An Assessment of Canopy Stratification and Tree Species Diversity Following Clearcutting in Central Appalachian Hardwoods

Mark Benjamin Brashears, Mary Ann Fajvan, and Thomas M. Schuler

ABSTRACT. On high quality growing sites in West Virginia, shade intolerant tree species have increased in importance in third-generation forests following clearcutting. We investigated the effect of tree species canopy position on the Shannon-Weiner Diversity Index (*H'*), Pielou's evenness index (*E*), and species richness (*S*) using a chronosequence of 13 clearcuts. Two to 26 yr after clearcutting, tree species diversity significantly decreased from 2.07 to 1.83, and evenness decreased from 0.80 to 0.71 while species richness was maintained. As the number of years since harvesting increased, the importance value of oaks (*Quercus* L.), hickories (*Carya* Nutt.), American beech (*Fagus grandifolia* Ehrh.), sugar maple (*Acer saccharum* Marsh.), and black birch (*Betula lenta* L.) decreased while the importance of yellow-poplar (*Liriodendron tulipifera* L.) increased. In these mixed-species stands with stratified canopies, species importance in overstory versus understory canopy layers was the best indicator of competitive success during stem exclusion. Second-generation forests that had almost equal representation of overstory sugar maple and yellow-poplar prior to harvesting had 43% yellow-poplar and 13% sugar maple overstory importance 22–26 yr after harvest. Forty-five percent of the dominant crown class stems and 54% of the codominant class were yellow-poplar. While sugar maple was also an important (13%) overstory species overall, it had no dominant and few codominant stems and over 30% importance as overtopped trees and in the understory. As these stands progress through the stem exclusion stage, richness and measures of diversity may continue declining as yellow-poplar basal area increases. FOR. SCI. 50(1):54–64.

Key Words: Species diversity, clearcutting, canopy structure, yellow-poplar.

THE CENTRAL APPALACHIAN hardwood forest region consists of maturing, second-growth stands. The high species and structural diversity of these forests was influenced by heavy logging, periodic fires, and the death of the American chestnut (*Castanea dentata* [Marsh.] Borkh.) (Hicks 1998, p. 80–106). Current stands typically contain more than 20 tree species representing a range of silvical characteristics (Miller and Kochenderfer 1998). As second-generation forests are harvested, maintenance of species diversity is an important consideration of forest managers. On federal land, the *National Forest Management Act of 1976* directs the Forest Service to maintain the diversity of tree species present at the onset of management activities. To establish new cohorts containing species representative of the forests that preceded them, some silvicultural recommendations include creating canopy openings >0.2 ha (Trimble 1973, Dale et al. 1995). However, the maintenance of preharvest species dominance in the overstory can be

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delayed or prevented by the presence of shade-tolerant advance regeneration (Wang and Nyland 1993, Arthur et al. 1997), and/or dominance of short-lived early successional species (Marquis 1967, Marks 1974, Walters and Nyland 1989, Wang and Nyland 2002).

Appropriately applied clearcutting removes an entire tree community creating sufficient growing space for the initiation of many woody and herbaceous species (Nyland 2002, p. 277–290). Species diversity is higher during stand initiation compared to later stages of development (Oliver and Larson 1996). However, exact developmental pathways for a given forest type are determined by variations in initial stand conditions and postharvest environmental conditions. During stem exclusion, species diversity decreases due to high mortality rates and competition. Tree species that can sustain rapid height growth will eventually dominate the overstory (Oliver and Larson 1996) and be indicative of the probable future species composition of the new community (Wang and Nyland 1993).

Comparisons of tree species composition before and after clearcutting eastern hardwoods indicate that species diversity and richness can increase soon after harvest and may become more like preharvest conditions as stand development proceeds (Elliott and Swank 1994, Elliott et al. 1997). These studies, and others, typically examine overall tree species composition without regard to canopy position to predict future structure. However, over the long term, third generation stands originating after clearcutting may actually become more homogeneous than previous stands because shade intolerant species tend to dominate the overstory (Wang and Nyland 1993).

On high quality sites in West Virginia, yellow-poplar (*Liriodendron tulipifera* L.), black locust (*Robinia pseudoacacia* L.), black birch (*Betula lenta* L.), and black cherry (*Prunus serotina* Ehrh.) have increased in importance following clearcutting (Trimble and Hart 1961, Trimble 1972, Trimble 1973). Similar trends have been noted for yellow-poplar, black locust, and black birch in the southern Appalachians (Parker and Swank 1982, Beck and Hooper 1986, Elliott et al. 1997). In all of these studies, yellow-poplar shows the greatest increase in species importance from stand initiation through early stem exclusion. Yellow-poplar is a long-lived species and sustains rapid height growth longer than its common hardwood associates (Doolittle 1958, Tift and Fajvan 1999). Early in stand development, yellow-poplar can achieve and maintain a dominant position in the overstory stratum (Beck 1990).

In this study, we investigated whether separating measures of species diversity by canopy position was a better indicator of probable future species dominance than the more typical method of calculating overall species importance. We examined a chronosequence of 13 clearcuts, representing 26 yr of development, to document the temporal changes in species composition and canopy structure of Appalachian hardwood tree species from stand initiation through early stem exclusion. We also assessed overall changes in tree species dominance through stand-level comparisons of preharvest and postharvest tree species diversity, evenness, and richness.

Methods

Study Areas

The study areas are located on the Fernow Experimental Forest (39.03N, 79.67W) in north-central West Virginia. The 1,900 ha Fernow is administered by the USDA Forest Service Northeastern Research Station's Timber and Watershed Laboratory in Parsons, WV. The land type association of the Fernow is the Allegheny Front Sideslopes (Ba10) (DeMeo et al. 1995), and the ecological land type is the Allegheny Mountain section (M221B) of the Central Appalachian Broadleaf Forest (M221) (McNab and Avers 1994). The forest vegetation type is classified as the Allegheny Mountain section of the mixed mesophytic forest (Braun 1950, p. 75–87). Average annual precipitation is 143 cm, with a mean of 71 cm during the growing season (May through October) (Pan et al. 1997). There is an average of 145 frost-free days per year.

The study areas lie generally within a north-facing cove with elevations ranging from 610 to 914 m above sea level. The study areas were selected to minimize variation in site factors. The topography is mountainous, with up to 60% slopes. Soils are classified as Dekalb, Calvin, and Belmont series, which are moderately deep to deep, well-drained, and medium-textured loams of shale and/or sandstone origin (Losche and Beverage 1967). Natural soil fertility is moderate to high with northern red oak (*Quercus rubra* L.) site indices$_{50}$ ranging from 23 to 24 m.

Stand History and Development

Current forest composition on the Fernow Experimental Forest was influenced by human and natural disturbances. Logging from 1903 to 1911 (Trimble 1977) was heavy, but left behind scattered unwanted trees because of poor form, inadequate size, or species type (Schuler and Gillespie 2000). At the time, species considered undesirable included sugar maple (*Acer saccharum* Marsh.), American beech (*Fagus grandifolia* Ehrh.), black birch, yellow birch (*Betula alleghaniensis* Britton) and hickory (*Carya* Nutt.). The chestnut blight fungus (*Cryphonectria parasitica*) caused a 25% volume reduction in stands on the Fernow during the 1930s (Weitzman 1949). Grazing and fire have been absent from these stands since 1915 (Schuler and Gillespie 2000). Species composition was dominated by the Appalachian mixed-hardwood forest type (Smith et al. 1983). The age structure of the second-growth stands evaluated exhibited dominance by a single cohort, but representation of up to three cohorts was possible.

Our study examined 13 strip clearcuts in 3 study areas. The clearcuts ranged in size from 0.32 to 2.09 ha, and the width of each strip was approximately 50 m (Table 1). These canopy openings are of sufficient size to provide suitable light conditions for the most shade-intolerant Appalachian hardwood species to regenerate (Trimble 1973, Smith 1981). Harvesting began in 1974 in Study Area 1, 1977 in Study Area 2, and 1978 in Study Area 3. Additional clearcuts were made 10 and 20 yr following the initial harvest on each of these areas. Thus, each area contained stands that were 22–26, 12–16, and 2–6 yr old. All study areas received silvicul-

Table 1. Measures of tree diversity (*H'*), richness (*S*), evenness (*E*) for preharvest trees > 12.7 cm dbh and postharvest seedlings (<2.54 cm dbh) and trees (≥2.54 cm dbh) combined. Preharvest mean stem densities and mean basal areas. Postharvest mean stem densities ± standard error (SE) and mean basal areas ± SE. Postharvest densities are shown separately for seedlings and trees.

Site characteristics					Preharvest					Postharvest								
Stand	Age	Size (ha)	Aspect	Slope (%)	*H'*	*S*	*E*	#/ha (≥12.7 cm)	Basal area (m²/ha)	*H'*	*S*	*E*	#/ha (< 2.54 cm)	SE	#/ha (≥ 2.54 cm)	SE	Basal area (m²/ha) (≥ 2.54 cm)	SE
1	2	2.09	355	30	1.890	15	0.698	285	29.03	1.744	13	0.680	38,575	7,079	0	0	0.00	0.00
2	3	2.06	330	5	2.400	21	0.789	320	32.23	2.159	21	0.709	53,185	6,715	365	252	0.34	0.23
3	3	1.05	0	55	2.180	15	0.804	287	38.33	2.031	15	0.750	37,683	6,227	700	302	0.71	0.31
4	6	0.61	25	60	1.680	8	0.809	236	24.66	1.357	8	0.691	16,062	5,094	329	198	0.41	0.31
5	6	0.40	295	60	2.251	14	0.853	267	28.57	1.655	12	0.666	98,840	10,008	0	0	0.00	0.00
6	12	1.86	340	30	1.919	14	0.727	194	25.53	1.577	12	0.635	5,628	2,093	3,638	478	14.14	1.48
7	13	0.77	0	55	2.285	15	0.844	351	40.99	2.443	16	0.881	7,688	4,249	6,035	744	14.90	1.26
8	16	1.17	285	45	2.232	15	0.824	237	26.36	1.655	15	0.611	5,972	1,535	4,962	348	19.54	1.09
9	16	0.32	290	60	2.145	13	0.836	284	28.07	2.016	12	0.811	4,448	1,977	3,944	692	13.80	2.39
10	22	2.08	350	30	n/a†	n/a	n/a	n/a	n/a	2.026	13	0.790	1,081	503	2,171	203	17.97	1.65
11	23	1.50	325	10	2.087	16	0.753	245	20.75	1.667	13	0.650	1,521	658	2,669	222	35.83	1.61
12	26	0.73	60	55	2.074	15	0.766	281	30.34	2.006	15	0.741	21,690	7,909	1,568	200	20.80	0.88
13	26	0.32	35	50	1.682	7	0.864	380	40.50	1.613	10	0.701	2,471	2,471	1,219	141	23.60	3.95

* *H'* = Shannon-Wiener Diversity Index; *S* = total number of species present on each stand; *E* = Pielou's evenness index; SE = Standard Error.

† Preharvest data not available for stand 10.

tural clearcuts where all stems greater than 2.54 cm diameter at 1.37 m above ground (dbh) were felled with chainsaws and removed using conventional ground-based logging methods. Nonmerchantable stems, cull trees, and tops were left on site.

Sampling Procedures

Immediately prior to each harvest, all trees >12.7 cm dbh were inventoried according to species and dbh. Concurrently, 0.0004 ha, circular sample plots were used to measure seedling advance regeneration <2.54 cm dbh, and 0.004 ha plots were used to measure understory trees ≥2.54 to <12.7 cm dbh. These nested sample plots were established along a central transect at a rate of about 1/0.5 ha.

During summer 2000, stand structure and species variables were measured in the 13 stands. Plots were systematically located along three transects running parallel to the longest side of each study area. Two transects were placed 10 m from the edges of the harvest unit. The third transect was placed in the center of the harvest unit. Plots were established equidistant along a transect, resulting in 1 to 7 plots per transect depending on the size of the clearcut. Using a nested plot design, circular 0.0004 ha plots were used to inventory seedlings <2.54 cm dbh, 0.004 ha plots were used to inventory trees ≥2.54 to <12.7 cm dbh, and 0.02 ha plots were used to inventory trees >12.7 cm dbh. Shrub species were typically omitted from the survey except for some species that had a well-developed central stem and were functioning as competitors with trees. Depending on the size and shape of each clearcut, plots were established at a rate of 7.4 to 9.9 ha^{-1}.

On the 0.0004 ha plots, trees were classified according to species, origin (seedling or sprout), and three height classes (<0.30 m, >0.30 m to <1.37 m, >1.37 m). On the 0.004 and 0.02 ha plots, trees were classified by species, dbh, origin, and canopy strata (overstory or understory). Trees were designated as overstory if they grew in the B-stratum (upper continuous canopy), according to the stratified mixed-species stand model described in Oliver and Larson (1996). All overstory trees were additionally classified as either dominant, codominant, intermediate, or overtopped, as defined by the Kraft Crown Classification system (Smith et al. 1997, p. 29–30). Stems >2.54 cm dbh with crowns located at least 3 m below the overstory canopy were classified as understory.

Data Analysis

Preharvest overstory densities were determined from the 100% inventories conducted immediately prior to each harvest. Preharvest understory and regeneration densities were determined from the sample plots in 1974, 1984, and 1994. In 2000, mean trees ha^{-1} and mean basal area ha^{-1} were calculated from sample plots for each species in each postharvest stand. Species relative density (number of trees per hectare of a species divided by the total number of trees per hectare of the stand) and species relative basal area (basal area per hectare of a species divided by the total basal area per hectare of the stand) were used to calculate species importance values (IV). Species importance values (IV = species relative density + species relative basal area/2) were determined for each stand, crown class. and canopy strata.

The Shannon-Wiener Diversity Index (H') (Whitaker 1972), Pielou's evenness index (E) (Pielou 1977), and species richness (S) were calculated for pre- and postharvest tree species densities for 12 of the harvest areas. S is the number of species present in a given stand, and E is a measure of the evenness of species abundance. The Shannon-Weiner Diversity Index is often used for quantifying aspects of woody species composition in second-growth and old-growth forests of the region (Elliott and Swank 1994, McCarthy and Bailey 1996, Jenkins and Parker 1998, Schuler and Gillespie 2000). This index of diversity is a simple quantitative expression that incorporates species richness and evenness of species abundance and is relatively independent of moderate variations in sample size (Magurran 1988). H' was calculated based on species importance values using the following equation: $H' = -(pi \ln pi)$, where pi is the proportion of importance of the *i*th species. Evenness was calculated as $E = H'/\ln S$. These values were calculated for all trees (<2.54 and ≥2.54 cm dbh) in each stand and, additionally, for just preharvest overstory trees and postharvest overstory trees in stands ≥12 yr old. Although canopy structure data were not collected in preharvest stands, we assumed that all trees ≥25.4 cm dbh would have been in the overstory. Preharvest H', E, and S could not be calculated for stand 10, because of missing inventory data.

We used a paired-sample *t*-test (Kent and Coker 1992, p. 131–133) to examine the stand-level differences in diversity, evenness, and richness for preharvest and the 2000 postharvest samples. Temporal trends for only postharvest densities, canopy structures, and species IV were examined by grouping stands into three similar age classes based on time since harvest: Class 1 = 2–6 yr, Class 2 = 12–16 yr, Class 3 = 22–26 yr.

Pre- and postharvest species importance values were contrasted using multiresponse permutation procedures (MRPP) and nonmetric multidimensional scaling (NMS) (McCune and Medford 1999). MRPP is a nonparametric multivariate test of differences between *a priori* groups (Mielke 1984) and NMS is an ordination technique especially suited for ecological applications (Clarke 1993). NMS, and other ordination techniques, reduce the number of response variables of complex multivariate data making interpretation feasible. Both MRPP and NMS were conducted using the Sofensen distance measure. NMS is an iterative procedure and was conducted using 60 runs of real data along with 50 runs of randomized data (a maximum of 200 iterations for each run) for a Monte Carlo test of significance that similar results could have been achieved by chance alone ($P = 0.039$).

Following Monte Carlo testing, a three-dimensional solution was chosen for the final iterative ordination using the best ending point in the preliminary analysis as the starting point in the final run. We report the final stress of the ordination and coefficients of determination (R^2) for each ordination axis calculated as a proportion of the variation explained in the reduced matrix relative to that in the original matrix. Ecological community data sets often have final stress values between 10 and 20. Values in the lower half of this range indicate reliable solutions (McCune and Grace 2002, p. 132). Unlike other ordination techniques, axis order does not correlate to the relative importance of each axis. A secondary matrix of site and stand characteristics including aspect, slope, size of opening, age of opening (preharvest samples were given an age of 0), and H' were used to help interpret the ordination results. Aspect was transformed (transformed aspect = cosine (45 − aspect) + 1) and the resulting values ranged from 0 (southwest) to 2 (northeast) (Beers et al. 1966).

Results

Preharvest Species Composition and Canopy Structure

Twenty-five tree species were represented across all stands prior to clearcutting (Table 2). Stands averaged 280 (±15) trees ha^{-1} and 30.5 (±1.9) m^2ha^{-1} of basal area. Sugar maple, yellow-poplar, and American basswood (*Tilia*

Table 2. Preharvest tree species importance values for advance regeneration*, understory,† and overstory†.

	Advance regeneration seedlings (< 2.54 cm dbh) Importance value*			Understory saplings (≤ 2.54 to < 12.7 cm dbh) Importance value †			Overstory poles and sawtimber (≥ 12.7 cm dbh) Importance value †		
Species	1974–1978	1984–1988	1994–1998	1974–1978	1984–1988	1994–1998	1974–1978	1984–1988	1994–1998
Acer pensylvanicum	3.80	6.45	22.39	1.79	4.03	9.83	0.00	0.00	0.00
A. rubrum	1.09	0.81	8.96	1.62	0.00	1.19	3.49	1.54	0.79
A. saccharum	71.20	75.81	32.84	62.38	63.18	62.55	24.24	24.34	22.60
Amelanchier arborea	0.00	0.00	0.00	0.76	0.00	0.00	0.24	0.00	0.06
Betula alleghaniensis	0.00	0.00	0.00	0.52	0.00	0.00	2.90	1.22	4.62
B. lenta	1.63	0.00	2.99	2.83	0.00	0.00	2.83	3.95	1.28
Carpinus caroliniana	1.09	0.00	0.00	0.00	1.25	0.00	0.00	0.00	0.00
Carya spp.	1.09	0.00	0.00	0.00	0.00	0.00	2.90	3.03	9.41
Cornus florida	0.00	0.81	0.00	0.61	0.91	0.00	0.00	0.00	0.26
Fagus grandifolia	9.24	8.06	17.91	20.02	19.21	17.69	9.22	12.69	6.41
Fraxinus americana	1.63	0.81	4.48	0.00	0.00	0.00	2.42	2.66	3.05
Juglans cinerea	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.18
J. nigra	0.00	0.00	0.00	0.00	0.00	0.00	0.04	0.00	0.00
Liriodendron tulipifera	0.00	0.00	4.48	1.55	0.00	0.00	16.87	13.61	23.28
Magnolia acuminata	1.09	0.00	0.00	2.29	0.00	0.00	2.43	3.14	1.75
Ostrya virginiana	0.54	0.00	1.49	1.50	2.86	1.02	0.43	0.48	0.62
Prunus pensylvanica	0.00	0.00	0.00	0.00	0.00	0.00	0.07	0.00	0.00
P. serotina	4.89	0.00	1.49	0.00	0.00	0.00	3.97	1.60	1.38
Quercus alba	0.00	0.00	0.00	0.00	0.00	0.00	0.32	0.46	0.00
Q. prinus	0.00	0.00	0.00	0.00	0.00	0.00	0.90	1.07	0.10
Q. rubra	1.09	3.23	0.00	0.00	0.00	0.00	8.87	8.51	4.92
Robinia pseudo-acacia	0.00	0.00	0.00	0.88	0.00	0.00	1.02	5.11	0.00
Sassafras albidum	0.00	0.00	0.00	0.00	0.00	0.00	0.05	0.00	0.00
Tilia americana	1.63	2.42	2.99	3.24	6.56	7.71	14.15	14.26	13.53
Ulmus rubra	0.00	1.61	0.00	0.00	1.99	0.00	2.63	2.31	5.77

* Species importance value = number of trees per ha of a species/the total number of trees per ha of the stand.
† Species importance value = (species relative density + species relative basal area)/2.

americana L.) were the most important overstory constituents ≥12.7 cm dbh).

The most important species in the sapling size class were American beech and sugar maple. Sugar maple saplings exceeded 60% IV for all three measurement periods. In the more ephemeral seedling size-class, sugar maple also dominated with an average IV of 73% (±10%) during the 1974 and 1984 measurement periods. However, in 1994, sugar maple seedling IV declined to 33%, and striped maple (*Acer pennsylvanicum* L.) IV increased from 6% in 1984 to 22% in 1994.

Chronosequence of Postharvest Species Composition and Canopy Structure

Species Composition.—Of the 26 species regenerating after clearcutting (Table 3), yellow-poplar and sugar maple were the only species present in all 13 stands. In 2 to 6 yr old stands, 70% of the regeneration (based on importance values) was contained in four species: yellow-poplar (24%), sugar maple (19%), black birch (16%), and striped maple (11%). These young stands had highly variable stem densities averaging 49,148 (±8,885) trees ha^{-1}(Table 1). Alternate-leaf dogwood (*Cornus alternifolia* L.f.), chestnut oak (*Q. prinus* L.), sassafras (*Sassafras albidum* [Nutt.] Nees), and white oak (*Q. alba* L.) were present only in the 2 to 6 yr old stands (Table 3).

In stands ≥12 yr old, the most important species were yellow-poplar and sugar maple. Sugar maple had the highest relative density, ranging from 31% to 47%, and yellow-poplar had the highest relative basal area, ranging from 31% to 53% (Table 3). For stems ≥2.54 cm, the 12 to 16 yr old stands averaged 4,645 (±566) trees ha^{-1} and 15.59 (±0.74) $m^2\ ha^{-1}$ of basal area, and the 22 to 26 yr old stands averaged 1,907 (±192) trees ha^{-1} and 24.55 (±2.18) $m^2\ ha^{-1}$ of basal area.

Yellow-poplar exhibited a progressive increase in IV in older cohorts. Conversely, black birch, a species that also aggressively invades clearcuts, decreased in importance over time. Black birch IV averaged 14% in the youngest stands and decreased to 6% and 3% in 12 to 16 and 22 to 26 yr old stands, respectively (Table 3).

Canopy Structure.—Assessment of species' crown class distribution through time reflects the aforementioned patterns in species densities. Stands ≥12 yr old were dominated by yellow-poplar in all crown classes except overtopped (Table 4). Sugar maple had the highest IV in the overtopped crown class and understory. Black locust (*Robinia pseudoacacia* L.) had low overall overstory importance but was similar in importance to yellow-poplar in the dominant crown class. American basswood had an overstory IV around 10%, but it was more important as a codominant tree in 12 to 16 yr old stands and as an intermediate and overtopped tree in older stands. Black cherry had a similar overstory IV to sugar maple in the 22 to 26 yr old stands but was more evenly distributed throughout all crown classes.

The 2 to 6 yr old stands were still in the stand initiation stage (Oliver and Larson 1996) and had not yet developed stratified canopies. Stems in the smallest height class (<0.31 m tall) were dominated by sugar maple and yellow-poplar. Stems ≥0.31 m were primarily black birch, yellow-poplar, sugar maple, and striped maple (Table 4). Yellow-poplar, sugar maple, basswood, and striped maple

Table 3. Postharvest species importance value (IV), relative density* (RD) and relative basal area (RBA) for all trees in each age class.

	2–6-yr-old stands			12–16-yr-old stands			22–26-yr-old stands		
Species	IV	RD	RBA	IV	RD	RBA	IV	RD	RBA
Acer pensylvanicum	11.00	3.68	18.32	2.43	2.81	2.05	10.19	19.88	0.51
A. rubrum	1.56	3.11	0.00	0.57	0.78	0.36	0.00	0.00	0.00
A. saccharum	19.35	25.49	13.20	20.47	30.79	10.15	26.02	46.71	5.32
Aralia spinosa	4.88	2.47	7.29	3.55	2.75	4.35	0.00	0.00	0.00
Betula alleghaniensis	0.00	0.00	0.00	0.52	0.64	0.39	0.88	0.80	0.97
B. lenta	15.65	22.84	8.46	6.22	6.94	5.51	2.29	0.94	3.64
Carpinus caroliniana	0.00	0.00	0.00	0.00	0.00	0.00	0.08	0.08	0.09
Carya spp.	0.21	0.43	0.00	0.55	0.87	0.23	1.23	1.16	1.30
Cornus alternifolia	0.05	0.10	0.00	0.00	0.00	0.00	0.00	0.00	0.00
C. florida	0.15	0.30	0.00	0.10	0.12	0.08	0.28	0.55	0.00
Fagus grandifolia	3.44	4.14	2.75	3.11	3.06	3.15	0.54	0.71	0.37
Fraxinus americana	1.36	2.72	0.00	9.60	16.61	2.58	4.49	5.51	3.46
Juglans cinerea	0.00	0.00	0.00	0.00	0.00	0.00	0.26	0.05	0.47
Liriodendron tulipifera	23.50	22.17	24.82	22.21	13.84	30.57	29.90	7.34	52.46
Magnolia acuminata	0.42	0.85	0.00	1.41	1.38	1.44	1.69	3.22	0.15
Ostrya virginiana	0.02	0.05	0.00	0.05	0.05	0.05	0.00	0.00	0.00
Prunus pensylvanica	0.63	0.23	1.02	0.99	0.13	1.86	1.07	0.16	1.99
P. serotina	1.44	2.88	0.00	0.94	1.76	0.12	8.64	2.12	15.15
Quercus alba	0.02	0.05	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Q. prinus	0.02	0.05	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Q. rubra	2.77	5.54	0.00	0.00	0.00	0.00	3.48	6.94	0.01
Rhus typhina	0.00	0.00	0.00	0.36	0.08	0.64	0.00	0.00	0.00
Robinia pseudo-acacia	3.40	0.75	6.04	10.76	3.32	18.20	1.14	0.17	2.10
Sassafras albidum	0.42	0.83	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Tilia americana	7.39	1.13	13.65	7.43	4.25	10.60	5.65	2.74	8.57
Ulmus rubra	2.33	0.21	4.45	8.75	9.82	7.67	2.18	0.93	3.42

* Includes seedlings.

Table 4. Postharvest tree species importance values for each age class, crown class*, and canopy strata†. Importance values for trees <2.54 cm dbh are determined from species relative densities and for trees ≥ 2.54 cm dbh from relative density + relative basal area. Overstory trees are those found in the upper continuous canopy and understory trees are stems ≥ 2.54 cm dbh with crowns ≥ 3m below the overstory.

	2–6 yr seedling heights (m)			12–16 yr crown classes/strata							22–26 yr crown classes/strata						
Species	<0.31	≥ 0.31–<1.37	≥ 1.37	D	CD	I	OT	OS	US	Seedlings	D	CD	I	OT	OS	US	Seedlings
Acer pensylvanicum	1.2	3.1	13.3	0.0	1.4	6.0	7.3	3.6	0.0	1.2	0.0	1.1	1.9	1.2	1.2	0.0	25.2
Acer rubrum	5.7	2.3	0.2	0.0	0.7	0.0	0.0	0.3	0.0	1.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0
A. saccharum	35.1	20.9	15.5	0.0	9.6	17.0	25.8	14.4	51.1	39.0	0.0	1.6	5.9	34.3	13.2	37.9	51.6
Aralia spinosa	0.7	3.1	5.6	2.9	5.1	7.9	6.5	5.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Betula alleghaniensis	0.0	0.0	0.0	0.0	0.4	0.0	1.4	0.6	0.0	0.6	0.0	0.2	3.9	0.0	0.5	9.7	0.0
B. lenta	9.1	25.5	24.4	2.8	8.1	12.7	5.9	7.5	0.0	5.2	0.0	5.0	10.3	3.6	5.0	0.0	0.0
Carpinus caroliniana	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.5	0.0
Carya spp.	0.2	1.0	0.0	0.0	0.4	0.0	0.5	0.3	0.0	1.2	0.0	2.6	1.3	2.8	2.4	1.0	0.7
Cornus alternifolia	0.0	0.1	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
C. florida	0.3	0.5	0.0	0.0	0.0	0.0	0.6	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.7
Fagus grandifolia	4.0	5.9	2.3	0.0	3.3	7.0	8.8	5.3	7.3	0.0	0.0	0.0	0.0	0.4	0.1	8.1	0.0
Fraxinus americana	2.1	4.3	0.7	0.0	3.1	4.4	5.3	3.6	0.0	25.2	0.0	4.6	4.4	2.3	3.8	2.1	6.2
Juglans cinerea	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.9	0.0	0.4	0.0	0.0
Liriodendron tulipifera	30.7	17.2	20.3	30.3	29.7	26.3	18.4	26.4	0.0	8.1	45.4	54.4	35.5	26.9	43.4	17.6	2.1
Magnolia acuminata	0.8	1.2	0.3	1.2	1.7	0.0	0.0	1.0	0.0	2.0	0.0	0.2	0.0	0.3	0.2	0.0	4.1
Ostrya virginiana	0.0	0.1	0.0	0.0	0.0	0.0	0.3	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Prunus pensylvanica	0.1	0.0	0.9	7.2	0.4	0.0	0.0	1.1	0.0	0.0	0.0	2.2	0.0	0.0	1.4	0.6	0.0
P. serotina	2.8	4.0	0.6	0.0	0.3	0.0	0.0	0.1	0.0	2.9	13.7	14.6	7.9	12.8	13.0	8.6	0.0
Quercus alba	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Q. prinus	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Q. rubra	4.0	8.4	1.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.2	0.0	8.9
Rhus typhina	0.0	0.0	0.0	0.0	0.9	0.0	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Robinia pseudo-acacia	0.2	0.7	3.9	52.9	13.5	3.6	4.6	13.2	0.0	0.0	40.9	2.1	0.0	0.0	1.7	0.0	0.0
Sassafras albidum	0.7	1.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Tilia americana	2.3	0.5	7.0	2.7	13.6	4.7	6.7	9.2	15.3	1.7	0.0	7.8	19.2	14.9	10.9	4.9	0.6
Ulmus rubra	0.0	0.0	2.6	0.0	7.8	10.4	7.9	7.2	26.3	11.8	0.0	3.6	5.8	0.2	2.8	8.0	0.0

* D = dominant crown class; CD = codominant crown class; I = intermediate crown class; OT = overtopped crown class.
† OS = total overstory (all crown classes); US = understory; seedlings = stems < 2.54 cm dbh.

together had the highest density of stems ≥2.54 cm dbh and composed 70% of the basal area in these young stands (Table 3).

The chronosequence indicated a temporal pattern of species dominance changes. In stands 2–6 yr old, yellow-poplar had a 20% IV in the largest stems (≥1.37 m), increasing to a 26% overstory IV in 12 to 16 yr old stands. The highest yellow-poplar overstory IV was in stands 22 to 26 yr old, where it was 43%. Conversely, black birch had the opposite pattern. Black birch had the highest IV (24%), for stems ≥1.37 m in the youngest stands. In the overstory of stands 12 to 16 and 22 to 26 yr old, black birch IV was only 8% and 5%, respectively. Black birch primarily occupied an intermediate crown position in these older stands, whereas in the 2 to 6 yr old stands, it was one of the most dominant species (Table 4).

Comparison of Preharvest and Postharvest Species Composition and Canopy Structure

In paired sample *t*-tests, H' declined significantly after harvest from 2.066 to 1.820 ($0.005 > P > 0.001$). H' declined because E declined significantly from 0.799 to 0.713 ($0.005 > P > 0.001$), while S did not change significantly ($0.20 > P > 0.10$). Mean S was 13.833 (±0.983) before harvest and 13.167 (±0.960) after harvest (Table 1). Similar to stand-level diversity measures, mean overstory H' of stands ≥ 12 yr old significantly decreased ($0.025 > P > 0.01$) from 2.024 to1.660 after clearcutting because E also significantly decreased ($0.025 > P > 0.01$) from 0.825 to 0.686. Mean overstory S was not significantly less ($0.25 > P > 0.10$) than prior to clearcutting.

In addition to changes in diversity, species composition in the clearcut strips 2 to 26 yr after harvesting differed significantly from the preharvest conditions (MRPP: $P < 0.001$). Average distance of the preharvest group was 0.383 and increased to 0.548 after harvesting, indicating greater heterogeneity among clearcut strips after disturbance. These results were corroborated by the NMS ordination of species composition (Figure 1). The final stress for the three-dimensional solution was 12.8. Preharvest strips clustered along axis 2 and 3 of the final three-dimensional solution while postharvest stands exhibited greater variability. The proportion of variance explained for each ordination axis was 21% for axis 2 and an additional 50% for axis 3 (axis 1 R^2 = 12.3%; cumulative R^2 = 83.2%). When assessed from a secondary matrix, axis 2 was positively correlated with H' ($r = 0.624$) and negatively correlated with the number of years since harvesting ($r = -0.542$) (Figure 1). Axis 1 also was correlated with H' ($r = 0.443$) but showed little correlation to stand age ($r = 0.108$). Interpretation of axis 2 suggests that the older clearcut stands were less diverse than either the younger clearcut stands or the preharvest stands. In addition, the ordination illustrates that the change in composition among stands, sometimes referred to as beta diversity, increased after clearcutting. In other words, stands were less similar to each other and less diverse internally after harvesting than

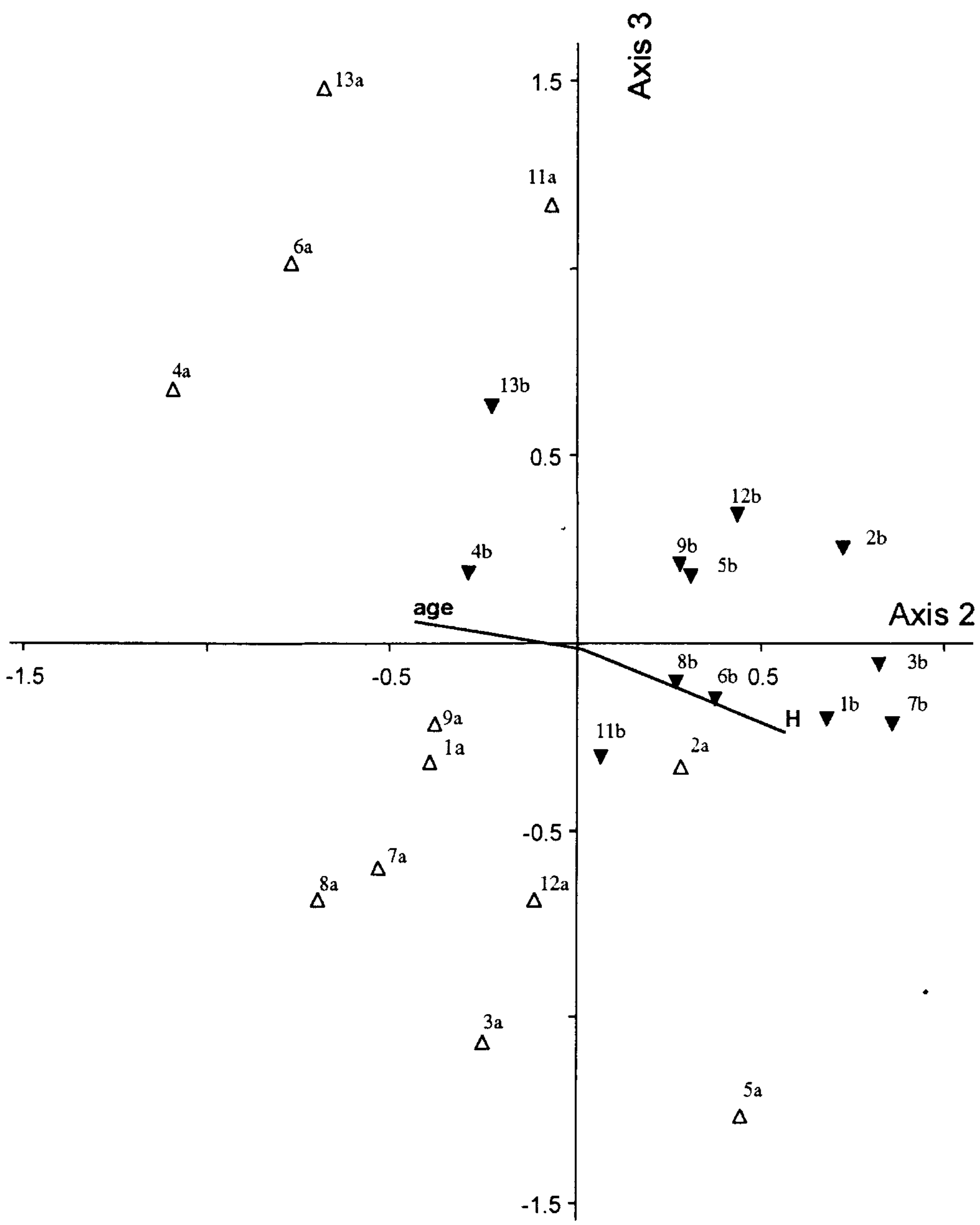

Figure 1. Nonmetric multidimensional scaling ordination of clearcut stands before (filled symbols) and after (open symbols) harvesting. Points are identified by clearcut designation. The correlation of the Shannon-Weiner Diversity Index (*H'*) and number of years since harvesting (age) with the ordination axes are represented by vectors.

before. As expected, the final ordination had little correlation with aspect, slope, or size of opening when evaluated from a secondary matrix.

The ordination provided additional insight into the effects of clearcutting on species composition. NMS axis 2 scores were most positively correlated with the IV of northern red oak ($r = 0.703$) and most negatively correlated with yellow-poplar IV ($r = -0.678$). Axis 3 was most positively correlated with importance of yellow-poplar ($r = 0.759$) and negatively correlated with sugar maple ($r = -0.556$) and black birch ($r = -0.574$), which indicated that not all postharvest stands were equally dominated by yellow-poplar and stands with high yellow-poplar importance had low sugar maple and black birch importance. In general, species associated with major disturbances were negatively correlated with axis 2 [e.g., black locust, pin cherry (*P. pensylvanica* L.f.), sumac (*Rhus typhina* L.), and yellow-poplar]. Shade intolerant black cherry was the exception and had a positive correlation with axis 2. However, all stands had low or no preharvest black cherry importance (Table 2), and only one of the oldest stands had postharvest cherry IV that exceeded 10%. Heavy seeded species (i.e., oaks, hickories, and American beech) were positively correlated with axis 2 and declined temporally following the harvest operations (Figures 1 and 2).

Discussion

After clearcutting, Appalachian hardwood stand development follows the single-cohort mixed-species model (Oliver and Larson 1996) where species assemble in various canopy strata according to their silvical characteristics. There are

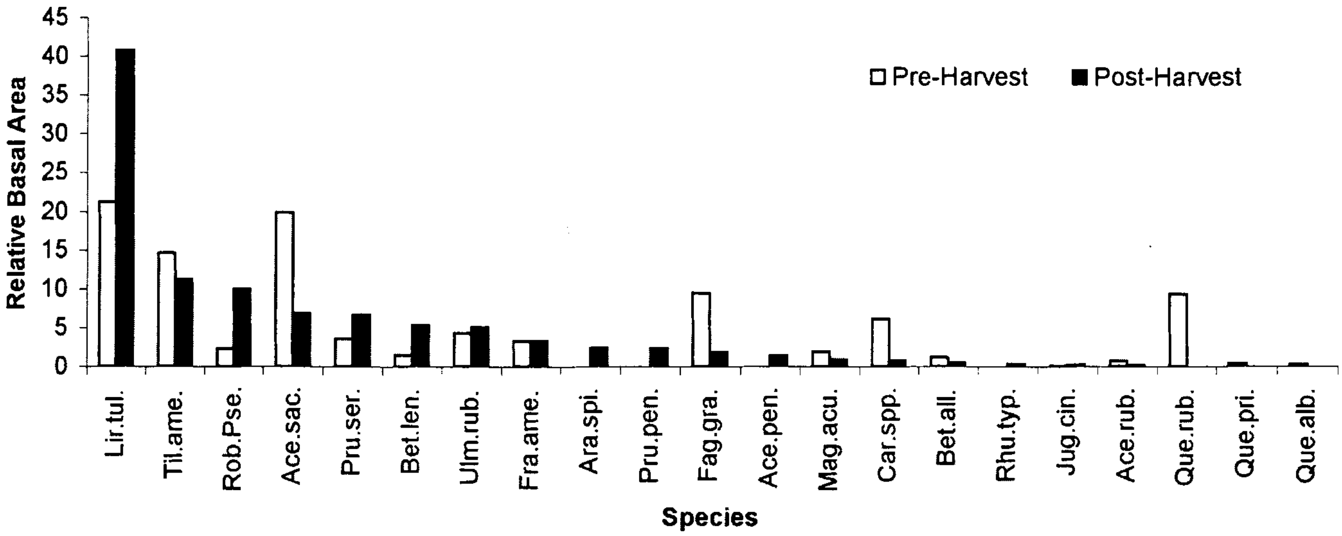

Figure 2. Changes in overstory species relative basal areas between preharvest stands and postharvest stands ≥12 yr old.

numerous factors that influence the establishment and subsequent development of tree regeneration after clearcutting. These include seedbed conditions, propagule supply, lighting, interfering plants, deer browsing, small mammal predation, insects and diseases, incidence and severity of fires, and site quality limitations. Species capable of prolific seed production followed by rapid germination, and/or high sprouting ability are likely to be most competitive. Yellow-poplar produces abundant seed almost annually, and seeds can remain viable in the forest floor for 3–5 yr (Beck 1990), whereas oaks produce bumper crops as infrequently as every 10 yr, and forest floor seed storage does not exceed the first winter (Sander 1990). Because of their high shade tolerance, sugar maple and striped maple tend to regenerate most effectively via a seedling bank strategy (Godman et al. 1990). Forest floor disturbance is also beneficial to germination of black birch and yellow-poplar (Beck 1990, Lamson 1990).

In our study, postharvest stands were less similar to each other than their preharvest condition partly because of the rapid changes in species composition common during early stand development. Species such as pin cherry (Marks 1974), black locust (Huntly 1990), and black birch display rapid early height growth, express early dominance, then die or regress to lower canopy strata. Black locust's height growth rates decrease rapidly after 30 yr, and it is highly susceptible to a variety of insects and diseases (Huntly 1990). Black birch can retain an overstory presence (up to 15% of basal area) primarily as intermediate and overtopped trees for over 80 yr (Oliver 1978, Ward and Stephens 1996). In our study, black birch had already been reduced to an intermediate crown position in the oldest cohort. Yellow-poplar also displays rapid early height growth (Beck 1990) that continues as the canopy stratifies. Alternatively, American basswood has been able to maintain its overstory component primarily because it grows rapidly from sprouts (Crow 1990). Eighty-nine percent of the American basswood stems in the overstory were of sprout origin. In time, we suspect that the variation in composition among the new stands will decline as yellow-poplar overstory dominance is anticipated in all stands by the third or fourth decade of stand development.

The maintenance of *S* while *H'* declined can be explained by a reduction in *E*. *S* was maintained because new species not present before clearcutting replaced some species that did not regenerate after clearcutting. Long-lived species such as northern red oak and chestnut oak were not found in four stands where they occurred prior to clearcutting. Species such as pin cherry, black birch, black locust, and Hercules' club (*Aralia spinosa* L.) aggressively colonized all stands where they had little or no preharvest presence. Butternut (*Juglans cinerea* L.) and flowering dogwood (*Cornus florida* L.) are currently rare and may succumb to species-specific pathogens. Staghorn sumac is a shrub species and cannot persist in the understory of a closed canopy forest. Similar species shifts have been noted in other eastern hardwood stands after clearcutting (Beck and Hooper 1986, Hix and Lorimer 1991, Wang and Nyland 1993, Elliott and Swank 1994, Arthur et al. 1997, Elliott et al. 1997). As these stands progress through the stem exclusion stage, *S* may also decline as short-lived and rare species die and are replaced by species already present. Once yellow-poplar has expressed dominance in the overstory of a stand, it will continue rapid height growth at least until age 30 (Beck 1990) or up to age 50 on high quality sites (Doolittle 1958), such as those of our study. Because yellow-poplar can maintain canopy dominance for up to 300 yr (Beck 1990), shade-tolerant species will attain canopy dominance at a rate functionally related to future canopy disturbances that result in yellow-poplar mortality.

Other studies of early stand development after clearcutting have suggested that advance regeneration of sugar maple may interfere with the early height growth of shade-intolerant species (Trimble 1972, Trimble 1973) and then achieve a strong presence in the overstory (Marquis 1981, Guldin and Lorimer 1985, Hix and Lorimer 1991, Wang and Nyland 1993). In our study, sugar maple comprised the majority of the seedling/sapling advanced regeneration. However, regardless of sugar maple's presence, yellow-poplar and black birch seedlings had the highest importance of the tallest stems and were expressing canopy dominance in the youngest stands. Marquis (1981), found that if silvicultural clearcutting of second generation stands removed large (>2.54 cm) sugar maple and American beech saplings, then the third generation stands showed reduced tree species diversity due to the dominance of black cherry. However, when sugar maple and American beech saplings >4 cm dbh were retained during clearcutting, these shade-tolerant species became important overstory components. Our study supports these findings to some extent. Sugar maple advance regeneration was probably not large enough to compete with yellow-poplar and attain codominant status in the overstory because all trees >2.54 cm dbh had been removed by the harvest. Hence, sugar maple will decrease in overstory importance, but will remain a major stand component due to high shade tolerance and longevity (Godman et al. 1990).

About 10% of the preharvest overstory was composed of northern red oak, but in stands >12 yr old, it was nearly absent. The decreased representation of oak in young stands after harvesting second-generation forests is a widespread problem in eastern hardwood forests (Brose et al. 2001). In the early 20th century, oak was able to compete following what were essentially clearcuts (Schuler and Fajvan 1999). It is a common hypothesis that fire exclusion during the past century is partially responsible for this functional change of oak in response to disturbance (Abrams 1992). Our results indicate that red oak did regenerate following overstory removal but was not able to compete with more aggressive species early in stem exclusion (Beck and Hooper 1986, Tift and Fajvan 1999). In 2 to 6 yr old stands, northern red oak had over 8% of the stems in the middle size class (0.31 m to 1.37 m tall) and 4% of the tallest stems (≥1.37 m). A postharvest prescribed fire within 6 yr after harvest may have partially released oak from fast-growing fire-sensitive species, such as yellow-poplar, that eventually dominated our sites (Brose et al. 1999).

Another contributing factor to the decrease in red oak importance and the increase in striped maple importance could be selective browsing by white-tailed deer (*Odocoileus virginianus*). Deer affect vegetation abundance and horizontal structure as well as height development (Russell et al. 2001). Deer favor species such as red oak, whereas striped maple is considered "browse resilient" (Horsely and Marquis 1983). A decline in oaks and other hard-mast-bearing species also has important implications for wildlife, especially since the virtual extirpation of American chestnut in the early 1900s (Brooks 1911, Weitzman 1949). Oaks provide an important winter food source for numerous wildlife game species, small mammals, and nongame birds (e.g., Bendell 1959, Wentworth et al. 1992, Wolff 1996, McShea 2000).

Our results illustrate that in young, mixed-species stands with stratified canopies, examination of species importance by canopy position gives a stronger indication of future overstory dominance than overall importance. For example, in the oldest stands, sugar maple's overall importance (OS and US combined) is 26%, decreasing to 13% for the overstory, and <1% for dominant and codominant crown classes. Yellow-poplar's overall importance in (OS and US) is 30%, whereas yellow-poplar's IV in the dominant and codominant crown classes are 50% and 43%, respectively. The canopy importance of each species, combined with knowledge of silvical and site characteristics, can be used to better predict the future development of young stands.

Conclusion

Silvicultural clearcutting favored the rapid, early height growth of shade-intolerant species and caused a shift in species composition early in stand development. These shifts were most evident when species composition and canopy stratification information were combined. Postharvest stands will continue to be less diverse than preharvest forest until yellow-poplar dominance is reduced from natural mortality or exogenous disturbance. Some shade-tolerant species are capable of persisting in the understory until canopy gaps permit attainment of overstory status. Other important species, such as red oak and black cherry, will not recover, and woody species diversity will be less in the third-generation forest as stand development proceeds. Additional silvicultural steps are needed to maintain diverse stands that include species with high economic value and ecological significance. At minimum, we recommend that silvicultural clearcutting be modified to retain large, desirable advance regeneration in order to give some species a better competitive position in postharvest stands. In addition, postharvest cleanings could be conducted early in stem exclusion to release stems of underrepresented species from more aggressive competitors (Schuler and Miller 1999).

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