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Forest Ecology and Management 224 (2006) 241–251
Forest Ecology and Management
www.elsevier.com/locate/foreco

Influence of individual reserve trees on nearby reproduction in two-aged Appalachian hardwood stands

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Abstract

In the 1970s, public opposition to clearcut harvesting in hardwood forests of the eastern United States led forest managers and scientists to consider alternative practices that retain a low-density overstory forest cover. From 1979 to 1984, a form of clearcut-with-reserves harvesting was applied in 80-year-old Appalachian mixed-hardwoods to create four experimental stands with two-aged structures. The residual stand basal area averaged 5.3 m^2/ha, comprising an average of 36 reserve trees/ha. The reserve trees were evenly distributed throughout the stand, initially with considerable space between their crowns, thus providing the sunlight and seedbed conditions needed to recruit desirable shade-intolerant reproduction after harvest. This study examined the response of the 100-year-old reserve trees and the development of the 20-year-old natural reproduction located in their immediate vicinity.

Diameter at breast height (Dbh), height, and relative position were recorded for all reproduction $\geq$2.5 cm within transects adjacent to northern red oak (*Quercus rubra* L.) and yellow-poplar (*Liriodendron tulipifera* L.) reserve trees. Each transect was divided into five zones, which represented positions relative to the reserve tree crown edge, and basal area was computed for each of three shade tolerance classes within each zone. A repeated measures ANOVA was used to compare basal area of reproduction by tolerance classes and zone. In general, basal area of reproduction, particularly that of shade-intolerant species, increased with distance from the reserve tree. Regression analyses also indicated that dbh and height of reproduction was positively related to distance from the reserve trees. Although height growth of reserve trees was similar for both species, northern red oak exhibited significantly greater dbh and crown radial growth than yellow-poplar.

The results indicated that reserve trees influence the growth rate and species composition of reproduction in their immediate vicinity. Basal area of reproduction increased from 10.1 to 17.7 m^2/ha with increasing distance from the reserve trees. Basal area of intolerant species more than doubled along the same gradient. Basal area of reproduction in the two-age stands was 30–40% less than that observed in even-aged stands on similar growing sites, but the reduction was offset by growth of the reserve trees. The surface area covered by the reserve tree crowns increased approximately 88% for northern red oak and 44% for yellow-poplar. Since the sphere of influence of reserve trees increases over time, forest managers must consider their long-term impact on reproduction when prescribing clearcut-with-reserves harvests and other practices that involve retaining trees for many years.

Keywords: Appalachian hardwoods; Continuous cover forestry; Two-age management; Reserve trees; Reproduction; Shade tolerance; Influence circle; Competition zones; Response gradient

1. Introduction

As forest management objectives become increasingly complex, innovations in harvest practices are needed to sustain the production of numerous desired outputs. An example of this process in Appalachian hardwood forests was the expanded use of clearcut harvests in the 1960s to increase regeneration of shade-intolerant species in even-aged stands, and the subsequent application of clearcut-with-reserves harvests in the 1980s to improve esthetics and vertical structure in two-aged stands. With each innovation, forest managers need additional information on stand development so that harvest prescriptions can be adjusted to meet long-term management objectives. Smith et al. (1989) installed experimental applications of a clearcut-with-reserves harvest in Appalachian hardwood stands to study the impacts of a low-density overstory forest cover. Over 20 years have elapsed, and there is now an opportunity to evaluate the effect of the reserve trees on nearby reproduction.

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0378-1127/$ – see front matter
doi:10.1016/j.foreco.2005.12.035

The production of woodland benefits is closely tied to species composition within a forest, thus harvesting disturbances should be planned to provide for successful recruitment of desired species. During the mid to latter part of the 1900s, the most common harvest practice in the region was market-based, diameter-limit cutting which left 40–60% of the initial stand in place (Trimble, 1971). Research indicated that repeated single-tree selection and diameter-limit harvests, practices that leave much of the canopy intact, promoted a gradual shift in species composition toward shade-tolerant species and a general loss of species diversity (Trimble, 1973). Partial harvest practices result in relatively small canopy gaps, which tend to favor recruitment of shade-tolerant species over time. Runkle (1990) noted that woody regeneration increased in density for 5–10 years after canopy gaps formed, followed by decreases in density as the gaps closed. The successful recruitment of various species was related to gap size, whereby intolerant and mid-tolerant species exhibited optimal response in large gaps, and tolerant species dominated small gaps.

A key justification for clearcut harvesting was that complete removal of the overstory and understory strata in relatively large gaps provided suitable sunlight and seedbed conditions for all woody reproduction, including desirable shade-intolerant species, to compete successfully in the new stand (Trimble, 1973). The open conditions after harvest allowed a diverse mix of hardwood species, valuable for both wildlife and timber, to develop from stored seed, advanced seedlings, and sprouts. Unlike the shift to tolerant species that followed partial harvesting practices, this response allowed forest managers to achieve the critical management objectives of regenerating shade-intolerant species and maintaining species diversity. In addition, clearcut harvesting resulted in new even-aged stands that allowed forest planners to manage mosaics of stands and balance the age distribution of large industrial and public forests. In the 1960s, clearcut harvesting was emerging as an alternative to partial harvesting practices because it was a more effective way to meet regeneration objectives within the biological constraints of the hardwood forest.

Along the way, public opposition to the initial appearance of clearcut harvests led forest managers and scientists to consider alternative practices that would sustain desirable species composition and maintain a somewhat continuous forest cover. In the late 1970s personnel with the Monongahela National Forest and Northeastern Research Station formed a partnership to study the effects of two-aged stand structures (Miller et al., 1997b). Both parties reasoned that retaining a few reserve trees/ha after harvest operations would still result in desirable reproduction but would be less disruptive to vertical structure, wildlife habitat, and esthetic quality compared to complete overstory removal.

From 1979 to 1984, a form of clearcut-with-reserves harvesting was applied in 80-year-old Appalachian mixed-hardwoods to create four experimental stands with two-aged structures. The residual stand basal area averaged 5.3 m^2/ha, comprising an average of 36 residual trees/ha. The reserve trees were evenly distributed throughout the stand, initially with considerable space between their crowns, thus providing the environmental conditions needed to recruit desirable shade-intolerant reproduction after harvest. Several previous reports on the experimental two-aged stands documented the initial response of the reserve trees (Smith and Miller, 1991; Smith et al., 1994; Miller, 1996) and the early development of reproduction (Miller and Schuler, 1995; Miller et al., 1997a). Preliminary information on reproduction and reserve tree quality was summarized from 20 two-aged stands on the Monongahela National Forest 2–5 years after clearcut-with-reserves harvests (Johnson et al., 1998). Duguay et al. (2000) studied the impact of a two-aged stand structure on insect and songbird habitat, but the overall impact of reserve trees on early succession habitat needs further evaluation.

As the experimental two-aged stands continue to develop, several key silvicultural questions remain. The objective of this study was to answer several exploratory questions about individual reserve trees and how they affect nearby reproduction: (a) how fast do the reserve trees grow over time? (b) How do the reserve trees influence the diameter at breast height (dbh) and height growth of reproduction? (c) How do the reserve trees influence the distribution and species composition of reproduction in their immediate vicinity? This study examined the response of the 100-year-old reserve trees and the growth, composition, and distribution of the approximately 20-year-old natural reproduction located in their immediate vicinity. Although the results presented here are relatively limited in scope, they shed light on important issues that forest managers need to consider when promoting two-aged stand structures and other continuous cover management systems in hardwood forests.

2. Study sites

Three stands are located on the Monongahela National Forest and one stand is located on the Fernow Experimental Forest in north-central West Virginia. Stand area ranged from 4 to 6 ha, northern red oak site index ranged from 21 to 24 (base age 50 years), and elevation ranged from 600 to 900 m. Soil depth to bedrock is typically 1 m or less, and annual precipitation averages 150 cm distributed evenly throughout the year. The soils are similar among the four stands, generally described as acidic, sandy-loam Inceptisols, with >60% sand, 10–15% clay, and 20–25% silt, underlain with fractured sandstone and shale. The soil series for the stands were described as follows: Stand 1 (Berks channery silt loam), Stand 2 (Calvin channery silt loam), Stand 3 (Berks channery silt loam), and Stand 4 (Dekalb stony loam), all characteristic of loamy-skeletal, mixed, mesic Typic Dystrochrepts (Soil Conservation Service, 1967, 1982).

Before the clearcut-with-reserves harvests, the four stands contained approximately 80-year-old, second-growth Appalachian hardwoods. These stands regenerated after heavy commercial harvests in the early 1900s, and several important factors influenced their early development. Unlike current conditions, periodic wildfires were common throughout the region from 1910 to 1930, browsing by whitetail deer (*Odocoileus virginianus* Boddaert) was not a limiting factor

(DeGarmo and Gill, 1958), and American chestnut (*Castanea dentata* Marsh.) was a significant component of forests in the region (Brooks, 1911). Later, the chestnut blight fungus (*Cryphonectria parasitica* (Murr.) Bar) caused significant mortality during the 1920s, thus reducing stocking in the young, second-growth stands. No other major disturbances occurred in these stands until the clearcut-with-reserves harvests were applied to begin studying the two-aged management system.

3. Methods

From 1979 to 1984, a clearcut-with-reserves harvest (Smith et al., 1989) was applied to four stands to remove merchantable products, regenerate a new age class of trees, and promote the development of a two-aged stand structure. The reserve trees were selected with preference for dominant and codominant, high-quality northern red oak (*Quercus rubra* L.) and yellow-poplar (*Liriodendron tulipifera* L.). A few other species including black cherry (*Prunus serotina* Ehrh.), white oak (*Q. alba* L.), chestnut oak (Q. *prinus* L.), and American basswood (*Tilia americana* L.) were retained to achieve somewhat uniform spacing. Residual stand density guidelines called for leaving 35–50 reserve trees/ha such that residual basal area did not exceed 7 m^2/ha. In general, reserve trees were spaced approximately 15 m apart to provide abundant sunlight for natural reproduction of hardwood species from all shade tolerance classes. During the commercial logging operations, all trees $\geq$2.5 cm dbh other than the reserve trees were cut. The boles of merchantable trees $\geq$12.7 cm dbh were removed, while their tops and all non-merchantable cut-trees were left on the site. The reserve trees were tagged for long-term monitoring. Dbh, total height, and crown radius were measured immediately after the logging operations. Crown radius was measured from the tree bole to a vertical projection of the crown edge along the four cardinal directions.

Stand-wide reproduction data were obtained before logging from 170 permanent sample points located along systematic grids throughout the four stands. Small reproduction, defined as woody stems $\geq$30 cm tall and <2.5 cm dbh, was tallied on 4 m^2 circular plots. Large reproduction, defined as woody stems $\geq$2.5 cm dbh, was tallied on 40 m^2 circular plots using the same center points. These plots provided a general inventory of stem counts and sizes of reproduction over time, but they did not indicate how reserve trees affected the growth and distribution of reproduction in their immediate vicinity.

Additional reproduction data were collected in 2001 and 2003 to assess the impact of individual reserve trees on nearby reproduction. The data were collected under and adjacent to the crowns of 6–8 randomly selected northern red oak and yellow-poplar reserve trees in each stand. These species were chosen because they represented distinct shade tolerance classes and were evenly distributed and relatively abundant on all four stands. Species, dbh, crown class, height, and distance to reserve tree crown edge were recorded for all reproduction $\geq$2.5 cm dbh within transects

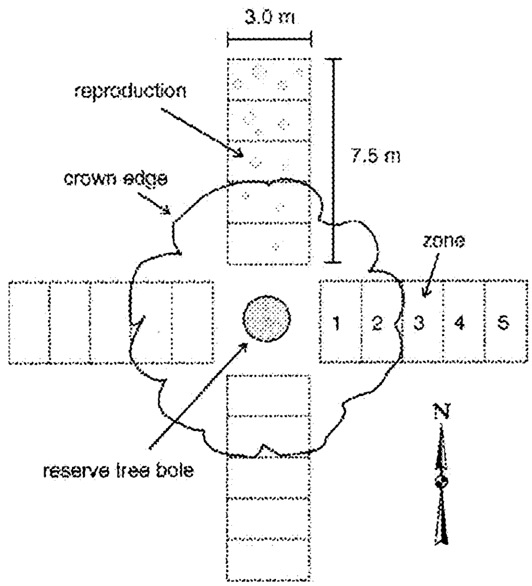

Fig. 1. Schematic of transects used to collect reproduction data under and adjacent to reserve trees.

aligned along the four cardinal directions from each reserve tree. The transects were 3.0 m wide and 7.5 m long, with a 3.0-m section located under the crown and a 4.5-m section located beyond the crown edge (Fig. 1). In addition, reserve tree dbh, height, and crown radius along each transect also were recorded to compare with original measurements. Crown class of the reproduction was based on the status of each tree relative to neighboring trees of the same age, without regard for the reserve trees (Smith, 1986). The relative position of each reproduction tree was defined as the positive or negative distance to reserve tree crown edge within each transect. Note that trees with relative position <0 were located under the reserve tree crown, while trees with relative position >0 were located beyond the edge of the reserve tree crown.

In addition, each transect was divided into five equal zones, each zone measuring 1.5 m $\times$ 3.0 m (Fig. 1). The zones provided a basis for assessing basal area/ha and species distribution of reproduction in relation to the edge of the reserve tree crown edge. Zones 1 and 2 were located under the crown, and zones 3, 4 and 5 were located beyond the crown edge in increasing order. The midpoints of the zones were −2.25, −0.75, 0.75, 2.25, and 3.75 m from the reserve tree crown edge for zones 1–5, respectively. For reproduction within each zone, basal area/ha was computed for each of three species groups according to shade tolerance defined by Trimble (1975). For example, intolerant species included yellow-poplar and black cherry; mid-tolerant species included northern red oak, white oak, chestnut oak, white ash (*Fraxinus americana* L.), and sweet birch (*Betula lenta* L.); tolerant species included American beech (*Fagus grandifolia* Ehrh.), red maple (*Acer rubrum* L.), sugar maple (*A. saccharum* Marsh.), and American basswood (Trimble, 1975). Sweet birch has been described as both intolerant (Lamson, 1990) and mid-tolerant (Trimble, 1975), but its relative competitiveness in canopy gaps suggests it is more characteristic of the mid-tolerant species (McClure and Lee, 1993; Ward and Stephens, 1996; Fownes and Harrington, 2004).

4. Analyses

The reserve tree data were analyzed to compare dbh, height, and crown radius growth between two reserve tree species for approximately 20 years after the clearcut-with-reserves harvest. The reproduction data were analyzed to determine if dbh, total height, and basal area/ha of reproduction by species group were related to distance from the reserve trees. For reserve trees and reproduction, the data relating to dbh, height, crown radius, and basal area were scaled to annual measurements to account for slight differences in the number of growing seasons that elapsed between harvest operations and the year in which data were collected in each stand.

The analysis of variance (ANOVA) procedure (SYSTAT, 2004) was used to compare dbh, height, and crown radial growth between 29 northern red oak and 24 yellow-poplar reserve trees in four stands. The model included the following terms (and degrees of freedom): reserve tree species (1), stand (3), and reserve tree species by stand interaction (3) and error (45). Normality and homogeneity of variances were examined using graphical analysis and the Levene test, respectively, and transformations were not necessary as data conformed to model assumptions. The initial analyses included post-harvest dbh, height, or crown radius as covariates to improve precision. The covariates were not significant, so they were excluded from subsequent analyses.

The general linear model (GLM) regression procedure (SYSTAT, 2004) was used to relate dbh and height of 317 dominant and codominant reproduction trees to their position relative to the reserve tree crown edge. The model included the following terms (and degrees of freedom): relative position (1), reserve tree species (1), stand (3), tolerance (2), relative position by reserve tree species interaction (1), relative position by stand interaction (3), relative position by tolerance interaction (2), and error (303). Dummy variables for the categorical effects of reserve tree species, stand, and tolerance were included in the regression analyses to test the assumption of common slopes. Log transformed values of the annual growth and relative position variables were used to achieve normality and homogeneity of variance.

A repeated measures GLM procedure (SYSTAT, 2004) was used to compare annual basal area/ha of reproduction by tolerance and zone. A total of 158 transects served as subjects, and the class variables included two reserve tree species, four stands, and four cardinal directions. The model included the following terms (and degrees of freedom): reserve tree species (1), stand (3), cardinal direction (3), and error (15) between subjects, and zone (14), zone by reserve tree species (14), zone by stand (42), zone by cardinal direction (42) and error (2100) within subjects. Log transformed values were used to achieve normality, and the compound symmetry assumption was feasible.

Table 1
Summary of stand characteristics before and after clearcut-with-reserves harvests in four Appalachian hardwood stands

Stand	Inventory	Density (stems/ha)	Basal area (m^2/ha)	Mean dbh (cm)	Volume (m^3/ha)
1	Initial	467	29.6	39	111
	Residual	31	4.0	42	23
2	Initial	299	29.7	43	177
	Residual	35	5.7	46	42
3	Initial	430	26.6	39	122
	Residual	32	4.7	43	33
4	Initial	459	41.1	39	233
	Residual	46	6.7	43	48
All	Initial	414	31.8	40	161
	Residual	36	5.3	44	36

Stand density and basal area include all trees ≥12.7 cm dbh. Mean dbh and volume include all trees ≥27.9 cm dbh.

5. Results

Pre-harvest inventories of the four stands indicated that they were fully stocked and contained significant volumes of merchantable sawtimber. Initial basal area ranged from 27 to 41 m^2/ha in trees ≥12.7 cm dbh, with an additional 1–2 m^2/ha in trees 2.5–12.6 cm dbh (Table 1). The overstory contained an average of 200 trees/ha ≥27.9 cm dbh and 214 trees/ha 12.7–27.8 cm dbh. The average size of sawtimber trees ranged from 39 to 43 cm dbh in the four stands. In general, yellow-poplar and northern red oak occupied most of the initial overstory, although black cherry, white oak, sugar maple, and American beech also occupied significant proportions of the overstory in individual stands (Table 2). For example, Stand 4 was 28% black cherry, a species noted for its relatively small crown, which resulted in a relatively high basal area in that stand compared to the others. The variability in species composition across the four stands is typical of hardwood stands that began after heavy commercial logging in the early 1900s (Trimble, 1973). Sugar maple, American beech, white ash, and northern red oak were the most abundant species in the pool of advanced reproduction before the clearcut-with-reserves harvests, although each stand had over 20 species of advanced reproduction in the pre-harvest inventory (Table 3).

Basal area in the residual stands averaged 5.3 m^2/ha, which included 36 trees/ha with an average dbh of 44 cm (Table 1). The residual stand accounted for an average of 23% of the initial stand merchantable volume. The reserve trees were among the most vigorous and valuable trees before the harvest, thus the reserve trees accounted for a relatively high proportion of the initial stand value. The composition of reserve trees averaged 50% yellow-poplar, 30% northern red oak, and 20% a mixture of other commercial species. After the harvest, the residual basal area ranged from 14 to 19% of the initial basal area in the four stands. In addition to advanced reproduction (Table 3), new reproduction that developed after the harvest came from seed stored in the forest floor and sprouts from cut and damaged stems. Trimble (1975) observed in nine even-aged

Table 2
Species composition in trees ≥12.7 cm dbh before harvests

Species	Stand 1 (% basal area)	Stand 2 (% basal area)	Stand 3 (% basal area)	Stand 4 (% basal area)	All stands (% basal area)
Sugar maple	2.4	6.9	4.0	2.0	3.8
American beech	1.9	14.6	9.3	0.5	6.6
Red maple	10.0	0.6	2.2	2.4	3.8
White ash	<0.1	1.5	4.9	2.5	2.2
White oak	20.0	0.0	1.6	0.0	5.4
Northern red oak	14.7	5.2	14.8	15.7	12.6
Yellow-poplar	13.4	38.4	46.7	46.7	36.3
Black cherry	<0.1	3.7	2.7	27.9	8.6
Other species	37.5	29.1	13.8	2.3	20.7
Total	100.0	100.0	100.0	100.0	100.0

Other species included 17 species. Stand 1 was 22% chestnut oak. Stand 2 was 18% American basswood.

stands following clearcut harvests in Appalachian hardwoods that 58% of reproduction came from sprouts, while the remainder came from advanced seedlings and stored seed.

5.1. Response of reserve trees

The initial mean dbh of reserve trees ranged from 36 to 49 cm varying by species and stand (Table 4). Annual dbh growth of northern red oaks exceeded that of yellow-poplar by an average of 27% ($p < 0.01$) (Fig. 2), even though yellow-poplar was slightly larger when harvests occurred. The ANOVA indicated that both stand ($p < 0.01$) and species ($p < 0.01$) were significant effects, with no evidence of interaction ($p = 0.94$), and the faster dbh growth of northern red oak was consistent in all four stands.

Yellow-poplar was slightly taller than northern red oak in each stand when the study began, but overall the two species exhibited similar annual height growth (Table 4). Height growth differed by stand ($p < 0.01$) but not species ($p = 0.14$), and significant interaction between stand and species was evident ($p = 0.02$). Yellow-poplar grew faster in the Stand 3 ($p = 0.02$), and northern red oak appeared to grow faster in Stand 4 ($p = 0.06$) (Fig. 2).

Similar to dbh growth, northern red oak had faster crown radial growth ($p < 0.01$) than yellow-poplar in each stand (Fig. 2). Unlike dbh growth, however, stand ($p = 0.66$) was not a significant effect in crown radial growth, and there was no evidence of interaction ($p = 0.13$) between stand and species. Crown radius of northern red oak and yellow-poplar reserve trees increased by an average of 1.6 and 0.8 m, respectively. As

Table 3
Density of advanced reproduction ≥30.5 cm tall and <2.5 cm dbh before harvests

Species	Stand 1 (stems/ha)	Stand 2 (stems/ha)	Stand 3 (stems/ha)	Stand 4 (stems/ha)	All stands (stems/ha)
Sugar maple	1841	2058	939	1379	1554
American beech	3892	1112	2965	516	2121
Red maple	840	0	0	116	239
White ash	106	494	1285	57	486
White oak	316	0	49	0	91
Northern red oak	630	82	99	346	289
Yellow-poplar	0	82	49	633	191
Black cherry	316	82	0	1782	545
Other species	418	44	346	689	374
Totals	8359	3954	5733	5518	5891

Other species included 15 species.

Table 4
Mean dbh, total height, and crown radius of reserve trees

Species	n	Year	Dbh (cm)	Total height (m)	Crown radius (m)
Northern red oak	29	1979–1984	41.1	29.0	4.3
		2001	62.0	32.0	5.9
Yellow-poplar	24	1979–1984	45.1	32.7	4.0
		2003	64.3	36.9	4.8

Harvest years varied from 1979 to 1984.

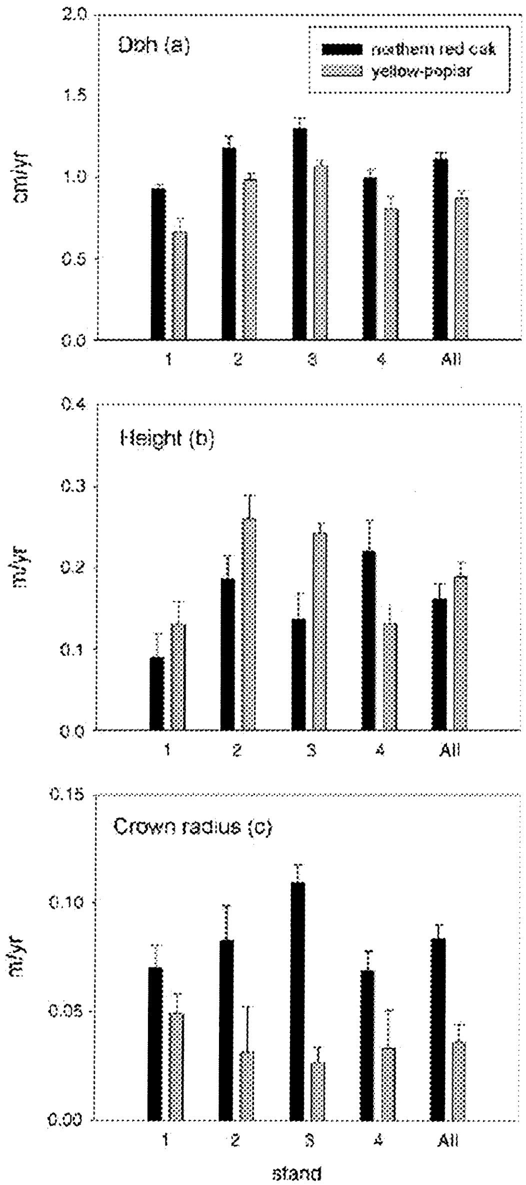

Fig. 2. Mean annual dbh, total height, and crown radius growth of reserve trees.

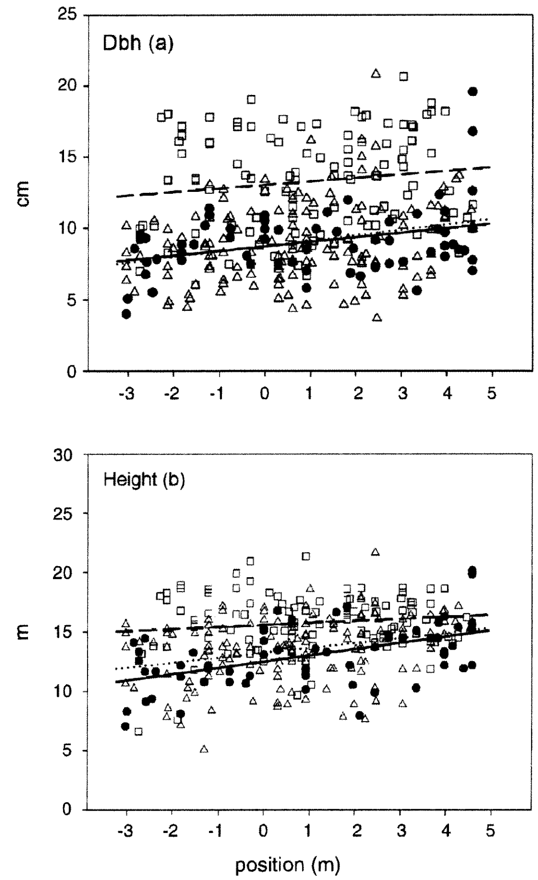

Fig. 3. Dbh and height scaled to age 20 years of dominant/codominant reproduction by position relative to reserve tree crown edge for intolerant (square/dashed line), mid-tolerant (triangle/dotted line), and tolerant (circle/solid line) species.

a result, the surface area covered by the reserve tree crowns increased approximately 88% for northern red oak and 44% for yellow-poplar in the 20 years since the harvests. Mortality of reserve trees averaged 10% since the harvests (Miller et al., 1997a), thus there were an average of 32 reserve trees/ha after 20 years.

5.2. Dbh and height of reproduction

The regression analyses indicated that position, a continuous variable representing relative distance from the reserve tree crown edge, had a significant positive influence on both dbh ($p < 0.01$) and height ($p < 0.01$) of reproduction. Reserve tree species, shade tolerance of reproduction, and stand also were significant categorical factors ($p < 0.01$ for each factor) that explained variation in dbh and height of reproduction. There was no evidence of interaction (p-values > 0.39 for dbh and p-values > 0.47 for height) between the categorical factors and relative position of reproduction, thus the slope coefficients were not significantly different. For example, intolerant species exhibited slightly greater dbh and height growth compared to mid-tolerant and tolerant species, but the relationship to distance from the reserve tree was similar (equal slopes) in all tolerance classes (Fig. 3). It is typical for black cherry and yellow-poplar reproduction, the most abundant intolerant species encountered in the reproduction pool, to exhibit slightly faster early growth compared to mid-tolerant and tolerant species after overstory removal on sites similar to the study areas (Smith, 1983).

Mean dbh of dominant and codominant reproduction, scaled to age 20 years for clarity, increased from 9.4 cm in zone 1 to 11.4 cm in zone 5, a difference of 21% (Table 5). Similarly, height increased from 12.5 m in zone 1 to 15.2 m in zone 5, a difference of 22%. By comparison, dbh and height of dominant and codominant trees in 11 nearby even-aged stands on similar growing sites averaged 12.7 cm and 15.2 m, respectively, when 20 years old (Miller et al., 2001). These findings support the

Table 5
Mean dbh and height (±standard error), scaled to age 20 years, of dominant and codominant reproduction near reserve trees

Species	Zone				
	1	2	3	4	5
Dbh (cm), $n = 317$ trees					
All	9.4 (0.7)	10.7 (0.5)	10.2 (0.4)	10.9 (0.5)	11.4 (0.5)
Intolerant	11.7 (0.8)	13.5 (1.0)	12.2 (0.8)	13.7 (0.5)	14.5 (0.8)
Mid-tolerant	7.4 (0.5)	8.9 (0.4)	9.1 (0.4)	9.4 (0.7)	9.7 (0.5)
Tolerant	7.6 (0.5)	9.7 (0.5)	8.6 (0.6)	8.6 (0.5)	10.2 (0.8)
Height (m), $n = 317$ trees					
All	12.5 (0.5)	14.0 (0.4)	14.0 (0.3)	14.5 (0.4)	15.2 (0.3)
Intolerant	14.6 (0.1)	16.1 (0.5)	15.2 (0.1)	16.1 (0.3)	16.1 (0.4)
Mid-tolerant	12.1 (0.7)	13.0 (0.5)	13.5 (0.4)	13.6 (0.7)	14.8 (0.4)
Tolerant	11.2 (0.6)	11.3 (0.2)	12.6 (1.2)	13.2 (0.9)	14.7 (0.6)

The midpoints of zones relative to the reserve tree crown edge are −2.25, −0.75, 0.75, 2.25, and 3.75 m for zones 1–5, respectively.

general conclusion that dbh and height of reproduction was strongly related to distance from the reserve trees.

5.3. Distribution and species composition of reproduction

The most recent inventories of the permanent sample points located in each stand indicated that yellow-poplar, black cherry, red maple, and sweet birch accounted for most of the dominant and codominant reproduction (Table 6). Other valuable species such as sugar maple and northern red oak reproduction were present in relatively smaller proportions. It was clear that the low-density residual stand had allowed species of all tolerance classes to compete in the new age class for many years. In fact, as many as 24 species were dominant or codominant in the stand-wide reproduction summary (Table 6). The stand-wide summary of reproduction provided only a snapshot of species composition at 17–22 years after harvest, but it did not provide information about the distribution of species around the reserve trees or the long-term trend in species composition.

Reproduction data collected within transects in 2001 and 2003 indicated that basal area of reproduction, particularly intolerant species, increased with distance from the reserve trees (Fig. 4). The preliminary repeated measures ANOVA included main effects of reserve tree species ($p = 0.30$), stand ($p = 0.15$), and cardinal direction (0.29), but they did not have a significant effect on mean basal area in the five zones. The main effects were dropped from further analyses. However, the first order polynomial contrast within zones indicated a strong linear increase in basal area ($p < 0.01$). From zone 1 to 5, basal area increased 75% considering all trees ≥2.5 cm (Fig. 4a) and 128% considering only dominant and codominant trees (Fig. 4b).

A comparison of mean basal area of dominant and codominant reproduction by zone and tolerance class indicated that distribution of species varied by distance from the reserve trees. For example, basal area was significantly greater in zone 5 compared to zone 1 for intolerant species ($p = 0.04$). This trend was less apparent for mid-tolerant species ($p = 0.07$). Basal area of tolerant species was unchanged from zone 1 to 5 ($p = 0.17$). In addition, basal area of intolerant species in zone 5 exceeded that observed for both mid-tolerant ($p = 0.04$) and tolerant species ($p = 0.03$).

Development of reproduction appeared to lag behind that observed in even-aged stands after clearcut harvests on similar

Table 6
Density of reproduction 17–22 years after clearcut-with-reserves harvests

Species	Stand 1 (stems/ha)		Stand 2 (stems/ha)		Stand 3 (stems/ha)		Stand 4 (stems/ha)		All stands (stems/ha)	
	All	D/C	All	D/C	All	D/C	All	D/C	All	D/C
Sugar maple	316	89	741	22	185	7	40	0	321	30
American beech	778	227	173	0	420	0	40	0	353	57
Red maple	462	247	17	7	124	15	138	12	185	70
White ash	15	0	62	5	84	0	30	0	48	1
White oak	84	15	0	0	0	0	0	0	21	4
Northern red oak	447	95	42	5	79	15	74	0	161	54
Yellow-poplar	215	111	469	193	539	40	1621	489	711	208
Black cherry	141	9	59	20	15	0	563	213	195	80
Sweet birch	662	326	264	67	143	35	1045	304	529	183
Other species	445	230	504	151	269	7	109	40	332	107
Totals	3566	1530	2333	469	1858	119	3660	1058	2854	794

Other species included 15 species. All reproduction included trees ≥2.5 cm dbh, and D/C included dominant and codominant trees. Stand ages were 22, 20, 19 and 17 years for Stands 1, 2, 3 and 4, respectively.

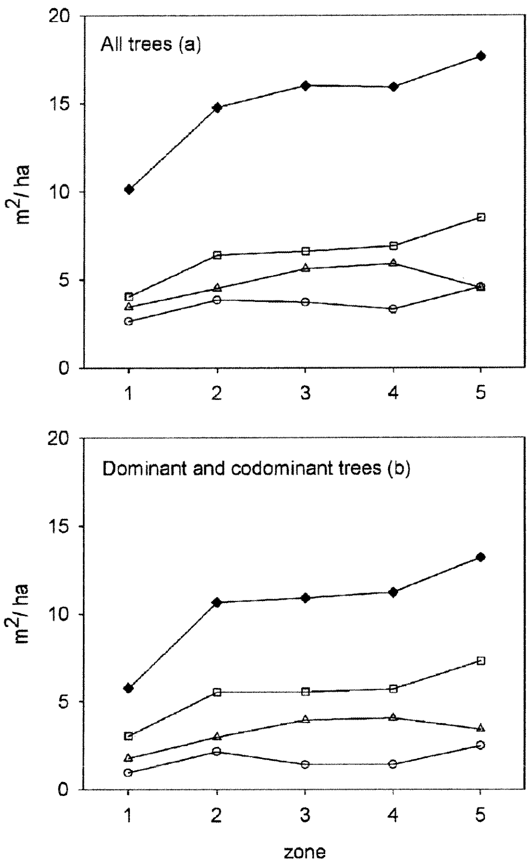

Fig. 4. Mean basal area scaled to age 20 years of reproduction developing in the vicinity of reserve trees. The midpoints of zones relative to the reserve tree crown edge are −2.25, −0.75, 0.75, 2.25, and 3.75 m for zones 1–5, respectively. Species groups based on shade tolerance include intolerant (square), mid-tolerant (triangle), tolerant (circle), and all species combined (solid diamond).

growing sites. Mean basal area including all trees ≥2.5 cm dbh, scaled to age 20 years, ranged from 10.1 to 17.7 m^2/ha in zones 1–5, respectively (Table 7). Virtually all of the stand area was located within 4.5 m of the reserve tree crowns (Table 4), thus the results provided a basis for estimating stand-wide basal area of reproduction. Applying the appropriate proportion of stand area and basal area observed in each zone, stand-wide basal area of reproduction averaged 15 m^2/ha. In contrast, basal area in 11 nearby even-aged stands totaling 64 ha on similar growing sites averaged 22 m^2/ha when 20 years old (Miller et al., 2001). Basal area in a 34-ha even-aged stand averaged 25 m^2/ha when 20 years old (Gilliam et al., 1995). While basal area growth of reproduction was less than that observed after clearcut harvests, the difference was essentially offset by 13 m^2/ha of basal area growth on the surviving reserve trees since the harvest.

6. Discussion

The initial concept of studying two-aged stand structures was based on retaining a low-density overstory cover for many years, even as long as an 80-year rotation (Smith et al., 1989). The results of this study suggest that retaining reserve trees for >20 years has a measurable effect on nearby reproduction. Also, retaining 36 reserve trees/ha affected reproduction on virtually all of the stand area. It is not clear if the impact of the reserve trees, particularly on intolerant reproduction, would be mitigated by their removal after 20 years. In light of these findings, it is important for forest mangers to consider the tradeoffs associated with retaining reserve trees and competing management objectives over the long term when deciding how many trees to retain and how long to retain them.

The analysis focused on the composition and development of dominant and codominant reproduction, while subordinate trees received less attention. At the 20-year stage of development, when crown classes are evident, dominant and codominant trees are those most likely to remain competitive for an extended time and eventually occupy considerable space in the overstory. For intolerant and mid-tolerant species, in particular, subordinate trees have little chance of exhibiting sufficient height growth to survive or maintain their position in the canopy of an aggrading stand (Trimble, 1973). Intolerant species also are more likely to lose competitiveness once they become subordinate to neighboring trees of the same age or receive overhead competition from older, taller trees.

The observed influence of reserve trees on reproduction is similar to that observed in several studies of gap dynamics in

Table 7
Mean basal area (±standard error), scaled to age 20 years, of reproduction near reserve trees

Species	Zone				
	1	2	3	4	5
All trees ≥ 2.5 cm dbh (m^2/ha), n = 1029 trees					
All	10.1 (2.4)	14.8 (3.6)	16.0 (3.3)	16.1 (3.9)	17.7 (4.0)
Intolerant	4.0 (1.2)	6.4 (1.9)	6.6 (1.5)	6.9 (1.7)	8.5 (1.7)
Mid-tolerant	3.5 (0.7)	4.5 (0.7)	5.6 (1.0)	5.9 (1.5)	4.5 (0.7)
Tolerant	2.6 (0.5)	3.9 (1.0)	3.7 (0.8)	3.3 (0.8)	4.6 (1.6)
Dominant and codominant trees (m^2/ha), n = 317 trees					
All	5.8 (1.9)	10.7 (3.2)	10.9 (2.7)	11.2 (3.5)	13.2 (3.7)
Intolerant	3.1 (1.1)	5.5 (1.8)	5.1 (1.3)	5.4 (1.5)	7.2 (1.5)
Mid-tolerant	1.8 (0.5)	3.0 (0.6)	4.5 (0.9)	4.4 (1.4)	3.2 (0.7)
Tolerant	0.9 (0.3)	2.2 (0.9)	1.4 (0.5)	1.4 (0.6)	2.8 (1.5)

The midpoints of zones relative to the reserve tree crown edge are −2.25, −0.75, 0.75, 2.25, and 3.75 m for zones 1–5, respectively. Means were computed from 158 transects.

eastern hardwoods, whereby distance from an individual reserve tree is similar to distance from a gap edge. Dale et al. (1995) analyzed 30-year-old natural hardwood reproduction in clearcut canopy gaps up to 1 ha in size and found that total basal area and basal area of intolerant species increased with gap size and distance from the gap edge. However, basal area was reduced by 20–60% compared to that observed in large clearcuts up to 20 m away from the gap edges. In other studies, small canopy gaps up to 1 ha in size also favored reproduction of tolerant species because a significant proportion of the gap area was influenced by trees on the gap edge (Walters and Nyland, 1989; Runkle, 1990). Relative species abundance among tolerance classes was related to gap age, with tolerant species increasing, as border trees expanded and gap size decreased over time (McClure and Lee, 1993). Species interactions in gaps are usually attributed to light availability, but soil nutrients are affected by gap size and may also influence competition among hardwood species (Fownes and Harrington, 2004).

Evidence from alternative applications of canopy retention systems indicated that individual reserve trees influence the development of new reproduction. Sprout or coppice reproduction was reduced within the first 10 years after disturbance where overstory density ≥40% (Joys et al., 2004). Shade from the reserve trees apparently can affect the species composition of reproduction even in the early stages of development. For example, seedling root mass of tolerant species varied little across various levels of available light, yet root mass of mid-tolerant and intolerant species decreased sharply as light decreased (Logan, 1965, 1973). Height and biomass of black cherry saplings were significantly related to distance from parent trees (Packer and Clay, 2003). Greenhouse experiments indicated that some of this distance-dependent relationship was explained by soil pathogens near the parent tree. However, field experiments indicated that competition with the parent tree also affected growth patterns. The results suggest that the probability of black cherry saplings reaching the canopy diminishes with proximity to adult trees. In another study, individual trees influenced nearby soil properties in relation to distance from the crown edge in Appalachian hardwoods (Boettcher and Kalisz, 1990), and by extension, they can also affect the growth and distribution of nearby vegetation. On a much larger scale, Zinge (1962) suggested that the distribution of vegetation within a stand or forest reflects the aggregated effect of many single-tree influence circles.

This study did not directly compare reproduction in two-aged stands to that observed in even-aged stands, but the results provided evidence that the reserve trees reduced the growth of reproduction throughout the stand. The mean basal area in zone 5, which was located 3.0–4.5 m from the reserve tree crown edge (Table 7), was about 20–30% less than that observed in even-aged stands on similar sites (Gilliam et al., 1995; Miller et al., 2001), and basal area decreased with proximity to the reserve trees. Similar reductions in dbh and height of individual trees also were observed. Although growth of the reserve trees essentially offset slower growth of the reproduction, the reserve trees will continue to influence the species composition of reproduction as their crowns expand. When data were collected, the reserve trees were approximately 100 years old, and the reproduction ranged from 17 to 24 years old. Reserve tree height exceeded 30 m, while most dominant and codominant reproduction was less than 15 m tall. Height growth of the reserve trees was relatively slow, about 0.2 m/year (Table 4), compared to 0.7 m/year for the reproduction (Table 5). At these growth rates, the reproduction will not reach the height of the reserve trees for 30–40 years. During that time, the crowns of the reserve trees will expand and continue to hinder the survival of intolerant reproduction for many years. This trend is apparent in zone 1, where reproduction has been under the reserve tree crown since the harvest, and basal area/ha among the species groups is not significantly different. Stocking of intolerant reproduction near the reserve trees will continue to decline due to its inability to persist under the shade of the reserve trees. Conditions in zone 1 and 2 now favor the survival of tolerant reproduction, and as the reserve trees expand in the future, the stand area suitable for survival of intolerant reproduction will diminish. In this study, retaining 36 trees/ha with an average crown radius of 4.1 m resulted in a 19% canopy cover immediately after the harvest. After 20 years, 90% of the reserve trees survived, average crown radius had increased to 5.3 m, and canopy cover had increased to 28% (Table 4). In a few more years, nearly half of the stand area will be located under the crowns of the reserve trees and much of the reproduction will be influenced by more than one reserve tree. Northern red oak and yellow-poplar have relatively large crowns compared to other species of the same dbh, particularly on productive sites (Lamson, 1987). Species with smaller crowns or less aggressive crown expansion would tend to have less impact on reproduction. Still, reserve trees of any species will expand over time, and forest managers need to consider their impact to achieve long-term management objectives.

Reproduction in the new age class would benefit from an intermediate cultural practice such as cleaning or crop tree release to favor trees that meet management objectives (Miller, 2000). Crown release treatments free selected trees from nearby competition, thus accelerating their growth and increasing their future competitiveness. In two-aged stands, however, opportunities to successfully release intolerant and mid-tolerant species may be limited to areas located between the reserve trees.

There are several alternative strategies for managing two-aged stands if the influence of reserve trees on reproduction is a concern:

(1) Retain fewer reserve trees/ha in the initial harvest operation.
(2) Leave species with relatively smaller crowns and less aggressive crown expansion.
(3) Leave clumps of residual trees to increase open space and reduce the effect of reserve tree crown expansion.
(4) Start with a given number of reserve trees/ha and later reduce the residual stand density by chemical or mechanical means.
(5) Plan to harvest some of the reserve trees once the new age class is established.

Forest managers should weigh the risks and benefits of harvesting the reserve trees in two-aged stands. Falling and skidding the reserve trees can cause significant damage to young trees in the new age class. Combining a thinning treatment in the new age class with the harvest of reserve trees would provide corridors in which to fall the reserve trees, but additional care is needed to minimize damage from skidding logs and the movement of logging equipment.

Finally, it is important to prepare for reproduction of desired species many years before conducting a clearcut-with-reserves harvest in hardwood stands (Miller and Kochenderfer, 1998). A regeneration assessment should be conducted before a planned harvest to determine if preparatory silvicultural treatments are needed. For example, interfering plants and adverse deer impacts must be controlled to allow desirable advanced reproduction to develop. Once competitive advanced reproduction is in place, and undesirable competition is under control, overstory removal can begin. A low-density overstory forest cover can be retained for many years, but the forest manger must consider the long-term impact of reserve trees on reproduction to fully meet management objectives.

Acknowledgements

The authors thank H. Clay Smith (retired), Neil I. Lamson (retired), Robert Rosier, Richard Hovatter, Frederica Wood, and staff at the Fernow Experimental Forest in Parsons, WV for their contributions in establishing and maintaining the study sites since 1979. The authors also thank Dave Feicht, Brian Simpson, John Juracko, Regis Young, Sandra Fosbroke and staff at the Forestry Sciences Laboratory in Morgantown, WV for their assistance in designing the transects and collecting the data used to measure the effect of the reserve trees on reproduction in 2001 and 2003. Finally, the authors thank Bob Schirk (retired), who first suggested leaving reserve trees in clearcut stands, and other personnel on the Monongahela National Forest for contributing three of the study sites.

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