

Productivity of New England Hemlock/Hardwood Stands as Affected by Species Composition and Canopy Structure

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ABSTRACT

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Canopy structure, yield, and current productivity of two even-aged stands (of ages 44 and 87 years) composed of hemlock (*Tsuga canadensis* (L.) Carr.) and hardwoods (primarily *Quercus rubra* L. and *Acer rubrum* L.) were compared with that of adjacent hardwood stands of the same age, site conditions, and hardwood species composition, but which lacked hemlock. In the hemlock/hardwood mixtures, hemlock formed a dense understory beneath the hardwood overstory, while hardwood stands lacked comparably dense understories of any species. The mixed stands were found to have significantly greater yields and current production rates in total stand basal area than adjacent hardwood stands. Basal area yield and production of the hardwood component of the mixed stands were not significantly different from that of the adjacent hardwood stands, indicating that the hemlock growth was largely additive to that of the hardwood overstory. Similar patterns were observed when data were converted to stemwood volume or above-ground biomass measures, although not all differences were statistically significant. Published yield tables for hemlock indicate that basal area and biomass yield of pure hemlock stands of similar age and site conditions was also exceeded by that of the hemlock/hardwood mixtures in the present study.

A review of plantation studies comparing mixed stands with adjacent pure stands of the component species indicates consistency with the results of the present study in the pattern of mixed stands with stratified canopies having greater yield than pure stands of the overstory species. There is some evidence to indicate that mixtures have greater yields than pure stands of the understory component as well, although fewer data exist for this comparison.

INTRODUCTION

One facet of the much-debated question concerning the relative merits of single-species and mixed-species stands is that of total stand productivity. This

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problem has often been approached in correlative studies of the relationship between species diversity and productivity in complex, natural stands. However, no broad generalizations concerning this relationship have been supported (Whittaker and Woodwell, 1972; Whitehead, 1982; Smith, 1986). One difficulty in such studies is that species diversity and site quality are often related, making it difficult to separate the effects of each on productivity.

Agronomists and plant population biologists have approached the same question by using much simpler experimental mixtures of herbaceous species. A standardized experimental design has been developed, called 'replacement series' studies, in which the productivity of stands growing in identical site conditions is compared. Total plant density is held constant across all stands, while the proportions of two species are varied, including pure stands of each species. These experiments generally have shown that mixtures are not more productive than pure stands of the highest-yielding component species (Trenbath, 1974), although some exceptions to this pattern do occur. This pattern may appear surprising because it is not necessary for a commensal relationship to exist between species (e.g., fixation of atmospheric nitrogen by one species which becomes available to the other through root exudation or litterfall) in order to have a higher-yielding mixture. All that is necessary for a mixture to more fully utilize a site for production is that a sufficient degree of niche separation exists in characteristics such as phenology, degree of shade tolerance, or shoot and root growth patterns that allow canopy or root stratification to occur. In replacement series experiments where mixtures have shown higher yields than either pure stand, species differences in one or more of these characteristics have been shown to exist (Ellern et al., 1970; Trenbath and Harper, 1973; Hill and Shimamoto, 1973). Harper (1977) suggested that the rarity of this result in experiments may be due to the use of crop cultivars bred for high production in monoculture, rather than pairs of species chosen for their ecological combining ability.

Although elegant experiments of the replacement series kind are not possible (or at least very difficult) with most forest stands, it is logical to apply this general approach to forest production where possible, as an alternative to the diversity/productivity correlative studies. In the present study, a comparison is made of naturally occurring, adjacent stands with varying species composition and results are compared with those from previous forest studies which follow the same basic study design.

The focus of the present study is a comparison between unthinned, even-aged stands of mixed-hardwood species and adjacent stands of similar age, history and composition but which also contain a component of hemlock (*Tsuga canadensis* (L.) Carr.). Thus, this study does not examine the productivity of mixtures of two species, as in experiments with herbaceous species, but of a species on one hand, and a group of species on the other – distinguished by differing basic growth characteristics. Hemlock is a shade-tolerant, evergreen

species, with slow juvenile height growth, whereas the important hardwood species in these stands – red oak (*Quercus rubra* L.), red maple (*Acer rubrum* L.), black birch (*Betula lenta* L.), paper birch (*Betula papyrifera* Marsh.) and black cherry (*Prunus serotina* Ehrh.) – are deciduous species of intermediate to low shade-tolerance, with much greater juvenile rates of height growth. This allows a canopy stratification to occur with the main hardwood canopy layer occurring above that of hemlock (Kelty, 1986). Ideally, a further productivity comparison would be made between the two previously described stands and pure hemlock stands, but no cases were found of all three types of stands occurring adjacent on the same site; thus, productivity estimates for pure hemlock stands were taken from the literature.

SITE DESCRIPTIONS

Two study areas were selected which had the following characteristics in common: (1) both were in the transition hardwood–hemlock–white pine (*Pinus strobus* L.) forest vegetation zone (Westveld, 1956); (2) both were on rolling, glaciated uplands with thin till soils that had never been cleared for agricultural use; (3) both had originated from a single, large-scale disturbance that completely (or nearly so) removed the previous overstory over at least several hectares; (4) neither had received any silvicultural treatment since establishment; and (5) the spatial distribution of hemlock was patchy, so that hardwood and hemlock/hardwood stands occurred in close proximity. One area is in the Harvard Forest in central Massachusetts and one on the Great Mountain Forest in northwest Connecticut, 110 km southwest of the Harvard Forest. The climate of both sites is a temperate, continental type, with precipitation evenly distributed through the year. Climatic conditions of the two sites are given in Table 1.

The 3-ha Harvard Forest (HF) site occupies the top and upper west-facing slope of a small hill at 300 m elevation. The soil is classified as well-drained

TABLE 1

Climatic conditions at the Harvard Forest (Murison, 1963) and the Great Mountain Forest (Winer, 1955)

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

^aMean number of days between last spring frost and first autumn frost.

Charlton, stony, fine sandy loam, derived from till of gneiss and schist origin (Simmons, 1940). Bedrock outcrops occur within the study area, with depth to bedrock varying from 0 to approximately 200 cm. Slopes on sample plots varied from level to 10%. The study site was never cleared for crop or pasture use because of its rocky and uneven terrain, although much of the adjacent land had once been farmed. Records from the mid-19th century indicate that it was used as a farm woodlot (Raup and Carlson, 1941). The present stand originated after hurricane winds destroyed the existing overstory in 1938. The stand age was 44 years at the time measurements for the present study were made.

The 8-ha Great Mountain Forest (GMF) site occupies the top and upper north-facing slope of a small hill at 460 m elevation. The soil is well-drained to somewhat excessively drained Hollis, extremely rocky, fine sandy loam (Anonymous, 1970), a till soil averaging 40 cm to bedrock, which is derived from gneiss and schist parent materials. Slopes on study plots were level to 10%. This study site is in an area where little agricultural development occurred in the 19th century. Extensive timber cutting began in the mid-19th century, with clearcutting of hardwoods for charcoal production accompanied by cutting of hemlock for sawlogs and tanbark, which resulted in nearly complete clearcutting. The study stand originated following this kind of cutting in 1895. Stand age at the time of measurement was 87 years, with some older hemlock occurring which had been understory trees left at the time of cutting (Kelty, 1986).

METHODS

Study design

Assessments of productivity in replacement series experiments involving herbaceous plant species are generally made in terms of biomass yield at the end of one growing season. This is accomplished by harvesting, drying, and weighing all above-ground vegetation on sample plots. In forest studies, productivity of trees can be assessed in terms of basal area, stemwood volume, or total tree biomass. Also, distinction can be made between yield (a measure of the accumulated basal area, volume, or biomass of all standing trees at a given time) and current production (current annual increment in any of these parameters at the time of measurement). All of these measures were used in the present study.

In this study, two sets of stands were compared. Each set consisted of a hardwood stand and an adjacent hemlock/hardwood mixture. Stand boundaries between the hardwood and hemlock/hardwood stands were irregular, with the two kinds of stands being intermixed across a slope with the same soil type. This situation occurs because of the regeneration characteristics of hemlock.

Hemlock seedlings frequently grow beneath the canopies of older stands, and successful regeneration of hemlock following overstory disturbance generally depends on the release of these advance-growth seedlings. These seedlings often occur in a patchy distribution, because seedling establishment appears to be restricted to limited areas surrounding overstory hemlocks acting as seed sources (Simmons, 1940; Winer, 1955). The patchiness is more pronounced than might be expected beneath a mature hemlock/hardwood canopy, because most hemlocks occur in a suppressed canopy position, but only dominant or co-dominant hemlocks produce seed. Thus, when the overstory is removed, new stands are composed predominantly of hardwood species, but often contain an irregular distribution of hemlock which is correlated, not to site differences, but to the presence of overstory hemlocks in the previous stand.

Stand measurements

In each set of stands, sample plots were located at fixed intervals along parallel transect lines. Plots were aggregated into stands according to the presence or absence of hemlock. Plots with 3 stems of hemlock or less 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. In the Harvard Forest stands, 20 circular 0.01-ha plots were established and all trees 1.3 m and greater in height were measured. In the Great Mountain Forest stands, 32 variable-radius plots were measured using a prism with a basal area factor of $2.3 \text{ m}^2 \text{ ha}^{-1}$. All trees judged borderline by prism measurement were verified with measuring tape. All trees at least 1.3 m in height were included.

Diameter at breast height (DBH) and total tree height were measured for all trees on all plots. A subsample of trees was selected for measurement of basal area growth, apportioned among species according to the relative stand basal area of each. For each of these trees, 2 increment cores at breast height were extracted, oriented at right angles to another, 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 by gypsy moths (*Lymantria dispar* L.). Since the purpose of this study 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 that had recently died from the effects of defoliation were counted as living trees. Second, present diameter growth rates were not estimated by averaging the most recent 5 years of growth, since growth during the previous 2 years was severely reduced due to defoliation. Instead, the growth from 1975 through 1979 was used, these being the least 5 years prior to defoliation. Thus, estimates of stand parameters reflect growth unaffected by defoliation.

Data analysis

Comparisons between stands were made in terms of basal area, stemwood volume, and total biomass. The stemwood volume of individual trees was estimated using regression equations developed by Scott (1981). These equations use DBH and stemlength from the top of a 30.5-cm stump to an upper limit of 10-cm outside-bark stem diameter as the 2 independent variables, and calculate total wood volume (excluding bark) within that length of stem. Only trees 12.7 cm and greater in DBH were included in volume calculations, since this was the limit used in developing the equations. Biomass calculations, estimating total above-ground dry weight of individual trees (including branches and foliage) were made using equations developed by Monteith (1979), in which the independent variables were DBH and total tree height. All trees 1.3 m and taller were included in biomass estimates.

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 2 increment cores of each subsampled tree, served as the estimate of current diameter growth rate. This was converted to current basal area growth which was then related to current basal area by linear regression following logarithmic transformation of both variables. The growth of species that occurred only in 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 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 from the original volume. Similar calculations were made for current annual biomass increment.

Yield estimation of pure hemlock stands

A direct comparison of mixed stands with pure hemlock stands was not possible because hemlock rarely occurs as an even-aged pure stand, 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 small stands of pure hemlock, enabled 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 hemlocks) were taken directly from the Merrill and Hawley yield tables. 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 were derived from the yield

tables using the 'mean-tree' approach (Madgwick, 1970; Parde, 1980): the biomass of the tree of mean basal area (which approximates the tree of mean biomass in even-aged, single-species stands) was determined using the same biomass equations as for the rest of the study, and was multiplied by tree density to estimate total stand biomass.

RESULTS

Stand characteristics

With the exception of hemlock, species composition was similar between the hardwood and hemlock/hardwood stands at each of the 2 study sites (Table 2). Red oak, red maple, black birch, and paper birch were the most common at the HF site, and red oak, red maple, American beech (*Fagus grandifolia* Ehrh.), and black cherry at the GMF site. Densities of red oak, black cherry, and the birch species were similar between stands at each site, with greater densities of red maple and beech occurring in the hardwood stands. Mixed stands had greater overall stem density because of the large number of hemlocks, which comprised 52% and 61% of the total stem density in the HF and GMF mixed stands, respectively. Differences in composition and density in the GMF stands are shown in Fig. 1.

Heights of the main overstory hardwood trees were 12–18 m in the HF stands and 15–21 m in the GMF stands (Fig. 2). Most hemlocks occurred in the understory canopy. In the HF mixture, hemlock occurred almost exclusively at heights of 12 m and less; in the GMF mixture, they were primarily less than

TABLE 2

Species composition of hardwood and hemlock/hardwood (mixed) stands at the Harvard Forest and Great Mountain Forest sites by tree density (trees ha⁻¹)

Species	Harvard Forest		Great Mountain Forest	
	Mixed stand	Hardwood stand	Mixed stand	Hardwood stand
Red oak	610	540	176	167
Red maple	340	640	190	273
Black cherry	—	—	29	25
Beech	—	—	164	306
Birch spp.	890	940	—	—
All hardwoods	2040	2720	565	811
Hemlock	2170	80	885	27
Total	4210	2800	1450	838

Totals include minor species not listed separately.

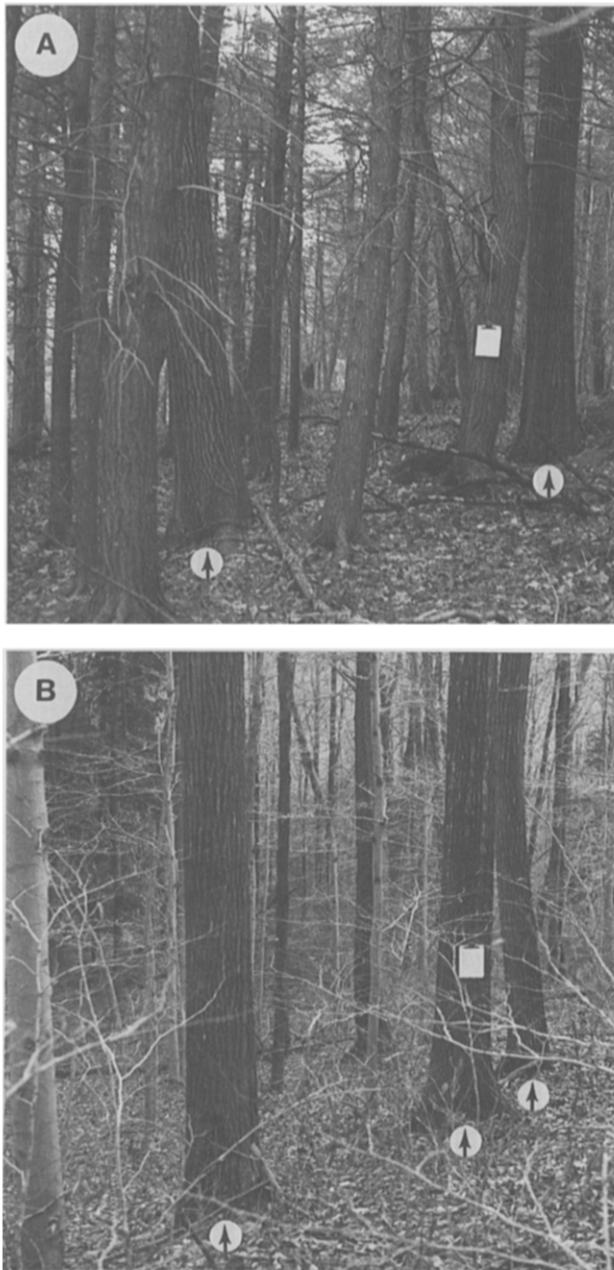


Fig. 1. Views of the hemlock/hardwood stand (A) and hardwood stand (B) at the Great Mountain Forest study site. Arrows indicate overstory red oaks. All other trees in foreground of A are understory hemlocks which are overtopped by the two red oaks. Other trees in B are maple, birch, and beech of varying crown positions.

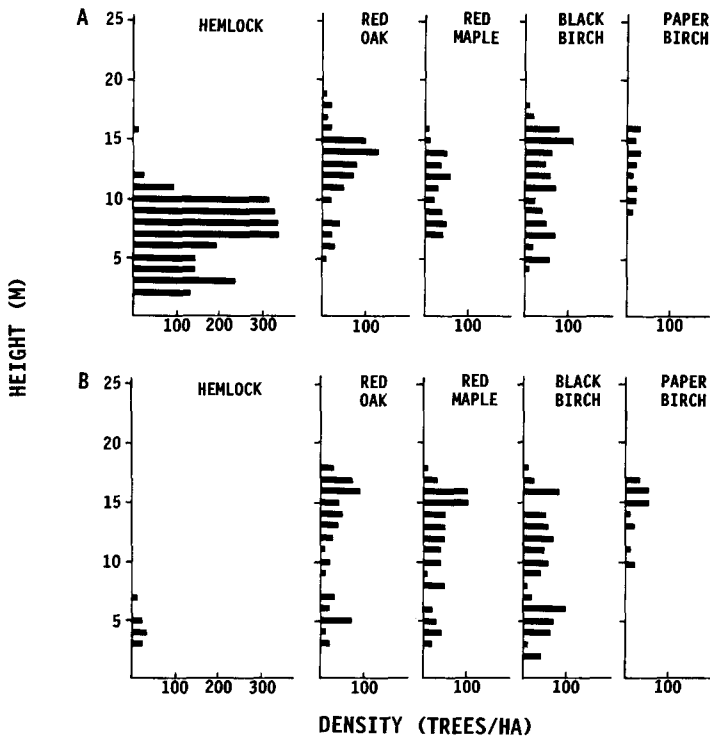
15 m but a small number of hemlocks occurred at heights of 15–18 m, similar to the tallest hardwoods.

Yield comparisons

For both forests, basal area of each hardwood species was similar between stands with and without a major hemlock component, except for beech at GMF, which showed a significantly greater basal area in the hardwood stand (Fig. 3). In both cases, the total basal area of the hardwood component in the mixed stand was less than that of the total hardwood stand, but differences were not significant. Stand comparisons that include all species showed that the mixed stands produced 64% and 43% greater basal area yield than adjacent hardwood stands in the HF and GMF sites, respectively.

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

Results from the GMF site showed smaller differences between stands, with a 19% greater volume yield in the hemlock/hardwood mixture, and an 11% greater biomass yield (Table 3). Unlike other stand comparisons, the hardwood stand biomass was significantly greater than that of the hardwood component of the mixture. One possible reason examined for these differences was that, while the HF hemlock/hardwood stand overstory was almost completely composed of hardwoods (less than 1% of overstory basal area was made up of hemlock), the GMF hemlock/hardwood overstory had a larger hemlock component (20% of overstory basal area). This resulted from understory hemlocks having been left at the time of cutting in 1895; these had an initial height advantage over newly established hardwoods that was sufficient to maintain an overstory position in spite of the more rapid height growth of the hardwoods (Kelty, 1986). This partial hemlock overstory would affect the biomass of the stand more than the basal area or volume because of the difference in wood density. Measures made in this stand indicated 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). This greatly affects the biomass per unit land area between individual overstory oak and hemlock trees. Furthermore, most overstory oaks had one or more understory



hemlocks growing beneath their crowns, occupying the same land area, whereas overstory hemlocks had deep crowns extending close to the ground, with no understory trees beneath them. To test the level of these effects on total biomass yield, stand biomass was recalculated by omitting the stand areas where hemlocks occupied overstory positions. This gives an estimate of the biomass in the GMF mixed stand as if no overstory hemlocks were present and instead a complete upper story of hardwoods had developed as in the HF stand. With this change, the hemlock/hardwood mixture would have a 28% greater biomass yield (298 t ha^{-1} compared to 233 t ha^{-1} for the hardwood stand), which is similar to the comparison between the HF stands.

Estimates of basal area, volume, and biomass yield for pure hemlock stands were derived from a yield study of hemlock stands in southern New England (Merrill and Hawley, 1924). These estimates (Table 4) indicate that the basal area of pure hemlock stands would exceed that of hardwood stands of similar age and site conditions but would be less than that of mixed stands. In volume, hemlock stands and mixtures would be 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 stand. Differences between

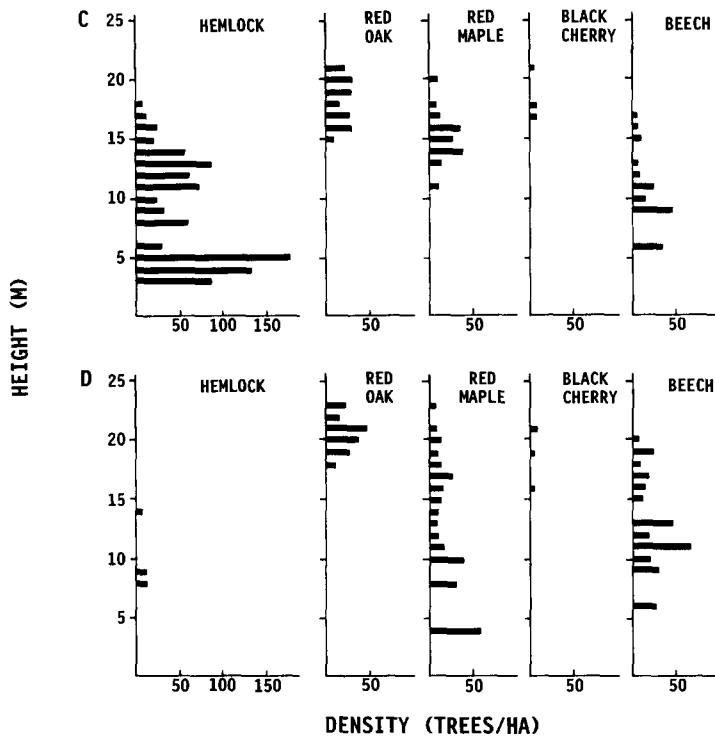


Fig. 2. Tree density distributions by species and 1-m height class for 44-year-old Harvard Forest hemlock/hardwood stand (A) and adjacent hardwood stand of same age (B); and for 87-year-old Great Mountain Forest hemlock/hardwood stand (C) and adjacent hardwood stand of same age (D).

the hemlock yield study estimates and data from the present study could not be statistically tested.

Current production comparisons

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 grown at approximately equal rates, with hemlock/hardwood mixtures having a greater yield at any time because of differential rates of survival 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. Current production levels were measured to assess the relative importance of these two alternatives.

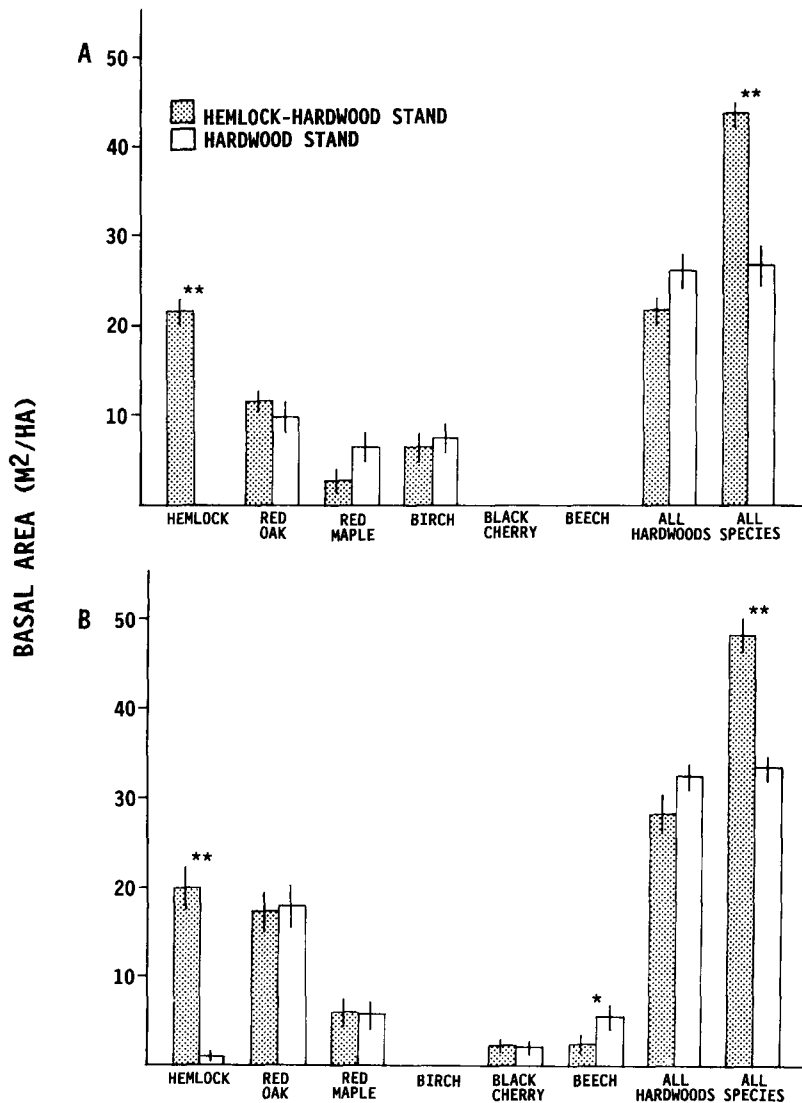


Fig. 3. Basal area yields of (A) Harvard Forest stands and (B) Great Mountain Forest stands by species and species groups. Vertical lines indicate \pm SE. Significant differences between hemlock/hardwood and hardwood stands by each species or species group are indicated by * and ** for $P < 0.05$ and $P < 0.01$, respectively.

Current growth rates of individual trees were measured across the range of stem sizes present, and regressions of basal area growth on present basal area were made for individual trees of each important species in each stand. Squared correlation coefficients ranged from 0.60 to 0.94 for all species except red maple (0.20) and black birch (0.36) in the HF stands. These were low because these

TABLE 3

Yield of stemwood volume and aboveground biomass of hemlock-hardwood mixed stands and hardwood stands at the Harvard Forest and Great Mountain Forest sites

Species	Volume ($\text{m}^3 \text{ha}^{-1}$)		Biomass (t ha^{-1})	
	Mixed	Hardwood	Mixed	Hardwood
Harvard Forest site				
Red oak	61.9 (5.3)	59.9 (9.4) ns	65.1 (5.8)	60.3 (9.6) ns
Red maple	7.7 (6.3)	27.1 (8.6) ns	10.6 (5.3)	29.3 (8.1) ns
Birch spp.	22.2 (4.5)	30.3 (7.8) ns	36.8 (8.3)	41.9 (9.2) ns
All hardwoods	95.4 (11.0)	120.8 (10.7) ns	117.8 (7.2)	141.8 (11.1) ns
Hemlock	58.2 (3.9)	0.0 — **	63.4 (4.1)	0.9 (0.5) **
All species	155.6 (9.6)	120.8 (10.7) *	182.4 (5.3)	143.6 (11.4) **
Great Mountain Forest site				
Red oak	134.6 (15.6)	149.6 (19.3) ns	124.9 (14.5)	137.7 (17.8) ns
Red maple	39.3 (9.8)	39.8 (9.9) ns	29.9 (7.3)	31.0 (7.5) ns
Black cherry	18.3 (5.3)	19.7 (6.2) ns	14.6 (4.2)	15.7 (5.0) ns
Beech	12.7 (4.6)	36.4 (9.9) *	13.5 (4.8)	36.2 (8.7) *
All hardwoods	206.6 (15.4)	251.9 (11.3) *	184.3 (13.9)	228.2 (10.6) *
Hemlock	99.4 (14.1)	6.1 (3.0) **	74.2 (8.8)	4.4 (2.2) **
All species	306.6 (11.3)	258.0 (12.1) **	258.5 (11.0)	232.6 (10.8) ns

Values in parentheses are standard errors.

Results of *t*-tests comparing mixed stand with hardwood stand by species or species groups are given by: *, $P < 0.05$ level; **, $P < 0.01$ level; ns, not significant.

TABLE 4

Summary of stand yields in basal area, stemwood volume, and biomass for stands of different species composition

Stand type	Basal area ($\text{m}^2 \text{ha}^{-1}$)	Volume ($\text{m}^3 \text{ha}^{-1}$)	Biomass (t ha^{-1})
Stand age: 44 years (Harvard Forest site)			
Hardwood	27	121	144
Hemlock/hardwood	44	156	182
Hemlock	30	159	102
Stand age: 87 years (Great Mountain Forest site)			
Hardwood	34	258	233
Hemlock/hardwood	48	306	259
Hemlock	44	320	189

Data for hardwood and hemlock/hardwood stands from the current study are compared with data for pure hemlock stands of the same age and site quality from the yield tables of Merrill and Hawley (1924).

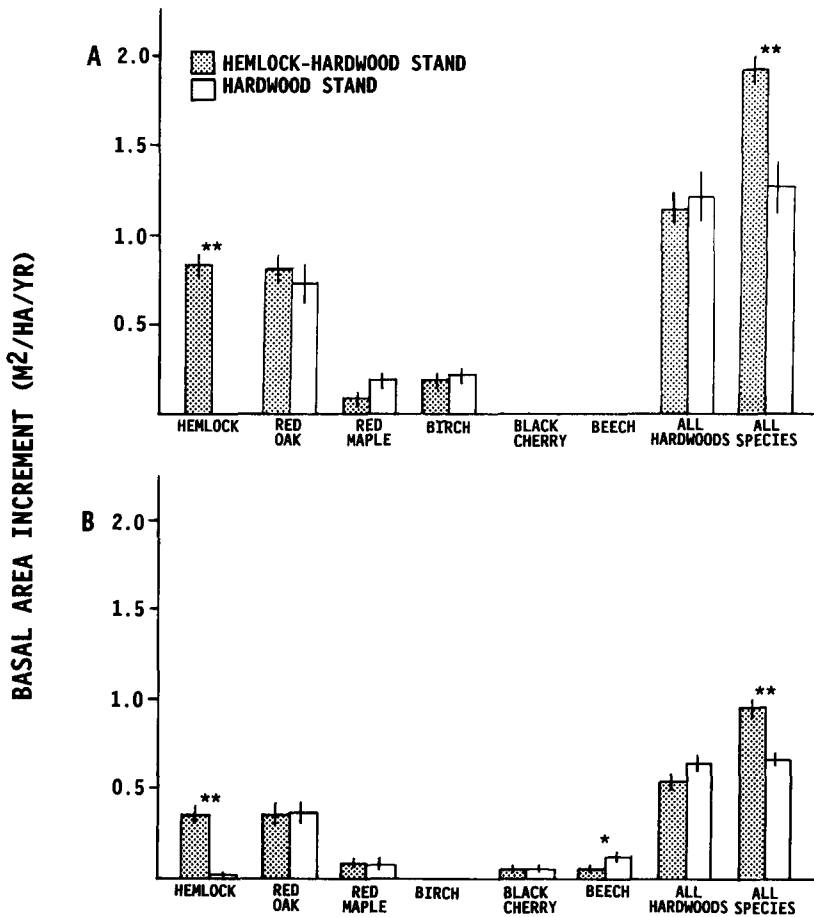


Fig. 4. Current basal area increment of (A) Harvard Forest stands and (B) Great Mountain Forest stands by species and species groups. Vertical lines indicate \pm SE. Significant differences between hemlock/hardwood and hardwood stands by each species or species group are indicated by * and ** for $P < 0.05$ and $P < 0.01$, respectively.

two species had consistently low growth regardless of present size. Basal area increment of the mixed stands was greater by 52% in the HF stands and by 38% in the GMF stands than adjacent hardwood stands (Fig. 4); these relationships are similar to values for basal area yield. As in yield comparisons, the current 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. When current increment was assessed in terms of volume and biomass, similar patterns were apparent (Table 5) but greater variability resulted in total stand differences falling below the level of significance. Thus, while

TABLE 5

Current annual increment of stemwood volume and above-ground biomass of hemlock/hardwood mixed stands and hardwood stands at the Harvard Forest and Great Mountain Forest sites

Species	Volume increment (m ³ ha ⁻¹ year ⁻¹)		Biomass increment (t ha ⁻¹ year ⁻¹)	
	Mixed	Hardwood	Mixed	Hardwood
Harvard Forest site				
Red oak	4.6 (0.4)	4.5 (0.7) ns	5.1 (0.5)	4.8 (0.8) ns
Red maple	0.2 (0.2)	0.7 (0.2) ns	0.4 (0.2)	0.8 (0.2) ns
Birch spp.	0.6 (0.1)	0.8 (0.2) ns	1.1 (0.3)	1.2 (0.3) ns
All hardwoods	5.7 (0.6)	6.2 (0.7) ns	6.9 (0.4)	7.4 (0.8) ns
Hemlock	1.7 (0.1)	0.0 (—) **	2.2 (0.1)	0.0 (—) **
All species	7.4 (0.5)	6.2 (0.7) ns	9.1 (0.3)	7.5 (0.9) **
Great Mountain Forest site				
Red oak	2.8 (0.3)	3.0 (0.4) ns	2.6 (0.2)	2.8 (0.4) ns
Red maple	0.6 (0.3)	0.6 (0.1) ns	0.4 (0.1)	0.4 (0.1) ns
Black cherry	0.3 (0.1)	0.3 (0.1) ns	0.2 (0.1)	0.3 (0.1) ns
Beech	0.3 (0.1)	0.8 (0.2) *	0.3 (0.1)	0.8 (0.2) *
All hardwoods	4.0 (0.3)	4.9 (0.3) ns	3.6 (0.3)	4.4 (0.3) *
Hemlock	1.7 (0.2)	0.1 (0.1) **	1.3 (0.2)	0.1 (0.04) **
All species	5.7 (0.3)	5.0 (0.3) *	4.8 (0.2)	4.5 (0.3) ns

Values in parentheses represent standard errors.

Results of *t*-test comparing mixed stand with hardwood stand by species or species group are given by: *, $P < 0.05$ level; **, $P < 0.01$ level; ns, not significant.

basal area comparisons indicate that current hemlock growth was an important component of growth at the stand level and yield differences were not due simply to the low mortality rate of hemlock, the results in terms of volume and biomass were not conclusive.

DISCUSSION

Yield comparisons

In the 44-year-old Harvard Forest stands, the hemlock/hardwood mixture had greater basal area, volume and biomass than the adjacent hardwood stand growing under the same site conditions. The yield of the hardwood component of the mixed stand was less than that of the adjacent hardwood stand, but the difference was not statistically significant. Thus, the hemlock yield can be considered as largely additive to that of the hardwoods.

Results were similar in the 87-year-old Great Mountain Forest 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 appeared to be due to the fact that some residual understory hemlocks had been left during the timber harvesting which initiated the mixed stand, and these residuals eventually came to occupy space in the overstory canopy, reducing the hardwood overstory component and the overall stand biomass.

The yield of pure hemlock stands relative to hemlock/hardwood mixtures depends upon the measurement units. In terms of volume, hemlock stands would have yields comparable to those of mixed stands, but in basal area or biomass, hemlock yield would be lower than that of mixed stands.

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. The most evident are differences in height of foliage among species (Fig. 2). Stratification on these mixed stands occurs early in development, with dominant oaks being twice as tall as the tallest hemlocks by age 25 (Kelty, 1986). After that, most hemlock foliage occurs in a lower stratum, with only limited vertical overlap with the foliage of the taller hardwoods. In contrast, hardwood stands lack a comparably dense understory. This canopy stratification provides one possible explanation for differences in production between mixtures and hardwood stands. Because of its high degree of shade tolerance, hemlock can 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 would be additive to that of the hardwoods in total stand production if light were the principal factor limiting growth.

Potential reasons for increased production of mixed stands over pure hemlock stands are not as evident. The dense canopy maintained by a pure stand of a shade-tolerant species intercepts a high proportion of available sunlight, suggesting that it would have highest production. However, studies comparing the physiology of sun- and shade-adapted plants (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 net photosynthetic rates 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 net photosynthetic rates. This suggests that hardwood foliage in the upper levels of the hemlock/hardwood canopy may use intercepted light more efficiently than the upper

levels of a hemlock canopy, while lower 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 the effects of foliage stratification in increasing the production of hemlock/hardwood mixtures. Hemlock may show biomass increases in late spring and early autumn when free of overstory shading, as do many evergreen species as long as temperatures are not too low (Kramer and Kozlowski, 1979). Furthermore, red oak, the dominant species of the overstory, comes into leaf 7–13 days later than other hardwoods (Swan, 1970) giving a longer period each spring when hemlock receives little overstory shading at a time when temperatures are usually not restrictive to photosynthesis.

Finally, differences in rooting depth may play a role in causing these species mixtures to more fully utilize a site by reducing direct competition for nutrient and water absorption. Red oak produces a strong taproot and a network of woody lateral roots at soil depths of 20–50 cm, while hemlock and other hardwood species produce lateral roots close to the surface of the mineral soil (Lyford, 1980). However, the deep oak lateral roots 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 competition in nutrient and water absorption is not clear.

Results from plantation experiments

A number of plantation experiments described by Assmann (1970) begun in the late 19th century in Germany and Switzerland address the problem of productivity in mixed and pure stands. These are quite valuable because they are essentially simple, long-term replacement-series experiments with various stands growing adjacent to one another for up to 90 years. Stands in these studies had received repeated, light thinnings, which are designed only to salvage suppressed trees before they die, without leaving significant gaps in the canopy. The trees removed in these thinnings were included as part of total yield, thus giving a complete measure 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 component species growing in a pure stand on the same site.

Four of these experiments compared pure stands of the shade-intolerant Scots pine (*Pinus sylvestris* L.) with mixtures of Scots pine and either Norway spruce (*Picea abies* (L.) Karst.) or European beech (*Fagus sylvatica* L.) as the shade-tolerant component. These showed that the presence of either of the last two species in an understory position decreased the production of the pine

overstory a small amount in both volume and biomass, but the understory production more than compensated for this decrease; mixed stands had yields in the range of 50% greater biomass than pure pine. No direct comparison with the growth of pure spruce or beech stands was made.

Mixtures of a sessile oak (*Quercus petraea* (Mattuschka) Lieblein) overstory with a European 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 described by Assmann compared mixed stands with pure stands of the shade-tolerant component species. In this case, production in a mixture of European larch (*Larix decidua* L.) and European beech exceeded that of 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 greatly out-produced pure larch stands, indicating that the mixture had higher yields than either pure stands.

Finally, one experiment included direct comparisons of pure stands of two species – Norway spruce and silver fir (*Abies alba* (Mill.)) – plus their mixture, all growing on similar sites. Although Norway spruce constitutes the more shade-tolerant understory component when mixed with pine, it is less shade-tolerant than fir and has more rapid juvenile height growth. Mixtures of these species developed a two-storied canopy with spruce above fir. At age 60, spruce and fir produced equal amounts of stemwood biomass in pure stands, but mixed stands exceeded that production by 15–37%.

A more recent study (Poleno, 1981) than those reviewed by Assmann also included comparisons of mixed stands with pure stands of both component species. In that study, comparisons were made of canopy development and basal area yield of stands of Scots pine and Norway spruce of varying ages, site qualities, and species proportions. In mixed stands, spruce had slower height growth than pine 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 plantation studies, plus the results of the present investigation, show consistency in one type of comparison: mixed stands produce greater yields than stands of the shade-intolerant overstory species alone, measured in basal area, volume or biomass. The comparison of mixed-stand yield with that of pure stands of the shade-tolerant understory species component is not as clear. The slower juvenile height growth of these species has made them less frequently used in forestry in pure stands, thus fewer comparisons are available. However, where direct comparisons were made in the plantation studies cited above, mixed stands were found to have greater volume

and biomass than pure stands of the tolerant species. In the present study, comparisons with yield tables for pure hemlock suggest that the mixtures produce greater biomass yields, although volume yields of the 2 types of stands would be approximately the same.

These studies do not indicate that species mixtures always outyield pure stands of the component species. Evidence from experiments with herbaceous species shows that mixtures involving species with little difference in morphology or phenology do not outproduce monocultures of the higher-yielding species (Harper, 1977), and similar patterns would be expected with forest stands as well. In all of the forest mixtures described above, component species have differing growth characteristics which cause a stratified canopy to be 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 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 of these species lying adjacent to one another, spruce outyielded beech in stemwood biomass by 10–100% 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 height growth of understory beech.

Site quality limitations

Site conditions are also important in controlling the situations where increased production of mixtures over pure stands may occur. The present study and the European plantation experiments were all carried out in moist climates where soil moisture is generally not critically limiting to stand production. This lack of moisture limitations has been demonstrated in experiments on New England sites similar to those of the present study, where removal of all understory trees failed to increase growth of the remaining overstory (Kelty et al., 1987). In areas of lower precipitation in the north-central U.S., similar treatments in oak-dominated stands did result in increased growth of overstory trees (Dale, 1975). The phenomenon of increased production of mixed stands with multiple canopy strata is likely to occur only where light rather than water or nutrients is the principal factor limiting stand production.

Management implications

The principal commodity objective of management in the forest type described in this study is the production of high-quality sawtimber from red oak

and, to a lesser extent, from other hardwood species. Hemlock is used for both sawtimber and pulpwood, but its value is lower than that of the hardwood species. Thus, while mixed stands have greater financial yield than hardwood stands because of the added hemlock production, the increase is not proportional to the increase in biological yield. However, two other factors associated with the presence of a hemlock understory further increase the potential merit of mixed stands for timber production. First, the deep shade cast by the hemlock greatly reduces the development of understory vegetation which can interfere with the establishment of advance regeneration of desirable tree species. A dense cover of shrubs and ferns often develops beneath hardwood canopies where hemlock is absent. Second, the shade cast by hemlock on the boles of overstory hardwoods may help to improve hardwood timber quality by suppressing the growth of epicormic branches. These considerations suggest that, during regeneration of mature stands, maintenance of a hemlock component in hemlock/hardwood mixtures, and conversion of hardwood stands to hemlock/hardwood mixtures would increase both the quantity and quality of timber produced.

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

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REFERENCES

- Anonymous, 1970. Soil survey - Litchfield County, Connecticut. USDA Soil Conservation Service, U.S. Government Printing Office, Washington, D.C.

- Assmann, E., 1970. *The Principles of Forest Yield Study*. Pergamon Press, Oxford, 506 pp.
- Boardman, N.K., 1977. Comparative photosynthesis of sun and shade plants. *Annu. Rev. Plant Physiol.*, 28: 355-377.
- Dale, M.E., 1975. Effects of removing understory on growth of upland oak. *USDA For. Serv. Res. Pap. NE-321*, 10 pp.
- Ellern, S.J., Harper, J.L. and Sagar, G.R., 1970. A comparative study of the distribution of roots of *Avena fatua* and *A. strigosa* in mixed stands using a ¹⁴C labelling technique. *J. Ecol.*, 58: 865-868.
- Harper, J.L., 1977. *Population Biology of Plants*. Academic Press, New York, 892 pp.
- Hill, J. and Shimamoto, Y., 1973. Methods of analysing competition with special reference to herbage plants. I. Establishment. *J. Agric. Sci.*, 81: 77-88.
- Kelty, M.J., 1984. *The Development and Productivity of Hemlock-Hardwood Forests in Southern New England*. Doctoral dissertation, Yale University, New Haven, Connecticut, 206 pp.
- Kelty, M.J., 1986. Development patterns in two hemlock-hardwood stands in southern New England. *Can. J. For. Res.*, 16: 885-891.
- Kelty, M.J., Gould, E.M., Jr. and Twery, M.J., 1987. Effects of understory removal in hardwood stands. *North. J. Appl. For.*, 4: 162-164.
- Kramer, P.J. and Kozlowski, T.T., 1979. *Physiology of Woody Plants*. Academic Press, New York, 811 pp.
- Lyford, W.H., 1980. Development of the root system of northern red oak (*Quercus rubra* L.). *Harv. For. Pap. No. 21*, 30 pp.
- Madgwick, M.A.I., 1970. Biomass and productivity models of forest canopies. In: D.E. Reichle (Editor), *Ecological Studies. Volume I. Analysis of Temperate Forest Ecosystems*. Springer, Berlin, pp. 47-54.
- Merrill, P.H. and Hawley, R.C., 1924. Hemlock: its place in the silviculture of the southern New England forest. *Yale Univ. Sch. For. Bull. No. 12*, 68 pp.
- Monteith, D.B., 1979. Whole tree weight tables for New York. *State Univ. N.Y. Appl. For. Res. Inst. Res. Pap. No. 40*, 69 pp.
- Murison, W.F., 1963. Records of experiment 63-4: Weather summary for 1913-1962. *Harvard Forest Records* (unpublished).
- Parde, J., 1980. Forest biomass. *For. Abstr.*, 41: 343-362.
- Poleno, Z., 1981. Vyojsmisenyh porostu. [Development of mixed forest stands]. *Prace Vyzkumneho Ustavu Lesniho Hospodarstvi a Myslivosti*, 59: 179-202.
- Raup, H.M. and Carlson, R.E., 1941. The history of land use in the Harvard Forest. *Harv. For. Bull. No. 20*, 64 pp.
- Scott, C.T., 1981. Northeast forest survey revised cubic-foot volume equations. *USDA For. Serv. Res. Note NE-304*, 3 pp.
- Simmons, C.S., 1940. Soil survey of Harvard Forest - Slab City Block. *Harvard Forest Report* (unpublished), 30 pp.
- Smith, D.M., 1986. *The Practice of Silviculture* (8th edition). Wiley, New York, 527 pp.
- Swan, J.M.A., 1970. Records of experiment 70-2: phenology study. *Harvard Forest Records* (unpublished).
- Trenbath, B.R., 1974. Biomass productivity of mixtures. *Adv. Agron.*, 26: 177-210.
- Trenbath, B.R. and Harper, J.L., 1973. Neighbour effects in the genus *Avena*. I. Comparison of crop species. *J. Appl. Ecol.*, 10: 379-400.
- 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. Abs.*, 43: 615-624.
- Whittaker, R.H. and Woodwell, G.M., 1972. Evolution of natural communities. In: J.A. Wiens (Editor), *Ecosystem Structure and Evolution*. Oregon State University Press, Corvallis, Oregon, pp. 137-159.
- Winer, H.I., 1955. *The History of the Great Mountain Forest*. Doctoral dissertation, Yale University, New Haven, Connecticut, 278 pp.