Indigenous Vegetation in a Southern Arkansas Pine-Hardwood Forest After a Half Century Without Catastrophic Disturbances

Michael D. Cain
Michael G. Shelton
U.S. Forest Service
Southern Forest Experiment Station
Monticello, Arkansas 71656-3516

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ABSTRACT: In 1992 we analyzed the composition of a 32-ha pine-hardwood forest that originated from the partial cutting of the existing virgin forest around 1915. The area has been reserved from timber management since 1935. Pines >9 cm in diameter at a height of 1.37 m accounted for 61% of overstory and midstory basal area but only 21% of density. Of those trees that had attained overstory status, loblolly pine (*Pinus taeda*) had the highest importance value based on relative density, relative basal area, and relative frequency. Following loblolly pine in importance were: white oak (*Quercus alba*), sweetgum (*Liquidambar styraciflua*), and shortleaf pine (*P. echinata*), respectively. Basal area of overstory and midstory trees (17 species) totaled 38 m^2/ha. Dominant trees ranged in age from 80 to 140 years. After 57 years without catastrophic disturbances, this forest was characterized by a multilayered, closed canopy. Canopy stratification generally reflected the shade tolerance of the represented species. Species intolerant of shade dominated the overstory, while shade-tolerant species dominated the midstory and understory. Without recruitment from the understory and in the absence of disturbance, data suggest that hardwood species will eventually replace the overstory pines as the dominant vegetative component.

INTRODUCTION

Large-scale removal of virgin loblolly pine (*Pinus taeda*) and shortleaf pine (*P. echinata*) timber began in southern Arkansas in the 1890s and was almost complete by the late 1920s (Reynolds 1980). Lumber companies usually cut only trees that were larger than 36 cm in stump diameter. When the old-growth timber was almost depleted, most sawmills shut down. In those days, lumber from second-growth trees was considered practically worthless because it would warp, shrink, or twist (Reynolds 1980). Nevertheless, a few companies decided to manage their second-growth forests for timber production. Owners of the Crossett Lumber Company opted for timber management on about 20,000 ha of their forestland in southern Arkansas and northern Louisiana. The company began leaving pine seed trees and instituted fire protection. By selectively cutting the old-growth pines and harvesting some second-growth pines, the Crossett Lumber Company was able to extend its dwindling supply of virgin timber and stay in business, while other timber companies failed.

In 1934 the Crossett Lumber Company made 680 ha of its cutover timberland available to the U.S. Forest Service to be used as an experimental forest and research center for studying ways of improving and rebuilding previously unmanaged second-growth pine stands. In 1935, 32 ha of the cutover timberland were selected as the most representative in terms of pine and hardwood stocking on the Crossett Experimental Forest; this area was set aside from future management. We describe the natural vegetation on these 32 ha after 57 years without catastrophic disturbances and explore overstory/understory relationships within this once cutover, pine-hardwood forest in the West Gulf Coastal Plain of southern Arkansas. Old-growth forests in the southern United States are fragmented and small in size (Devall and Ramp 1992), but protected areas, such as the one under consideration, can be considered natural laboratories with historical and biological importance (Fountain and Sweeney 1987). These areas also contribute to an understanding of vegetation dynamics (Hemond et al. 1983). This 32-ha pine-hardwood forest is currently being considered for designation as a research natural area.

METHODS

Description of the Study Area

The 32-ha study area is located in Ashley County, Arkansas at 33°02'N mean latitude and 91°56'W mean longitude. It is dissected by several ephemeral drainages (Figure 1), and soil types are oriented in relation to these drainages. Arkabutla silt loam (Aeric Fluvaquents) occurs in the floodplain along the drainages (U.S. Department of Agriculture 1979). These somewhat poorly drained soils have a site index of about 30 m at 50 years for loblolly pine, cherrybark oak (*Quercus falcata* var. *pagodifolia*), green ash (*Fraxinus pennsylvanica*), sweetgum (*Liquidambar styraciflua*), and water oak (*Q. nigra*). 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 site index is 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.

Elevation of the area ranges from 37.0 to 42.3 m above sea level. The growing season is about 240 days, and annual precipitation averages 140 cm, with wet winters and dry autumns. The climate is subtropical humid (Trewartha 1968). The area is currently bordered by anthropogenic ecosystems (Tansley 1935) that have been managed during the last 50 years for pine timber production using single-tree selection, seed-tree cuts, and 2-ha block clearcuts.

Historical Background

Preharvest conditions are not known, but virgin forests in southern Arkansas consisted of mixed pine-hardwood, with 54% 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*), post oaks (*Quercus stellata*), water oaks, and elms (*Ulmus* spp.) were left. Residual trees also included merchantable size pines, red oaks (principally *Q. falcata*), and white oaks (*Q. alba*) that were of poor quality. Since 1935, management practices have not been conducted on this area, with the exception of fire protection and measures to control an infestation of southern pine beetles (*Dendroctonus frontalis*) that reached epidemic levels in southern Arkansas in the early 1970s (Ku et al. 1981). In the early 1970s 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 (~0.5 tree/ha) across the 32 ha.

Inventory Procedures

Understory component

Sixty circular quadrats of 8 m^2 (radius = 1.6 m) each were systematically established within the 32-ha study area. There were three line-transects at 60-m intervals, with sample quadrats at 40-m intervals along the transects. All live pine stems and woody rootstocks (>15 cm tall but <9 cm in diameter at a height of 1.37 m [dbh]) were measured within these quadrats in the summer of 1992.

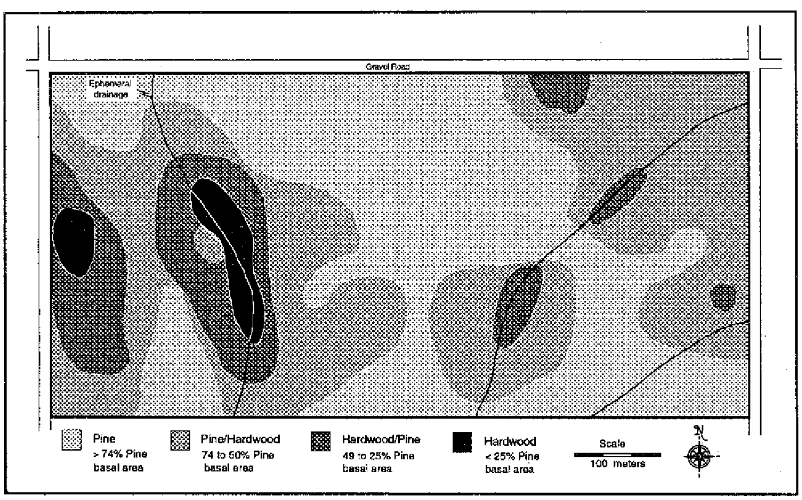

Figure 1. Overstory-midstory cover types in a 32-ha, unmanaged, pine-hardwood forest.

Woody rootstocks consisted of either single or multiple stems (clumps) that obviously arose from the same root system. Each rootstock was identified by species, and its location was mapped with respect to quadrat center. For the dominant stem per rootstock, total height was measured to an accuracy of 3 cm and, for stems taller than 1.37 m, dbh was measured to an accuracy of 0.25 cm. Other understory assessments in 1992 included percent of each 8-m^2 quadrat that was occupied by herbaceous vegetation (grass, woody and semiwoody vines, and forbs) and number of pine seedlings ≤15 cm tall.

Overstory component

During the winter of 1992–93, composition of overstory and midstory trees was determined using a 10 basal area factor prism at the center point of each 8-m^2 quadrat. For each tree >9 cm dbh that was tallied by prism, species was identified, distance from quadrat center was measured to an accuracy of 3 cm, and dbh was measured to an accuracy of 0.25 cm. These data were used to partition vegetative cover types and to compute basal area and competition index (Daniels 1976). Four cover types were identified (Figure 1): *pine* (20 quadrats), *pine-hardwood* (25 quadrats), *hardwood-pine* (11 quadrats), and *hardwood* (4 quadrats). Ages of dominant pines and oaks (>50 cm dbh) were determined by counting annual growth rings on increment cores taken at a height of 1.37 m from a random sample of more than 100 overstory trees. Three years were added to ring counts to adjust age for growth to 1.37 m in height.

Other measurements

Photosynthetically active radiation (PAR) was determined at a height of 1.37 m above ground, during clear sky conditions on August 8, 1991, using an 80-sensor Sunfleck Ceptometer (Decagon Devices, Inc., Pullman, WA). Determinations were made on 100 temporary points systematically located around each of a subsample of 12 of the 60 8-m^2 quadrats. All measurements were taken between 1130 and 1330 solar time. Several measurements were also made in full sunlight, which permitted the calculation of relative intensity (PAR at 1.37 m expressed as a percent of PAR in full sunlight).

In February 1993 an alidade and stadia rod were used to run a topographic survey for determining the elevation of each 8-m^2 sample quadrat. The survey was tied to a known elevation point on the Crossett Experimental Forest.

Data Analysis

For the 1992 data, understory components were divided into seedlings (<1 cm dbh) and saplings (1 cm–9 cm dbh). For both seedling-size and sapling-size species, importance value (IV) was calculated as relative density + relative height + relative frequency. For trees >9 cm dbh, species IVs were calculated as relative density + relative basal area + relative frequency. Importance value, as proposed by Curtis and McIntosh (1951), 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' contribution to the total for all species.

Diversity of woody species was determined for both the understory and overstory-midstory components according to Simpson's index of dominance (Odum 1975). Relative basal area was calculated for the pine and hardwood overstory-midstory components, and was classified into cover types. These classifications were used in conjunction with a 1986 aerial photograph and ground surveys to prepare a type map of the overstory and midstory vegetation (Figure 1). In this paper, we classified species by their potential position within the canopy (i.e., shrubs, midstory, and overstory).

To simplify analyses and data summaries, species were categorized into five groups: pines, oaks, other overstory species, midstory species, and shrubs. Individual species within each of the four groups are listed in Table 1. Nomenclature follows Little (1979).

Analysis of variance was used to compare understory and overstory-midstory variables between vegetative cover types. Percent ground cover by herbaceous vegetation, density of understory rootstocks, overstory-midstory competition index, overstory-midstory basal area, species diversity, and species richness were analyzed. Percent ground cover was analyzed following arcsine transformation. Differences between cover-type means were isolated by the Ryan-Einot-Gabriel-Welsch Multiple

Table 1. Common and scientific names of woody species recorded in a 32-ha unmanaged pine-hardwood forest in southern Arkansas.

Common Name	Scientific Name
Pines:	
shortleaf pine	*Pinus echinata* Mill.
loblolly pine	*Pinus taeda* L.
Oaks:	
white oak	*Quercus alba* L.
southern red oak	*Quercus falcata* Michx.
blackjack oak	*Quercus marilandica* Muenchh.
water oak	*Quercus nigra* L.
willow oak	*Quercus phellos* L.
post oak	*Quercus stellata* Wangenh.
Other overstory species:	
hickory	*Carya* Nutt. spp.
ash	*Fraxinus* L. spp.
sweetgum	*Liquidambar styraciflua* L.
blackgum	*Nyssa sylvatica* Marsh.
Midstory species:	
red maple	*Acer rubrum* L.
American hornbeam	*Carpinus caroliniana* Walt.
eastern redbud	*Cercis canadensis* L.
flowering dogwood	*Cornus florida* L.
persimmon	*Diospyros virginiana* L.
American holly	*Ilex opaca* Ait.
red mulberry	*Morus rubra* L.
eastern hophornbeam	*Ostrya virginiana* (Mill.) K. Koch
black cherry	*Prunus serotina* Ehrh.
sassafras	*Sassafras albidum* (Nutt.) Nees
elm	*Ulmus* L. spp.
Shrubs:	
hawthorn	*Crataegus* L. spp.
deciduous holly/yaupon	*Ilex decidua* Walt./*I. vomitoria* Ait.
plum	*Prunus* L. spp.
sparkleberry	*Vaccinium L. spp.*
American beautyberry	*Callicarpa americana* L.
sumac	*Rhus* L. spp.
viburnum	*Viburnum* L. spp.
devils-walkingstick	*Aralia spinosa* L.
witch-hazel	*Hamamelis virginiana* L.
privet	*Ligustrum* L. spp.
sweetleaf	*Symplocos tinctoria* (L.) L'Her.

Table 2. Descriptive variables for the overstory and midstory components[a] in a 32-ha, unmanaged, pine-hardwood forest.

Species by Group	IV[b] (%)	Density (no./ha)	Basal Area (m^2/ha)	Frequency[c] (%)	DBH (cm) Mean[d]	DBH (cm) Min.	DBH (cm) Max.
Pines:							
loblolly pine	26.6	64	17.95	98.3	59.7	24.9	94.5
shortleaf pine	11.7	34	5.39	70.0	44.7	23.4	74.2
Group total or (mean)	38.3	98	23.34	100.0	(55.1)	—	—
Oaks:							
white oak	12.9	48	4.87	80.0	35.8	9.1	111.8
southern red oak	7.3	19	2.53	56.7	40.9	11.9	76.2
post oak	4.6	16	1.72	30.0	37.3	18.0	77.5
water oak	1.6	5	0.41	13.3	33.0	19.6	63.5
Group total or (mean)	26.3	88	9.53	93.3	(37.1)	—	—
Other overstory species:							
sweetgum	11.9	84	2.59	56.7	19.8	9.1	77.5
blackgum	6.6	54	0.92	30.0	14.7	9.1	28.4
ash	2.1	15	0.39	11.7	18.3	14.5	24.4
hickory	0.6	2	0.16	5.0	33.0	26.9	45.7
Group total or (mean)	21.2	155	4.06	80.0	(18.3)	—	—
Midstory species:							
elm	5.9	52	0.62	25.0	12.2	9.1	22.1
eastern hophornbeam	3.0	28	0.34	11.7	12.7	10.2	17.5
flowering dogwood	2.2	21	0.18	8.3	10.7	9.1	13.7
American holly	1.3	12	0.11	5.0	11.2	9.4	15.2
red maple	1.1	9	0.11	5.0	12.7	9.4	25.9
sassafras	0.3	3	0.05	1.7	13.0	13.0	13.0
American hornbeam	0.3	2	0.05	1.7	14.0	14.0	14.0
Group total or (mean)	14.2	127	1.46	50.0	(12.2)	—	—
Forest total or (mean)	100.0	468	38.39	—	(12.7)	—	—

[a] Data taken at the 60 understory sample quadrats using a 10 basal area factor prism positioned over quadrat center.

[b] Importance value = relative density + relative basal area + relative frequency.

[c] (Quadrats occupied by individual species/total number of quadrats) x 100. Frequency totals represent frequency of occurrence for all species within a group.

[d] Quadratic mean.

Range Test ($p \leq 0.05$) because it is one of the most powerful step-down multiple-stage tests available and it controls the experiment-wise error rate (SAS Institute 1990:946-947).

RESULTS AND DISCUSSION

Overstory and Midstory Components

In 1992 total basal area in overstory and midstory trees (stems >9 cm dbh) averaged 38 m^2/ha with 468 trees/ha (Table 2). Only 21% of these trees were pines, but that group accounted for 61% of overstory and midstory basal area. Dominant pines and oaks (>50 cm dbh) ranged in age from 80 to 140 years. According to the successional development of forest communities proposed for the Gulf Coastal Plain by Switzer et al. (1979), most of the vegetation within this 32-ha forest is in the veteran period of late succession, which is a transitional phase when dominance shifts from pines to hardwoods. This stand differs from those described by Switzer et al. (1979) principally by a low representation of hickories.

Loblolly pines had three times as much basal area and twice as many overstory stems as shortleaf. Pines were well distributed over the area, with 100% frequency of occurrence on the variable-radius plots. About half of the 32 ha was classified as pine type (Figure 1). The pines tended to predominate on upland flats between the ephemeral drainages, as verified by the topographic survey. Variation in relative pine basal area was significantly related to elevation (relative pine basal area = 421–14,300/meters elevation, r^2=0.23, RMSE=18.3, p=0.0001). The associated values of percent pine basal area to elevation were 35% at 37.0 m and 83% at 42.3 m above sea level.

This phenomenon is most likely a phytological "footprint" that reflects conditions during the early years of stand development. The vegetative cover types may be a remnant of historical wildfire effects before fire protection was initiated in the 1930s, but are more likely related to 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 precluded pines from establishing once the canopy closed near the drains or, at least, could have reduced pine numbers.

Although pines were the most important overstory group, minimum diameters of 23.4–24.9 cm suggest that few recruits will be available to replace the old-growth relics as they die from natural causes. Diameters for these overstory pines exhibited a normal, bell-shaped distribution characteristic of even-aged stands (Figure 2). However, age determinations showed an irregular, uneven-aged pattern, with dominant pines varying in age by as much as 60 years. Similarly, Glitzenstein et al. (1986) reported that loblolly pines (20 to 65 cm dbh) in an old-growth pine-hardwood forest in East Texas exhibited a normal diameter distribution. In contrast, diameters of midstory and overstory hardwoods in our study followed the negative exponential or reversed-J distribution that is characteristic of uneven-aged stands (Figure 2).

Only four oak species occurred within the variable-radius plots. White oaks were the most important oaks in terms of density, basal area, and frequency of occurrence (Table 2). White oaks also had the largest dbh (111.8 cm) of any species that was inventoried. There were about as many oaks per hectare as pines, but the pines had 145% more basal area than the oaks. The oaks were well distributed, with 93% frequency of occurrence.

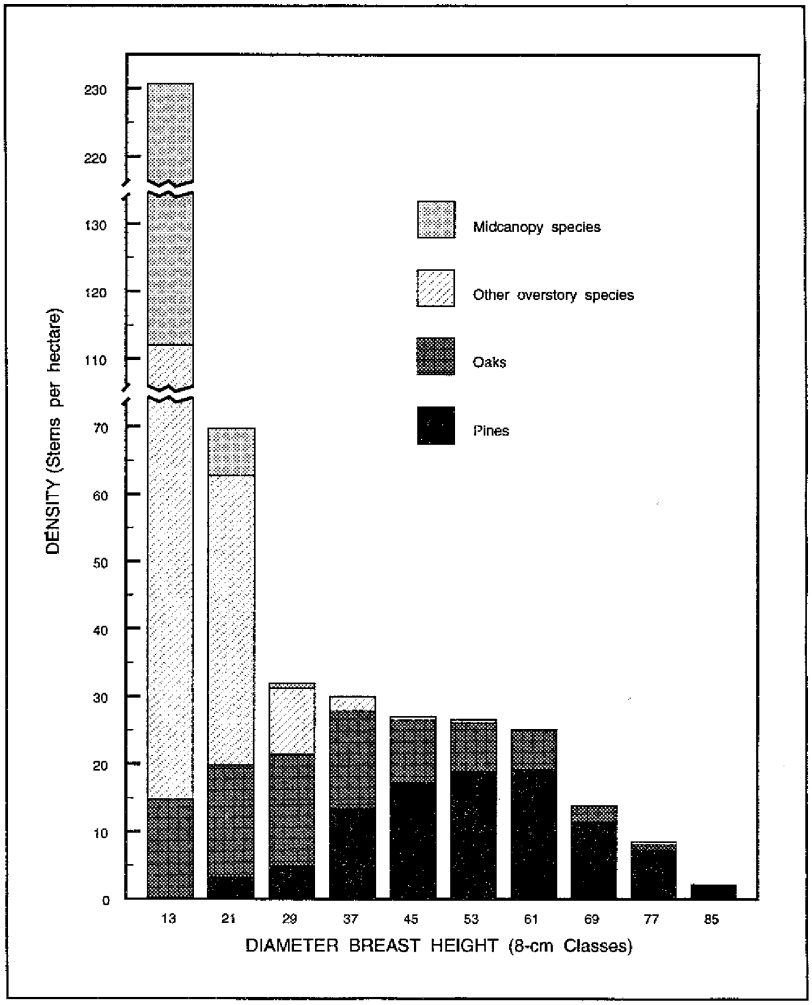

Figure 2. Diameter distribution of the overstory and midstory components in a 32-ha unmanaged pine-hardwood forest.

Among other overstory species, sweetgums were the most important and had a maximum diameter comparable to that of the pines and oaks (Table 2). Although sweetgums are somewhat intolerant (Preston 1965), they were present in smaller size classes (minimum dbh = 9.1 cm) when compared to the pines (minimum dbh = 23.4 cm). The species in this group accounted for one-third of total density and had about twice as many stems as the oaks, but oak basal area was 135% greater than the basal area for these species. Members of this group occurred on 80% of the variable-radius plots.

Among midstory species, elms were the most important, with twice the density and frequency of any other species in that group (Table 2). Out of the seven species in the midstory group, red maples attained the largest size (25.9 cm dbh). As a group, these midstory hardwoods accounted for 27% of total density but only 4% of total basal area; their frequency of occurrence was 50%.

During the 1991 growing season at a height of 1.37 m, relative intensity of photosynthetically active radiation (PAR) averaged 3.6% of full sunlight and ranged only from 2.5% to 5.3% for the 12 quadrats that were evaluated. Variation was not significantly related to overstory pine and hardwood basal area (p=0.85). Low PAR values indicate a closed canopy, which suggested that overstory and midstory vegetation had essentially reached the carrying capacity of the site. Low PAR values also indicated that dense shade characterized the understory environment. Only regeneration of the more shade-tolerant species can subsist in such an environment for prolonged periods. The narrow range in PAR values also indicated that canopy gaps created by overstory mortality were usually too small to be detected, or the gaps have been obscured by the dense midstory and upper portion of the understory.

Understory Components

Although pines were the most important species group in the overstory, pine seedlings accounted for only 10% of total importance values for understory plants of seedling size (Table 3), and there were no pines of sapling size (Table 4 and Figure 3). Likewise, Glitzenstein et al. (1986) reported an absence of pine saplings in an old-growth pine-hardwood forest in East Texas, where 35% of total basal area (33 m^2/ha) was in loblolly pines.

Because there were unusually large annual pine seed crops (1.5 to 4.2 million potentially viable seeds/ha) during the two winters preceding the 1992 inventory and favorable soil moisture during the two growing seasons that followed seed fall, pine seedlings averaged 2471 stems/ha and occurred on 45% of all quadrats. However, their small size (24 cm tall) suggested that most were first-year or second-year seedlings that are not likely to survive under this closed canopy. This observation is substantiated by the fact that, ten years earlier, the importance value of understory pines on this area was <1% of total (Cain 1987). Bormann (1956) reported that loblolly pine seedlings can become established under dense forest canopies because of their early ability to utilize low light intensities; but when secondary foliage develops, seedlings are unable to photosynthesize effectively and die out. Toumey (1929) concluded that failure of eastern white pine (*Pinus strobus*) reproduction under closed forest canopies was as much the result of

Table 3. Descriptive variables for seedling-sized woody plants in a 32-ha unmanaged pine-hardwood forest.

Species by Group	IV[a] (%)	Density (rtstks/ha)[c]	Total Height (m)[d]	Frequency[b] (%)
Pines:				
pine total or (mean)	10.3	2471	(0.24)	45.0
Oaks:				
white oak	11.7	2080	0.40	63.3
southern red oak	2.9	453	0.43	18.3
willow oak	2.8	391	0.24	23.3
water oak	1.2	144	0.34	10.0
post oak	1.0	103	0.64	8.3
blackjack oak	0.2	21	0.46	1.7
Group total or (mean)	19.8	3192	(0.40)	76.7
Other overstory species:				
blackgum	1.9	227	0.55	13.3
ash	1.3	185	0.52	8.3
sweetgum	0.8	82	0.55	6.7
hickory	0.7	62	1.01	5.0
Group total or (mean)	4.7	556	(0.58)	31.7
Midstory species:				
red maple	10.3	1750	0.52	50.0
flowering dogwood	8.5	1339	0.61	40.0
eastern hophornbeam	3.9	536	0.70	20.0
american holly	1.8	144	1.19	11.7
sassafras	1.5	227	0.27	11.7
elm	0.7	62	0.94	5.0
red mulberry	0.4	41	0.82	3.3
black cherry	0.4	41	0.30	3.3
Group total or (mean)	27.4	4140	(0.58)	73.3
Shrubs:				
sparkleberry	23.5	5148	0.52	48.3
American beautyberry	9.3	1359	0.76	38.3
deciduous holly/Yaupon	1.4	185	0.55	10.0
hawthorn	1.3	144	0.34	11.7
sweetleaf	0.8	144	0.52	3.3
witch-hazel	0.8	103	1.22	1.7
viburnum	0.4	41	0.40	3.3
privet	0.2	21	0.27	1.7
sumac	0.2	21	0.15	1.7
Group total or (mean)	37.8	7166	(0.58)	78.3
Forest total or (mean)	100.0	17525	(0.49)	—

[a] Importance value = relative density + relative height + relative frequency.

[b] (Quadrats occupied by individual species/total number of quadrats) x 100. Frequency totals represent frequency of occurrence for all species within a group.

[c] Rootstocks per hectare.

[d] Group means weighted by number of stems per species.

root competition for soil moisture as it was the shade effect of the overstory.

Table 4. Descriptive variables for sapling-sized woody plants in a 32-ha, unmanaged, pine-hardwood forest.

Species by Group	IV[a] (%)	Density (stems/ha)	Total height (m)[c]	Frequency[b] (%)
Pines: —	—	—	—	
Oaks:				
white oak	4.4	103	4.54	5.0
water oak	1.0	21	3.14	1.7
Group total or (mean)	5.3	124	(4.30)	6.7
Other overstory species:				
blackgum	10.0	206	4.39	15.0
sweetgum	7.3	124	6.98	10.0
hickory	1.3	21	8.44	1.7
ash	1.1	21	4.85	1.7
Group total or (mean)	19.6	372	(5.49)	23.3
Midstory species:				
elm	18.8	432	4.08	25.0
flowering dogwood	16.2	412	4.18	16.7
eastern hophornbeam	11.2	206	6.86	13.3
red maple	7.0	144	3.84	11.7
American holly	7.0	165	3.51	10.0
sassafras	1.1	21	5.24	1.7
black cherry	1.1	21	5.76	1.7
Group total or (mean)	62.4	1401	(4.45)	65.0
Shrubs:				
witch-hazel	5.3	165	3.60	3.3
sparkleberry	3.6	103	2.13	5.0
hawthorn	1.8	41	2.77	3.3
American beautyberry	1.0	21	3.47	1.7
deciduous holly/yaupon	0.9	21	2.99	1.7
Group total or (mean)	12.6	351	(3.02)	13.3
Forest total or (mean)	100.0	2248	(4.39)	—

[a] Importance value = relative density + relative height + relative frequency.

[b] (Quadrats occupied by individual species/total number of quadrats) x 100. Frequency totals represent frequency of occurrence for all species within a group.

[c] Group means weighted by number of stems per species.

Shrubs occurred on 78% of sample quadrats and were the most important group of seedling-size rootstocks in the understory, representing 38% of total importance values (Table 3). Sparkleberries (*Vaccinium* spp.) accounted for 24% of importance values and were the most important species in the understory. About 93% of shrub density was attributed to sparkleberries, American beautyberry (*Callicarpa americana*), and deciduous holly (*Ilex decidua*) or yaupon (*I. vomitoria*). All of these shrubs have been identified as valuable to wildlife in southern forests (Oefinger and Halls 1974).

Seedling-size white oaks and southern red oaks were present in substantial numbers (>2500 rootstocks/ha) and, as a group, oak seedlings occurred on 77% of sample quadrats (Table 3). Oaks accounted for 20% of total importance values in the seedling size class and were second only to *Vaccinium* in importance. In contrast, sapling-size oaks accounted for only 5% of total sapling importance values (Table 4), with white oaks and water oaks being the only species represented in the sapling size class. Frequency of occurrence for oaks of sapling size was only 7%.

Oak seedlings have been reported to occur in other forests where oak saplings were rare (Parker et al. 1985). According to Lorimer (1981), oak saplings that originate under shade are prone to repeated topkill when they do not receive substantial direct solar radiation. Abrams and Downs (1990) surmised that the small number of hardwood saplings in a mixed mesophytic forest of Pennsylvania was the result of monopolization of resources and canopy closure by older trees.

As a group, midstory species of seedling size were more important than the oaks or other overstory species (Table 3). In this group, seedling-size red maples predominated in density and frequency of occurrence, but American hollies (*Ilex opaca*) had the tallest seedlings (1.2 m) of any midstory species. This group had the highest importance value (62%) for stems of sapling size (Table 4). Elms and flowering dogwoods (*Cornus florida*) accounted for 60% of midstory density in stems of sapling size. Most sapling-size stems were in the smallest dbh class (2 cm), and sapling density exhibited a reversed-J distribution (Figure 3).

Relationship of Understory to Overstory

Ground cover from herbaceous vegetation tended to decline as relative basal area of the cover types changed from predominantly pine to predominantly hardwood (Table 5). On quadrats with more than

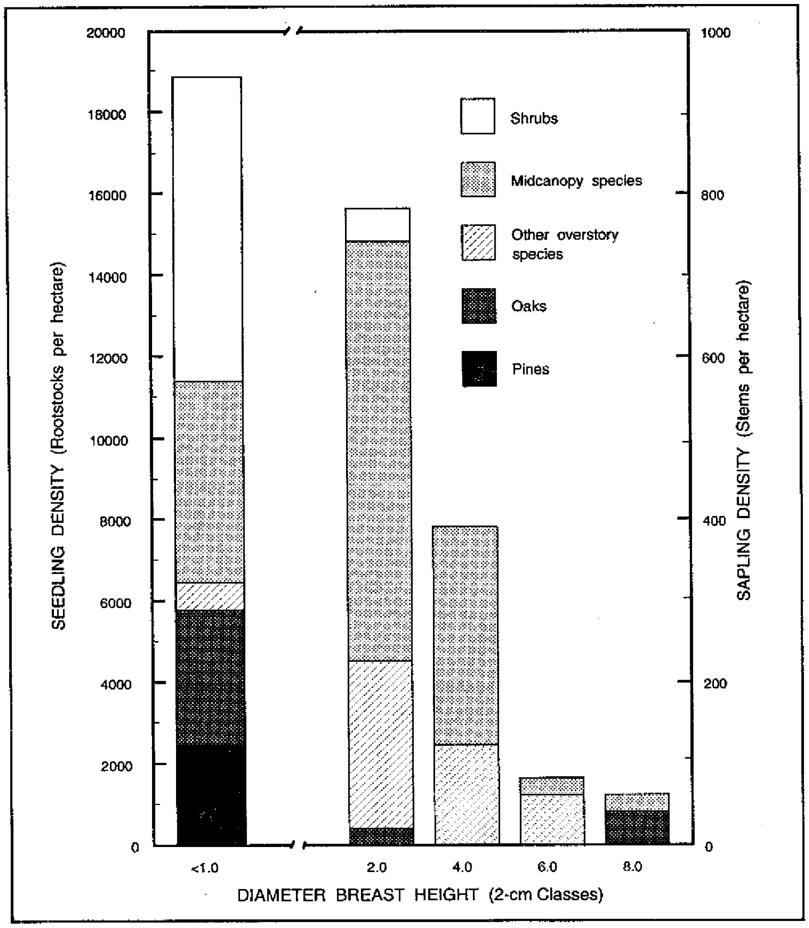

Figure 3. Diameter distribution of the understory component in a 32-ha unmanaged pine-hardwood forest.

75% hardwood basal area, ground cover from grass averaged only 10%, which was significantly less (p=0.049) than the 31% ground cover that was estimated under the other three cover types. The lack of herbaceous vegetation under the hardwood cover type may be owing to low light intensity at the ground surface throughout the growing season, allelopathy (Hook and Stubbs 1967), and periodic flooding along the ephemeral drains. When catastrophic perturbations occur in pine-hardwood stands, natural pine regeneration tends to be enhanced in the absence of herbaceous groundcover (Cain 1991).

Density of understory rootstocks, within five species groups, were compared among cover types (Table 5). The trend was for woody rootstock density of understory species in all five groups — pines, oaks, other overstory species, midstory species, and shrubs — to average higher in either the pine-hardwood or the hardwood-pine cover types as compared to the pine or hardwood cover types. However, differences in rootstock numbers between types were not statistically significant (p=0.124 to 0.784).

Competition Measures and Species Diversity

Overstory competition index and overstory basal area in the pine cover type were, respectively, 43% (p=0.0461) and 44% (p=0.0042) more than in the hardwood cover type (Table 6). Most of the pine biomass was concentrated in a few trees with large diameters, as compared to the hardwoods, which consisted of many stems of smaller diameter. Since there was a positive correlation (r^2=0.35, p=0.0001) between competition index and basal area, then basal area is probably as good a predictor of competitive effects as competition index for old-growth stands with widely dispersed trees of large diameter.

For trees in the overstory and midstory, species diversity and species richness were highest (p=0.0001 and p=0.0015, respectively) in the hardwood-pine and pine-hardwood cover types and lowest in the hardwood cover type (Table 6). There were no statistically significant differences for understory species diversity (p=0.2239) or species richness (p=0.5667) between cover types. For understory woody plants, diversity averaged 59% and richness averaged 5.2 species per plot, across cover types. These results are consistent with findings reported by Collins and Good (1987), who found few significant relationships between canopy type and ground layer species in oak-pine forests of New Jersey. They concluded that biotic interactions within the ground layer of the forest have more effect on species distribution than does canopy type.

SUMMARY AND CONCLUSIONS

After 57 years without catastrophic disturbance by human or natural sources, this 32-ha pine-hardwood forest was characterized by a multilayered, closed canopy. Canopy stratification generally reflected the shade tolerance of the represented species. Species intolerant of shade dominated the overstory, while shade-tolerant species dominated the midstory and understory.

Ten species of woody plants were identified in the overstory and seven species were found in the midstory. At least six of the overstory species were represented by individuals of large diameter (≥ 74 cm dbh), and those six species are prized for their commercial timber value. An additional 18 species of woody plants were recorded in the understory. Although many

Table 5. Relationship of overstory-midstory cover types to woody and herbaceous understory components in a 32-ha unmanaged pine-hardwood forest.

Understory Component	Cover types: Pine	Pine Hardwood	Hardwood Pine	Hardwood	Mean square error	P>F
Herbaceous vegetation:		*Percent cover*				
Grass	33A[a]	35A	25AB	10B	0.052	0.049
Forbs	5.0	2.2	2.0	1.8	0.028	0.935
Vines	1.4	1.0	0.4	0.0	0.008	0.420
Woody density:		*Rootstocks/ha*				
Pines	2039	1581	5617	1544	5.4E7	0.480
Oaks	2903	4003	3032	1853	1.6E7	0.667
Other overstory species	926	988	1010	309	1.6E6	0.784
Midstory species	4324	5535	9098	1853	3.7E7	0.124
Shrubs	5992	8846	8760	3398	1.2E8	0.702
Total	16184	20953	27517	8957	2.9E8	0.189

[a] Row means followed by different letters are significantly different.

Table 6. Relationship of overstory-midstory cover types to measures of competition and diversity in a 32-ha, unmanaged, pine-hardwood forest.

Forest Component	Cover types: Pine	Pine Hardwood	Hardwood Pine	Hardwood	Mean square error	P>F
		Competition index[a]				
Overstory-midstory	105.5A[b]	97.4AB	84.2AB	73.9B	626	0.0461
		Basal area (m^2/ha)				
Overstory-midstory	42.9A	37.9AB	33.7B	29.8B	65	0.0042
		Species diversity (%)[c]				
Overstory-midstory	61B	73A	76A	49C	96	0.0001
Understory	62	67	54	53	362	0.2239
		Species richness (number/plot)				
Overstory-midstory	4.4BC	5.7AB	5.9A	4.0B	1.8	0.0015
Understory	5.2	5.9	5.6	4.0	6.9	0.5667

[a] $CI_i = \sum_{j=1}^{N} D_j/Dist_{ij}$; Where:
D_j = Dbh of competitor (j).
$Dist_{ij}$ = Distance between plot center (i) and the competitor (j).
N = Number of competitors counted with a 10 basal area factor prism.

[b] Row means followed by different letters are significantly different.

[c] Diversity for woody species was calculated from Simpson's index of dominance using species importance values from individual 8-m^2 quadrats. Importance values were based on relative density and relative dominance (*i.e.*, basal area for the overstory and height for the understory). Percent diversity = 100 $(1 - \Sigma p_i^2)$. Where: p_i is the proportion of the total importance values in the i_{th} species.

of these understory species have little commercial importance as a timber resource, they contribute to a diverse wildlife habitat and enhance the recreational and aesthetic values of the forest.

Pines were the most important species in the overstory but were not represented in the sapling size class of the understory. If succession proceeds without catastrophic disturbance, then hardwoods will eventually replace the pines. According to Glitzenstein et al. (1986), the order of canopy stratification is crucial to subsequent patterns of succession because the number of releases and the length of time required to attain overstory size are directly related to the position of a tree in the stratification sequence. Although an oak-hickory climax has been proposed for the Gulf Coastal Plain (Oosting 1956), data from the present investigation suggest that the climax vegetation in this forest will be mixed hardwoods (Quarterman and Keever 1962), with an overstory dominated by oaks, gums, and elms.

Michael D. Cain and Michael G. Shelton are Research Foresters with the U.S. Forest Service, Southern Forest Experiment Station. Their research emphasis is on silvicultural practices for natural stand establishment and monitoring of stand dynamics.

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