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Secondary forest succession following reproduction cutting on the Upper Coastal Plain of southeastern Arkansas, USA

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Abstract

To contribute to an understanding of forest management on secondary forest succession, we conducted vegetation surveys in a chronosequence of pine stands ranging in age from 1 to 59 years. Adjacent areas were compared at 1, 7, 12, and 17 years following two reproduction cutting methods (clearcuts or pine seed-tree cuts); a 59-year-old pine stand that was periodically thinned was also included to represent conditions before reproduction cutting. Because average or better natural loblolly and shortleaf pine (*Pinus taeda* L. and *P. echinata* Mill.) seed crops coincided with the planned site disturbances, pines dominated the seedling-size classes at 1 and 7 years after reproduction cutting, the sapling-size classes at 7, 12, and 17 years after reproduction cutting, and the small- and large-tree size classes at 12, 17, and 59 years after reproduction cutting. For seedling-size classes, three measures of woody plant diversity (Shannon's (H'), Simpson's (D), and evenness (e) indices) tended to increase from 1 to 12 years after reproduction cutting. In the sapling-size classes, H' and D diversity indices were highest at 17 years and lowest at 59 years after reproduction cutting. For small-tree size classes, H', and D were highest at 7 years and lowest at 12 years after reproduction cutting. Across all but the large-tree size classes, woody species richness peaked 7 years after reproduction cutting. Naturally regenerated pines achieved complete crown closure by 17 years after reproduction cutting; consequently, the presence of shade-tolerant woody plants increased in the understory, and shade-intolerant herbaceous plants disappeared from the forest floor. Published by Elsevier Science B.V.

Keywords: Density; Natural regeneration; *Pinus echinata; Pinus tueda;* Upper Coastal Plain; Woody plant diversity

1. Introduction

In the southeastern United States, a major physiographic subregion is the Upper Coastal Plain, where loblolly and shortleaf pines (*Pinus taeda* L. and *P. echinata* Mill.) predominate (Baker and Langdon, 1990; Lawson, 1990). In the West Gulf Region, which extends from the Mississippi River into East Texas and southeast Oklahoma, loblolly and shortleaf pines occur naturally in pure stands or mixed with hardwoods. Since these two southern pines regenerate from wind-disseminated seeds and are shade-intolerant, they comprise an early seral stage in forest succession on Coastal Plain sites. However, in the absence of recurring human or natural disturbances, vegetation on these sites will likely evolve into a climax forest of mixed hardwoods (Quarterman and Keever, 1962; Cain and Shelton, 1994, 1995; Shelton and Cain, 1999).

An increasing emphasis on ecosystem management of forests within the United States (Brooks and Grant, 1992; Swank and Van Lear, 1992; Irland, 1994; Kaufmann et al., 1994; Salwasser, 1994) has necessitated that

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forest managers understand the role of major forest disturbances, such as clearcuts, on successional changes in woody vegetation diversity through time. Such investigations have been conducted in the Southern Appalachians (Boring et al., 1981; Parker and Swank, 1982; Elliott and Swank, 1994; Elliott et al., 1997), western Oregon (Gholz et al., 1985), and northeastern hardwood forests (Hornbeck et al., 1987; Gove et al., 1992; Reiners, 1992). However, there is a lack of information on early successional trends following reproduction cutting of southern yellow pine stands on the Upper Coastal Plain.

Desirable forest species can be naturally perpetuated by the application of silvicultural techniques, which include various reproduction cutting methods (Smith, 1986). In 1980, two 16 ha management areas were set aside on the Upper Coastal Plain of southeastern Arkansas to demonstrate even-aged regulation of naturally regenerated loblolly and shortleaf pines by using clearcuts and seed-tree reproduction cutting methods on contiguous 2 ha blocks and strips at 5-year intervals. In order to understand the role of early and late successional species in the recovery of forest structure, the present study was initiated to document successional changes in woody plant species composition and diversity using a chronosequence of adjacent stands that developed on these management areas at 59, 1, 7, 12, and 17 years after reproduction cutting. By substituting space for time, we inferred change in woody vegetation by assuming that the only difference between disturbed sites was time and that the chronological sequence should represent vegetation change through time (Laven, 1982). Billings (1938) employed a chronosequence of different aged pine stands to detail the structure and development of old-field shortleaf pines in the Piedmont region of North Carolina. Analysis of chronosequences of forest stands that represent different ages has been widely used to evaluate successional change (Peet and Loucks, 1977; Christensen and Peet, 1984; Finegan, 1984; Roberts and Christensen, 1988; Vankat, 1991).

2. Methods

2.1. Study area

This investigation was conducted within two adjacent 16 ha forest management units on the Upper Coastal Plain in southeastern Arkansas, USA, at 33°02′N and 91°56′W. The area has an elevation of about 40 m. Soils are Arkabutla and Bude silt loams (Aeric Fluvaquents and Typic Fragiudalfs, respectively) with a site index of 27 m at 50 years for loblolly and shortleaf pines. Site index is a measure of the relative productive capacity of a site for the trees that are being studied and is based on the height of the dominant trees at an arbitrarily chosen age (Ford-Robertson, 1971). When the reproduction cutting methods were initiated in 1980, the two 16 ha management units were homogeneous in stand composition as well as in soils, climate, topography, and site index.

The growing season is about 240 days, and annual precipitation averages 140 cm. Seasonal extremes are wet winters and dry autumns. Daily temperatures average 22°C during the growing season — March to September — and 11 °C during the dormant season — October to February (USDA, 1979).

2.2. Management history

From the mid-1930s to the late-1960s, the study sites were managed for pine timber production using single-tree selection, which involves periodic harvesting of the poorest trees while retaining the best trees within specified size classes for future harvests and natural seeding (Reynolds, 1969). From 1970 to 1980, the areas were not managed and became overstocked (basal area >23 m^2 ha-‘) with pines that ranged from 25 to 60 cm in diameter at breast height (DBH), taken 1.37 m above ground. When the two areas were selected for study installation in 1980, there was a mixture of understory and midstory hardwood species beneath the pine canopy. Prescribed burns were conducted on both areas in March 1980 to reduce hardwood competition and the hazard from potential wildfires.

Each 16 ha management unit was divided into eight subunits containing 2 ha each. One management unit was subdivided into strips (50 m x 400 m) and the other into blocks (100 m×200 m), with the long axes oriented north to south. At approximately 5-year intervals, reproduction cutting progressed from east to west in each 16 ha management unit to ensure that pine seeds from residual trees bordering the cuts would be disseminated downwind and across the clearcuts (Fig. 1).

Clearcutting or seed-tree cutting were completed during the following time frames: spring 1981,

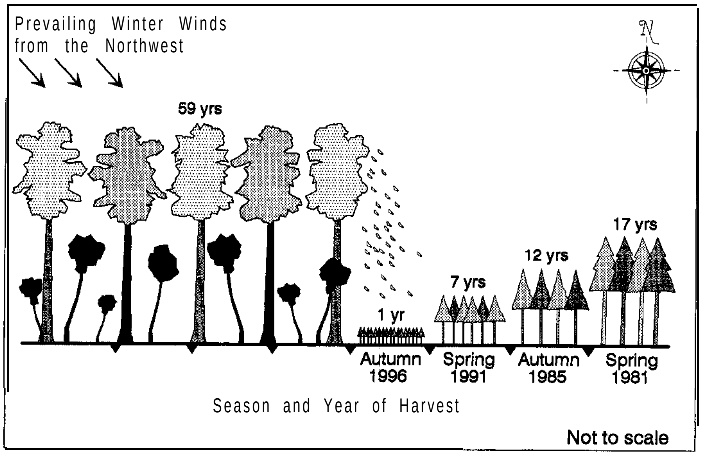

Fig. 1. Schematic diagram representing a chronosequence of naturally established loblolly-shortleaf pine stands at 59, 1, 7, 12, and 17 years after reproduction cutting on the Upper Coastal Plain of southeastern Arkansas.

autumn 1985, winter and spring 1991, and autumn 1996. Trees were cut at a height of ≤0.3 m above ground. After being felled, trees ≥24 cm DBH were delimbed on site, then logs were removed in 11 m lengths or tree length by use of articulated rubber-tired skidders. During the 1981 and 1985 harvests, trees of pulpwood size (9.1-23.9 cm DBH) were delimbed on site, sawn into 2.4 m lengths, loaded onto forwarders, and removed by use of crawler or rubber-tired tractors. In 1991 and 1996, pulpwood-sized trees were skidded tree length from the site after they were delimbed. At the time of each 2 ha clearcut, pines on the remaining uncut subunits were thinned to a residual basal area of 18 m^2 ha-’ by harvesting merchantable trees in the smaller DBH classes. With this management technique, pines on the initial clearcuts would be 40 years old at the end of eight harvests, and the process could conceivably be repeated indefinitely.

When measurements were taken for the present investigation in 1997, trees on four of the eight subunits in each 16 ha study area had been cut. In each 2 ha subunit where pines were designated for reproduction cutting, all pines were clearcut with the following exceptions. In 1985, approximately 30 seed trees ha^{-1} were retained on the strip subunit for 5 years, then were harvested. Similarly, 30 seed trees ha^{-1} were retained on the block subunit in 1996.

By autumn 1997, the cutting schedules employed between 1981 and 1996 resulted in a chronosequence of vegetation that became established 59, 1, 7, 12, and 17 years after harvest of the merchantable-tree component (Fig. 1). We determined age of the oldest stands by taking increment cores at 1.37 m in height from 20 dominant and codominant pines and counting growth rings. We added 5 years to the ring count as the time required for pine seedlings to grow to a height of 1.37 m in uneven-aged stands. The mean tree age was 59 years with a standard deviation of 13 years. When the virgin forests were cut in southeastern Arkansas around 1915, the harvesting technique was basically an economic clearcut, where all merchantable trees were removed to a 36 cm stump diameter. To facilitate discussion in this paper, we refer to the oldest stand as being 59 years in age.

To promote the establishment of natural pine regeneration, prescribed winter burns were periodically conducted in advance of reproduction cutting to temporarily topkill small hardwoods and create favorable pine seedbed conditions by reducing litter on the forest floor as follows: November 1986, February 1987, December 1989, and December 1995. All 2 ha subunits that had previously received a clearcut or seed-tree cut were excluded from these bums.

In the summer of 1980, a basally injected herbicide’ (0.03 kg picloram plus 0.12 kg 2,4-D L^{-1} as amine

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[1] This publication reports research involving herbicides. It does not contain recommendations for their use nor does it imply that the uses discussed here have been registered. All uses of herbicides must be registered by appropriate State and/or Federal agencies before they can be recommended.

salts) was used to control nomnerchantable hardwoods on the 2 ha block and strip designated for clearcutting in 1981. Likewise, in the summer of 1984, a soil-applied herbicide (3.4 kg a.i. ha-' of hexazinone dispersed from spotguns on a 0.9 mx0.9 m grid) was used for hardwood control on the 2 ha block and strip where cutting was done in autumn 1985. At the time of the 1991 and 1996 clearcuts, no herbicides were used because repeat burning and disturbance from harvesting eliminated the need for understory vegetation control. Although minor disturbances varied across ages, harvesting was the major disturbance that established the chronosequence consistently across ages.

2.3. Measurements

In autumn 1997, a grid of 4, 40, and 400 m^2 circular quadrats (subplots) was systematically established within each of five 2 ha strips and five 2 ha blocks, representing successional ages of 1, 7, 12, 17 and 59 years after reproduction cutting. Blocks contained fifty 4 m^2 quadrats and twenty-five 40 m^2 quadrats; strips contained fifty-two 4 m^2 quadrats and twenty-six 40 m^2 quadrats. Both blocks and strips had ten400 m^2 quadrats.

Within each 4 m^2 quadrat, ocular estimates were made of percent ground cover from: herbaceous vegetation by type (graminoids, forbs, vines, and semi-woody plants); understory (≤ 9.0 cm DBH) pines, hardwoods, and nonarborescent woody plants; overstory-midstory (≥ 9.1 cm DBH) pines and hardwoods. The 4 m^2 quadrats were also used for rootstock counts of seedling-sized (<1.3 cm DBH) stems by species. A rootstock was comprised of either single or multiple stems (clump) which obviously arose from the same root system. No distinction was made between regeneration from seeds and vegetative reproduction. The 40 m^2 quadrats were used for counts of woody saplings (stems $\geq$ 1.3-9.0 cm DBH within 2.5 cm DBH classes) by species, and the 400 m^2 quadrats were used for counts of overstory-midstory trees (stems >9.0 cm DBH within 2.5 cm DBH classes) by species. The overstory-midstory component was split into small trees (9.1-24.0 cm DBH) and large trees (>24.0 cm DBH).

2.4. Data analyses

We characterized the successional ages using simple descriptive statistics. To express the variation in vegetative properties within a successional age, we grouped the subplots in each 2 ha block and strip into equal north and south halves to form four pseudo-replications (Hurlbert, 1984). We calculated means and standard errors for various vegetative properties by using these pseudoreplicates to represent a successional age. Means were calculated for density (number of stems or rootstocks) and basal area (for saplings and overstory-midstory trees only) by species. To simplify data summaries, we categorized species into five groups: pines, oaks, other overstory species, midstory species, and nonarborescents. Pines and oaks were classified by genera, while the other groups were classified by their potential position within the canopy (Cain and Shelton, 1994). Frequency of occurrence was determined as the percentage of subplots with at least one representative of the species.

For seedlings, importance values (IVs) of species groups were calculated on the basis of relative density+relative frequency. For saplings, midstory, and overstory trees, IVs of species were calculated as relative density+relative basal area+relative frequency. Curtis and McIntosh (1951) proposed the concept of “importance value”, which is commonly used to characterize vegetative composition and to distinguish the dominant vegetation of an area. In this paper, the term “relative” refers to an individual species group’s contribution to the total for all species groups. Diversity of woody species was determined by size class (seedlings, saplings, small trees, and large trees) by years after reproduction cutting. Measures of diversity included Shannon’s index (H'), Simpson’s index (D), evenness index (e), and species richness (S) (Odum, 1971, 1975).

3. Results

3.1. Species composition

Across all five disturbance intervals, there were two *Pinus* species, six ***Quercus*** species, and 14 hardwood species with midstory or overstory potential (Table 1). Another 15 genera were categorized as nonarborescent woody plants.

Seedling-sized pines were present on all sites except 17 years after disturbance (Table 1). Lack of seedling pines at that age indicated their intolerance to

Table 1
Woody species presence relative to size class and years after reproduction cutting on five, 4 ha sites managed for natural pine productivity in southeastern Arkansas

Pines, oaks, and other woody species by potential canopy position	Species presence (+) or absence (0) by size class and years after reproduction cutting																			
	Seedlings (<1.5 cm DBH)					Saplings (1.5–9.0 cm DBH)					Small trees (9.1–24.0 cm DBH)					Large trees (>24.0 cm DBH)				
	59	1	7	12	17	59	1	7	12	17	59	1	7	12	17	59	1	7	12	17
Pines																				
Pinus echinata and *P. taeda*	+	+	+	+	0	+	0	+	+	+	+	+	+	+	+	+	+	0	0	+
Oaks																				
Quercus alba	+	+	+	+	0	+	+	+	+	+	0	+	+	0	0	0	0	0	0	0
Q. falcata	+	+	+	+	+	+	+	+	+	+	0	+	+	0	+	0	0	0	0	0
Q. marilandica	+	0	+	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Q. nigra	+	+	+	+	+	0	0	+	+	+	0	0	+	0	+	0	0	0	0	0
Q. phellos	+	+	+	+	0	0	0	+	0	0	0	0	0	0	0	0	0	0	0	0
Q. stellata	+	+	+	+	0	0	0	+	+	+	0	0	0	0	0	0	0	0	0	0
Other overstory hardwoods																				
Carya spp.	0	0	+	0	0	+	+	+	0	+	0	0	0	0	0	0	0	0	0	0
Fraxinus spp.	+	+	+	0	0	0	+	+	+	+	0	0	+	0	0	0	0	0	0	0
Liquidambar styraciflua	+	+	+	+	+	+	+	+	+	+	+	0	+	0	0	0	0	0	0	0
Nyssa sylvatica	+	+	+	+	+	0	0	+	+	+	0	+	0	0	0	0	0	0	0	0
Midstory hardwoods																				
Acer rubrum	+	+	+	+	+	+	+	+	+	+	+	0	+	0	+	0	0	0	0	0
Cornus florida	+	+	+	+	+	0	+	+	+	+	0	+	+	+	0	0	0	0	0	0
Diospyros virginiana	+	+	+	+	+	0	+	+	+	+	0	0	0	0	0	0	0	0	0	0
Ilex opaca	+	0	+	+	+	0	0	+	+	+	0	0	0	0	0	0	0	0	0	0
Morus rubra	0	0	+	0	0	0	0	0	+	0	0	0	0	0	+	0	0	0	0	0
Ostrya virginiana	+	+	+	+	0	0	0	+	+	0	0	0	0	0	0	0	0	0	0	0
Prunus serotina	+	0	+	+	0	0	0	+	+	+	0	0	0	0	0	0	0	0	0	0
Salix nigra	+	0	0	0	0	0	0	+	0	0	0	0	0	0	0	0	0	0	0	0
Sassafras albidum	+	+	+	+	0	+	+	+	+	0	0	0	0	0	0	0	0	0	0	0
Ulmus alata	+	+	+	+	+	0	+	+	+	+	0	0	+	0	0	0	0	0	0	0

Table 1 (*Continued*)

Pines, oaks, and other woody species by potential canopy position	Species presence (+) or absence (0) by size class and years after reproduction cutting																			
	Seedlings (<1.5 cm DBH)					Saplings (1.5–9.0 cm DBH)					Small trees (9.1–24.0 cm DBH)					Large trees (>24.0 cm DBH)				
	59	1	7	12	17	59	1	7	12	17	59	1	7	12	17	59	1	7	12	17
Nonarborescents																				
Aralia spinosa	+	+	+	0	+	0	0	+	+	+	0	0	0	0	0	0	0	0	0	0
Callicarpa americana	+	+	+	+	+	0	0	0	+	0	0	0	0	0	0	0	0	0	0	0
Castanea spp.	0	+	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cephalanthus occidentalis	+	0	0	0	0	+	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Crataegus spp.	+	+	+	+	+	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hamamelis virginiana	+	+	+	0	0	0	0	+	0	0	0	0	0	0	0	0	0	0	0	0
Ilex decidua/I. vomitoria	+	+	+	+	+	0	0	+	+	+	0	0	0	0	0	0	0	0	0	0
Ligustrum spp.	+	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Prunus spp.	+	+	+	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rhamnus caroliniana	0	0	0	0	+	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rhus spp.	+	+	+	+	0	+	0	+	+	+	0	0	0	0	0	0	0	0	0	0
Styrax americanus	0	0	0	0	0	0	+	0	0	0	0	0	0	0	0	0	0	0	0	0
Symplocos tinctora	+	+	+	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Vaccinium spp.	+	+	+	+	+	0	0	0	0	+	0	0	0	0	0	0	0	0	0	0
Viburnum spp.	0	0	0	0	0	0	0	0	0	+	0	0	0	0	0	0	0	0	0	0

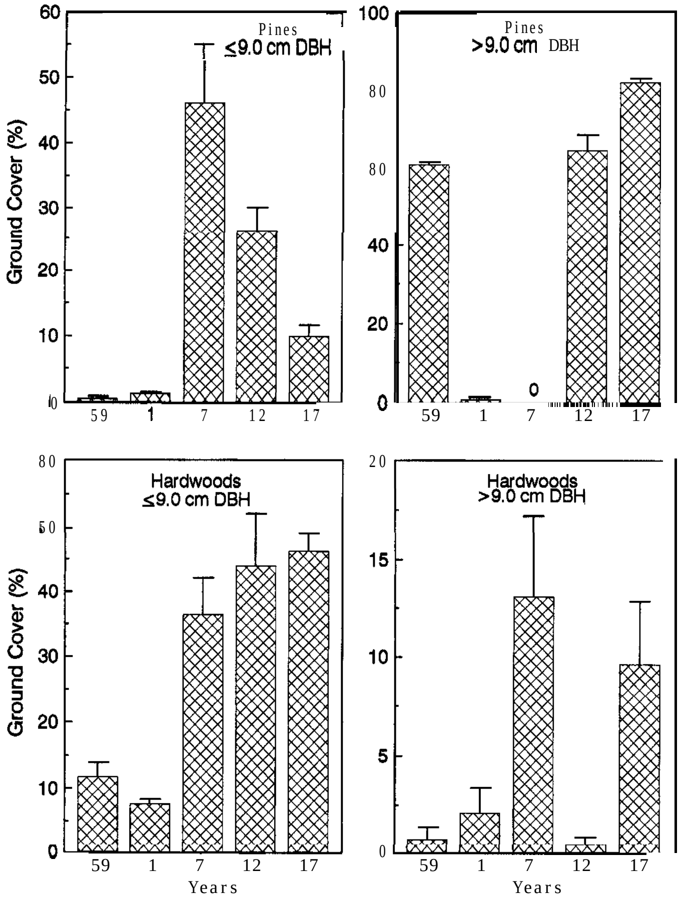

Fig. 2. Percent ground cover (mean+S.E.) from pines and hardwoods by size class relative to years after reproduction cutting of natural loblolly-shortleaf pine stands on a Coastal Plain site.

shade under a closed canopy. A measure of canopy closure was percent ground cover which averaged 82% from overstory pines and 56% from all hardwoods at year 17 (Fig. 2).

Shade-intolerant herbaceous vegetation (graminoids, forbs, vines, and semi-woody plants) also responded negatively to canopy closure (Fig. 3). Percent ground cover from graminoids, forbs, and semi-woody plants declined across the chronosequence beginning at 1 or 7 years after disturbance by reproduction cutting to near zero at 17 years after disturbance. Ground cover from these herbaceous species was also high at 59 years after reproduction cutting because periodic thinning permitted sunlight to reach the forest floor beneath the high crowns of mature pines. Once vines became established, they also exhibited a decline in percent ground cover from 7 to 17 years after disturbance, but their cover did not drop to zero because they were not restricted to the forest floor. Vines grew into the canopy where they were exposed to partial sunlight which sustained their presence.

Sapling-sized pines were found on all but the 1-year-old disturbed sites; they were absent because loblolly and shortleaf pines will not grow to sapling size within 1 year after establishment from seed (Table 1). All sites had pines in the small-tree size class; their presence at 1 and 7 years indicated that some suppressed pines from the initial stand survived the most recent disturbances. At 7 and 12 years after disturbance, pines had not attained diameters >24 cm (i.e., large trees), but these size classes were found 1,

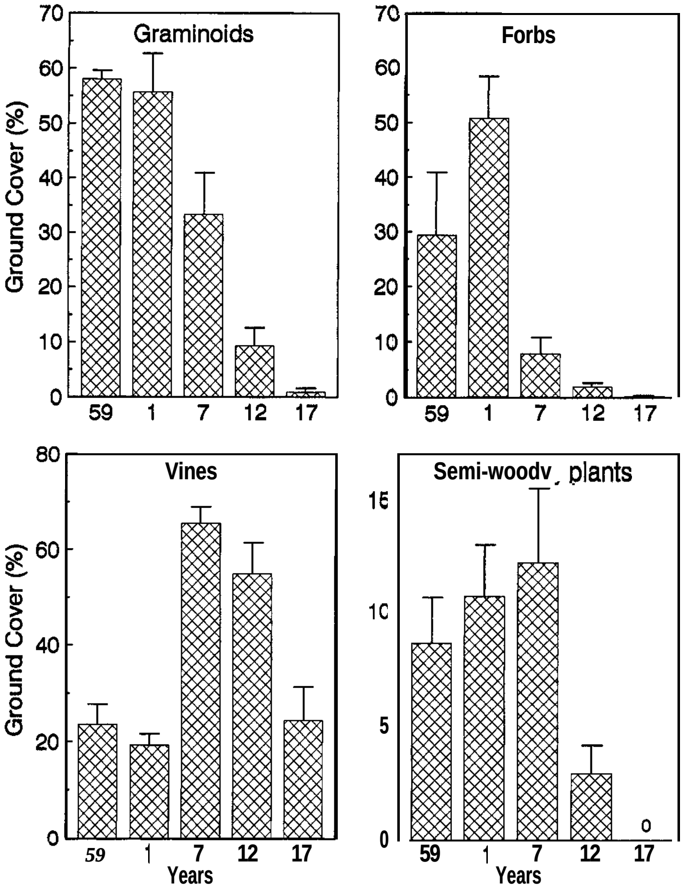

Fig. 3. Percent ground cover (mean+S.E.) from herbaceous vegetation relative to years after reproduction cutting of natural loblolly-shortleaf pine stands on a Coastal Plain site.

17, and 59 years after reproduction cutting. The presence of pines >24 cm on l-year-old disturbed sites was the result of seed-tree retention.

For seedling-sized oaks, all six species (Table 1) occurred on sites 7 and 59 years after reproduction cutting, and five species were also present at 1 and 12 years after reproduction cutting. Because of their intolerance to deep shade, the fewest number of seedling-sized oaks (two species) occurred 17 years after disturbance due to the closed canopy. For the sapling size class, both ***Quercus falcata*** Michx. and *Q. alba* L. were present across all sites. These were also the only two sapling-sized oak species at 1 and 59 years after reproduction cutting. In the small-tree category, three of the six oak species were found on sites 7 years after reproduction cutting, only two oak species were found 1 and 17 years after reproduction cutting, and no small-tree oaks occurred on sites that were cutover 12 and 59 years earlier. In the large-tree size classes, no oaks occurred on any of the sites. The absence of oaks in the small- and large-tree categories across all sites is attributed to harvesting of those size classes and the use of prescribed fires and herbicides to enhance pine establishment and growth.

For the other four hardwood species that have overstory potential, only sweetgum ***(Liquidambar*** *styraciflua* L.) was present across all sites in both the seedling and sapling size classes (Table 1). Seedling-sized blackgums (*Nyssa sylvatica* Marsh.) were also present across all sites, and sapling-sized blackgums occurred on sites clearcut 7, 12, and 17 years earlier. For the small-tree size classes, only ash

(*Fraxinus* L. spp.), blackgum, and sweetgum were present and only at 1, 7, and 59 years after reproduction cutting. Because of harvesting and competition control measures, none of these potential overstory species were found in the large-tree size classes on any site.

Of the 10 hardwood species with midstory potential, only red maple (*Acer rubrum* L.), flowering dogwood (*Cornus florida* L.), common persimmon (*Diospyros virginiana* L.), and winged elm (*Ulmus alata* Michx.) were present across all sites in seedling-size classes (Table 1). Although these same four species had sapling-sized stems on sites that were cutover 1, 7, 12, and 17 years earlier, red maple was the only species in the midstory group with sapling-sized stems across all sites. The highest richness (9 of 10 species) for sapling size classes from these species occurred on sites cutover 7 and 12 years earlier, whereas the lowest richness (2 of 10 species) occurred in the 59-year-old stand. For the small-tree size classes, only flowering dogwood, red maple, red mulberry (*Morus rubra* L.), and winged elm were

Table 2

Mean (S.E.) importance values[a] for woody vegetation components relative to size class and years after reproduction cutting on five, 4 ha sites managed for natural pine productivity

Woody vegetation components by years after reproduction cutting	Importance values (percent) by woody vegetation size classes			
	Seedlings (<1.5 cm DBH)	Saplings (1.5–9.0 cm DBH)	Small trees (9.1-24.0 cm DBH)	Large trees (>24.0 cm DBH)
59 Years				
Pine	43.8 (7.24)	7.0 (6.90)	77.9 (22.08)	100.0 (0.00)
Oak	14.9 (2.50)	21.8 (12.6)	0.0 (0.00)	0.0 (0.00)
Other overstory hardwoods	4.0 (0.98)	34.5 (23.6)	14.0 (13.99)	0.0 (0.00)
Midstory hardwoods	23.6 (5.82)	22.2 (14.5)	8.1 (8.09)	0.0 (0.00)
Nonarborescents	13.7 (0.76)	14.5 (9.30)	0.0 (0.00)	0.0 (0.00)
1 Year				
Pine	56.2 (0.84)	0.0 (0.00)	27.5 (15.90)	100.0 (0.00)
Oak	9.0 (0.67)	34.7 (15.66)	17.1 (17.10)	0.0 (0.00)
Other overstory hardwoods	4.0 (0.84)	21.1 (7.10)	10.9 (10.90)	0.0 (0.00)
Midstory hardwoods	13.4 (1.67)	39.2 (15.73)	44.5 (20.88)	0.0 (0.00)
Nonarborescents	17.4 (3.66)	5.0 (4.97)	0.0 (0.00)	0.0 (0.00)
7 Years				
Pine	50.5 (4.06)	56.5 (8.05)	3.6 (3.60)	0.0 (0.00)
Oak	9.0 (0.65)	16.9 (3.63)	49.0 (9.24)	0.0 (0.00)
Other overstory hardwoods	5.3 (1.69)	8.0 (1.55)	18.0 (6.23)	0.0 (0.00)
Midstory hardwoods	22.2 (1.97)	14.1 (2.47)	29.4 (4.38)	0.0 (0.00)
Nonarborescents	13.0 (2.26)	4.5 (1.55)	0.0 (0.00)	0.0 (0.00)
12 Years				
Pine	8.0 (2.25)	56.0 (3.08)	99.0 (0.97)	0.0 (0.00)
Oak	11.2 (1.33)	10.6 (1.47)	0.0 (0.00)	0.0 (0.00)
Other overstory hardwoods	0.7 (0.73)	5.3 (1.80)	0.0 (0.00)	0.0 (0.00)
Midstory hardwoods	53.8 (2.14)	23.4 (2.19)	1.0 (0.97)	0.0 (0.00)
Nonarborescents	26.3 (2.77)	4.7 (0.78)	0.0 (0.00)	0.0 (0.00)
17 Years				
Pine	0.0 (0.00)	46.5 (2.25)	93.6 (1.71)	100.0 (0.00)
Oak	11.3 (3.15)	18.7 (2.29)	5.0 (1.30)	0.0 (0.00)
Other overstory hardwoods	5.6 (2.24)	6.7 (2.09)	0.0 (0.00)	0.0 (0.00)
Midstory hardwoods	33.4 (1.66)	22.3 (1.85)	1.4 (0.82)	0.0 (0.00)
Nonarborescents	49.7 (3.84)	5.8 (0.18)	0.0 (0.00)	0.0 (0.00)

[a] IV for seedlings=$\frac{1}{2}$(relative density+relative frequency); IV for saplings, small trees, and large trees=$\frac{1}{3}$(relative density+relative basal area+relative frequency).

present on any of the disturbed sites, and none of these 10 midstory species occurred in the large-tree size classes because of competition control with prescribed fires and herbicides.

Of the 15 woody genera categorized as nonarborescents, only American beautyberry (*Callicarpa* L.), deciduous holly/yaupon ***(Ilex decidua* Walt./*I. vomitoria*** Ait.), hawthorn ***(Crataegus*** spp.), and huckleberry (*Vaccinium* spp.) occurred across all sites in the seedling size classes (Table 1). For sapling size classes, American snowbell ***(Styrax americanus*** Lam.) was the only nonarborescent found on the site disturbed 1 year earlier, and only three nonarborescents ***(Ilex*** spp., ***Aralia spinosa*** L., and ***Rhus*** spp.) consistently occurred in the sapling size classes 7, 12, and 17 years after reproduction cutting. Common buttonbush ***(Cephalanthus occidentalis*** L.) and sumacs ***(Rhus*** spp.) were the only sapling-sized nonarborescents found in the 59-year-old stand. Because of their natural habit, none of the 15 nonarborescent genera occurred in the small- or large-tree size classes.

3.2. Woody vegetation importance

At 1, 7, and 59 years after reproduction cutting, pines had the highest IV for seedling-sized stems, averaging from 44 to 56% of the total (Table 2). Although midstory hardwoods and other overstory hardwoods dominated the sapling size classes at 1 and 59 years after disturbance from reproduction cutting, respectively, sapling pines had the highest IVs at 7, 12, and 17 years after disturbance, with from

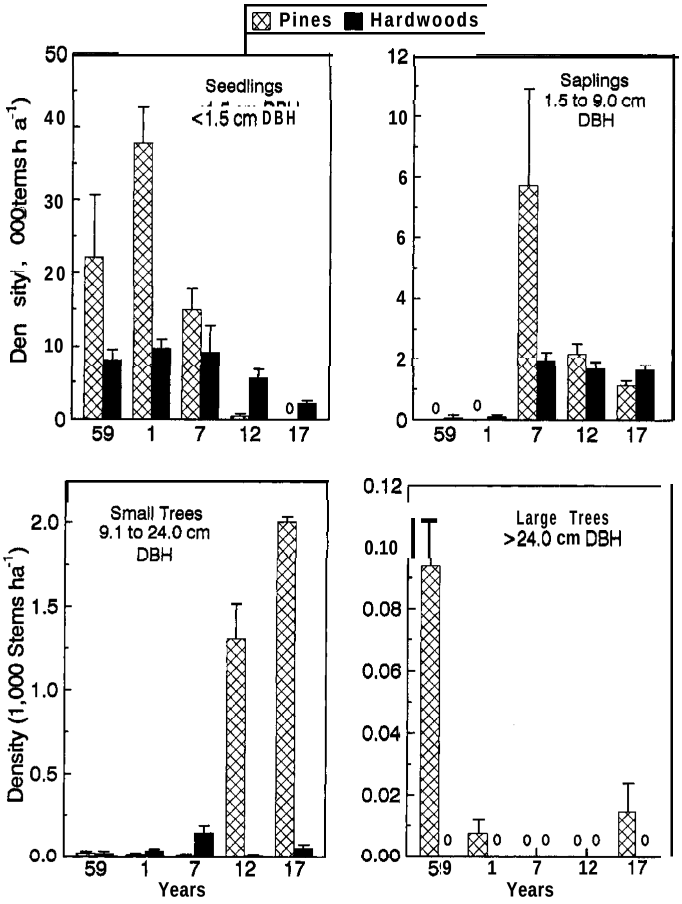

Fig. 4. Pine and hardwood density (mean+S.E.) by size class relative to years after reproduction cutting of natural loblolly-shortleaf pine stands on a Coastal Plain site.

47 to 57% of total importance. Midstory hardwoods were the dominant small-tree component 1 year after reproduction cutting, but they were displaced by oaks at 7 years and by pines at 12, 17, and 59 years. Because of seed-tree retention, pines were the only large-tree component 1 year after disturbance. There were no large-tree pines at 7 and 12 years after disturbance, but pines completely dominated that size class at ages 17 and 59.

Because average or better loblolly and shortleaf pine seed crops tend to occur in southeastern Arkansas during 3 out of every 4 years (Cain and Shelton, 1996a), pine seedlings attained dominance within 1 year after their establishment on these disturbed sites (Table 2) and density approached 40 000 stems ha-’ (Fig. 4). As these pines grew into sapling size classes by age 7, their numbers decreased to about 7500 stems ha-’ because of self-thinning. Since natural thinning proceeds from smaller to larger individuals (White and Harper, 1970; Cain, 1996), residual pines had grown into small-tree size classes by 12-17 years after reproduction cutting, with densities of from 1300 to 2000 stems ha-‘, respectively (Fig. 4). At 59 years after reproduction cutting, stand management for pine timber production assured full stocking of pines with >90 trees ha^{-1} that were >24 cm DBH.

For the seedling and sapling size classes, hardwoods exhibited trends in density somewhat similar to the pines (Fig. 4). There was a measurable decline in density of seedling-sized hardwoods from 10 000 rootstocks ha^{-1} 1 year after disturbance to 2000 rootstocks ha-’ 17 years after disturbance. About 50% of seedling-sized hardwoods might be expected to attain sapling size, with densities ranging from 1900 to 1600 stems ha-’ at 7-17 years after reproduction cutting, respectively.

Within 2.5 cm DBH classes, nonarborescents were the dominant seedling-sized nonpine woody plants 1 and 17 years after reproduction cutting with 50–30% of total nonpine stems, respectively (Fig. 5). When reproduction cutting occurred 7, 12, and 59 years earlier, hardwood species with midstory potential were dominant in seedling size classes with about 40% of total nonpine stems. For hardwoods larger than

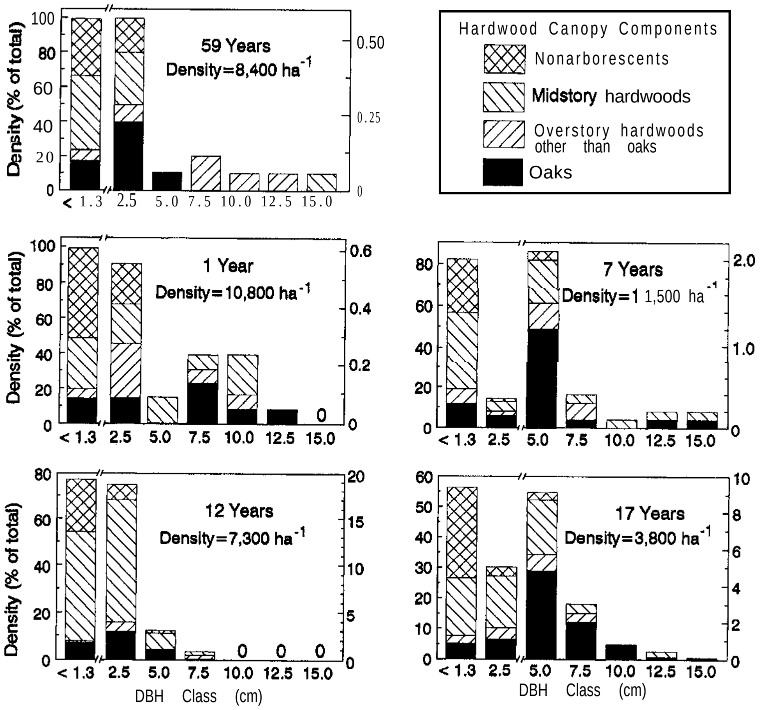

Fig. 5. Hardwood diameter distribution by potential canopy component at 59, 1, 7, 12, and 17 years after reproduction cutting of natural loblolly-shortleaf pine stands on a Coastal Plain site. A break in the X-axis indicates whether the left or right Y-axis was used for scaling.

the seedling size class, midstory species again had the most stems, but their density was <20% of the total within any DBH class. For hardwoods ≥2.5 cm DBH, oaks contributed <15% and overstory species other than oaks contributed <5% of hardwood density within any one disturbance interval (Fig. 5). Since the stands were managed for pine timber production by harvesting the hardwoods or controlling them with prescribed fires and herbicides, only a few hardwoods attained small-tree size across all disturbed sites, and none were >24 cm DBH (Fig. 4).

For seedling size classes, woody plant diversity based on Simpson's index *(D)* and evenness index (e) averaged lowest 1 year after reproduction cutting, whereas Shannon's index (H') and species richness were lowest at year 17 (Table 3). The highest H' diversity for seedling size classes occurred 59 years after reproduction cutting. ***D*** and e diversity peaked at years 12 and 17, respectively, and species richness averaged highest at 7 years after reproduction cutting.

Based on ***H', D,*** and species richness, sapling diversity of woody plants was lowest 59 years after reproduction cutting (Table 3). However, evenness for sapling sized stems was lowest at 7 years. The highest ***H'*** and ***D*** diversity for sapling size classes occurred at *17* years; evenness peaked at 1 year; species richness for saplings was highest 7 years after disturbance by reproduction cutting.

Table 3
Measures of woody plant diversity (S.E.) relative to years after reproduction cutting on five, 4 ha sites managed for natural pine productivity

Years after reproduction cutting by woody vegetation size classes	Measures of diversity			
	Shannon index (H')”	Simpson index (D)[b]	Evenness index (e)[c]	Species richness (S)[d]
Seedlings (<1.5 cm DBH)				
59	2.15 (0.10)	78 (3.72)	0.74 (0.04)	18.50 (0.87)
1	1.88 (0.02)	70 (0.84)	0.65 (0.00)	18.25 (0.48)
7	2.06 (0.13)	74 (3.94)	0.69 (0.03)	19.75 (1.49)
12	2.11 (0.09)	83 (1.72)	0.84 (0.02)	12.75 (1.44)
17	1.87 (0.14)	80 (2.82)	0.88 (0.02)	8.50 (1.04)
Saplings (1.5-9.0 cm DBH)				
59	0.70 (0.25)	44 (15.17)	0.96 (0.01)	2.25 (0.48)
1	1.18 (0.26)	66 (7.16)	0.98 (0.01)	3.75 (1.11)
7	1.78 (0.23)	67 (8.01)	0.64 (0.07)	16.00 (0.91)
12	1.79 (0.12)	69 (3.20)	0.66 (0.03)	15.00 (1.47)
17	1.92 (0.06)	76 (1.65)	0.71 (0.01)	15.25 (0.75)
Small trees (9.1-24.0 cm DBH)				
59	0.36 (0.36)	22 (21.70)	–[e]	1.67 (0.67)
1	0.61 (0.23)	41 (14.36)	0.99 (0.00)	2.00 (0.41)
7	1.46 (0.17)	74 (3.49)	0.95 (0.02)	5.00 (1.08)
12	0.04 (0.04)	2 (1.87)		1.25 (0.25)
17	0.26 (0.06)	12 (3.02)	0.28 (0.04)	2.50 (0.29)
Large trees (>24.0 cm DBH)				
59	0.00 (0.00)	0.00 (0.00)	–	1 (0.00)
1	0.00 (0.00)	0.00 (0.00)	–	1 (0.00)
7	–			0 (0.00)
12				0 (0.00)
17	0.00 (0.00)	0.00 (0.00)		1 (0.00)

[a] $H' = -\sum(n_i/N)\log_e(n_i/N)$, where N is the total of importance values and n_i the importance value for each species.

[b] $D = 100(1 \quad \sum(n_i/N)^2)$.

[c] e = $H'/\log_e S$, where S is the number of species.

[d] S is number of species.

[e] Insufficient data or no data for calculations.

Table 4
Woody species similarity by size classes relative to years after reproduction cutting on five, 4 ha sites managed for natural pine productivity

Years after reproduction cutting by size class	Years after disturbance (percent similarity[a])			
	1	7	12	17
Seedlings (<1.5 cm DBH)				
59	84	85	47	33
1		75	37	29
7			52	43
12				51
Saplings (1.5-9.0 cm DBH)				
59	52	23	24	27
1		20	17	22
7			81	77
12				81
Small trees (9.1-24.0 cm DBH)				
59	29	28	63	64
1		22	30	30
7			4	9
12				94

[a] Within a size class, percent similarity$=[2w/(a+b)] \times 100$, where w is the sum of lower importance value for each species being compared between two years, and $a+b$=sums of the species importance values in the 2 years being compared.

For small-tree size classes, H', D, and species richness were highest 7 years after reproduction cutting, but the evenness index was maximum at year 1 (Table 3). At 12 years, H', D, and species richness were lowest for small-tree size classes. Species richness was the only measure of diversity for large-tree size classes because pines were the only species present, and they occurred only at 1, 17, and 59 years after reproduction cutting.

3.4. Stand similarity

Seedling sized woody plants were most similar at 7 and 59 years and also at 1 and 59 years after reproduction cutting (Table 4). The least similarity for woody plants of seedling size occurred between areas that were cutover 1 and 17 years earlier. Sapling-sized species were most similar at 7 and 12 years and also at 12 and 17 years after reproduction cutting (Table 4). Similarity between cutover areas was lowest for sapling size classes when reproduction cutting occurred 1 and 12 years earlier.

In the small-tree category, the greatest similarity occurred between areas disturbed 12 and 17 years earlier, and the lowest similarity was found between years 7 and 12 (Table 4). Since pines were the only large trees across the chronosequence, similarity for that component was 100% between cutover areas after 1, 17, and 59 years.

4. Discussion

Plant succession has been interpreted using a number of models (Clements, 1916; Egler, 1954; Drury and Nisbet, 1973; Connell and Slatyer, 1977; Finegan, 1984). Although successional models contribute to a conceptual understanding of community development, many are not readily adapted to forest management. Based on studies and observations in the northeastern and northwestern United States, Oliver (1981) proposed a pattern of forest development following major disturbance (i.e., forest clearcutting) that appears to also have application in temperate regions such as the southeastern United States. In the present study, Oliver's four stages of forest development (stand initiation, stem exclusion, understory reinitiation, and old growth) were used to facilitate our discussion.

Early successional species are generally shade-intolerant while climax or late successional species are shade-tolerant, being found under their own canopy or that of early successional species (Govindaraju, 1984). This premise is supported by linking the early successional trends of this study with other studies of forest succession in the South that have focused on more long-term changes (Coile, 1940; Oosting, 1942; Switzer et al., 1979; Cain and Shelton, 1996b). These studies consistently show a progressive decline in the importance of the shade-intolerant pines and an accompanying increase in the more shade-tolerant hardwoods, especially the oaks. Through time, the canopy becomes multi-layered with the intolerant pines occupying the upper-most layer followed by the oaks and other canopy species, which are mostly intermediate in tolerance. A midcanopy also develops with the most shade-tolerant members of the community; these species do not have the growth potential to attain dominant canopy positions. Achievement of dominant canopy position by the oaks and other canopy species is inhibited by the pines until they begin to lose dominance due to individual mortality from senescence or collective mortality from catastrophic disturbance.

4.1. Stand initiation stage

Because of shade intolerance and their ability to colonize disturbed areas, both loblolly and shortleaf pines are categorized as early successional species. The tendency of pines to invade old fields, for example, has been attributed to their wind-disseminated seeds (Billings, 1938). Thus, by maintaining a pine seed source on or adjacent to cutover sites and by timing harvests to coincide with good seed years, forest managers are able to exploit the natural seeding potential of pines and thereby perpetuate the species for timber production.

Although reproduction cutting occurred at 5- to 6-year intervals, this chronosequence of stands on the Upper Coastal Plain was dominated by naturally seeded loblolly and shortleaf pines from seedlings through large-tree size classes. One year after clear-cutting or seed-tree cutting of the second-growth forest, pines had the highest IV of all woody plants in the seedling size class.

The stand initiation stage at 1 year after disturbance was also reflected in the high percentage of ground cover from shade-intolerant grasses and forbs. These herbaceous species are opportunist (Connell and Slatyer, 1977) with liberal representation in the soil seed bank (Thompson and Grime, 1979), broad dispersal ability, and rapid growth to maturity; but they are unable to invade and grow in the presence of adults of their own or other species.

In the present investigation, sites disturbed from 1 to 12 years earlier were generally in the stand initiation stage of development, during which species diversity increased. Pines were dominant as saplings in the 7-year-old stand. By 12 years after disturbance, pine saplings and small trees had the highest IVs compared to other canopy components.

4.2. Stem exclusion stage

By 7 years after disturbance, the stand initiation stage was in transition, as indicated by a reduction in ground cover from herbaceous vegetation and density of seedling-sized pines. Between 7 and 12 years after disturbance, pines increased in size but their density declined drastically due to self-thinning. From 12 to 17 years, pines and hardwoods had achieved crown closure; thus, stand development moved into the stem exclusion stage, in which woody species richness declined because of shade intolerance. Pines retained their dominance in importance as small trees and large trees at 17 years after reproduction cutting.

Because of complete crown closure at 17 years after disturbance, 11 of the 16 seedling-sized woody species present in the understory were shade-tolerant — *Acer rubrum* L., ***Callicarpa americana*** L., *Cornus florida* L., ***Crataegus*** L. spp., ***Diospyros virginiana*** L., *Ilex* ***decidua*** Walt,, ***I. opaca*** Ait., ***I. vomitoria*** Ait., ***Nyssa sylvatica*** Marsh., *Ulmus* ***alata*** Michx., and ***Vaccinium*** L. spp. Cain and Shelton (1995) examined understory dynamics over a period of 38 years in a mature, closed-canopy, pine-oak forest in southeastern Arkansas and found trends similar to those reported in the present investigation. In that earlier study, relative importance for woody understory species tended to increase through time for shade-tolerant genera and decrease for shade-intolerant genera.

In a study of northern hardwood forest succession in New Hampshire, Bormann and Likens (1979) found that species richness reached a maximum shortly after disturbance, then declined. Similarly, in the present investigation, species richness of woody plants increased for the seedling, sapling, and small-tree size classes between 1 and 7 years after disturbance from reproduction cutting. By 12 years after disturbance, species richness had declined for those same size classes and continued to decline through 17 years for seedlings.

4.3. Understory reinitiation stage

Since the 59-year-old stand received periodic thinnings, sunlight filtered through to the forest floor, thereby facilitating the understory reinitiation stage of development. That trend was most apparent when considering the increase in ground cover from grasses, forbs, and semi-woody herbaceous vegetation at 59 versus 17 years after reproduction cutting. The density of nonpines in the 59-year-old stand averaged 8400 stems ha-^{1}, and this component only increased by an additional 3500 stems ha-’ 7 years after reproduction cutting. So, most of the hardwoods developed from advanced regeneration and sprouting of stems that were present when reproduction cutting occurred. In addition, this resulted in a relatively high initial importance of oaks in the hardwood component of these stands. In contrast, the successional pattern described by Switzer et al. (1979) for old-field sites with no existing woody vegetation showed a high contribution of light seeded hardwoods, such as *Liquidambar styraciflua* L. and *Ulmus alata* Michx., that became established either with or shortly after the pines. In that earlier study, oaks did not appear in substantial numbers until the middle successional stage (beginning at 45 years) and did not achieve main canopy positions until late succession (beginning at 100 years), when the pines began to lose dominance due to the mortality of large, dominant trees.

4.4. Old growth stage

Oliver (1981) proposed that forest development concludes in an old growth stage. However, as long as the pines are managed for timber production in the present study, the old growth stage will not be attained on these sites. In an adjacent 32 ha pine-hardwood stand where anthropogenic perturbations had been excluded since 1935, Cain and Shelton (1996b) found that overstory pines were dying as a result of senescence and bark beetle infestations, which permitted midstory and understory hardwoods to move into the canopy, thereby forming an uneven-aged mosaic pattern described by Oliver (1981).

Forest succession is difficult to evaluate because of the long timescale involved (Hibbs, 1983). Nevertheless, the 17-year results of woody species dynamics presented in this study contribute to our understanding of forest succession on the Upper Coastal Plain in the absence of catastrophic disturbance following reproduction cutting.

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