SURVIVAL PATTERNS OF UNDERSTORY WOODY SPECIES IN A PINE-HARDWOOD FOREST DURING 28 YEARS WITHOUT TIMBER MANAGEMENT[1/]

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Abstract. In 1935, 32 ha on the Crossett Experimental Forest in southern Arkansas were set aside from future timber management. Between 1937 and 1983, eight inventories were made of the overstory component. Understory species were inventoried annually between 1954 and 1960, then again in 1963 and 1982.

Although the overstory pine-hardwood ratio remained stable in terms of relative basal area, merchantable pine density in stems/ha decreased with a commensurate increase in merchantable hardwood density. Understory species importance values tended to increase for the more shade tolerant genera and decrease for less tolerant genera. Survival of most understory species improved as greater size was attained.

Keywords: Succession, tolerance, Pinus, Quercus

INTRODUCTION

Private nonindustrial forest landowners (PNIFL's) control more than 70 percent of the forest land in the South, yet many do not perceive timber production as their principal goal of ownership (Porterfield 1984). Some of these landowners have allocated their forest holdings to wildlife habitat, recreational areas, or aesthetically pleasing landscapes and do not practice forest management. Boyce and Knight (1980) reported that it is not uncommon for PNIFL's, who derive income from timber sales on their property, to passively permit biologically better adapted hardwoods to increase on pine sites after pines are harvested. Evidence is sufficient to conclude that, in the absence of forest management or other external disturbances on pine sites of the southeastern Coastal Plain, natural plant succession eventually culminates in a climax forest of mixed hardwoods (Oosting 1956, Quarterman and Keever 1962).

Because many PNIFL's have demonstrated interest in nontimber resources on their properties, it is incumbent upon forest land managers to study the long-term consequences of nonmanagement on plant population trends. Although considerable published information traces successional trends over long periods of time in the northeastern United States (Lorimer 1981, Pickett 1982, Hemond and others 1983, Hibbs 1983, Metzger and Schultz 1984, Whitney 1984, McCune and Cottam 1985), less information covers the southern United States (Christensen 1977, Della-Bianca 1983, McGee 1984, Guldin and Baker 1985).

One aspect of successional trends is the ability of species to compete for limited sunlight, growing space, soil moisture, and nutrients. Good and Good (1972) reported that chances of survival for tree seedlings and saplings increased as greater size was attained in a mature, eastern hardwood forest. Similarly, Keever (1983) surmised that much of a plant's ability to compete is determined by the relative size of individuals. Even though such generalizations are quite plausible, the correlation of initial size with subsequent survival for individual species is not well documented. The purpose of this paper is to address that lack of information by investigating the survival patterns of understory woody species over a period of almost three decades in an undisturbed, old-growth, pine-hardwood forest in southeastern Arkansas.

[1/] Paper presented at the Sixth Central Hardwood Forest Conference, Knoxville, TN, February 24-26, 1987.

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STUDY AREA

Data for this paper were collected within a pair of 16-ha management units on the Crossett Experimental Forest, Ashley County, Arkansas, at 33°02'N mean latitude and 91°56'W mean longitude. Annual precipitation there averages 140 cm with extremes being wet winters and dry autumns. Elevation of the area averages about 53 m with nearly level topography. Soils are Bude (Glossaquic Fragiudalfs), Providence (Typic Fragiudalfs), and Arkabutla (Aeric Fluvaquents) silt loams (U.S.D.A. 1979). Bude and Providence soils were formed in thin loessial deposits and have an impervious layer at 46 to 102 cm that impedes internal drainage. Arkabutla soil formed in silty alluvium and is subject to flooding in late winter and early spring. These soils have excellent potential for growth of cherrybark oak (*Quercus falcata* var. *pagodifolia* Ell.), sweetgum (*Liquidambar styraciflua* L.), and loblolly pine (*Pinus taeda* L.) for which the site index is 27 m at 50 years.

Old-growth pine timber on the area was cut before 1915 to a 30-cm d.b.h. limit. In 1935, the 32 ha were set aside from future management. With the exception of fire protection and occasional cut-and-leave or salvage of small bark beetle infestations, no management practices have been undertaken.

METHODS

Overstory Inventories

Eight inventories of the overstory component (trees 9 cm d.b.h. and larger) were conducted between 1937 and 1983 at 5- to 10-year intervals. Inventories before 1983 recognized three species groups: pines (*Pinus* L. spp.), oaks (*Quercus* L. spp.), and other hardwoods. All stems were recorded by 2.5-cm d.b.h. classes. In 1983, a fourth group, gums (*Liquidambar* L. and *Nyssa* L.), was added to the inventory. Loblolly (*P. taeda* L.) and shortleaf (*P. echinata* Mill.) are the only two species of pines growing on the 32 ha, and they were never inventoried separately.

Understory Inventories

Prior to the 1954 growing season, 60 permanent circular quadrats of 8 m^2 each were systematically established on the 32 ha to monitor understory vegetation dynamics. Inventories of understory (stems less than 9 cm d.b.h.) pines, hardwoods, and shrubs were conducted annually from 1954 through 1960 and again in 1963 and 1982. Individual species were identified according to Little (1979) and their heights measured to the nearest 0.03 m. Species' azimuth and distance from each quadrat center were recorded to permit periodic remeasurement of previously identified stems.

The overtopping condition for each understory quadrat was subjectively assessed in 1954 as open, pine, pine/hardwood, or hardwood. Those categories were reassessed for each quadrat at the time of the 1982 inventory.

Importance values were calculated for each understory species on the basis of relative number and relative height:

$$\text{Relative number} = \frac{\text{Number of stems for an individual species}}{\text{Number of stems for all species}} \times 100$$

$$\text{Relative height} = \frac{\text{Mean height for an individual species}}{\text{Sum of mean heights for all species}} \times 100$$

$$\text{Importance value} = \text{Relative number} + \text{Relative height}$$

Simple correlation coefficients were computed to determine the degree of linear association between initial height and subsequent years of survival for each understory species. Regression analyses provided equations for expressing the linear relationship between survival and height. All analyses were carried to the 0.05 level of significance.

RESULTS AND DISCUSSION

Overstory Component

Temporal trends in overstory density (stems/ha) and basal area for pines and hardwoods are illustrated in Figure 1. Although relative basal area for each component remained stable during the 46 years without stand management, the relative proportion of pine and hardwood stems completely reversed.

Overstory pine basal area was concentrated in stems 10 to 51 cm d.b.h. in 1937 and averaged 13 m^2/ha. By 1983 overstory pine basal area averaged 22 m^2/ha and had shifted to the larger (38- to 76-cm) d.b.h. classes. Between 1937 and 1983 merchantable pine basal area increased 69 percent, but the number of merchantable pines decreased 65 percent, from 321 stems/ha to 111 stems/ha. Because of intolerance, pines in the smaller size classes were unable to survive competition with the increasing number of shade tolerant hardwoods and the persistent dominance from mature overstory pines. As a result, there was no ingrowth of pines into the merchantable size classes to replace natural mortality of old-growth pines.

In contrast to the pines, hardwood species had a substantial army of recruits in this 32 ha forest. As such, merchantable (trees 9 cm d.b.h. and larger) hardwood density increased from 101 stems/ha in 1937 to 299 stems/ha in 1983. The major hardwood component in 1937 was oak, which accounted for 57 percent of total hardwood density. By 1983, overstory hardwood density was almost equally divided among oaks (30 percent), gums (31 percent), and other hardwoods (39 percent). Although the proportion of oaks to all

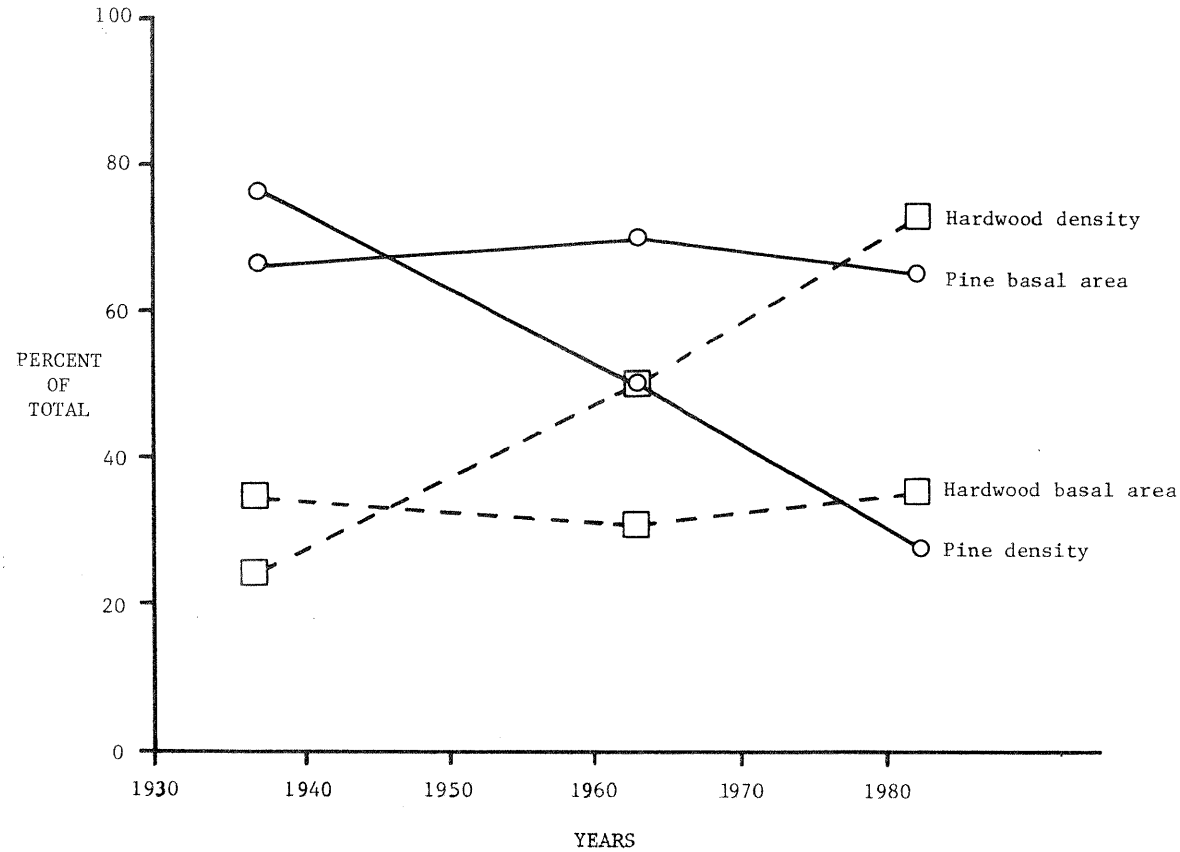

Figure 1.--Relative density and basal area for overstory pine and hardwood components between 1937 and 1983

hardwoods declined by 27 percentage points between 1937 and 1983, actual numbers of merchantable-size oaks increased by about 5 stems/ha during the 46-year period.

Merchantable hardwood basal area increased from 7 m^2/ha in 1937 to 12 m^2/ha in 1983. Oaks maintained basal area dominance with 61 percent of the hardwood total in 1937 and 64 percent in 1983.

Understory Component

On the original 52 quadrats that were found again in 1982, the major 28-year trend showed an increase in percent hardwood or pine/hardwood overtopping (60 percent in 1954 to 74 percent in 1982) with a corresponding decrease in pine or open overtopping conditions (40 percent in 1954 to 26 percent in 1982). Such trends are consistent with the decline in number of overstory pines and the increase in number of overstory hardwoods during 46 years of nonmanagement. It was assumed that overtopping conditions, from open to hardwood, should correspond to decreasing light intensities at the forest floor.

Increasing levels of overstory basal area, as well as increasing numbers of overstory hardwoods, between 1937 and 1983 suggest that the understory environment became more favorable for the growth of shade tolerant species. Ranking of understory species by relative importance (Table 1), between 1954 and 1982, reflects species' potential to persist in the shade of a changing overstory component. For those species that are capable of growing into tree size, the Quercus group was by far the most important in 1954 (16 percent) and 1982 (12 percent). The importance of that genus in both the overstory and understory after 46 years of nonmanagement favors the contention that oaks are a major component of the climax forest in the southeastern United States (Oosting 1956).

Published tolerance classifications were used in this investigation as a standard for comparing the 28-year change in relative species importance. During 28 years of nonmanagement, 73

Table 1.--Understory species importance expressed as a percent of total importance in 1954 and 1982

Species	1954	1982
	Percent importance values	
Acer rubrum L.	4.3	7.2
Aralia spinosa L.	5.1	0.4
Callicarpa americana L.	3.5	5.7
Carya spp. Nutt.	1.1	7.3
Cercis canadensis L.	3.3	---
Cornus florida L.	5.2	7.4
Crataegus spp. L.	5.8	2.6
Diospyros virginiana L.	2.1	4.3
Fraxinus spp. L.	3.7	2.5
Hamamelis virginiana L.	2.6	4.9
Ilex decidua Walt./Ilex vomitoria Ait.	2.4	1.9
Ilex opaca Ait.	2.7	3.7
Liquidambar styraciflua L.	8.5	6.1
Morus rubra L.	---	0.4
Nyssa sylvatica Marsh.	6.4	4.2
Ostrya virginiana (Mill.) K. Koch	6.3	4.9
Pinus spp. L.	3.1	0.8
Prunus americana Marsh.	1.9	0.4
Prunus serotina Ehrh.	3.8	1.5
Quercus spp. L.[1/]	3.9	2.4
Quercus alba L.	4.3	5.9
Quercus nigra L.	3.2	1.2
Quercus phellos L.	1.2	1.3
Quercus stellata Wangenh.	3.4	1.0
Rhus spp. L.	---	0.9
Sassafras albidum (Nutt.) Nees	1.8	1.0
Symplocos tinctoria (L.) L'Her.	---	0.9
Ulmus spp. L.	10.3	6.1
Vaccinium spp. L.	---	13.1

1/ Species of oak other than those listed, principally Q. falcata Michx.

percent of the tolerant species gained in relative importance; whereas, 80 percent of the intolerant and 67 percent of those intermediate in tolerance declined in relative importance. Tolerance classifications were derived from Putnam and others (1960), Preston (1965), Grelen and Duvall (1966), and Hicks and Stephenson (1978).

Although change in relative importance values provides a measure of species interaction through time, those values are not indicative of species' survival patterns. Of the 30 understory species that were identified from 1954 to 1982, 18 had sufficient survival data between measurement periods for correlation with initial size (Table 2). Correlation coefficients were statistically significant for 10 of those 18 species.

Two intolerant species, Pinus and Sassafras, had understory survival patterns that were well correlated with initial height. Even though correlation coefficients for the remaining 8 species were rather low, ranging from 0.31 for Cornus to 0.65 for Ulmus, all of these statistically significant correlations were positive. These data provide support to the supposition that survival of perennial plants tends to increase as size increases. That fact seems to hold true for a broad range of understory species, especially those that attain tree size. Those species with nonsignificant correlations were mostly shrubs or small trees where size differentials between youth and maturity are generally small.

Regression analyses were used to provide equations with years of understory survival as a function of initial height in meters for each species where there was significant correlation (Table 2). The general tendency was for understory species that are tolerant or intermediate in tolerance to survive longer in the shade of an overstory pine-hardwood component than an intolerant understory species with the same initial height. For example, an intolerant understory species such as Pinus might be expected to survive an additional 4 years given a height of 1.5 m. With the same height, the tolerant species Acer rubrum might be expected to survive an additional 15 years. Significant

Table 2.--Correlation and regression coefficients for the linear relationship of survival years (Y) to initial height (X) for understory species

Species	n	r	Regression coefficients a	b
Acer rubrum L.	40	0.57*1/	5.0904	6.5133
Aralia spinosa L.	6	.68		
Callicarpa americana L.	25	.12		
Carya spp. Nutt.	--2/	--		
Cercis canadensis L.	--	--		
Cornus florida L.	43	.31*	7.1364	1.6210
Crataegus spp. L.	45	.19		
Diospyros virginiana L.	--	--		
Fraxinus spp. L.	19	.14		
Hamamelis virginiana L.	7	-.01		
Ilex decidua Walt./Ilex vomitoria Ait.	--	--		
Ilex opaca Ait.	10	-.12		
Liquidambar styraciflua L.	58	.34*	7.1400	1.7110
Morus rubra L.	--	--		
Nyssa sylvatica Marsh.	47	.41*	8.8926	2.6999
Ostrya virginiana (Mill.) K. Koch	33	.59*	8.4557	2.3337
Pinus spp. L.	9	.89*	0.6117	2.2183
Prunus americana Marsh.	--	--		
Prunus serotina Ehrh.	--	--		
Quercus spp. L.3/	35	.10		
Quercus alba L.	45	.37*	8.1255	3.0031
Quercus nigra L.	20	.46*	5.9949	1.7850
Quercus phellos L.	--	--		
Quercus stellata Wangenh.	5	.31		
Rhus spp. L.	--	--		
Sassafras albidum (Nutt.) Nees	5	.95*	0.5157	2.8482
Symplocos tinctoria (L.) L'Her.	--	--		
Ulmus spp. L.	81	.65*	5.1899	5.2144
Vaccinium spp. L.	--	--		

1/ Significant at the 0.05 level.
2/ Lack survival data.
3/ Species of oak other than those listed, principally Q. falcata Michx.

linear relationships of survival to height for the other understory species in this investigation ranged between these two extremes.

Light and soil moisture have been demonstrated as competition factors that can reduce growth of understory plants or prevent many species from becoming established in forest stands (Shirley 1929, Korstian and Coile 1938, Bormann 1956, Horn 1985). In terms of timber management, release treatments have been recommended to free species from competition when those overtopped species have valuable utilization characteristics (Miller and Tissue 1956, Minckler and others 1961, Williston 1977). Data in the present investigation suggest that release must be done within a narrow time frame of a few years if established understory plants of intolerant species are to survive.

Of the 18 species where correlation analyses were done, only two species, Hamamelis virginiana and Ilex opaca, had negative but nonsignificant correlations. Both of these species are small trees, somewhat tolerant, and relegated to the understory. As such, they may become established as seedlings or sprouts in rather fragile microenvironments where they can persist as small plants for a number of years, completely shaded by canopy species. But a fragile microenvironment that sustained them as small plants may not support their continued survival once a critical size is reached.

MANAGEMENT IMPLICATIONS

Many people are often attracted by the beauty of what they consider to be pristine forests. Yet, even in the absence of management or disturbance by man, forests are a network of complex interactions that result in continuous change. In fact, species' presence within a forest at one point in time might best be maintained with management rather than without.

For example, two of the principal overstory components in this 32 ha forest are Pinus and Liquidambar. Once these two species approach maturity, they are commercially prized as lumber,

veneer, or pulpwood. However, the number of overstory pines declined between 1937 and 1983; and both of these intolerant species had declining understory importance during the last 28 years of nonmanagement. It was also found that a substantial size (height) was required for these two species to survive for a number of years as understory plants beneath a pine-hardwood canopy and in the absence of disturbance. In contrast, Acer rubrum is considered to be a tree of medium size at maturity compared to the larger size of Pinus or Liquidambar. Yet, A. rubrum increased in understory importance between 1954 and 1982. Because of shade tolerance, A. rubrum was able to persist in the understory even as small-sized plants. The commercial value of A. rubrum has been mainly for furniture stock, but the spectacular coloration of its foliage in autumn is aesthetically pleasing.

Species' survival patterns that occur in the absence of disturbance may be altered with proper forest management. If management objectives call for the continued presence of intolerant species within mixed pine-hardwood forests, then established understory plants of intolerant species will most likely require release from overtopping vegetation within a relatively short period of time. If not released, the smaller plants of intolerant species within the understory will most likely die and be replaced by species that are able to thrive in the shade of overtopping vegetation.

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