

## Structure and short-term dynamics of the tree component of a mature pine-oak forest in southeastern Arkansas

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SHELTON, M. G. AND M. D. CAIN (USDA Forest Service, Southern Research Station, Monticello, AR 71656-3516). Structure and short-term dynamics of the tree component of a mature pine-oak forest in southeastern Arkansas. *J. Torrey Bot. Soc.* 126:32–48. 1999.—The R.R. Reynolds Research Natural Area is a 32-ha second-growth forest with little human intervention for nearly 60 years. In this paper, we characterize the existing vegetation, which represents 60 years of successional change with no major disturbances, and report vegetative changes over a 5-year period, which suggest the future successional direction. Trees  $\geq 9.0$  cm DBH were inventoried in twenty 0.1-ha plots and placed into four species groups: pines, oaks, other overstory trees, and midstory trees. Loblolly pine (*Pinus taeda* L.) was the dominant tree species, accounting for 51% of the total basal area and having the largest mean DBH (56.5 cm) and height (35.7 m). Tree ages ranged from 50 to 140 years for the pines and from 40 to 150 years for the oaks. However, 70% of the pines became established in the 4 decades that followed harvest of the virgin forest in the 1910s, while the oaks showed two peaks of establishment (one after harvest and one 50 years before harvest). The pines displayed a bell-shaped DBH-class distribution, while the oaks displayed a gradual decline in numbers as DBH-class increased. In contrast, the other overstory trees and midstory trees had negative exponential distributions. Multiple occupancy was common within the canopy, which had a horizontal coverage of 97%. Canopy positions of the species groups were as follows: pines>oaks>other overstory trees>midstory trees. The growth of individual trees was positively related with tree size. Stand-level survivor growth was positively related with the basal area of the species group. Recruitment was greatest for the other overstory trees and midstory trees (totaling 6.2 trees  $\text{ha}^{-1} \text{yr}^{-1}$ ), but did not occur for the pines and oaks. Mortality of large pines during the observation period (averaging 3.3 trees  $\text{ha}^{-1} \text{yr}^{-1}$ ) resulted in net losses in basal area and volume for that species group. By contrast, hardwood species groups displayed net increases, totaling 0.17  $\text{m}^2 \text{ha}^{-1} \text{yr}^{-1}$  for basal area and 1.59  $\text{m}^3 \text{ha}^{-1} \text{yr}^{-1}$  for volume. Stand dynamics suggest that the shade-intolerant pines are rapidly being replaced by more shade-tolerant hardwoods.

Key words: forest growth, old-growth forests, *Pinus echinata* Mill., *P. taeda* L., research natural areas, succession.

In virgin forests of the Eastern United States, the early harvesting policy was almost universally one of 'high grading' in which forest stands were repeatedly cutover and only the best trees were taken (Della-Bianca 1983). In southern Arkansas, large-scale removal of virgin loblolly and shortleaf pines (*Pinus taeda* L. and *P. echinata* Mill., respectively) began in the 1890's and was almost complete by 1930 (Reynolds 1980). During that time, lumber companies usually cut only high-quality trees that were  $>36$  cm in stump diameter. Since most hardwoods had little merchantable value in those days, many were left standing. Residual pines of cone-bearing size seeded these cutover areas and residual hardwoods grew and reproduced, thereby resulting in second-growth stands with multiple diameter classes of pines and mixed hardwoods.

In 1934, the USDA Forest Service acquired 680 ha of forestland in southeastern Arkansas that originated from diameter-limit cutting of the virgin forest before 1915. This forest property was to be used as an experimental forest to study

ways of improving and rebuilding previously unmanaged second-growth pine stands in the West Gulf Coastal Plain. In 1935, 32 ha were selected as having the most representative stand conditions throughout the experimental forest and were set aside from future timber management. Major anthropogenic disturbances have been excluded from this 32-ha forest for over half a century, and it has been designated as the R.R. Reynolds Research Natural Area (RNA). The USDA Forest Service developed the RNA program to protect small areas of old growth on national forest lands (Devall and Ramp 1992). These protected RNAs are considered to be natural laboratories with historical and biological significance (Fountain and Sweeney 1987) and contribute to an understanding of long-term vegetation dynamics and forest succession (Hemond et al. 1983).

In southeastern Arkansas, the USDA Forest Service has accumulated more than 50 years of growth and yield research data from managed, natural stands of loblolly and shortleaf pines (Baker and Murphy 1982; Murphy and Farrar 1985; Baker 1986). Even in the present RNA, long-term growth trends at the stand level have

Received for publication January 18, 1998, and in revised form July 23, 1998.



been reported (Guldin and Baker 1985). However, there has been no previous effort to monitor mortality, growth, and development of individual trees in this 32-ha forest.

Our objective in this paper is to provide baseline information on the structure, survival, and growth of pines and hardwoods in this closed-canopy, mature forest between 1989 and 1994. These data should improve our ability to predict changes in the relative growth rates and relative shade tolerance of different plant species in response to natural perturbations. Such prediction mechanisms are critical if natural-resource managers are to anticipate how plant communities, ecosystems, and landscapes respond to environmental changes in the next century (Huston 1991). Understory dynamics and the effects of natural stand perturbations in this RNA have been previously documented (Cain and Shelton 1995, 1996).

**Methods. STUDY AREA.** The 32-ha RNA is located in the West Gulf Coastal Plain of southeastern Arkansas at 33°02'N and 91°56'W. It is dissected by several intermittent drainages, and soil types are oriented in relation to these drainages. Arkabutla silt loam (Aeric Fluvaquents) occurs in the floodplain along the drainages (USDA 1979). On these somewhat poorly drained soils, dominant tree height is expected to be about 30 m at 50 years for loblolly pine, cherrybark oak (*Quercus pagoda* Raf.), green ash (*Fraxinus pennsylvanica* var. *lanceolata* [Borkh.] Sarg.), sweetgum (*Liquidambar styraciflua* L.), and water oak (*Q. nigra* L.). (Botanical nomenclature follows Little [1979]). Providence silt loam (Typic Fragiudalfs) usually occurs on side slopes along the drainages, and Bude silt loam (Glossaquic Fragiudalfs) is found on upland flats. Providence and Bude soils were formed in thin loessial deposits, and the dominant tree height is expected to be 26 m at 50 years for loblolly pine, shortleaf pine, and sweetgum. A number of pimple mounds or Mima mounds (Cox 1984) occur on the flats between the drains.

Elevations within the sampled area of the RNA range from 38 to 41 m above sea level. The growing season is about 240 days, and annual precipitation averages 140 cm, with extremes being wet winters and dry autumns. The area is currently bordered by stands being managed during the last 50 years for pine timber production using single-tree selection, seed-tree cuts, and 2-ha block clearcuts.

Preharvest stand conditions are not known, but virgin forests in southern Arkansas consisted of mixed pine-hardwood stands, with about one-half of the volume in the pine component (White 1984). By 1915, old-growth pine timber on the study area had been cut to a 36-cm stump diameter (Reynolds 1959). Because only the very best hardwoods were cut with the pines, all hickories (*Carya* spp.), sweetgums, blackgums (*Nyssa sylvatica* Marsh.), post oaks (*Quercus stellata* Wangenh.), water oaks, and elms (*Ulmus* spp.) were left. Residual trees also included merchantable-sized pines, red oaks (principally southern red oak [*Quercus falcata* Michx.]), and white oaks (principally white oak [*Quercus alba* L.]) that were of poor quality. Since 1935, no management practices have been conducted on this area with the exception of fire protection and measures to control an infestation of southern pine beetles (*Dendroctonus frontalis* Zimm.) that reached epidemic levels in southern Arkansas in the early 1970's (Ku et al. 1981), when a 0.4-ha beetle infestation was salvaged along the perimeter of the study area, and a cut-and-leave treatment was imposed on infested but isolated pines ( $\approx 0.5$  tree  $\text{ha}^{-1}$ ).

**SAMPLING AND MEASUREMENTS.** Twelve square, 0.1-ha plots were systematically located within the area in March 1989. All trees with  $\text{DBH} \geq 9.0$  cm were given a permanent number, and distance and azimuth from plot center was determined. A mark was painted on the stem at 1.37 m in height so that DBH (diameter at breast height) could be measured at the same location during subsequent inventories. The DBH mark was offset if some stem abnormality was judged as influencing diameter growth at 1.37 m. Numbered trees were measured for DBH to 0.3 cm. To simplify sampling and measurements, species were sometimes categorized into four groups: pines, oaks, other overstory trees and midstory trees. Pines and oaks were grouped by genera, while other overstory trees, and midstory trees were species grouped by their potential size and position within the canopy (Cain and Shelton 1994). A representative subsample of about one-third of the pines and oaks and one-fifth of the other overstory and midstory tree species was measured for total height to the apex, height to the base of the live crown, and crown width. Heights were measured to an accuracy 0.3 m using a clinometer. Crown width was measured to an accuracy of 0.3 m using a tape along the long and short axes projected to ground level.

Crown length was the difference between total height and height to crown base. For determining age, an increment core was obtained from tree boles to the pith at 1.22 m in height from most of the oak and pine sample trees. A lower proportion of trees was aged for other overstory and midstory trees because of their narrower range in DBH, their lower contribution to stand basal area and volume, and the difficulty in counting their rings. Tree age was determined by counting growth rings under 20X magnification on a cleanly cut face of each core. Three years were added to the ring count to obtain tree age to adjust for growth to a height of 1.22 m (Cain and Shelton 1994).

Eight additional plots were systematically established and measured as described above during March 1991, except that no trees were subsampled for heights, crown dimensions, and age. At this time, DBH was also remeasured for surviving trees in the initial series of plots. The elevation of all 0.1-ha plots was determined using an alidade and stadia rod during February 1993, and the survey was tied to a point of known elevation.

Surviving trees in all plots were remeasured in February 1994 in an identical manner as the initial measurements. Plots were also examined for ingrowth of trees past the 9.0 cm DBH threshold, and these trees were given a permanent number, measured for DBH, identified by species, and their location mapped. Whenever possible, the cause of tree mortality was recorded for numbered trees.

Photosynthetically active radiation was determined at 1.37 m above ground during clear skies on August 8, 1991 using an 80-sensor Sunfleck Ceptometer (Decagon Devices, Inc., Pullman, WA). Determinations were made on 10 temporary points systematically located within each of the initial 12 measurement plots. Measurements were taken between 1030 and 1330 solar time. Several measurements were also made in full sunlight, which permitted calculation of relative light intensity (photosynthetically active radiation in sample plots at 1.37 m expressed as a percent of that in full sunlight). During the summer of 1993, canopy coverage was determined using a spherical densiometer positioned at 3 m above ground near plot center.

**CALCULATIONS AND STATISTICAL ANALYSIS.** Regression equations for sample trees and trends for the 20 plots were investigated using both linear and nonlinear regression, depending on the

particular data pattern (SAS 1988, 1989). The fit index reported for nonlinear equations is analogous to the coefficient of determination ( $r^2$ ) reported for linear equations. The reported root mean square error (RMSE) is an unbiased estimator of the equation's error variance. All reported coefficients were significantly different from zero at  $P \leq 0.10$ . Regression equations were developed for the relationships between total height and crown dimensions to DBH for the sample trees measured for these parameters, combining data from the 1989 and 1994 inventories (Table 1). The age structure of the forest was summarized by grouping trees into 10-year age classes (e.g., the 70-year age class included trees from 66 to 75 years old). The DBH structure was summarized by grouping trees into 5-cm DBH classes (e.g., the 11-cm DBH class included trees ranging from 9.0 to <14.0 cm in DBH). Stem volumes were calculated to express the combined effects of tree diameter and height and to allow growth comparisons with other forests. Inside-bark volume equations from Farrar et al. (1984) were used for the pine component and Clark et al. (1986) for the hardwood component. Heights for applying volume equations were calculated using the appropriate height-DBH prediction in Table 1. Mean height of species was calculated by applying developed prediction equations to the measured DBH's in 1991, and then calculating means. Frequency of occurrence of species refers to the percentage of the plots containing at least one individual of that species.

Canopy structure was calculated by applying regression equations for predicting height and crown dimensions from DBH (Table 1) to the measured DBH's in 1991. The width of each crown was calculated at 1-m intervals by assuming a parabolic shape. Crown cross-sectional area was then calculated from the crown width for the 1-m intervals and summed for each species group.

Calculations were made for three growth components: survivors, mortality, and recruitment (Husch et al. 1982). Growth was converted to an annual basis because the observation interval varied for the initial series of plots (a 5-year period) and the second series of plots (a 3-year period). Differences between the two series of plots were tested using a *t* test, but none were found to be significant at  $P=0.05$ , and thus, the mean annual growth data were combined from the 20 plots for analysis.

Table 1. Regression coefficients and associated statistics for predicting the total height and crown dimensions from DBH.

Species group	Regression coefficients		Mean value	Root mean square error	Fit index
	$b_0$	$b_1$			
Total height <sup>a</sup>					
Pines	3.795	-11.64	35.3	1.94	0.63
Oaks	3.683	-14.62	24.6	2.78	0.80
Other overstory trees	3.691	-13.70	17.2	2.46	0.83
Midstory trees	3.468	-11.76	12.9	1.97	0.76
Crown length <sup>b</sup>					
Pines	1.730	0.01148	10.6	2.16	0.41
Oaks	1.778	0.01642	11.0	2.60	0.60
Other overstory trees	1.462	0.02747	7.2	2.59	0.43
Midstory trees	1.044	0.05329	6.0	2.38	0.39
Crown width <sup>b</sup>					
Pines	1.422	0.01485	9.5	1.46	0.66
Oaks	1.601	0.01819	9.9	1.76	0.76
Other overstory trees	1.410	0.02199	6.2	1.32	0.52
Midstory trees	1.480	0.03056	6.7	1.10	0.49

<sup>a</sup> The equation for total height is:

$$H = \exp(b_0 + b_1 DBH^i)$$

where  $H$  is total height in m and  $DBH$  is in cm. Degrees of freedom are 158 for pines, 125 for oaks, 108 for other overstory trees, and 66 for midstory trees.

<sup>b</sup> The equation for specified crown dimension is:

$$CD = \exp(b_0 + b_1 DBH)$$

where  $CD$  is the specified crown dimension in m and  $DBH$  is in cm.

**Results.** SPECIES COMPOSITION. Tree density in the RNA averaged 453 trees ha<sup>-1</sup> with a basal area of 37 m<sup>2</sup> ha<sup>-1</sup> and a volume of 347 m<sup>3</sup> ha<sup>-1</sup> (Table 2). A total of 20 species and/or genera were recorded: two pine species, six oak species, four other overstory tree genera, and eight midstory tree genera. The order of importance by species groups in terms of DBH, height, basal area, and volume was as follows: pines>oaks>other overstory trees>midstory trees. Thus, the overall composition of the RNA was classified as pine-oak.

The dominant species was clearly loblolly pine, which had the largest stature (mean DBH and height of 56.5 cm and 35.7 m, respectively) and accounted for the greatest percentage of total basal area and volume (51 and 53%, respectively). In addition, loblolly pine was well distributed across the area with a 100% frequency of occurrence. White oak was the second most important species and was followed by shortleaf pine. By contrast, the least important species were red mulberry (*Morus rubra* L.) and sweetleaf (*Symplocos tinctoria* (L.) L'Her.), which are shade-tolerant small trees or shrubs that rarely reach midstory status.

Some spatial variation was observed in the

distribution of species within the RNA. Although both pines and hardwoods occurred in all plots, the pines tended to dominate the broad upland flats between intermittent drainages, while a mixed pine-hardwood or hardwood-pine composition occurred along the drainages. An inverse relationship was observed in the basal areas of pines and hardwoods (Fig. 1a). Evidence of the effects of topography on pine-hardwood composition is presented in Fig. 1b. Variation in elevation explained 46% of the variation in the percentage of total basal area in hardwoods. Areas with lower elevations tended to have more hardwoods than areas with higher elevations, although elevations differed by only 3 m across the twenty 0.1-ha plots. In addition, shortleaf pine tended to be more common on the areas with higher elevations, and there was a positive correlation between shortleaf pine basal area and elevation ( $r=0.56$ ,  $P=0.01$ ).

TREE SIZE AND CANOPY STRUCTURE. Species groups displayed strong differences in size-class distribution. The pines displayed a normal DBH-class distribution, with a range of 16 to 91 cm and a modal class of 56 cm (Fig. 2). By contrast, the other overstory and midstory tree groups dis-

Table 2. Mean characteristics of the trees occurring in twenty 0.1-ha plots located in the R.R. Reynolds Research Natural Area during 1991 (2 years after monitoring began).

Group and species	Density (trees ha <sup>-1</sup> )	Basal area (m <sup>2</sup> ha <sup>-1</sup> )	Volume (m <sup>3</sup> ha <sup>-1</sup> )	Frequency (%)	Mean DBH (cm)	Mean height (m)
<b>Pines</b>						
<i>Pinus echinata</i>	25.2	3.9	37.5	60	44.5	33.1
<i>Pinus taeda</i>	75.1	18.8	182.6	100	56.5	35.7
Group total or (mean)	100.3	22.7	220.1	100	(53.7)	(35.0)
<b>Oaks</b>						
<i>Quercus alba</i>	43.5	5.5	56.1	95	40.0	24.8
<i>Q. falcata</i>	13.8	2.0	19.5	70	43.0	25.8
<i>Q. nigra</i>	11.4	0.8	7.0	55	29.4	18.8
<i>Q. pagoda</i>	8.4	0.6	5.9	50	31.1	19.7
<i>Q. phellos</i>	1.0	0.1	0.7	10	31.2	24.4
<i>Q. stellata</i>	11.4	1.2	11.5	50	36.6	24.2
Group total or (mean)	89.5	10.2	100.7	100	(38.0)	(23.6)
<b>Other overstory trees</b>						
<i>Carya</i> spp. <sup>a</sup>	3.5	0.2	1.7	35	26.9	20.5
<i>Fraxinus</i> spp. <sup>b</sup>	11.4	0.3	1.9	55	17.4	16.6
<i>Nyssa sylvatica</i>	30.1	0.5	3.2	90	14.5	13.9
<i>Liquidambar styraciflua</i>	101.3	1.9	12.7	100	15.6	14.8
Group total or (mean)	146.3	2.9	19.5	100	(15.9)	(14.9)
<b>Midstory trees</b>						
<i>Acer rubrum</i>	11.4	0.1	0.8	55	12.7	11.8
<i>Cornus florida</i>	20.7	0.2	0.7	80	10.4	10.2
<i>Ilex opaca</i>	12.8	0.1	0.5	35	10.9	10.7
<i>Morus rubra</i>	0.5	<0.1	<0.1	5	9.1	8.7
<i>Ostrya virginiana</i>	39.0	0.4	1.9	80	11.6	11.3
<i>Sassafras albidum</i>	2.5	<0.1	0.2	20	12.7	12.2
<i>Symplocos tinctoria</i>	0.5	<0.1	<0.1	5	9.7	9.5
<i>Ulmus</i> spp. <sup>c</sup>	29.1	0.4	2.4	85	13.8	12.5
Group total or (mean)	116.5	1.3	6.5	100	(12.0)	(11.4)
Overall total or (mean)	452.6	37.1	346.8	100	(26.0)	(20.2)

<sup>a</sup> Principally *Carya tomentosa*.

<sup>b</sup> Both *Fraxinus americana* and *F. pennsylvanica* var. *lanceolata*.

<sup>c</sup> Principally *Ulmus alata*.

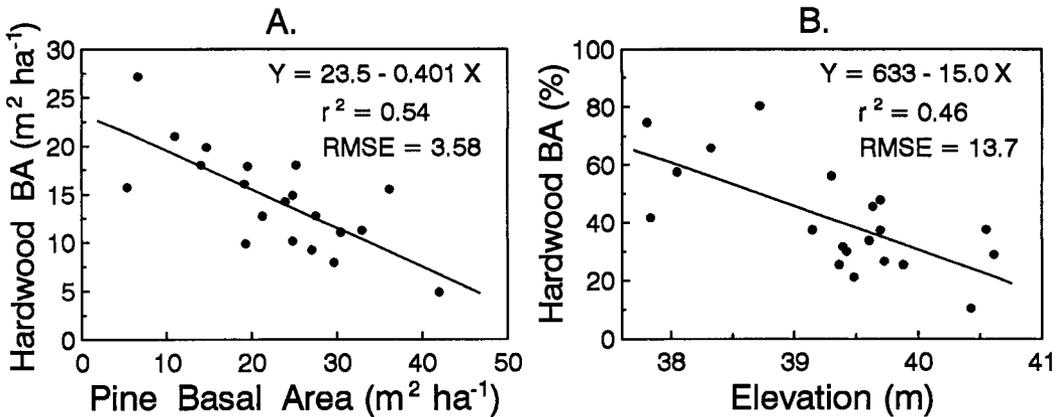


Fig. 1. Basal area (BA) relationships for twenty 0.1-ha plots located within R.R. Reynolds Research Natural Area in 1991: (A) hardwoods versus pines, and (B) the percentage of total basal area in the hardwood component related to plot elevation.

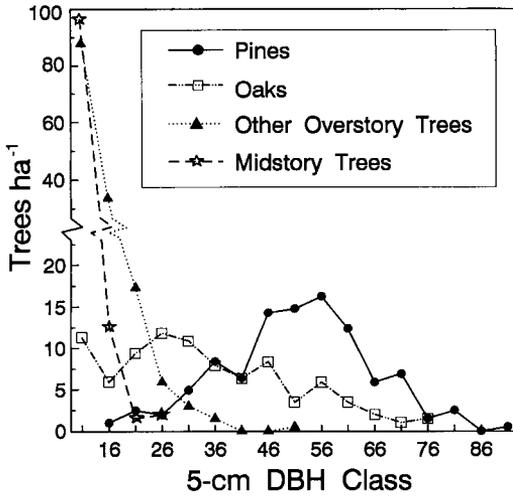


Fig. 2. The DBH-class distribution by species groups for the R.R. Reynolds Research Natural Area in 1991.

played a negative exponential DBH-class distribution, where the number of trees per DBH class decreased sharply as DBH increased. Most of the midstory and other overstory trees were less than 21 and 31 cm in DBH, respectively. The number of oaks gradually declined with increasing DBH, and thus were intermediate in pattern between the pines and the midstory trees. Overall, the smaller DBH classes were principally the midstory and other overstory trees, while the larger DBH classes were mainly the pines and oaks.

Species groups were also differentiated by canopy position (Fig. 3). Crown positions were

in the following order: pines>oaks>other overstory trees>midstory trees. Pine crowns occupied the upper portion of the canopy, with cross-sectional areas reaching a peak of 5,500 m<sup>2</sup> ha<sup>-1</sup> at 28 m in height but extending from 20 to 40 m. Oak crowns extended over a broader height zone than any other species group, ranging from 5 to 33 m and reaching a peak of 5,500 m<sup>2</sup> ha<sup>-1</sup> at 20 m in height. The lower portion of the canopy was composed of the crowns of other overstory and midstory trees, having peak cross-sectional areas of 1,200 and 2,000 m<sup>2</sup> ha<sup>-1</sup>, respectively. The peak cross-sectional areas for all groups totaled 14,200 m<sup>2</sup> ha<sup>-1</sup>. Expressed as a percentage of ground area, the total cross-sectional area for all groups was 142%, which reflected the closed nature of the canopy and a high degree of multiple occupancy. This finding was confirmed by determining the canopy coverage using a spherical densiometer at 3 m in height; canopy coverage averaged 96.6% of the area with only 3.4% of the area in openings. Little sunlight penetrates through the closed canopy during the growing season. For example, the photosynthetically active radiation at 1.37 m in height averaged only 3.6% of full sunlight for the original set of 12 plots during August of 1991, and values ranged from only 2.5 to 5.3%.

Figure 3 shows that pines and oaks were equal in the peak cross-sectional area of their crowns (both 5,500 m<sup>2</sup> ha<sup>-1</sup>), while basal area of the pines was twice that of the oaks (23 versus 10 m<sup>2</sup> ha<sup>-1</sup>, respectively, Table 2). This difference validates what one might intuitively expect, that oaks have a larger crown width than pines of the

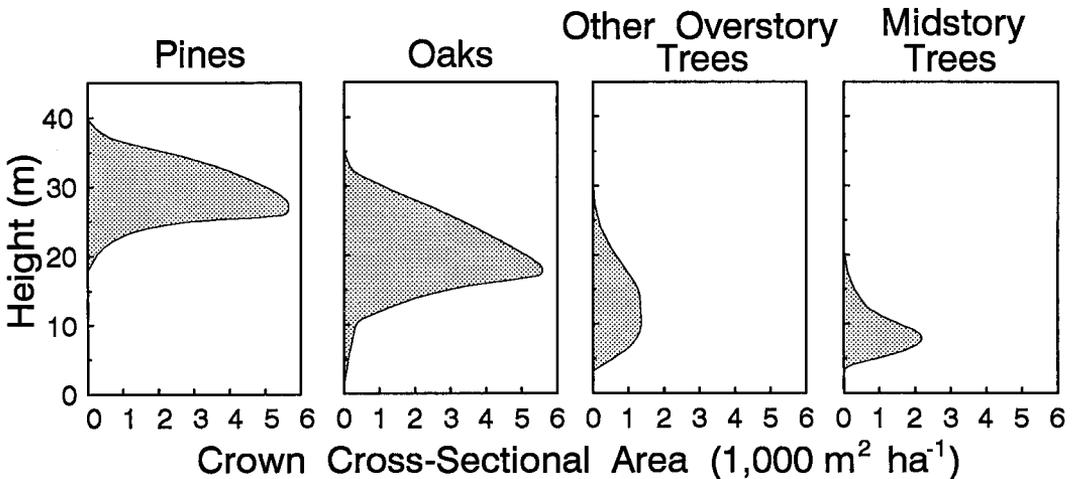


Fig. 3. Vertical canopy structure by species groups for the R.R. Reynolds Research Natural Area in 1991.

same DBH. For example, an oak 45 cm in DBH was predicted to have a crown width of 11.2 m compared to 8.1 m for a pine of the same DBH (equations presented in Table 1); this represents almost a two-fold difference in crown cross-sectional area. In addition, the equations relating crown width to DBH were significantly different for the oaks and the pines ( $P=0.0001$ ).

The high degree of multiple occupancy by trees is illustrated for a typical 0.1-ha plot in Fig.

4. The pine and hardwood basal areas of this plot (24.8 and 14.9  $\text{m}^2 \text{ha}^{-1}$ , respectively, in 1991) were close to the overall means for all plots. Also apparent in this illustration is the closed nature of the canopy, and the relatively large crown size of the oaks when compared to the pines. The clustering displayed by the pines is common in natural stands that have been partially harvested (Shelton and Murphy 1994), and it reflects the suppression of pine reproduction

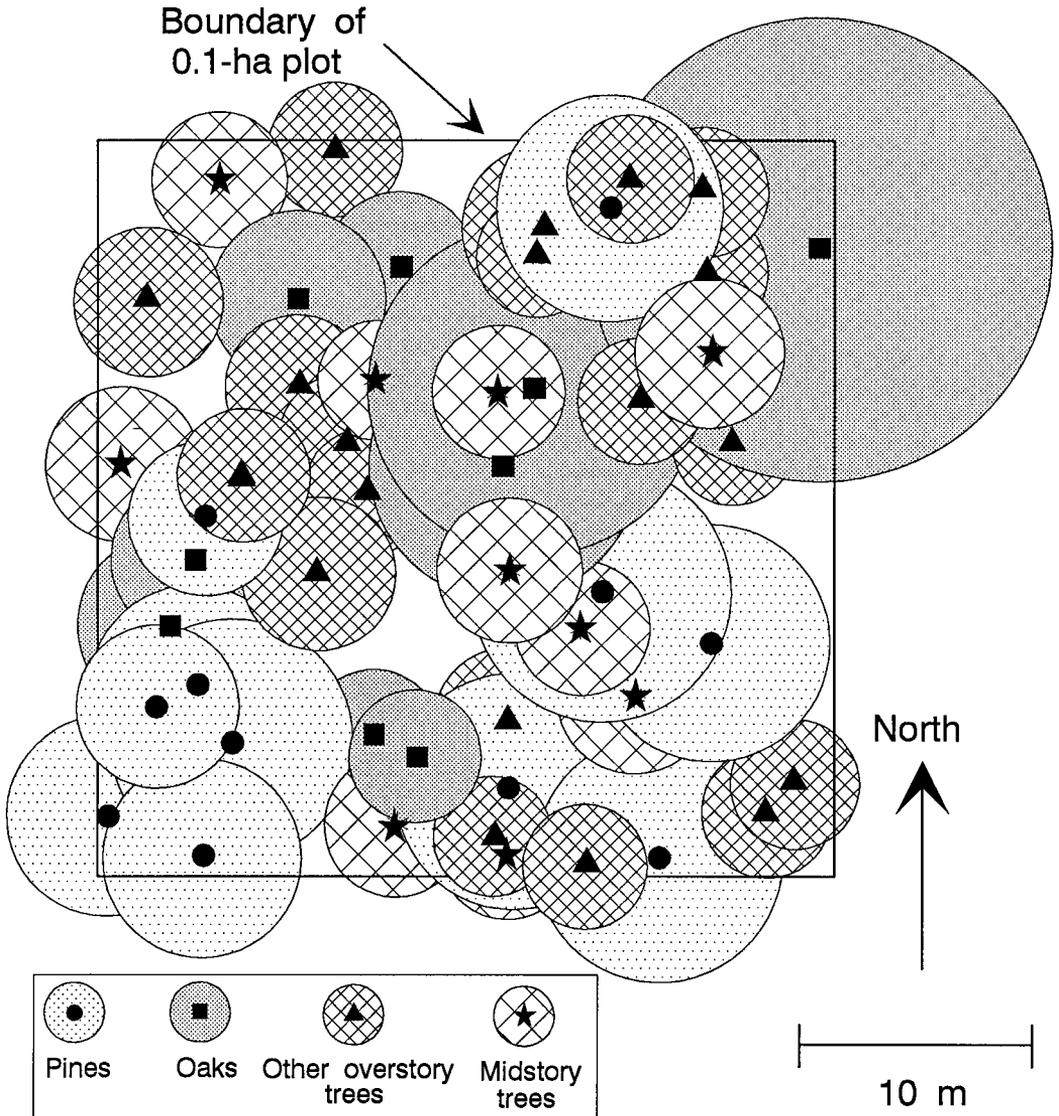


Fig. 4. Horizontal distribution of tree crowns on a 0.1-ha plot, which was close to the overall mean pine-hardwood basal area of the R.R. Reynolds Research Natural Area. The oak near the northeast corner was 78 cm in DBH. Crown width was calculated from equations presented in Table 1 and the tree's DBH in 1991. Horizontal tree position was based on a stem map. The vertical overlaying was varied to enhance clarity and does not reflect vertical position.

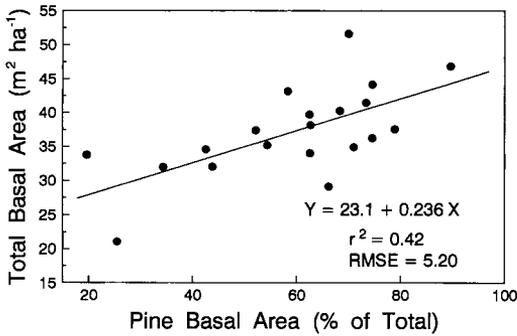


Fig. 5. The relationship between total basal area and the percentage of total basal area in the pine component for twenty 0.1-ha plots located within R.R. Reynolds Research Natural Area in 1991.

by trees in the residual stand and perhaps the disturbed seedbed conditions resulting from harvesting the virgin forest.

Another difference noted between pines and hardwoods was that areas dominated by pines tended to be higher in total basal area than areas with more hardwoods (Fig. 5). For example, when the pine basal area was 90% of the total, total basal area was predicted to be  $44 \text{ m}^2 \text{ ha}^{-1}$ , but total basal area decreased to  $28 \text{ m}^2 \text{ ha}^{-1}$  when pine basal area was 20%. This difference probably reflected the previously noted difference in the crown size of pines and hardwoods, which was also observed by Reynolds (1950).

**AGE STRUCTURE.** The age-class distributions for the pines and oaks observed in 1989 are presented in Fig. 6. The pines ranged in age from 50 to 140 years. However, 70% of the pines became established in the 4 decades that followed harvest of the virgin forest in the mid 1910s (i.e., the 50- to 80-year age classes). Ages for the pines showed a single peak, centered around the 70-year age class. The age-class distribution for the oaks was somewhat broader than for the pines, extending from 40 to 150 years. Two peaks were apparent for the oaks, one for the 70-year age class (17% of the oaks) and one for the 120-year age class (21%). The peak for the 120-year age class may reflect some earlier unidentified stand disturbance. The low representation of pines in the 120-year-old cohort (6% of the pines) may have resulted from harvesting in the 1910s, when they would have been about 50 years old. Forty-six percent of the oaks were established in the 40- to 70-year age classes.

The age-class distribution of other overstory and midstory trees was not shown in Fig. 6 because so few trees were aged. However, the age

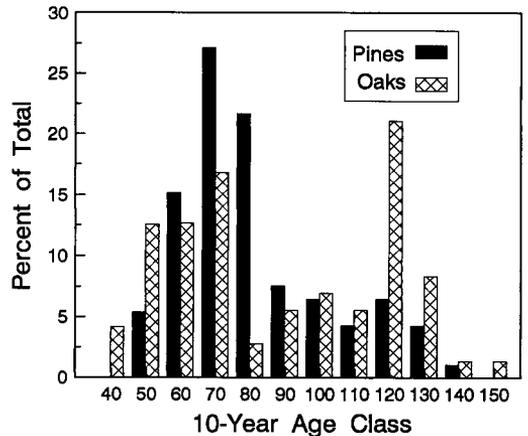


Fig. 6. The age-class structure of pines and oaks within R.R. Reynolds Research Natural Area. Based on 92 pines and 71 oaks aged in 1989.

of 10 trees in the other overstory group ranged from 37 to 67 years old and averaged 53 years; a 30-cm DBH hickory (*Carya tomentosa* (Poir.) Nutt.) was 136 years old. The midstory group contained the youngest trees recorded, which included a 19-year-old sassafras (*Sassafras albidum* (Nutt.) Nees) and a 26-year-old winged elm (*Ulmus alata* Michx.). Overall, trees in the midstory group ranged from 19 to 93 years old with a mean of 51 years for 16 trees.

A positive relationship was observed between tree size and age (Table 3). Tree age explained 23 to 51% of the variation in tree DBH and height for all species groups except other overstory trees, where the relationship was not significant for height ( $P=0.23$ ). Thus, trees existing when the virgin forest was cut in the 1910s had a growth advantage over reproduction becoming established afterward.

**TREE AND STAND GROWTH.** The basal area growth of individual trees was positively related to their basal area, which explained from 23 to 47% of the variation in this relationship for the four species groups (Table 4). Equations were solved for the observed range in tree basal areas for each species group, and values are plotted in Fig. 7. For the smaller trees within the forest (i.e.,  $<1,200 \text{ cm}^2$  in basal area or 39 cm in DBH), basal area growth rates for the other overstory and midstory groups exceeded that of the pines and the oaks. For example, a tree with a basal area of  $500 \text{ cm}^2$  was predicted to be growing at an annual rate of 14 and  $8 \text{ cm}^2$  for the other overstory and midstory groups, respectively, while a tree of the same basal area

Table 3. Regression coefficients and associated statistics for the relationship between tree size and age.

Variable and species group	Regression coefficients		Mean value	Root mean square error	Fit index
	$b_0$	$b_1$			
<b>DBH<sup>a</sup></b>					
Pines	3.23	0.00829	50.3	10.35	0.47
Oaks	2.60	0.00952	32.9	9.68	0.51
Other overstory trees	2.47	0.00674	18.0	7.42	0.23
Midstory trees	2.28	0.00804	15.0	4.81	0.24
<b>Total height<sup>b</sup></b>					
Pines	3.99	-39.6	32.5	4.98	0.39
Oaks	3.60	-38.7	22.7	4.46	0.41
Other overstory trees	ns <sup>c</sup>	ns	—	—	—
Midstory trees	3.02	-18.5	13.8	3.71	0.29

<sup>a</sup> The equation is:

$$DBH = \exp(b_0 + b_1 AGE)$$

where *DBH* is in cm and *AGE* is the tree age in years. Degrees of freedom are 90 for pines, 69 for oaks, 9 for other overstory trees, and 14 for midstory trees.

<sup>b</sup> The equation is:

$$TH = \exp(b_0 + b_1 AGE^{-1})$$

where *TH* is total height in m.

<sup>c</sup> The regression coefficient was not significantly different from zero at  $P \leq 0.10$ .

was growing at only 3 cm<sup>2</sup> for both the pines and oaks. For trees with basal areas over 1,200 cm<sup>2</sup>, growth of the pines slightly exceeded that of the oaks, and the oaks exceeded that of the other overstory trees for their mutual range in tree basal area. For the larger trees (e.g., a basal area of 4,000 cm<sup>2</sup> or 71 cm in DBH), annual growth of the pines was predicted to be 48 cm<sup>2</sup>, while a comparable value for the oaks was 43 cm<sup>2</sup>.

Stand-level survivor growth for pines and hardwoods from the twenty 0.1-ha plots is shown in Fig. 8. The growth of each component was positively related to that component's basal area, as is typically observed in studies of stand-level growth (Farrar et al. 1989; Shelton and Murphy 1997). Although pine basal area did not

significantly reduce the growth of the hardwood component ( $P=0.85$ ) nor did hardwood basal area affect pine growth ( $P=0.93$ ), the competition between pines and hardwoods is often found to be a significant factor in studies of the growth interactions within pine-hardwood stands (Farrar et al. 1989; Shelton and Murphy 1997). Possible explanations for these conflicting results are that the present RNA has reached the site's carrying capacity or trees from outside the plot boundary may have influenced the growth within the plot without being accounted for. For the same basal area, the pines and hardwoods were growing at about the same rate. For example, the annual basal area growth is predicted to be 0.35 m<sup>2</sup> ha<sup>-1</sup> for both pines and hardwoods when the basal area of each group is 25 m<sup>2</sup> ha<sup>-1</sup>.

Table 4. Regression coefficients and associated statistics for predicting the annual basal area growth of individual trees from the trees mean basal area during the growth period.

Species group	Regression coefficients <sup>a</sup>		Mean value	Root mean square error	Fit index
	$b_0$	$b_1$			
Pines	4.275	-1591	33.0	15.8	0.39
Oaks	4.137	-1509	15.9	12.9	0.47
Other overstory trees	3.201	-296	5.0	5.0	0.45
Midstory trees	2.385	-158	2.6	2.9	0.23

<sup>a</sup> The equation is:

$$\Delta B = \exp(b_0 + b_1 B^{-1})$$

where:  $\Delta B$  is tree basal area growth in cm<sup>2</sup> yr<sup>-1</sup>, and *B* is mean basal area of the tree during the growth period in cm<sup>2</sup>. Degrees of freedom are 180 for pines, 173 for oaks, 312 for other overstory trees, and 247 for midstory trees.

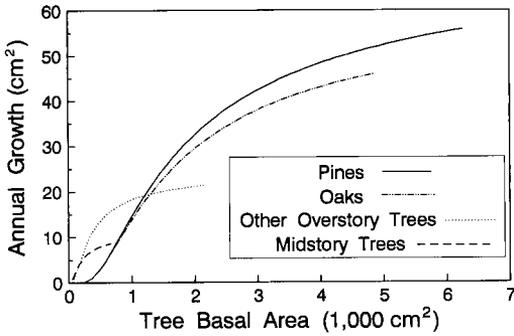


Fig. 7. Relationship between the mean annual basal area growth of individual trees within the R.R. Reynolds Research Natural Area to the tree's mean basal area during the observation period. Values calculated from prediction equations presented in Table 4.

The components of stand-level growth are presented by species groups in Table 5. Recruitment was only 0.1 tree  $\text{ha}^{-1} \text{yr}^{-1}$  for the oaks and was 0.0 tree  $\text{ha}^{-1} \text{yr}^{-1}$  for the pines. By contrast, recruitment totaled over 6 trees  $\text{ha}^{-1} \text{yr}^{-1}$  for the other overstory and midstory trees. The three species contributing the most to recruitment were: eastern hophornbeam (*Ostrya virginiana* (Mill.) K. Koch), sweetgum, and winged elm (25, 23, and 13%, respectively). Pines had the greatest mortality rates, which averaged 3 trees  $\text{ha}^{-1} \text{yr}^{-1}$ , while the lowest mortality was for the other overstory tree group. Most pine mortality was judged to be the result of insect damage (82%), while hardwood mortality was from unknown causes (79%). The combined effect of recruitment and mortality reduced the pine and oak density but increased the number of other overstory and midstory trees.

Survivor growth in basal area was by far greatest for the pines, which was twice that of

the oaks and over ten times that of the midstory trees. Basal area recruitment was nil for the pines and the oaks, but recruitment for the midstory trees was just about equal to survivor growth. Because pine mortality was in trees averaging 48 cm in DBH, the mortality losses in basal area were substantial and resulted in a net decline over the observation period. By contrast, mortality losses in the hardwood groups were mainly trees in the smaller DBH classes. Thus, hardwood losses did not completely offset the gains from survivor growth and recruitment, and net growth was small but positive for these groups.

The growth components for volume were similar to those of basal area. Both survivor growth and mortality losses were greatest for the pines, which showed net losses for the observation period. The hardwood groups showed net increases in volume growth, which was greatest for the oaks and least for the midstory trees. Because of the large losses in the pines, there was an overall net decrease in total volume through time.

**Discussion.** THE STANDING CROP AND ITS SPATIAL DISTRIBUTION. Total basal area within the RNA averaged 37  $\text{m}^2 \text{ha}^{-1}$  with the pines accounting for about 60% of the total. This basal area is remarkably similar to those of other forests with a comparable history. For example, Switzer et al. (1979) reported that even-aged pine stands in the veteran stage of succession ( $\approx 130$  years old) averaged 35  $\text{m}^2 \text{ha}^{-1}$  of total basal area with the pines accounting for about 50 to 60% of the total. Fountain and Sweeney (1987) found total basal areas of 33  $\text{m}^2 \text{ha}^{-1}$  with 72% in the pine component for a virgin pine-

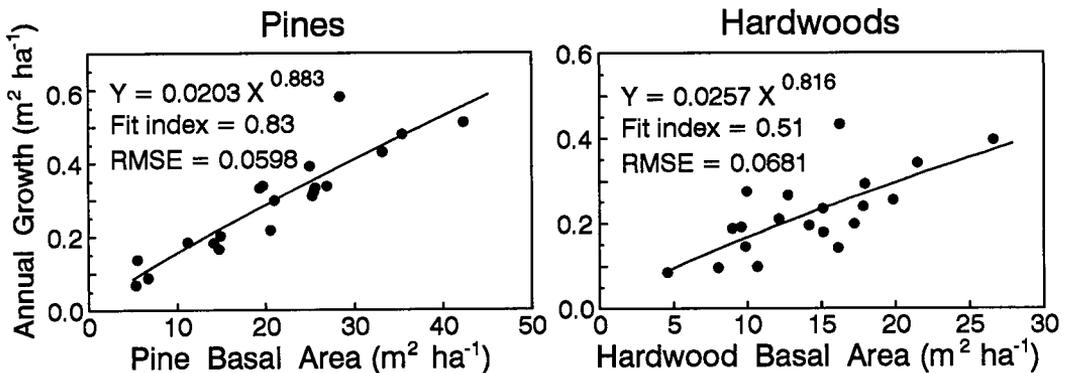


Fig. 8. Relationship between mean annual survivor growth and stand-level basal area from twenty 0.1-ha plots located within R.R. Reynolds Research Natural Area.

Table 5. Mean annual growth for species groups within the R.R. Reynolds Research Natural Area. The observation period was from 1989 to 1994 for twelve 0.1-ha plots and from 1991 to 1994 for eight 0.1-ha plots.

Variable and species group	Survivor growth	Recruitment	Mortality	Net growth <sup>a</sup>
Density (trees ha <sup>-1</sup> )				
Pines	0 <sup>b</sup>	0.00	3.33	-3.33
Oaks	0	0.10	1.25	-1.15
Other overstory trees	0	2.37	0.92	1.45
Midstory trees	0	3.78	1.68	2.10
Total	0	6.25	7.18	-0.93
Basal area (m <sup>2</sup> ha <sup>-1</sup> )				
Pines	0.295	0.000	0.601	-0.306
Oaks	0.137	0.001	0.065	0.073
Other overstory trees	0.064	0.017	0.015	0.066
Midstory trees	0.022	0.026	0.017	0.031
Total	0.518	0.044	0.698	-0.136
Volume (m <sup>3</sup> ha <sup>-1</sup> )				
Pines	2.809	0.000	6.327	-3.518
Oaks	1.543	0.002	0.640	0.905
Other overstory trees	0.572	0.062	0.093	0.541
Midstory trees	0.153	0.096	0.103	0.146
Total	5.077	0.160	7.163	-1.926

<sup>a</sup> Net growth = Survivor growth + Recruitment - Mortality.

<sup>b</sup> By definition, there is no change in the number of survivors for a period because a tree must be living at both inventories to be a survivor.

oak stand in the Ouachita Mountains, where the dominant trees were 150- to 200-years old. Wahlenberg (1960) reported that fully stocked, undisturbed loblolly pine stands generally fluctuate around an equilibrium basal area of 29 to 42 m<sup>2</sup> ha<sup>-1</sup>. In the present RNA, pine basal areas averaged 23 m<sup>2</sup> ha<sup>-1</sup>, but a maximum of 42 m<sup>2</sup> ha<sup>-1</sup> was measured for one of the permanent plots and one-quarter of the plots were  $\geq 29$  m<sup>2</sup> ha<sup>-1</sup>. Schnur (1937) reported that upland oak stands on good sites will approach basal areas of 34 m<sup>2</sup> ha<sup>-1</sup> at 100 years of age.

Pine basal area was mainly in loblolly pine which accounted for over 80% of the pine total. Hardwood basal area was concentrated in white oak (5.5 m<sup>2</sup> ha<sup>-1</sup>) which had 54% of total oak basal area and 38% of total hardwood basal area. The second highest concentration of hardwood basal area was in southern red oak which was followed by sweetgum. Halls and Homesley (1966) reported a similar species composition in a mature pine-hardwood forest of southeastern Texas.

The stem volume within the RNA averaged 347 m<sup>3</sup> ha<sup>-1</sup> with 63% in the pine component. This total volume was close to that reported for mature, even-aged stands growing on similar sites. In northern Louisiana, Meyer (1942) reported that fully stocked loblolly pine stands will have a volume of 385 m<sup>3</sup> ha<sup>-1</sup> at 100 years. Even-aged upland oak stands on good sites have

a volume of 395 m<sup>3</sup> ha<sup>-1</sup> at 100 years (Schnur 1937).

Very minor differences in topographic relief had a pronounced influence on species composition within the RNA, with overstory pines dominating the broad upland flats (about 40 m in elevation) and pines-hardwoods or hardwoods-pines occurring along the intermittent drainages (about 37 m in elevation). This variation in species composition may be a remnant of historical wildfire effects before fire protection began in the 1930s, but it may also reflect differences in site quality. Soils nearest the ephemeral drainages are the best sites for forest growth. These good sites are rapidly invaded by both woody and herbaceous vegetation which could have prevented the establishment of pine reproduction once the canopy closed near the drains or, at least, could have reduced pine numbers. Brender and Davis (1959) also found that hardwood development in pine stands was strongly related to topographic position in the Georgia Piedmont.

**AGE STRUCTURE.** The RNA has a wide range of tree ages because of its disturbance history. For trees  $\geq 9.0$  cm in DBH, ages ranged from 50 to 140 years for the pines and from 40 to 150 years for the oaks. These trees developed from three different sources: (1) a remnant of the virgin forest that was not harvested due to species,

stem size or stem quality (2) seedlings and saplings that existed as advanced reproduction when the virgin forest was harvested, and (3) seedlings and sprouts that became established after harvest.

A substantial remnant of the virgin forest was still present in the RNA. About 20% of the pines and 40% of the oaks were in the 100-year age class and older. The higher representation of the older oaks infers that few hardwoods were harvested from the virgin stand, because of the lower demand for hardwood lumber at that time or the poor stem quality due to repeated wildfires. When released by the harvest of the virgin forest, many of the residual trees developed to become the dominant members of the new forest. Some species are able to withstand a fair degree of suppression and recover following release, especially in the open stand conditions that existed after harvest of the virgin forest. Recovery of suppressed trees has been demonstrated in both pines (Chapman 1923; Reynolds 1952) and hardwoods (Minckler 1957; Schlesinger 1978). Residual trees from the virgin forest had a distinct growth advantage over newly established seedlings or advanced reproduction because of their larger stature.

The presence of the older oaks in the RNA suggests that the original virgin forest contained a major hardwood component. This observation is confirmed by Olmstead (1902), who described a virgin forest in Arkansas that averaged 46% of its volume in hardwoods. In the Ouachita Mountains of Arkansas, virgin forests were reported to contain about 20% of the total merchantable volume in hardwoods (American Lumberman 1904).

The wide range of tree ages in the older classes (i.e., 100 to 150 years) suggests that the trees in the original virgin forest also displayed a fair degree of age variation. Similar observations have been made by others. For example, Pederson et al. (1997) found that five of the six old loblolly pine stands examined on a floodplain site in South Carolina had multiple age classes. Turner (1935) reported that the oldest trees in three virgin pine stands in the Ouachita Mountains were about twice as old as the youngest trees; however, about two-thirds of trees became established during a one-decade period. Turner emphasized the importance of natural catastrophes (frequent tornadoes in conjunction with periodic fires) in modifying the composition and structure of the virgin forests of the region.

Most of the pines in the RNA became estab-

lished following harvest of the virgin forest. For example, over 70% of the pines were established in the 4-decade period following harvest and were represented by the 50- to 80-year age classes. The prolonged establishment period for the pines may reflect the fact that wildfires frequently occurred until fire control was implemented in the early 1930s (Reynolds 1980). Seeds for this recruitment came from the residual pine trees of seed-producing sizes. Two environmental requirements for sustaining pine reproduction are that overstory basal areas should not exceed  $17 \text{ m}^2 \text{ ha}^{-1}$  (Cain 1993; Shelton and Murphy 1994) and that pine reproduction should not be overtopped by hardwoods (Cain 1994). Because these two requirements were not met, no recruitment of pines into the overstory has occurred during the last 40 years of stand development regardless of topographic position. About 46% of the oaks were in the 40- to 70-year age classes. Recruitment of the oaks into the overstory was similar in pattern to that of the pines, and the youngest tree that was aged was in the 40-year age class.

Virtually all of the other overstory trees and midstory trees became established after harvest of the virgin forest in this 32-ha area. Only 4% of the aged trees in these species groups were older than 100 years, and mean age was about 50 years. The apparent low representation of these species groups in the virgin forest was probably due to the fire history of the area (Reynolds 1980). Their establishment and subsequent development were principally associated with the implementation of fire control in the 1930s.

In the RNA, a positive relationship was observed between tree size and tree age, with age accounting for 39 to 51% of the variation in DBH and height for the pines and oaks. Similar relationships have been reported for other natural stands with a history of disturbance—southern Appalachian forests (Lorimer 1980), table mountain pine (*Pinus pungens* Lamb.) stands in southwestern Virginia (Williams and Johnson 1990), and shortleaf pine-oak stands in the Ouachita Mountains (Shelton and Murphy 1991). In addition, the size-age relationship in the RNA is very similar to that described for loblolly pine trees in virgin forests of South Carolina (Chapman 1905). The positive relationship between size and age was partially due to the fact that DBH and height growth are cumulative processes. Another contributing factor was that stand conditions in the RNA have changed fol-

lowing harvest of the virgin forest. Open conditions existed immediately after harvest, and residual trees and advanced reproduction developed in a relatively free-to-grow environment. In contrast, seedlings becoming established later in stand development grew under competition from the older trees.

**SIZE STRUCTURE.** Tree size within the RNA is comparable to that reported for the virgin forest of the region. For example, Wahlenberg (1960), who compiled data regarding the size of loblolly pine in virgin stands, reported an average DBH of about 60 cm with heights of 34 to 37 m on good sites. Within the RNA, DBH for loblolly pine averaged 56 cm in 1991, and mean height was 36 m. The largest loblolly pine trees observed in virgin stands were 90 to 150 cm in DBH with heights of 40 to 43 m (Wahlenberg 1960). In addition, diameters of old-growth pines in the Boiling Springs Natural Area in South Carolina ranged from 90 to 110 cm with heights of 40 to 48 m (Jones et al. 1981). However, this large-tree component is lacking in the present RNA, probably because the larger trees were cut in the 1910s and sufficient time has not allowed for their development. The largest loblolly pine measured on the 20 permanent plots was 89 cm in DBH and the tallest tree was 41 m in height. The largest pine observed in the entire 32-ha RNA was 97 cm in DBH in 1993. Shortleaf pine trees in the RNA were generally smaller than loblolly pine trees by 27% in mean DBH and 8% in mean height. Such size differences are commonly observed when these two species occur in mixed stands (Reynolds 1959; Harrington 1987).

Published data are lacking for the size of hardwoods in virgin stands on uplands of the southern United States. In a mature shortleaf pine-white oak stand in Texas, Wilson and Hacker (1986) reported a 256-year-old white oak that was 32 m tall, and in the 51- to 60-cm DBH class. Within the RNA, the largest hardwood recorded in the permanent plots was a white oak with a DBH of 73 cm, and the tallest hardwood, also a white oak, was 36 m. However, a white oak with DBH of 112 cm was measured in 1993 outside the permanent plot boundaries of the RNA.

Each species group had a unique diameter-class distribution, reflecting differences in shade tolerance, growth habit, life history, and age structure. The pines (the most shade-intolerant species group) displayed a normal distribution,

while the other overstory trees and midstory trees (the most shade-tolerant groups) had a negative exponential pattern. By contrast, the distribution curve for the oaks was intermediate in form. Glitzenstein et al. (1986) reported a similar pattern of diameter-class distributions in an old-growth pine-hardwood forest in East Texas. The paucity of pines in the smaller diameter classes suggests that few recruits will be available to replace the old-growth relics as they die from natural senescence. The absence of large trees in the other overstory tree and the midstory tree groups also suggests that these groups were poorly represented before harvest of the virgin forest.

Historical records indicate that diameter-class distributions for the pines have changed dramatically through time in the RNA. In 1937, DBH classes for both pines and hardwoods followed negative exponential distributions (Cain and Shelton 1996). By 1963, overstory basal area for pines and hardwoods averaged 30 m<sup>2</sup> ha<sup>-1</sup> which prohibited the development of juvenile pines in the understory because of a closed canopy, and the negative exponential structure for pines began to disappear. Cain and Shelton (1994) reported that there were numerous pine seedlings present in the RNA in 1993, but reported no pines of sapling size (1-cm to 9-cm DBH).

**CANOPY STRUCTURE.** The RNA currently has a closed canopy, in which the species groups are vertically stratified by shade tolerance. Tree species in the upper portion of the canopy are shade intolerant or intermediate in tolerance (the pines and oaks) while the lower canopy is populated with mainly shade-tolerant species (the other overstory and midstory tree groups). In addition, many of the trees in the lower canopy were poorly and irregularly formed indicating that they had developed under a high degree of physiological stress. The vertical stratification of species within the canopy by shade tolerance has often been observed in mature forests of widely different cover types, for example: mixed mesophytic hardwoods (Runkle 1981; Abrams and Downs 1990; Brothers 1993); pine-oak (Halls and Homesley 1966; Switzer et al. 1979); mixed oaks (Parker et al. 1985; McCarthy et al. 1987; Abrams and Nowacki 1992); oak-hickory (Pallardy et al. 1988; Shotola et al. 1992); southern mixed hardwoods (Hartnett and Krofta 1989). The RNA, however, differs from many of these other forest cover types because it lacks shade-

tolerant, late-successional species that have overstory potential.

Associated with the closed canopy was a corresponding decrease in photosynthetically active radiation at the understory level to only 3.6% of full sunlight. The narrow range in canopy coverage observed for the permanent plots (86.5 to 100%) indicated that canopy gaps created by overstory mortality were too small to be detected, or the gaps have been obscured by the mid-story and upper portion of the understory canopy. As mature pines died, they remained vertical and gradually decayed into snags; there was no evidence of major windthrow during the inventories from 1989 to 1994. Instead of collapsing, large dead pines tend to remain erect and gradually deteriorate as snags over many years (Jones et al. 1981).

**FOREST GROWTH.** Individual trees within the RNA were growing very little in DBH, especially compared to trees in younger, managed stands. This was due to their large size and the fact that basal areas were higher in the RNA. A pine tree at the mean DBH was growing at an annual rate of 0.43 cm in DBH, while an oak at the mean DBH was growing at 0.33 cm. A pine in a managed stand with the same mean DBH as the RNA should be growing at an annual rate of 1.3 cm in DBH (Murphy and Shelton 1996). In an old-growth pine-hardwood stand in eastern Texas, Glitzenstein et al. (1986) reported mean annual DBH growth rates of 0.21 cm for pines and 0.14 cm for white oak (means for all trees  $\geq 20$  cm in DBH). Chapman (1905) reported that loblolly pine trees in virgin forests of South Carolina grew an average of 0.38 cm  $\text{yr}^{-1}$  in DBH from 71 to 104 years of age.

Annual stand-level survivor growth in the RNA averaged 0.52  $\text{m}^2 \text{ha}^{-1}$  for total basal area and 5.1  $\text{m}^3 \text{ha}^{-1}$  for stem volume, with the pines accounting for about 57% of the total. These values are considerably below those observed in younger, managed stands. For example, Shelton and Murphy (1997) reported that annual growth averaged 0.87  $\text{m}^2 \text{ha}^{-1}$  for basal area and 12.1  $\text{m}^3 \text{ha}^{-1}$  for volume in a 35-year old natural pine-hardwood stand on a site similar to the RNA. Because of the large standing tree crop in the RNA, a high proportion of gross primary productivity must be allocated to stand respiration, and thus fewer resources are available for growth (Larcher 1975).

The progression of trees from the understory to the overstory is crucial to sustain the com-

position of a forest. Over the 5-year monitoring period in the RNA, recruitment of trees into the overstory (i.e., growth past the 9.0-cm DBH limit) was clearly greatest for the other overstory tree and midstory tree groups, averaging 6 trees  $\text{ha}^{-1} \text{yr}^{-1}$ . This relationship was due to the presence of saplings of these species groups in the understory and the ability of these shade-tolerant saplings to grow despite intense competition for limited resources within the understory.

Mortality dominated stand-level growth of the pine component for all growth parameters. Mortality losses exceeded the gains from survivor growth, which resulted in a net decline in pine density, basal area, and volume over the monitoring period. Others have observed high mortality rates for canopy trees in old-growth stands (Jones et al. 1981; McGee 1984; McCune et al. 1988). In contrast to the pines, all hardwood groups increased in net basal area and volume during the monitoring period. Thus, the contribution of the pines to the standing crop declined, while the contribution of hardwoods increased.

**SUCCESSIONAL TRENDS.** Harvest of the virgin forests and the implementation of fire control were the two most significant events affecting the successional development of the RNA, and these same events also strongly affected the historical stand development throughout the South (White 1984). The short-term stand dynamics described in this paper show a decreasing importance for the pines and a commensurate increasing importance for the hardwoods, especially in the more shade-tolerant species groups. These short-term dynamics are supported by the long-term successional changes described by Cain and Shelton (1996), who reported stand-level changes in overstory trees in the RNA over a 56-year period beginning in 1937. During that time, development of overstory pines and hardwoods created an understory environment that was generally unfavorable for the survival, growth, and development of shade-intolerant species.

Cain and Shelton (1995) described the dynamics within the understory of the RNA over a 38-year period beginning in 1956. Shade-tolerant species (especially red maple [*Acer rubrum* L.], dogwood [*Cornus florida* L.], and hollies [*Ilex* spp.]) tended to increase in importance in the understory throughout this period, while the shade-intolerant species sharply declined during the same interval. Although pine seedlings periodically became established in the un-

derstory, none developed into saplings because of the unfavorable environmental conditions for these shade-intolerant species. Our findings are generally consistent with those of Harcombe and Marks (1978) who reported that an under representation of saplings of dominant overstory tree species (e.g., loblolly and shortleaf pines, American beech [*Fagus grandifolia* Ehrh.], southern magnolia [*Magnolia grandiflora* L.], water oak, and sweetgum) was common in mesic and wet forests of southeast Texas. They considered the phenomenon to be geographically widespread and attributed sapling mortality to competition from both overstory and understory species.

The perpetuation of the pine forest type is strongly dependent on periodic disturbances, which occur through several different mechanisms. Common natural disturbances include physical factors, such as fires and tornadoes, and pathological factors, such as insects and diseases. Man also contributes to disturbance through timber harvests, forest management, and fires, both prescribed and otherwise. The development of a substantial hardwood component during the natural succession of the pine-dominated forest is well known (e.g., Wahlenberg 1960; Blair and Brunett 1976; Finegan 1984; Huston and Smith 1987). Without periodic disturbance, successional development is characterized by the progressive replacement of pines with hardwoods. The progression to a hardwood-dominated forest reflects differences in the relative physiology of the associated species occurring in southern forests, which affect establishment, development, and survival. Compared to shade-intolerant pines, some hardwood species have a distinct ability to persist and develop in the shade (Cain and Shelton 1995). It is doubtful that the overstory of the present 32-ha forest will continue to be dominated by pines in the absence of large-scale perturbations that would facilitate the development of younger cohorts from these shade-intolerant species (Oliver 1981).

The RNA had developed relatively free of catastrophic disturbance from the 1930s until the 1994 inventory that was conducted in conjunction with this paper. However, a pine bark-beetle infestation began in 1993 and spread over considerable area ( $\approx 5$  ha) within the RNA during the 1994 growing season, killing most of the pines within the infected area (Cain and Shelton 1996). Despite this disturbance, the canopy below the dead and dying old-growth pines remained closed during the 1994 growing season

because of the combined effect from understory, midstory, and overstory hardwoods. This observation was confirmed by measuring photosynthetically active radiation beneath the forest canopy at a height of 1.37 m. Photosynthetically active radiation was not significantly related to the intensity of the southern pine beetle infestation, and averaged 7.9, 5.4, and 7.2% of full sunlight for areas where pine mortality was complete, partial, and none, respectively. Thus, we anticipate that shade-intolerant pines are not likely to become established and to achieve overstory status unless some factor removes the hardwood component within the infected areas, such as wildfire or major windthrow of the pine snags or dominant hardwoods.

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