition in applying the concept of stratification to the structure of temperate forests, and it is in this sense that it is used in the current study. Thus, the foliage of the total forest canopy may form a fairly continuous vertical distribution, but if the upper portions are composed of different species than the lower, these portions are considered different strata. The terms "upper and lower canopy positions" and "overstory and understory" are equivalent to "upper and lower canopy strata" in the present study, as they were in Richards' and Smith's terminology. Such terms are preferable to those of "dominant, codominant, intermediate, and overtopped canopy positions" as frequently used in forestry literature. These latter terms were developed for even-aged, single-species stands, and carry with them connotations of vigor and growth rate that may not hold for trees in mixed-species or uneven-aged stands.