

Wood volume increment in thinned, 50- to 55-year-old, mixed-species Allegheny hardwoods

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Abstract: A thinning study in 50- to 55-year-old, even-aged, mixed species Allegheny hardwoods produced highly variable merchantable stemwood volume increment responses. Regression equations relating parameters of stand growth (ingrowth, mortality, survivor growth, net growth, and gross growth) to relative stand density had R^2 values ranging from 0.07 to 0.48. When study plots with similar pretreatment species composition were assigned to four groups using cluster analysis, R^2 values were increased to 0.94–0.99. There were significant differences in the relationships between relative stand density and growth response variables among all plot groups. At all densities, plots with a high percentage of black cherry (*Prunus serotina* Ehrh.) had the highest volume increment. Plots with a high percentage of black cherry and a low percentage of sugar maple (*Acer saccharum* Marsh.) showed a decrease in volume increment, relatively high ingrowth, and relatively low mortality with a decrease in relative stand density. Plots with a high percentage of sugar maple and low percentage of black cherry showed an increase in volume increment, relatively low ingrowth, and relatively high mortality with decreases in relative stand density. Guidelines for thinning Allegheny hardwoods recommend a residual relative stand density of 60%. These guidelines may need to be revised to incorporate considerations of species composition. Stands of pole-size to small sawtimber-size trees dominated by black cherry may require a residual density higher than 60% to maximize the volume increment of merchantable stemwood. The volume increment in similarly structured stands dominated by sugar maple might be maximized at densities lower than 60%.

Résumé : Une étude sur l'éclaircie de peuplements équiennes mixtes de feuillus des Alleghanys de 50 à 55 ans a engendré des réactions très variables de croissance en volume marchand des tiges. Les équations de régression reliant les paramètres de croissance (recrutement, mortalité, croissance des survivants, croissance nette et brute) à la densité relative du peuplement présentaient des R^2 variant de 0,07 à 0,48. Lorsque les parcelles d'étude comportant des compositions semblables avant la coupe étaient réparties en quatre groupes à partir d'une étude de groupement, les valeurs de R^2 montaient à 0,94–0,99. Des différences significatives entre tous les groupes ont été observées dans les relations entre la densité relative et la réaction en croissance. À toutes les densités, les parcelles présentant un pourcentage élevé de cerisier tardif (*Prunus serotina* Ehrh.) présentaient les croissances les plus fortes en volume. Les parcelles avec un fort pourcentage de cerisier tardif et un faible pourcentage d'érable à sucre (*Acer saccharum* Marsh.) montraient une baisse de l'accroissement, un recrutement relativement important et une mortalité plutôt faible lorsque la densité relative diminuait. Les parcelles avec un fort pourcentage d'érable à sucre et un faible pourcentage de cerisier tardif montraient une augmentation de la croissance en volume, un recrutement relativement faible, une mortalité plutôt élevée lorsque la densité diminuait. Des prescriptions pour l'éclaircie des feuillus des Alleghanys recommandent une densité résiduelle de 60%. Ces recommandations pourraient nécessiter une révision afin de considérer la composition du peuplement. Des peuplements aux stades de perchis ou de jeune futaie dominés par le cerisier tardif pourraient nécessiter une densité résiduelle supérieure à 60% afin de maximiser la croissance en volume marchand. L'accroissement en volume dans des peuplements de structure semblable dominés par l'érable à sucre pourrait être maximisé à des densités inférieures à 60%.

[Traduit par la Rédaction]

Introduction

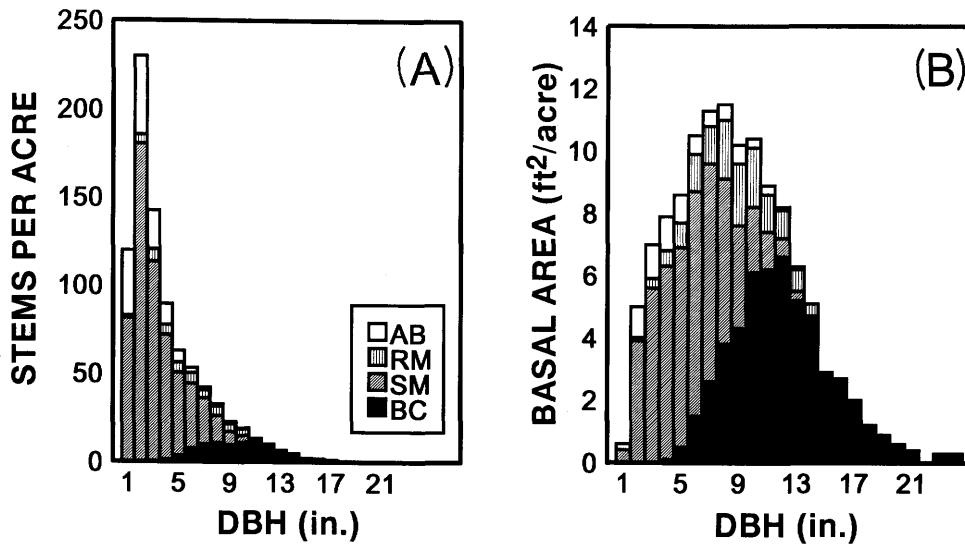
The relationship between volume increment of merchantable stemwood and stand density is fundamental to the development of thinning guidelines (Smith 1986). This relationship is usually difficult to derive accurately and precisely because

volume increment responses are often highly variable (Smith 1986; Oliver and Larson 1990). It can vary with differences in stand density, composition of tree species, site quality, units of measure, and stand age (Smith 1986). Stand structure (Marquis and Ernst 1991) and measurement period (Oliver 1979; Curtis and Marshall 1986) also can affect response. In this paper I report an analysis of the volume growth of merchantable stemwood following changes in stand density with thinning in 50- to 55-year-old, even-aged, mixed-species Allegheny hardwoods. Data used by Marquis (1986) and Ernst (1987) and a subset of data used by Marquis and Ernst (1991) were combined with

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Fig. 1. Distributions of number of stems (A) and basal area (B) by 1-in. diameter (at breast height) class, based on the average of all study plots before treatment.
AB, American beech; RM, red maple; SM, sugar maple; BC, black cherry.



subsequent remeasurements of the study plots to the end of the first 15-year thinning cycle. This differs in approach from previous work in that a rigorous attempt was made to understand how the interactions of species composition and relative stand density (RSD) influenced the volume increment of merchantable stemwood.

Background

Species composition in Allegheny hardwood stands

The Allegheny hardwood type, often referred to as the black cherry – maple type (SAF forest type 28; Marquis 1980), covers about 12×10^6 acres (1 acre = 0.40 ha), and is mostly on the Allegheny Plateau in southern New York and northern Pennsylvania, but is also common in West Virginia and Maryland (Marquis and Gearhart 1983). The type is characterized by stratified, mixed-species, even-aged forests that originated from landscape-scale heavy harvests during the last half of the 19th and early 20th centuries (Marquis 1975). The majority of stocking consists of black cherry (*Prunus serotina* Ehrh.), sugar maple (*Acer saccharum* Marsh.), American beech (*Fagus grandifolia* Ehrh.), red maple (*Acer rubrum* L.), and white ash (*Fraxinus americana* L.) (Marquis 1980). Proportions of each species range from an absence of one or more species to nearly pure stands of a single species (Marquis 1980).

Black cherry and white ash are fast-growing, shade-intolerant species; sugar maple and American beech are slower growing, shade-tolerant species; red maple is intermediate (Burns and Honkala 1990). Even-aged mixtures of these species have a diameter distribution that follows a reverse J shape (Fig. 1), characteristic of mixed-species, even-aged stands with an important shade-tolerant component (Oliver and Larson 1990). Among stands with a high proportion of black cherry and white ash, shade-tolerant species are concentrated in the smaller diameter classes and lower crown canopy strata. Shade intolerants

dominate the larger diameter classes (Marquis 1992) and may form a nearly continuous upper crown canopy stratum.

Shade-tolerant species are found in the main crown canopies of even-aged, second-growth Allegheny hardwood forests only if they were left as residual saplings or pole-size trees after the turn of the century logging. These usually ranged from 50 to 400 trees per acre, were 2 to 8 in. DBH (1 in. = 2.54 cm), and most commonly were sugar maple and American beech with some eastern hemlock (*Tsuga canadensis* (L.) Carr.) (Marquis 1981a, 1981b, 1992).

Study areas

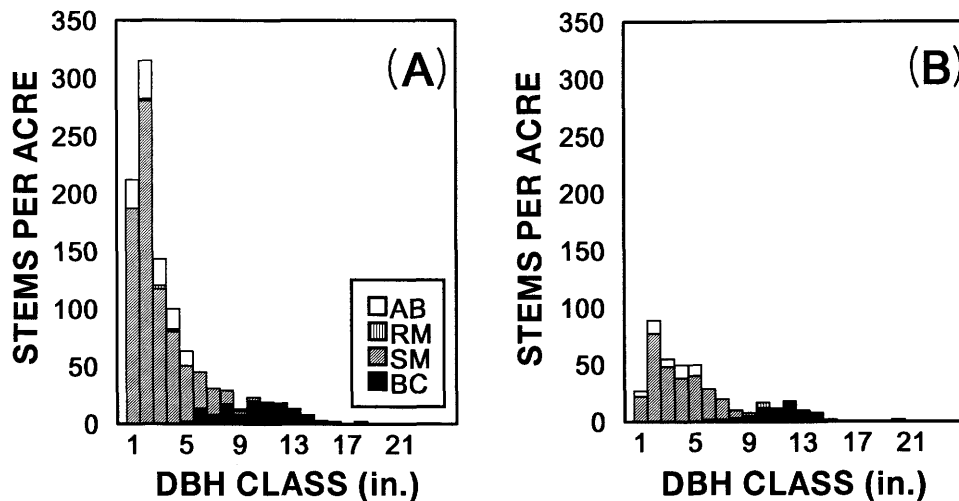
The study was conducted in northwestern Pennsylvania in two areas of 50- to 55-year-old, even-aged Allegheny hardwood forest located about 0.6 mi (1 mi = 1.6 km) apart (41°35'–41°37'N, 78°45'–78°50'W). The study areas were described by Ernst (1987) and Marquis and Ernst (1991). Both areas extended across toposesquences with soil associations representative of the unglaciated portion of the Allegheny Plateau (Aguilar and Arnold 1985). Elevations ranged from 2000 to 2080 ft (1 ft = 0.30 m). Landforms ranged from convex ridgetops, through flat side slopes, to concave foot slopes. Soil series included Buchanan silt loam (fine-loamy, mixed, mesic Aquic Fragiudult), Cookport channery loam (fine-loamy, mixed, mesic Aquic Fragiudult), Hartleton channery silt loam (loamy-skeletal, mixed, mesic Typic Hapludult), and Hazleton channery loam (loamy-skeletal, mixed, mesic Typic Dystrochrept) (Soil Conservation Service 1993).

Materials and methods

Experiment design and treatments

Twenty-three experimental units (plots) were randomly installed in 1973–1976, when the stands were 50 to 55 years old; 11 in area 1 and 12 in area 2. Plots generally were adjacent to each other with narrow (<66 ft), untreated strips between some plots to avoid wet areas and a railroad grade. Each plot was a

Fig. 2. Distributions of number of stems by 1-in. diameter (at breast height) class on one study plot from cluster 1 that was thinned to 60% relative density by methods described by Roach (1977). (A) Before treatment. (B) After treatment. AB, American beech; RM, red maple; SM, sugar maple; BC, black cherry.



2-acre rectangle (264 × 330 ft) composed of a 0.6-acre interior measurement subplot surrounded by a 66 ft wide isolation strip. The measurement subplot was further divided into 0.1-acre squares for plot measurements and treatment applications. Each square was treated to achieve the prescribed stand density and structure. Both the measurement subplot and the isolation strip were treated.

Treatments were reductions in stand density. Plots had prescribed RSDs of 30, 40, 50, 60, 70, 80, or 100% (unthinned control). RSD measures were used because of the stratified, mixed-species nature of Allegheny hardwoods and inherent differences in requirements for growing space among species (Roach 1977; Stout and Nyland 1986). Treatments were assigned randomly to each plot. Roach's (1977) stocking guide and marking procedures were used to determine the stocking level and to apply the prescribed thinning treatment. The cut was distributed by combining low and crown thinnings (after Smith 1986). Trees were removed from two species groups, the sugar maple – beech group and the black cherry – red maple group. The average diameter of each group was calculated, then within each species group two-thirds of the cut basal area was removed in trees from below each group's average diameter and one-third from above until the prescribed relative density was achieved (Roach 1977; Fig. 2). Marquis and Ernst (1991) referred to this as a combined thinning.

Area 1 plots were cut during February and March 1973; area 2 plots were cut during December 1974 and January 1975. Two control plots in area 2 were installed in January 1976. Trees of merchantable size were removed under a commercial timber sale. Nonmerchantable trees were cut and left after the commercial cuttings were complete.

The post-thinning RSDs of each plot were within 1–2% of the prescribed treatment levels based upon Roach's (1977) stocking guide. RSDs were recalculated using the current version of the Allegheny hardwood stocking guide (Stout and Nyland 1986; Stout et al. 1987), as programmed into the stand analysis, prescription, and management simulator program for Allegheny hardwoods known as SILVAH (Marquis and Ernst 1992; Marquis et al. 1992; Marquis 1994). In SILVAH, growing space requirements for red maple, which is intermediate between black cherry and sugar maple, are accounted for; in the Roach

guide they are not. Recalculated average relative densities were 1% greater than those from the Roach guide. Recalculated RSDs achieved for each treatment plot ranged from –8 to 7% of the prescribed level. Recalculated post-thinning RSDs were used in the analysis reported in this paper.

Field measurements

All trees 1.00 in. DBH or larger in each 0.6-acre measurement plot were numbered and remeasured periodically at breast height (nearest 0.01 in.) with a steel diameter tape. Data were taken at approximately 5-year intervals for 15 years after treatment, except for two control plots in area 2, which were measured for 14 years. Only the measurements taken immediately before and after treatment, and those made at 14 or 15 years post-treatment, are included in this paper.

Data analysis

Merchantable cubic-foot volume was calculated for all trees ≥5.50 in. DBH using local height and volume equations (Marquis 1977; Marquis et al. 1992). Volume responses of merchantable stemwood were calculated on a per-acre basis and separated by component after Beers (1962) and Marquis and Beers (1969) as follows:

- (1) Ingrowth. End of study period merchantable cubic-foot volume of trees that grew across the lower DBH threshold (5.50 in. DBH) by the end of the period.
- (2) Mortality. Pretreatment merchantable cubic-foot volume of residual trees that died during the study period, excluding trees that were cut during thinning.
- (3) Survivor growth. End of study period merchantable cubic-foot volume added to trees that were 5.50 in. DBH or larger at the beginning of the study period.
- (4) Gross growth. Survivor growth plus ingrowth.
- (5) Net growth. Gross growth minus mortality.

Pretreatment species composition of study plots

A preliminary analysis of plot-level growth response was done by graphing annual volume increment for all growth components as a function of RSD. The variation in volume increment response of merchantable stemwood was apparently too great

Table 1. Average pretreatment tree species composition across the study areas.

Species*	No. of stems per acre	Basal area (ft ² /acre)	Relative value (%)			Importance value [†]
			No. of stems	Basal area	Frequency [†]	
Sugar maple (<i>Acer saccharum</i> Marsh.)	584.4 (27.5)	49.5 (4.4)	68.6 (3.4)	39.5 (3.9)	15.5	123.6
Black cherry (<i>Prunus serotina</i> Ehrh.)	89.6 (11.7)	52.8 (3.7)	9.7 (1.1)	40.4 (2.5)	15.5	65.5
American beech (<i>Fagus grandifolia</i> Ehrh.)	131.5 (22.9)	7.2 (1.4)	14.3 (2.3)	5.6 (1.1)	15.5	35.4
Red maple (<i>Acer rubrum</i> L.)	53.4 (16.9)	13.3 (3.3)	5.7 (1.7)	9.8 (2.3)	14.2	29.7
Birch (<i>Betula alleghaniensis</i> Britton and <i>Betula lenta</i> L.)	6.9 (2.5)	2.2 (0.9)	0.7 (0.3)	1.7 (0.7)	12.2	14.6
Yellow-poplar (<i>Liriodendron tulipifera</i> L.)	1.9 (0.6)	1.6 (0.5)	0.2 (0.1)	1.2 (0.4)	6.7	8.2
Eastern hemlock (<i>Tsuga canadensis</i> (L.) Carr.)	2.3 (0.7)	0.3 (0.1)	0.3 (0.1)	0.3 (0.1)	6.7	7.3
Cucumbertree (<i>Magnolia acuminata</i> L.)	2.7 (1.4)	1.5 (0.7)	0.3 (0.1)	1.1 (0.6)	4.7	6.1
Other hardwoods	1.0 (0.6)	0.3 (0.2)	0.1 (0.1)	0.2 (0.2)	2.7	3.0
White ash (<i>Fraxinus americana</i> L.)	0.2 (0.1)	0.1 (0.1)	<0.0 (0.0)	<0.0 (0.0)	1.4	1.5
Pin cherry (<i>Prunus pensylvanica</i> L.f.)	0.2 (0.1)	0.1 (0.0)	<0.0 (0.0)	<0.0 (0.0)	1.4	1.5
Striped maple (<i>Acer pensylvanicum</i> L.)	0.2 (0.2)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	1.4	1.4
Downy serviceberry (<i>Amelanchier arborea</i> (Michx. f.) Fern)	0.3 (0.2)	<0.0 (0.0)	<0.0 (0.0)	<0.0 (0.0)	1.4	1.4
Eastern hophornbeam (<i>Ostrya virginiana</i> (Mill.) K. Koch)	0.3 (0.3)	0.1 (0.1)	<0.0 (0.0)	<0.0 (0.0)	0.7	0.8
Total	875	129.0				

Note: Values are based on all stems ≥ 1.00 in. DBH. Values in parentheses are standard errors ($n = 23$).

*Nomenclature follows Little (1979).

[†]Frequency and importance values were calculated after Barbour et al. (1987) as the sum of relative number of stems, relative basal area, and relative frequency.

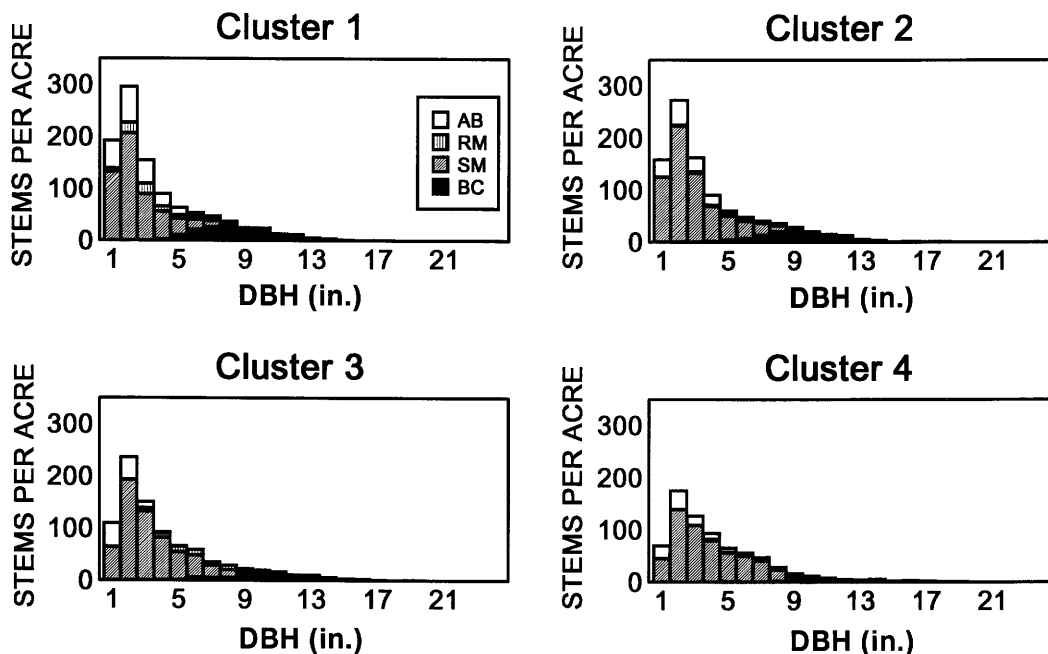
to elicit any meaningful treatment effects. Marquis (1986) and Ernst (1987) demonstrated that survivor, net, and gross volume increment were positively related to the proportion of black cherry in a stand. Hence, I suspected that variability in merchantable stemwood increment unrelated to stand density could be explained by differences in initial species composition. A review of pretreatment diameter distributions on a plot by plot basis supported the idea that some of the unexplained plot-level variation in volume increment response could be related to composition of all species, rather than variation only in black cherry. Black cherry, sugar maple, red maple, and American beech abundances all varied highly among plots. Aerial photographs of the study areas from 1940, 1962, and 1972 (just before treatment) confirmed that pretreatment overstory species composition was variable among plots.

Cluster analysis was used to group plots with similar pretreatment stand structure and species composition; variables chosen for the cluster analysis included pretreatment total stand basal area per acre, total number of stems per acre, and

proportion of black cherry, sugar maple, red maple, and American beech by basal area and number of stems. These four species accounted for 95% of the average total stand basal area and 98% of the average total number of stems (Table 1). The other 10 tree species were excluded to reduce dimensionality of the analysis.

Ward's minimum variance method and the cubic clustering criterion were used as guides in defining the number of clusters, i.e., plot groups with similar pretreatment overstory structure and species composition (SAS Institute Inc. 1988). Outlier plots were defined using the "Trim" routine in PROC CLUSTER of the SAS computer software program (SAS Institute Inc. 1988; $\alpha = 0.05$, $K = 2$). A canonical variate analysis (Jongman et al. 1987) and three-dimensional graphing techniques were used to interpret differences in species composition among clusters using PROC CANDISC in SAS (SAS Institute Inc. 1988). Canonical variates, represented by three-dimensional graph axes, were interpreted using both the standardized and unstandardized canonical coefficients. Graphs of the diameter and

Fig. 3. Pretreatment distributions of the number of stems by 1-in. diameter (at breast height) class, based on the average of all study plots within a cluster before treatment. AB, American beech; RM, red maple; SM, sugar maple; BC, black cherry.



basal area distributions from each cluster and analysis of variance of clusters (Scheffé's mean separation procedure; $\alpha = 0.10$) were also used.

Regression analysis of plot-level responses

Least-squares regression analysis with a quadratic model was used to model how ingrowth, mortality, survivor growth, net growth, and gross growth varied as a function of RSD. A priori selection of the quadratic model was done based on preliminary graphs of the data and use of curvilinear response curves by Marquis (1986) and others (Nelson et al. 1961; Oliver 1979; Beck 1986; Curtis and Marshall 1986). Regression equation intercept and slope coefficients were compared among clusters using a dummy variable approach (F -tests, $\alpha = 0.10$; Cunia 1973). Slopes were defined to include both the linear and quadratic coefficients from each regression equation. Pairwise comparisons were made between clusters. The comparisons of both slopes and intercepts were graphed to allow the reader to interpret study results beyond the critical level of statistical significance used in this paper.

Results and discussion

Analysis of pretreatment species composition

Cluster analysis

Four clusters of plots with similar pretreatment species composition were defined. There were 5, 4, 7, and 5 plots in clusters 1, 2, 3, and 4, respectively. Each cluster had at least one control plot. Other plots within a cluster were generally spread across the range of treatments to a lower RSD limit near 40%. Cluster 2 was an exception: three of four plots were grouped at the lower end of the RSD range.

Two plots (37% and 56% RSD plots) were "trimmed" by cluster analysis as outliers and excluded from further analysis. Both plots appeared to belong to a fifth cluster, but a

separate cluster could not be formed because there were too few observations. These plots were at the lowest end of the toposequence, where soils were very poorly drained. Black cherry, which grows well on all soils except the wettest and the driest (Marquis 1990), had extremely low growth responses on the wettest of these two plots.

Graphical analysis

Pretreatment diameter distributions (Fig. 3) and basal area distributions (Fig. 4) indicated that the proportion of black cherry progressively decreased, and that sugar maple increased, from clusters 1 through 4. Cluster 3 appeared to have more red maple and cluster 1 more American beech than the other clusters. Cluster 1 appeared to have more basal area and more total stems than the other clusters; the reverse was true of cluster 4. Cluster 2 was intermediate between clusters 1 and 3.

Analysis of variance

All variables used in the cluster analysis, except red maple, were statistically different among clusters for either basal area or number of stems (Table 2). The total number of stems and the proportion of black cherry was highest for cluster 1, and progressively decreased through cluster 4. The percentage of sugar maple followed a reverse pattern, increasing from clusters 1 through 4. Basal area was generally equivalent for clusters 1 and 3. Both were higher than cluster 4. Cluster 3 had a lower percentage of American beech. Cluster 2 was similar to clusters 1 and 3, except for total number of stems. Cluster 1 had the highest total number of stems, followed by clusters 2 and 3.

Canonical variate analysis

Clusters differed from each other when all variables were collectively compared (multivariate analysis of variance;

Fig. 4. Pretreatment distributions of the basal area by 1-in. diameter (at breast height) class, based on the average of all study plots before treatment. AB, American beech; RM, red maple; SM, sugar maple; BC, black cherry.

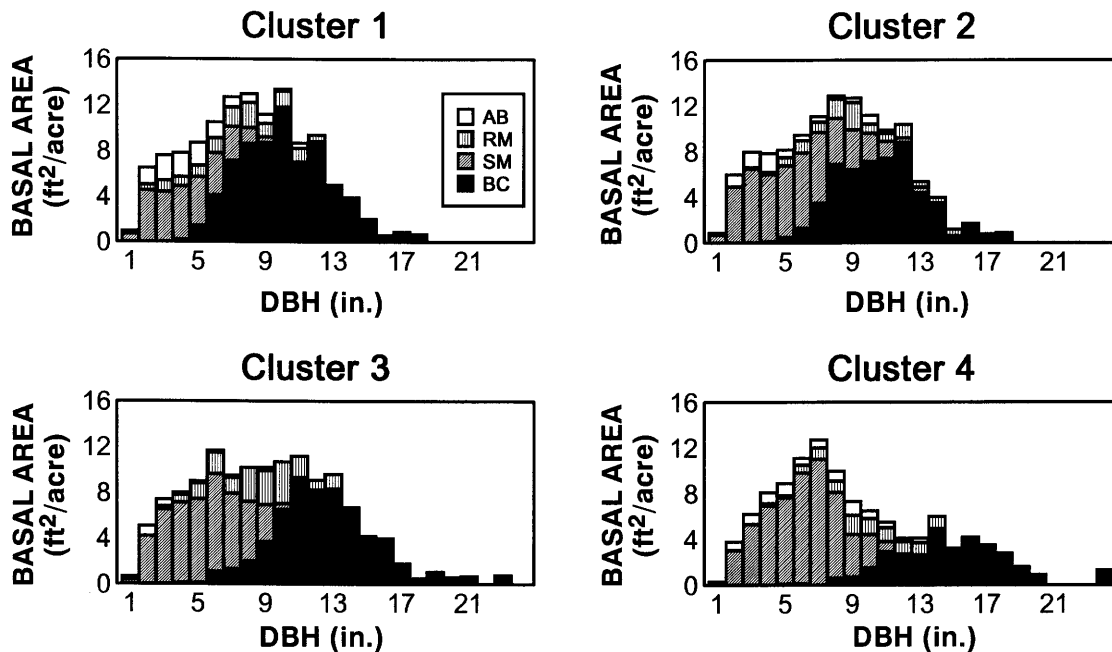


Table 2. Average pretreatment species composition characteristics of the four clusters of study plots.

Variable	Cluster 1		Cluster 2		Cluster 3		Cluster 4		P-value*
	n	Avg.	n	Avg.	n	Avg.	n	Avg.	
Total number of stems (stems/acre)	5	1047 ^a (8.5)	4	976 ^b (7.6)	7	896 ^c (10.7)	5	735 ^d (10.0)	<0.01
Total basal area (ft²/acre)		133 ^a (1.5)		127 ^{ab} (2.2)		140 ^a (3.8)		118 ^b (5.1)	<0.01
% of total number of stems									
Black cherry		15.1 ^a (1.9)		10.8 ^{ab} (1.9)		9.7 ^{ab} (1.7)		4.7 ^b (0.8)	<0.01
Sugar maple		52.6 (8.9)		69.7 (3.0)		68.6 (5.8)		75.5 (4.9)	0.12
Red maple		8.7 (6.1)		3.7 (1.4)		7.7 (3.1)		3.6 (2.4)	0.72
American beech		21.2 (6.9)		14.5 (3.9)		11.9 (3.6)		15.0 (4.4)	0.56
% of total basal area									
Black cherry		52.7 ^a (1.8)		42.6 ^a (5.2)		43.1 ^a (2.8)		28.4 ^b (2.7)	<0.01
Sugar maple		20.8 ^a (6.0)		39.0 ^{ab} (2.7)		36.4 ^{ab} (6.3)		50.9 ^b (6.3)	0.03
Red maple		9.9 (5.5)		9.0 (2.5)		13.6 (5.3)		8.5 (4.8)	0.87
American beech		9.7 ^a (3.7)		6.1 ^{ab} (1.0)		2.1 ^b (0.7)		7.9 ^{ab} (1.5)	0.05

Note: Values are based on all stems ≥ 1.00 in. DBH. Means within a row followed by the same letter are not statistically different from each other; means followed by a different letter are different from each other (Scheffé's tests; $\alpha = 0.10$). Rows without letters were not separated because the observed significance level (*P*-value) was greater than 0.10. Standard errors are in parentheses below each mean.

*From analysis of variance among the four clusters.

Wilks' λ ; $P < 0.01$). Pairwise comparisons using Mahalanobis' distances showed that all of the clusters differed from one another (P -values: <0.01 – 0.02).

Three-dimensional graphs of the clusters using canonical variates indicated that clusters 1 and 4 were the most different, and clusters 2 and 3 were the most similar and intermediate to clusters 1 and 4 (Fig. 5 and Table 3). The first canonical variate explained 87% of the variation in pretreatment species composition among clusters. Differences among the clusters along this variate were attributed to species composition, with emphasis on differences in the amount of black cherry and the total number of stems (Table 3). Squared canonical correlations were similarly high for variates 1 and 2 (0.98 and 0.89), indicating meaningful separations among the clusters along both axes. Separation along the second axis was between clusters 1 and 4 versus cluster 2 versus cluster 3 (Figs. 5A and 5C), and was interpreted to represent differences in percentages of sugar maple, red maple, and American beech. The third canonical variate provided less meaningful separation among clusters; the squared canonical correlation was 0.54. Only 1% of added variation was explained by this variate. Separation along the third axis was between clusters 1, 3, and 4 versus cluster 2 (Figs. 5B and 5C) and was interpreted to be due to the percentages of black cherry, sugar maple, and American beech.

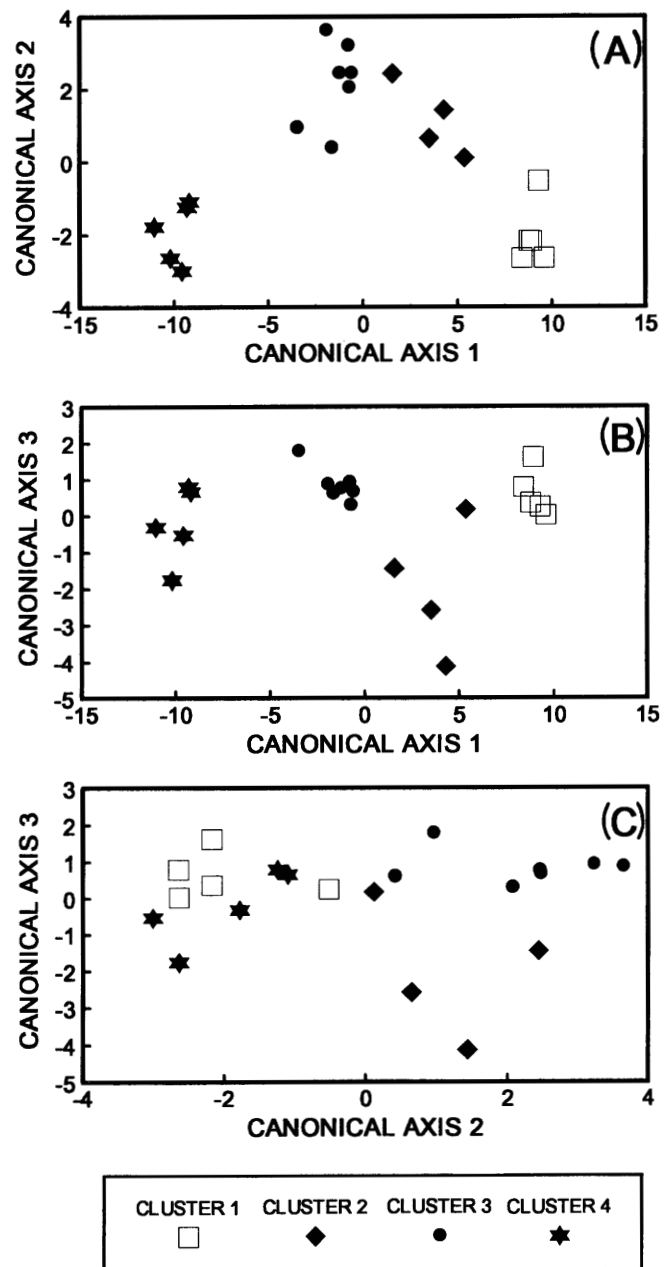
Cherry-maple relationships

Black cherry and sugar maple were the most important species accounting for the differences among clusters. Amounts of red maple and American beech varied somewhat among clusters, but this was minor compared with the large amount and variation in black cherry and sugar maple across the study plots. Black cherry and sugar maple represented nearly 80% of the total basal areas in the study plots.

The proportion of black cherry in a plot was negatively correlated with sugar maple ($r = -0.74$; $n = 23$; $P < 0.01$). This inverse relation was observed in other studies (Hough and Forbes 1943; Marquis 1981b). Cluster 1 had a high proportion of black cherry and a low proportion of sugar maple; the reverse was true for cluster 4. Clusters 2 and 3 were intermediate between clusters 1 and 4, and had generally equal proportions of basal area in black cherry and sugar maple. While average percentages of these species were different among clusters, there was overlap in the ranges of percentages expressing the presence of the species across the clusters. Hence, using the percentage of total stand basal area in black cherry alone to account for some of the unexplained variation in thinning response, as done in the other studies in which the same study plots were used (Marquis 1986; Ernst 1987), would not produce the same groupings of study plots described in this paper.

Stand structure was variable among clusters before thinning (Figs. 3 and 4), but was made more similar with thinning (Fig. 6). Cluster 4 plots, both thinned and unthinned, had less pole-size tree basal area and more sawtimber basal area than cluster 1 (Fig. 6). These differences in stand structure are related to differences in species composition. In cluster 4, the individual black cherry are few but are relatively large compared with the high abundance and

Fig. 5. Distributions of plots, by clusters, along canonical axes representing stand structure and species composition.



small size of black cherry in cluster 1. Average DBH of black cherry before thinning in cluster 4 was 14.9 in., compared with 10.1 in. in cluster 1. The large size of cherry in cluster 4 must be related to individual trees reaching dominant crown positions more quickly than in cluster 1. In cluster 1, cherry must have competed more often with other trees, likely cherry, in similar crown positions. In cluster 4, cherry often competed with sugar maple and beech, with the latter two relegated to lower crown positions through time because of the differences in growth rate and shade tolerance. In cluster 1, 60% of the pole-sized tree basal area was cherry and 7% was maple, compared with cluster 4, in which 12% of poles were cherry and 32% were sugar maple. In cluster 1, 79% of the sawtimber size

Table 3. Factor loadings of the canonical variates describing the four clusters of study plots with similar pretreatment species composition.

Variable	Canonical variate		
	1	2	3
Standardized			
Total no. of stems (stems/acre)	7.116	0.049	-1.456
Total basal area (ft ² /acre)	0.063	1.929	0.911
% of total no. of stems			
Black cherry	-2.913	-4.123	-4.091
Sugar maple	-4.535	-23.642	-7.042
Red maple	-2.369	-15.624	0.021
American beech	-5.066	-13.471	-4.109
% of total basal area			
Black cherry	1.569	4.380	3.452
Sugar maple	-0.247	12.215	2.165
Red maple	0.040	8.815	-1.877
American beech	1.916	-0.186	1.070
Unstandardized			
Total no. of stems (stems/acre)	0.025	-0.000 17	-0.0050
Total basal area (ft ² /acre)	0.023	0.716	0.338
% of total no. of stems			
Black cherry	-0.570	-0.807	-0.800
Sugar maple	-0.286	-1.491	-0.444
Red maple	-0.285	-1.880	0.002
American beech	-0.472	-1.254	-0.383
% of total basal area			
Black cherry	0.144	0.401	0.316
Sugar maple	-0.015	0.731	0.130
Red maple	0.004	0.802	-0.171
American beech	0.365	-0.035	0.204
Eigenvalue	62.94	8.38	1.18
Eigenvalue proportion	0.87	0.12	0.01
Squared canonical correlation	0.98	0.89	0.54

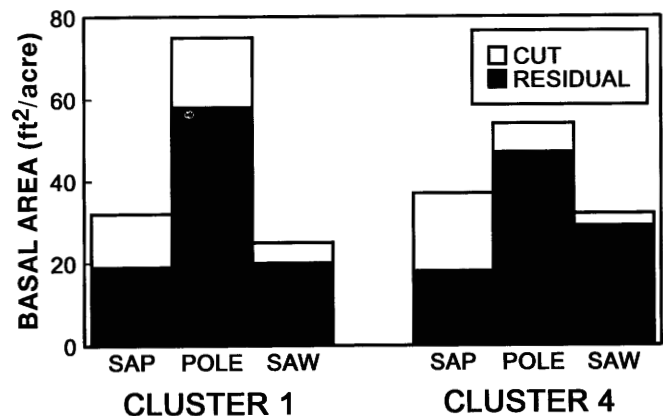
Note: Values are based on all stems ≥ 1.00 in. DBH.

tree basal area was cherry, compared with 87% in cluster 4. Cluster 1 had only 1% of sawtimber basal area in stems ≥ 17.50 in. DBH, compared with 21% in cluster 4. Differences in stand structure among clusters is related to the differences in species composition. But, separating the two effects would be difficult. Any differences in productivity relations among clusters could be related to both species composition and stand structure

Regression analysis of plot-level volume responses

Unexplained variation

When regression equations relating stand growth parameters to RSD were fit using data from all clusters, R^2 values

Fig. 6. Average basal area distribution by size class across treatments within clusters 1 and 4. Sapling, 1.00–5.49 in. DBH; pole, 5.50–11.49 in. DBH; sawtimber, ≥ 11.50 in. DBH.

ranged from 0.07 to 0.48 (Table 4). The high levels of unexplained variation were related to pretreatment species composition among the study plots. When plots with similar pretreatment species composition were assigned to groups by cluster analysis, R^2 values were increased to range from 0.77 to 0.99 (Table 5) and 0.94 to 0.99 (Table 6).

Ingrowth and mortality

Ingrowth generally increased and mortality decreased with decreases in RSD. Slopes of the ingrowth regression equations were equal among clusters, but intercepts were different (Tables 4–7, Fig. 7). Cluster 1 had 31 and 27% more ingrowth than clusters 3 and 4. Slopes of the mortality regression equations differed among all clusters, except that clusters 1 and 3 were equal (Tables 4–7, Fig. 8).

Fifty- to 55-year-old Allegheny hardwood stands are in the “stem-exclusion” (*sensu* Oliver and Larson 1990) stage of development. During this stage, competition for site resources is high, mortality is high, and ingrowth is low. Release of site resources, specifically light, by thinning increased ingrowth and reduced mortality in residual trees because trees in the lower stratum were allowed to grow in a less competitive environment.

Light is the most limiting resource in the study area. Removal of trees from below the main crown canopy to a residual of 60% relative density did not affect the growth of trees in the main crown canopy on plots adjacent to area 2 (Marquis and Ernst 1991). This lack of response indicated that resources derived from the soil, water and nutrients, were not limiting on the study area. This is consistent with the view of Kelty et al. (1987) that soil resources are generally not limiting for hardwoods in the northeastern United States.

Most of the mortality in all clusters was black cherry (mean: 56% of total mortality by basal area; range: 45–64%). Cluster 4 had the most mortality, cluster 1 had the least, and clusters 2 and 3 were intermediate between the two. Relatively high amounts of sugar maple mortality in cluster 4 account for it having the highest amount of mortality. The amount of sugar maple mortality across clusters averaged 17%, ranging from a low of 6% in cluster 2 to 33% in cluster 4. High amounts of sugar maple

Table 4. Regression parameters from curves fit to growth response data for all clusters.

Dependent variable*	n	Regression coefficient			$S_{y,x}^{\dagger}$	R^2
		b_0	b_1	b_2		
Ingrowth	21	16.43	-0.2378	0.001 236	2.69	0.20
Mortality	21	20.00	-0.6386	0.005 975	5.14	0.48
Survivor growth	21	29.85	1.5893	-0.011 407	14.07	0.08
Net growth	21	26.28	1.9901	-0.016 15	17.71	0.19
Gross growth	21	46.28	1.3514	-0.010 171	15.05	0.07

Note: Regression equations were fit to the data using a quadratic model: $y = b_0 + b_1RD + b_2RD^2 + e$, where y is the dependent variable, RD is relative stand density as a percent, b_0 , b_1 , and b_2 are estimated regression coefficients, and e is unexplained variation, or error.

*Dependent variables are in annual cubic foot volume increment of merchantable stemwood (minimum DBH 5.50 in.).

[†]Standard error.

Table 5. Regression parameters from volume increment equations with equal slope and cluster specific intercept.

Dependent variable*	n	Regression coefficients						$S_{y,x}^{\dagger}$	R^2
		b_{10}	b_{20}	b_{30}	b_{40}	b_1	b_2		
Ingrowth	21	18.97	15.76	14.45	14.97	-0.2313	0.001 249	2.08	0.94
Mortality	21	15.57	18.41	16.82	19.09	-0.5614	0.005 449	5.40	0.77
Survivor growth	21	28.32	17.05	12.96	-0.07	1.9768	-0.013 597	10.20	0.99
Net growth	21	31.73	14.39	10.60	-4.19	2.3069	-0.017 796	12.72	0.98
Gross growth	21	47.29	32.81	27.42	14.90	1.7455	-0.012 348	9.76	0.99

Note: Regression equations were fit to the data using a quadratic model with dummy variables: $y = b_{10} + b_{20} + b_{30} + b_{40} + b_1RD + b_2RD^2 + e$, where y is the dependent variable, RD is relative stand density as a percent, b_{10} , b_{20} , b_{30} , and b_{40} are dummy variable regression intercept coefficients for clusters 1, 2, 3, and 4, respectively, b_1 and b_2 are regression slope coefficients, and e is the unexplained variation, or error.

*Dependent variables are in annual cubic foot volume increment of merchantable stemwood (minimum DBH 5.50 in.).

[†]Standard error.

mortality in cluster 4 was related to it generally being a smaller size, lower crown canopy stratum species. Also, in northwestern Pennsylvania, sugar maple has been in a decline syndrome for decades (Kolb and McCormick 1993). In the study area, crown dieback and other decline symptoms were observed for sugar maple across all tree size classes and all treatment plots (Redding 1987). One of the two control plots for cluster 4 was located at the top of the toposequence on a ridge of excessively to well-drained Hartleton and Hazelton soils. Moisture stress has been cited as an important contributing factor in the decline of sugar maple (Kolb and McCormick 1993). Trees growing in drought-prone areas likely would have experienced more persistent and intense decline. The ridgetop control plot had 29 ft³ of annual mortality, while the other control plot in cluster 4, located on a midslope position on a moderately well to somewhat poorly drained Cookport soil, had only 9 ft³ of annual mortality and less severe decline symptoms.

Survivor growth

Slopes of the survivor volume increment regression equations were different between clusters 1 and 4, and 2 and 4

(Tables 4–7, Fig. 9). Intercepts were different between clusters 1 and 2, 1 and 3, and 3 and 4 (Tables 4–7, Fig. 9). Clusters 1 and 2, and 2 and 3, were alike in response (Tables 4–7 and Fig. 9). Cluster 1 had a 24% decrease in volume increment with a reduction in RSD from 100 to 40%. The magnitude of decrease is statistically meaningful as expressed by a quadratic equation ($F_{[2,2]} = 4.77$, $P = 0.17$). The slope of a linear response curve is significantly different from zero ($F_{[1,3]} = 6.75$, $P = 0.08$). Cluster 4 had a 46% statistically significant ($F_{[2,2]} = 77.93$, $P = 0.01$) increase in volume increment with a reduction in RSD from 100 to 40%. The responses for clusters 2 and 3 were intermediate between clusters 1 and 4.

Average percentage of survivor growth in black cherry across all plots within a cluster was 69, 55, 57, and 41% of the total increment for clusters 1, 2, 3 and 4, respectively. Sugar maple accounted for 9, 27, 17, and 27% of the survivor growth for clusters 1, 2, 3, and 4, respectively. Most of the remaining growth was produced by red maple, which accounted for 11, 12, 19, and 15% of the survivor growth for clusters 1, 2, 3, and 4, respectively. While the primary differences in volume increment among clusters is related

Table 6. Regression parameters from volume increment equations with cluster-specific slope and intercept.

Dependent variable*	n	Regression coefficient														$S_{y,x}^{\dagger}$	R^2
		b_{10}	b_{20}	b_{30}	b_{40}	b_{11}	b_{21}	b_{31}	b_{41}	b_{12}	b_{22}	b_{32}	b_{42}				
Ingrowth	21	7.87	-36.28	42.01	17.05	0.1886	1.4517	-0.9712	-0.3237	-0.002 267	-0.010 723	0.005 939	0.002 068			1.78	0.97
Mortality	21	-3.92	-127.54	16.04	81.33	0.1399	4.3107	-0.4690	-2.6435	0.000 237	-0.030 460	0.004 399	0.021 314			3.58	0.94
Survivor growth	21	86.38	31.35	-59.46	118.07	-0.2186	1.4021	3.9843	-0.9653	0.004 786	-0.008 579	-0.026 731	0.003 697			9.55	0.99
Net growth	21	98.17	122.61	-33.49	53.80	-0.1700	-1.4570	3.4822	1.3545	0.002 755	0.011 158	-0.025 191	-0.015 549			12.12	0.99
Gross growth	21	94.25	-4.93	-17.44	135.12	-0.0301	2.8537	3.0131	-1.2890	0.002 519	-0.019 302	-0.020 793	0.005 767			9.66	0.99

Note: Regression equations were fit to the data using a quadratic model with dummy variables: $y = b_{10} + b_{20}RD + b_{30}RD^2 + e$, where y is the dependent variable, RD is relative density as a percent (40–100%), b_{10} , b_{20} , and b_{30} are regression intercept coefficients, where $i = 1$ to 4 for clusters 1, 2, 3, and 4, and e is the unexplained variation, or error.

*Dependent variables are in annual merchantable cubic foot volume increment (minimum DBH 5.50 in.).

[†]Standard error.

to the relative proportions of black cherry and sugar maple, red maple was also an important component.

Differences in species composition and stand structure among clusters led to different proportions of volume increment occurring from different size classes and species of trees. In cluster 1, 70% of the volume increment was in pole timber, compared with 54% in cluster 4. Sugar maple and black cherry accounted for 17 and 58% of the pole-timber volume increment in cluster 1, compared with 50 and 15% in cluster 4. In cluster 1, 30% of the volume increment was in sawtimber, compared with 46% in cluster 4. Sugar maple and black cherry accounted for 0 and 79% of the sawtimber volume increment in cluster 1, compared with 0 and 72% in cluster 4.

Because black cherry grows faster in height and diameter than most of its associates (Ernst 1987; Marquis and Ernst 1991) and has less stem taper (Wenger 1984), a higher amount of black cherry results in higher total volume increment. Higher pretreatment percentage of black cherry in cluster 1 accounts for its greater survivor volume increment of $112 \text{ ft}^3 \cdot \text{acre}^{-1} \cdot \text{year}^{-1}$ at 100% relative density, compared with cluster 4 at $59 \text{ ft}^3 \cdot \text{acre}^{-1} \cdot \text{year}^{-1}$ increment (Fig. 9).

Thinning treatments reduced the total amount of black cherry in all plots. Plots with a high percentage of black cherry had a greater reduction in the total amount of black cherry basal area than plots with less cherry. In cluster 1, thinning reduced basal area of black cherry by an average of 24%, with a maximum decrease of 45%. Cluster 4 had an average decrease of 11%, with a maximum decrease of 22%. Thinning stands with different species composition to the same residual stand structure, but leaving different proportions of species as residual trees, resulted in plots with more similar species composition than before thinning. The result was a convergence of volume increment between clusters at lower relative densities. Lowered volume increment in cluster 1 can be attributed in part to large reductions in the amount of black cherry on the plots.

Because of its predominance in the upper crown canopy strata, black cherry may grow nearer to its potential maximum rate than most other Allegheny hardwood forest tree species, especially sugar maple (Hough and Taylor 1946; Ernst 1987). As a result, the potential for thinning to increase volume increment was likely higher in sugar maple than in black cherry.

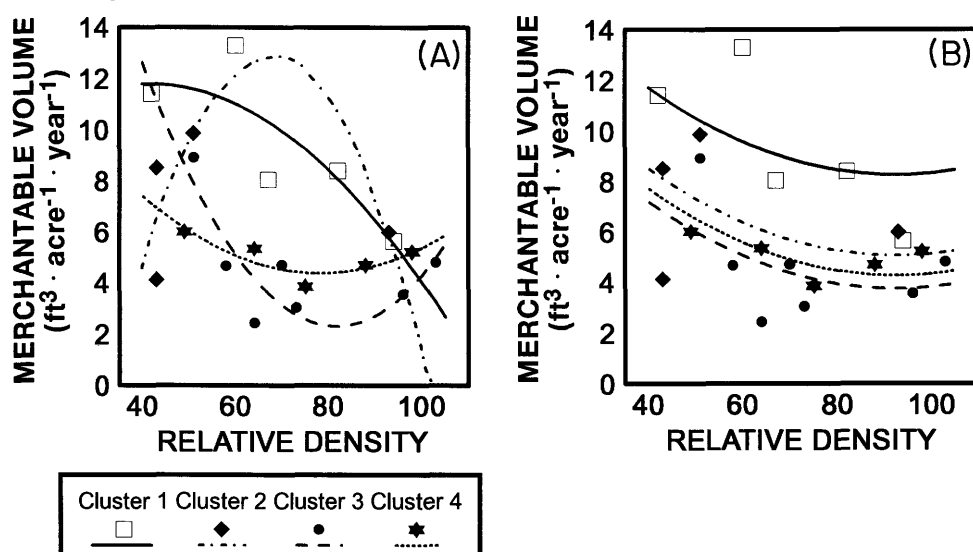
Volume increment in a thinned stand is affected by how quickly residual trees regain full site occupancy, i.e., how quickly canopy closure recurs as light is the most limiting resource. Rates of crown closure were observed to be high in cluster 4 plots and low in cluster 1 (J. Redding 1995, personal communication). Evidence of the low rate of crown closure in stands dominated by black cherry was demonstrated by the higher amount of ingrowth in cluster 1 compared with the other clusters (Fig. 7B). More light was able to reach trees in lower crown canopy strata in cluster 1 plots because main crown closure did not occur as quickly as in the other plots. Volume increment in plots with a large component of sugar maple did not decrease because the trees were able to quickly reoccupy the growing space released by thinning. The decrease in volume increment in cluster 1 indicates that black cherry could not quickly

Table 7. *P*-values from *F*-tests comparing volume increment regression equation slopes and intercepts among and between clusters.

Clusters compared	Comparison of slope parameters						Comparison of intercept parameters					
	df*	Ingrowth	Mortality	Survivor	Net	Gross	df*	Ingrowth	Mortality	Survivor	Net	Gross
All	6/9	0.18	0.03	0.33	0.37	0.45	3/15	0.01	0.74	0.01	<0.01	<0.01
1 vs. 2	2/3	0.46	0.13	0.54	0.83	0.54	1/5	0.32	0.22	0.03	0.01	0.01
1 vs. 3	2/6	0.15	0.72	0.34	0.52	0.51	1/8	0.01	0.43	0.05	0.03	0.02
1 vs. 4	2/4	0.25	0.10	0.01	0.04	0.02	1/6	0.02	0.45	0.01	0.01	<0.01
2 vs. 3	2/5	0.12	0.07	0.92	0.80	0.99	1/7	0.47	0.56	0.37	0.50	0.29
2 vs. 4	2/3	0.34	0.07	0.07	0.06	0.02	1/5	0.33	0.75	0.12	0.14	0.08
3 vs. 4	2/6	0.20	0.04	0.38	0.43	0.50	1/8	0.49	0.52	0.09	0.12	0.09

Note: Comparison of regression equation parameters was done using a dummy variables approach (Cunha 1973) using the full and reduced equations described in Tables 4–6.

*Degrees of freedom for *F*-tests: numerator/denominator.

Fig. 7. Annual ingrowth, by cluster, as a function of relative density. (A) Regression curves with cluster-specific slopes and intercepts. (B) Regression curves with equal slopes among clusters and cluster-specific intercepts. See Tables 5 and 6 for regression equation parameters.

regain full site occupancy. The rate of crown expansion and crown densification in black cherry was insufficient to compensate for the loss of volume growth attributable to the trees removed by thinning. Beck (1986) and Trimble (1968) demonstrated similar decreases in annual merchantable volume increment with reductions in density of stands dominated by yellow-poplar (*Liriodendron tulipifera* L.). Yellow-poplar and black cherry have similar silvical characteristics (Roach 1977; Stout and Nyland 1986; Burns and Honkala 1990). Stands dominated by one or the other species can be expected to respond similarly to thinning.

Differences in the ability of black cherry and sugar maple to occupy newly released crown space may be related to inherent differences in crown architecture. I have observed black cherry to have a compound umbel-shaped crown with low crown thickness, compared with sugar maple, which appears to have a more full, ovoid crown

with high crown thickness. Canham et al. (1994) reported that crown thickness (referred to as depth) was greatest for shade-tolerant hardwoods and least for shade intolerants. Differences in crown shape and thickness could lead to differences in response to increased growing space. Sugar maple crowns may be more responsive because of their high potential for branch expansion, which can occur laterally in all directions of the crown. This responsiveness in sugar maple has been referred to as its plasticity (Smith 1986; Canham 1988). By contrast, black cherry has limited opportunities for expansion and can be considered a less plastic species. Ellis (1979, p. 187) indicated that "shade tolerant sugar maple responds more readily to release than do less tolerant species" (such as black cherry and white ash).

There are a number of mechanisms that might explain potential differences in crown shape and thickness between black cherry and sugar maple. On black cherry, lower

Fig. 8. Annual mortality, by cluster, as a function of relative density. (A) Regression curves with cluster-specific slopes and intercepts. (B) Regression curves with equal slopes among clusters and cluster-specific intercepts. See Tables 5 and 6 for regression equation parameters.

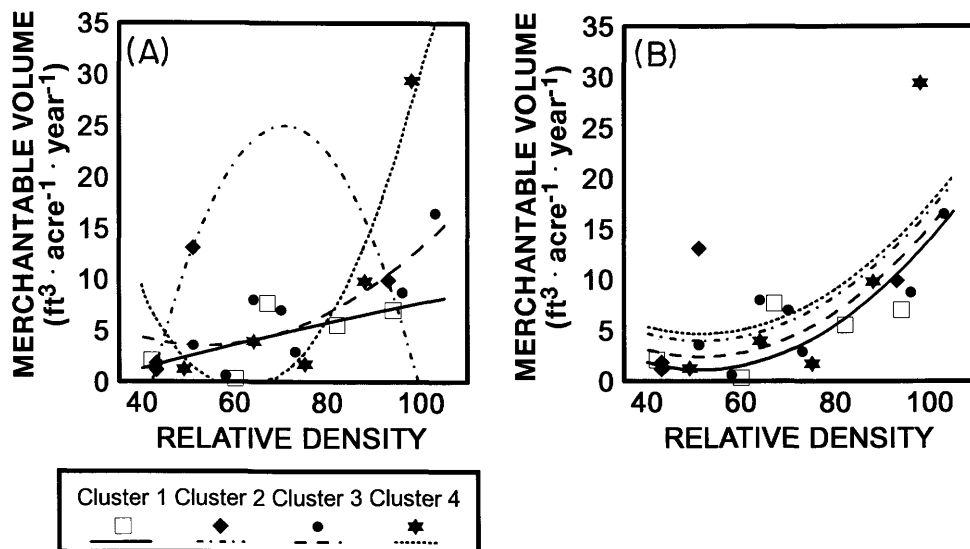
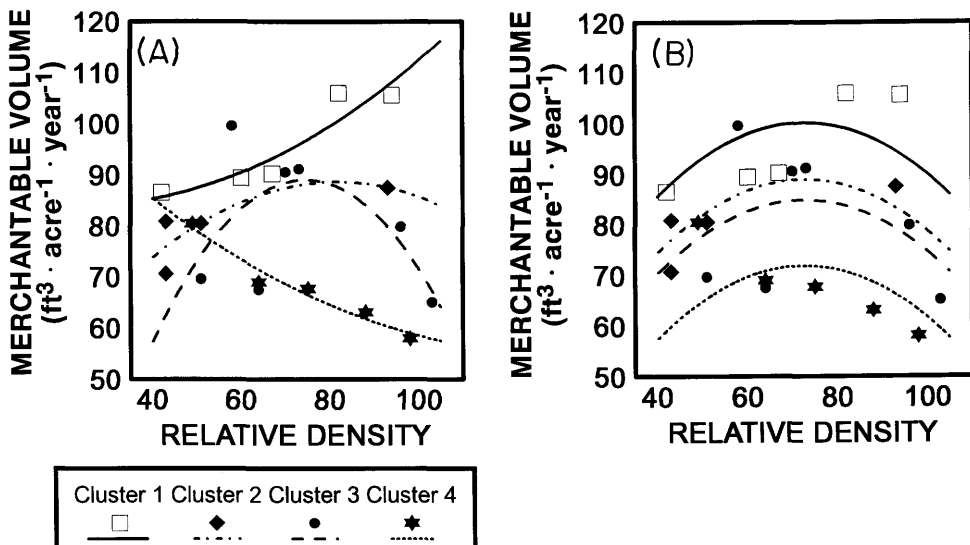


Fig. 9. Annual survivor growth, by cluster, as a function of relative density. (A) Regression curves with cluster-specific slopes and intercepts. (B) Regression curves with equal slopes among clusters and cluster-specific intercepts. See Tables 5 and 6 for regression equation parameters.



branches and branches away from the crown edge and near the main stem are shed earlier and more often than similarly positioned branches on sugar maple, a phenomenon related to shade tolerance. Hallé et al. (1978) described similar differences in crown architecture in tropical trees with long-lived branches (model 17a, Roux's model: ovoid crown) versus trees with short-lived branches (model 17b; Cook's model: umbel crown). Branching habit can result in different crown forms. Ward (1909) (as cited in Wilson 1970) used silhouettes to show how alternate branching habits such as in black cherry can lead to what I have called an umbel crown. Opposite branching in sugar maple

and other species can lead to an ovoid crown form. Horn (1971) speculated that there are adaptive patterns of crown architecture for woody species, and that midsuccessional trees like black cherry have a persistent multilayer strategy for crown development that leads to an umbel crown. According to Horn, late successional species like sugar maple have a monolayer strategy that leads to an ovoid crown (Horn 1971). In one of the few studies to examine crown architecture of trees in temperate hardwood forests, Tucker et al. (1993) presented diagrams of sugar maple that portrayed ovoid-shaped crowns among trees of different crown class. Leaf area per unit of crown radius was

Fig. 10. Annual net growth, by cluster, as a function of relative density. (A) Regression curves with cluster-specific slopes and intercepts. (B) Regression curves with equal slopes among clusters and cluster-specific intercepts. See Tables 5 and 6 for regression equation parameters.

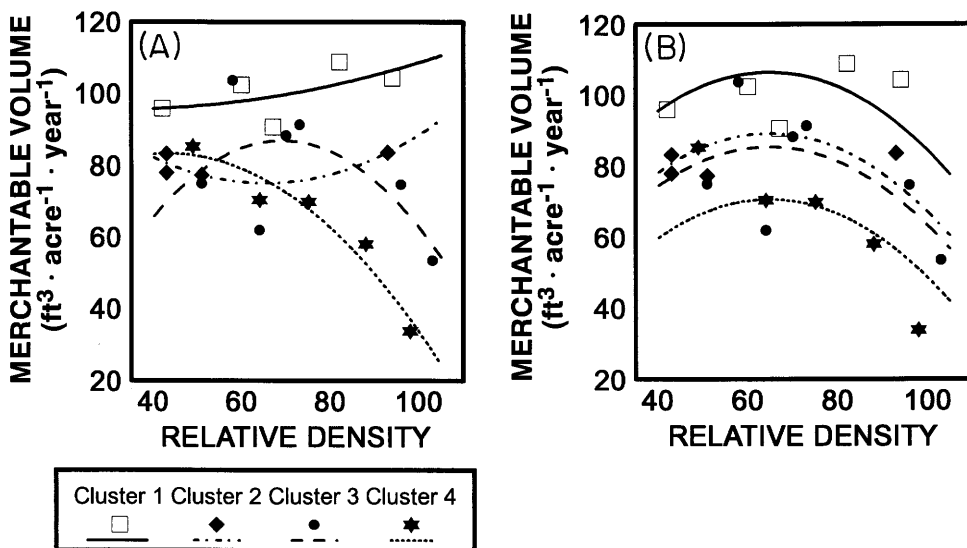
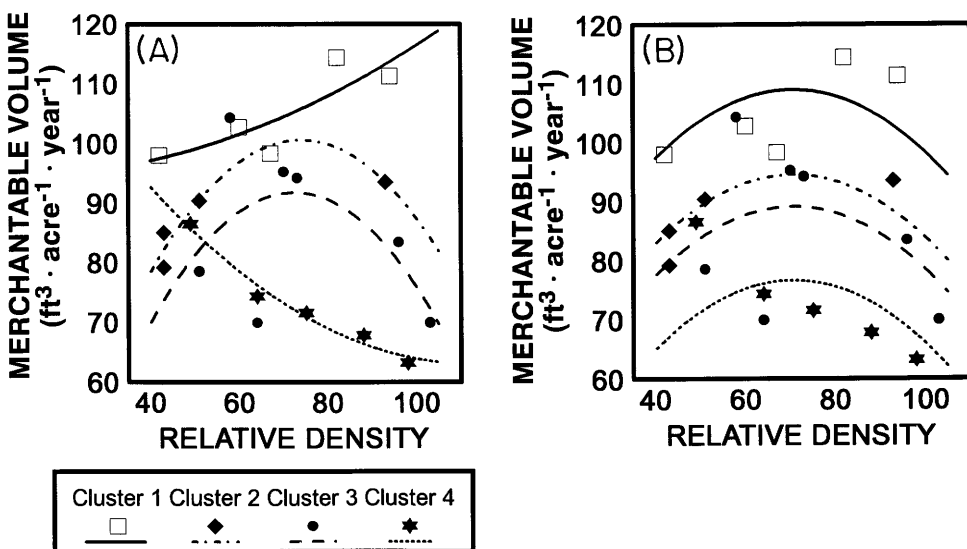


Fig. 11. Annual gross growth, by cluster, as a function of relative density. (A) Regression curves with cluster-specific slopes and intercepts. (B) Regression curves with equal slopes among clusters and cluster-specific intercepts. See Tables 5 and 6 for regression equation parameters.



generally constant across all crown classes, indicating that crown thickness is maintained at relatively high levels in all sizes of sugar maples.

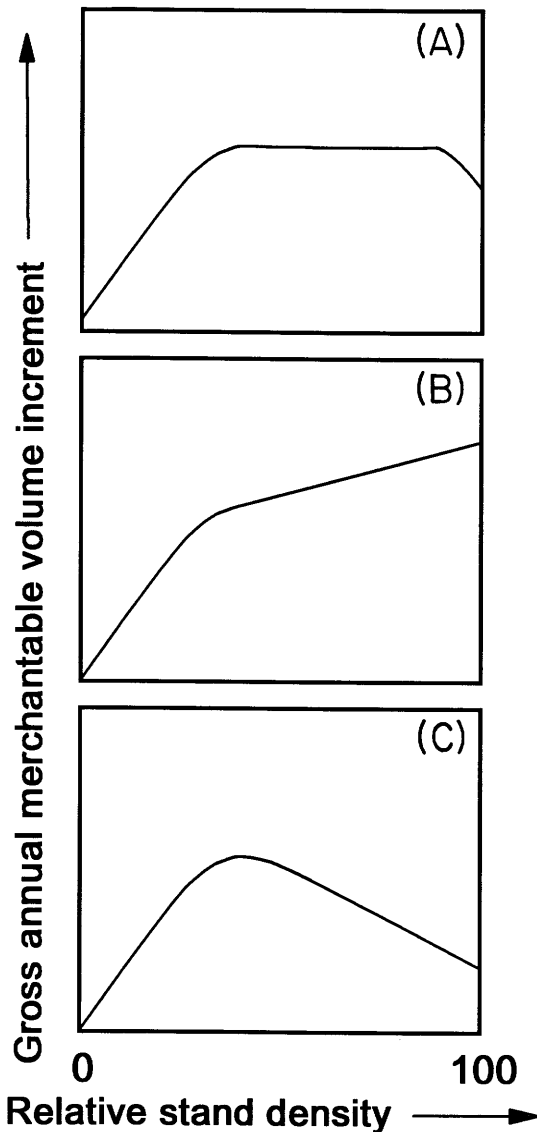
The increased volume increment with reductions in RSD observed in cluster 4 may be related to an increase in stand-level growth efficiencies due to increased foliar leaf area or improved photosynthetic efficiency. Thinning can increase stand growth efficiencies by removing suppressed and intermediate crown class trees (Assmann 1970; Oliver and Larson 1990), unhealthy trees, and other trees that inefficiently occupy their growing space. The decline of

sugar maple observed in the study area may have been mediated by thinning, causing higher growth efficiencies because healthy, vigorous trees were favored.

Net and gross growth

Regression equations for net and gross volume increment followed the same patterns of shape and difference among clusters as observed for survivor growth. Slopes were different between clusters 1 and 4, and 2 and 4 (Tables 4–7, Figs. 10 and 11). Clusters 2 and 3 were similar and intermediate between clusters 1 and 4 (Tables 4–7, Figs. 10

Fig. 12. Models of annual volume increment of wood in response to changes in stand density. (A) Langsaeter's model (Langsaeter 1941, as cited in Braathe 1957). (B and C) Modified after Smith (1986).



and 11). Similar response curves among survivor, net, and gross growth is due to the relatively low amounts of ingrowth and mortality across treatments. Ingrowth averaged 7% of gross volume production across all plots, with values ranging from 3 to 13%. Mortality averaged 7% across all plots and ranged from 1 to 24%, excluding the lone sugar maple control plot on the ridgetop position. Here the mortality level was 46% of gross production.

Comparison of volume increment responses with other studies

Langsaeter's (1941) model (cited in Braathe 1957) (Fig. 12A) is the most commonly used model of gross volume increment of merchantable stemwood following reductions in stand density with thinning. This model, along

with a similar model developed by Mar: Möller (1954), has had a pervasive influence on the fitting and interpretation of response curves that describe volume increment as a function of stand density. The key concept of these models is that wood production, i.e., volume increment, is constant across a wide range of stand densities. Smith (1986) presented two alternative models. One model describes a decline in volume increment over a wide ranging decrease in stand density (Fig. 12B). The other shows an increase in volume increment with reductions in stand density, to a point, followed by a decrease in volume increment thereafter (Fig. 12C). At low stand densities (likely lower than those presented here in this paper) all models have decreasing volume increment with reductions in stand density. If a Langsaeter – Mar: Möller model is used to generate thinning guidelines, stands might be over- or under-thinned if they respond according to one of the two other models described by Smith (1986).

Past studies of thinning in Allegheny hardwoods have followed the Langsaeter and Mar: Möller models in describing volume increment following thinning in Allegheny hardwoods. Using 10-year data from the same study plots used in this paper, Ernst (1987) graphically described average annual volume increment across three classes of RSD: low (less than 55%), medium (55–80%), and high (>80%). He concluded that survivor growth and net growth were nearly constant across these classes. Using the same data along with unpublished simulations of stand development, Marquis (1986) concluded that volume increment was constant across a broad range of RSDs. Roach (1977) apparently used earlier data from the same study to propose constant volume increment with reductions in relative density. In West Virginia, Lamson and Smith (1988) showed that the 5-year net volume increment in a 60-year-old thinned Allegheny hardwood stand was constant with reductions in RSD to 45%. Lamson (1985) showed that survivor volume increment of 60-year-old cherry-maple stands was increased with reductions in RSD to 66%.

Differences between published study results and those presented here can be attributed to the interpretation of plot-level variation in growth responses related to differences in species composition of the plots. Thinning studies often generate highly variable plot-level response data. Smith (1986; p. 56) noted that "part of the difference in interpretation between [models 1A, 1B, and 1C, Fig. 12] results merely from the bewildering variability that would become obvious in the scatter of points representing the actual observations." Langsaeter (1941, as cited in Braathe 1957) acknowledged the variation within his model. He referred to the section of the model curve where volume increment is constant with reductions in stand density as a line representing a broad band of responses (Braathe 1957). Mar: Möller (1954) derived his model by hand-fitting response curves through density class means (10% wide classes) based on highly variable plot data. In one of the few studies to report the high variation in thinning volume increment response, Oliver and Murray (1983) presented response curves for Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) with relatively low R^2 values (0.45–0.53). Oliver and Larson (1990; p. 345) concluded that "stand density does not define a unique growth condition and can give misleading results

when used as a refined correlate of growth (Bickford et al. 1957; Assmann 1970; Oliver and Murray 1983)."

Single response curves for volume increment fit through the highly variable data used in this paper had R^2 values of 0.07–0.48 (Table 4). The inference "no treatment effect" would result using these curves because the variation was too high to discern trends. With no treatment effect, the response curve slope would be zero, a result that could be interpreted as consistent with Langsaeter's model: no slope can be interpreted to mean constant volume increment with reductions in RSD. Nelson et al. (1961), Trimble (1968), and Beck and Della-Bianca (1975) apparently used an approach similar to mine in understanding volume increment in loblolly pine (*Pinus taeda* L.) and yellow-poplar. Variation in plot-level volume increment was explained by plot differences in site quality. Nelson et al. (1961) and Beck and Della-Bianca (1975) developed sets of response curves, one curve for each site quality class rather than a single response curve for all sites.

Implications for thinning practice in Allegheny hardwoods

Guidelines for thinning pole- and small sawtimber-sized Allegheny hardwoods were first described by Roach (1977) and were later modified by Marquis (1986, 1994) and Marquis et al. (1992). These guides were developed in part using average plot-level responses and a Langsaeter model of stand-level response to reductions in relative density with thinning. In these guidelines, thinnings are prescribed to leave an RSD of 60%. This level is consistent with most stocking guides (Leak 1981; Ernst and Knapp 1985). Prescriptions for stand structure are similar to those of Roach (1977), except that the cut is focused on the main crown canopy: two-thirds of the cut is from below the average medial stand diameter (after Marquis 1991; Marquis et al. 1992) and one-third is from above (Marquis 1986).

Results of my study show that thinning all Allegheny hardwood stands to 60% relative density may not maximize stemwood volume production. Leak (1981) reported similar results for a variety of New England forest types. Thinning guidelines for Allegheny hardwoods may need to reflect differences in species composition. Stands of pole- to small sawtimber-size trees dominated by black cherry may require a residual density that is higher than 60% to maximize volume increment of merchantable stemwood. The volume increment of merchantable stemwood in similarly structured stands dominated by sugar maple would be maximized at RSDs lower than 60%.

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