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# Thirty-eight years of autogenic, woody understory dynamics in a mature, temperate pine–oak forest

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**Abstract**: In 1935, 32 ha of a pine–hardwood forest were set aside from future timber management in southern Arkansas, U.S.A. Old-growth timber had been cut to a 36-cm stump diameter before 1915. Between 1952 and 1993, four inventories were made of the overstory and midstory components (number of live trees ≥9 cm in diameter breast height (DBH) taken at 1.37 m, by 2.54-cm DBH classes). Between 1954 and 1992, four corresponding inventories were made of the woody understory vegetation (>15 cm tall but <9 cm DBH) by counting rootstocks within 52 systematically spaced 8-$m^2$ circular quadrats. Understory species importance values (relative density + relative height + relative frequency) were used to compute diversity and similarity indices. During 38 years of assessment, no catastrophic disturbances occurred within the 32-ha forest. Although loblolly pine (*Pinus taeda* L.) and shortleaf pine (*Pinus echinata* Mill.) dominated the overstory (64% of basal area in 1954 and 63% in 1993), pines were absent from the understory in all but seedling size classes for the last 38 years. Woody understory diversity indices were essentially stable for 38 years, but the similarity of understory species tended to decline as the time between inventories increased. Relative importance values for woody understory species tended to increase for the more shade-tolerant genera and decrease for less tolerant genera. Survival and height growth of woody understory species were also found to be positively correlated with shade tolerance.

**Résumé** : Dans le sud de l'Arkansas, aux États-Unis, en 1935, 32 ha d'une forêt de pin et de feuillus ont été exclus du futur aménagement pour la matière ligneuse. Avant 1915, des arbres vierges ayant plus de 36 cm de diamètre à la souche y avaient été coupés. De 1952 à 1993, on a effectué quatre inventaires des composantes des étages dominant et intermédiaire des peuplements (nombre d'arbres vivants ≥9 cm de diamètre à hauteur de poitrine (DHP), mesuré à 1,37 m, par classes de 2,54 cm au DHP). Entre 1954 et 1992, quatre inventaires de la végétation ligneuse du sous-bois (>15 cm de hauteur mais <9 cm DHP) ont aussi été réalisés en comptant les plantes-mères dans 52 places-échantillon circulaires de 8 $m^2$, distribuées systématiquement. La valeur d'importance des espèces du sous-bois (densité relative + hauteur relative + fréquence relative) a été utilisée afin de calculer les indices de diversité et de similarité. Pendant les 38 ans du suivi, aucune perturbation catastrophique ne s'est produite à l'intérieur des 32 ha de cette forêt. Bien que le pin à encens (*Pinus taeda* L.) et le pin jaune (*Pinus echinata* Mill.) aient dominé l'étage supérieur (64% de la surface terrière en 1954 et 63% en 1993), les pins ont été absents du sous-bois pendant les 38 dernières années dans toutes les classes de diamètre, à l'exception de celle des semis. Durant ces 38 ans, les indices de diversité du sous-bois ligneux ont été essentiellement stables, mais la similarité des espèces du sous-bois tendait à diminuer à mesure que l'intervalle entre les inventaires augmentait. Les valeurs relatives d'importance des espèces ligneuses du sous-bois tendaient à s'accroître chez les genres plus tolérants à l'ombre et diminuaient dans le cas des genres moins tolérants. La survie et la croissance en hauteur des espèces ligneuses du sous-bois ont montré une corrélation positive avec la tolérance à l'ombre.
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## Introduction

On the Upper Coastal Plain of the southeastern United States, the loblolly pine (*Pinus taeda* L.) – hardwood forest type (Society of American Foresters 1954) in the southeastern evergreen forest region (Braun 1950) has experienced extreme anthropogenic perturbations during the past 100 years. In southern Arkansas, large-scale removal of the virgin loblolly and shortleaf pine (*Pinus echinata* Mill.) timber began in the 1890s and was almost complete by the late 1920s (Reynolds 1980). During that period, lumber companies usually cut only trees that were larger than 36 cm in stump diameter. Because loblolly pine is a prolific seed producer in southern Arkansas (Cain 1991), residual cone-bearing trees naturally regenerated the cutover sites, and the second-growth forests became dominated by loblolly pine – hardwood communities (Braun 1950).

Only remnants of these second-growth pine – hardwood forests are still available for investigation. In 1934, the USDA Forest Service acquired 680 ha of cutover timberland in southeastern Arkansas as an experimental forest for studying ways of improving and rebuilding previously unmanaged second-growth pine stands. In 1935, 32 ha of that experimental forest were selected as having the most representative forest conditions and were set aside from future timber management. Even though old-growth forests in the southern United States are fragmented and small (Devall and Ramp 1992), Fountain and Sweeney (1987) characterized these protected forests as natural laboratories that have historical and biological importance. Hemond et al. (1983) proposed that long-term studies in permanently protected areas can contribute significantly to an understanding of vegetation dynamics.

After a lengthy review of forestry research practices in the United States, the National Research Council (1990) reported a need to expand the knowledge of long-term changes in the composition, structure, and function of forest ecosystems as they are associated with natural succession. To that end, our objective in this paper is to document the long-term dynamics of survival, height growth, recruitment, disappearance, and reappearance of woody plant species in the understory of a mature, closed-canopy pine–oak forest. Although the 32-ha forest has been protected from devastation by wildfire and insect epidemics since 1935, it is unique because of the absence of catastrophic disturbances during the 38 years that measurements were taken.

## Study site

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 two ephemeral drainages, and soil types are oriented in relation to these drainages. Arkabutla silt loam (Aeric Fluvaquents) occurs in the flood plain along the drainages (U.S. Department of Agriculture 1979). Although flooding may occur along these drains every 3 to 4 years during heavy spring rains, water recedes in less than 24 h. These somewhat poorly drained soils have a site index of about 30 m at 50 years for *P. taeda*, *Quercus falcata* var. *pagodifolia* Ell., *Fraxinus pennsylvanica* Marsh., *Liquidambar styraciflua* L., and *Quercus nigra* L. Species nomenclature follows Little (1979). Providence silt loam (Typic Fragiudalfs) usually occurs on side slopes along the drainages, and Bude silt loam (Glossaquic Fragiudalfs) is found on upland flats. Providence and Bude soils were formed in thin loessial deposits, and site index is 26 m at 50 years for *P. taeda*, *P. echinata*, and *L. styraciflua*. 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. Daily temperatures average 22°C during the growing season (March through September) and 11°C during the dormant season (October through February). During summer, moist tropical air from the Gulf of Mexico persistently covers the area (U.S. Department of Agriculture 1979). The 32-ha forest might best be described as a natural, pine–oak biome 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 stand conditions are not known, but virgin forests in southern Arkansas consisted of mixed pine–hardwood stands, 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 *Carya* spp., *L. styraciflua* L., *Nyssa sylvatica* Marsh., *Q. nigra*, *Quercus stellata* Wangenh., and *Ulmus* spp. were left. Residual trees also included merchantable-sized *P. taeda*, *P. echinata*, *Quercus alba* L., and *Q. falcata* Michx. that were of poor quality. Since 1935, no silvicultural practices have been conducted on this area with the exception of fire protection and measures to control an infestation of southern pine beetles (*Dendroctonus frontalis* Zimm.) that reached epidemic levels in southern Arkansas in the early 1970s (Ku et al. 1981). At that time, cut-and-leave treatments were imposed to control beetle infestations but only on isolated pines (≈0.5 tree/ha) across the 32 ha.

## Methods

### Inventory procedures

*Overstory–midstory component*

All living trees ≥9 cm DBH (diameter at breast height, taken 1.37 m above the soil surface) were inventoried by 2.5-cm DBH classes within eight 4-ha subunits on the 32-ha study area. These inventories were conducted in 1952, 1963, 1983, and 1993. Trees were categorized into three species groups: pines, oaks, and other hardwoods. During the winter of 1992–1993, ages of dominant (>50 cm DBH) pines and oaks were determined by counting annual growth rings on increment cores taken at breast height 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.

*Understory component*
In 1954, 60 circular quadrats of 8 $m^2$ each were systematically established within the 32-ha study area. There were three parallel 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 DBH) were measured within these quadrats in 1954 and 1963.

Woody rootstocks were composed 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 tallest stem per rootstock, total height was measured to an accuracy of 3 cm for calculating growth.

In 1981, 52 of the original 60 quadrats were identified. The locations of the remaining 8 quadrats were indefinite; therefore, data from those 8 quadrats were excluded from our analyses. Understory woody vegetation on the original 52 quadrats was remeasured in 1982 and 1992. Rootstocks were counted by species, and survivors were identified from earlier inventories. Total height of dominant stems per rootstock was measured as in earlier inventories. Overstory and midstory stems that grew within the circular quadrats were not measured unless they were ingrowth from size classes <9 cm DBH that were mapped before 1982. In 1992, all pine seedlings were counted, even if they were <15 cm tall. Shade-tolerance classifications were derived from Putnam et al. (1960), Preston (1965), Grelen and Duvall (1966), Hicks and Stephenson (1978), Daniel et al. (1979), and Burns and Honkala (1990). For species lacking published shade-tolerance criteria, ratings were based on the authors' observations. It should be noted that shade-tolerance ratings are based on subjective assessments and may vary according to geographic location, habitat type, species composition of the canopy, and stand density (Lorimer 1983).

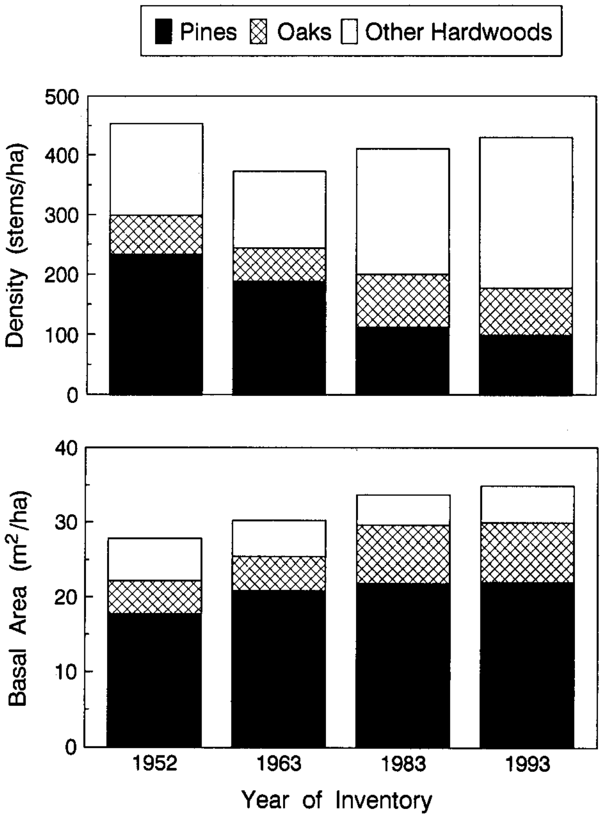
*Other measurements*
During the summer of 1993, canopy coverage was determined using a spherical densiometer positioned at two heights above the center point of each 8-$m^2$ quadrat. Heights were at 1.37 and 3 m, or below and above the major understory components, respectively.

### Data analysis

Importance values (IVs) were calculated for understory species on the basis of relative density + relative height + relative frequency. IVs were used to characterize woody understory composition and to distinguish the dominant vegetation on the area (Curtis and McIntosh 1951). In this paper, the term "relative" refers to an individual species' contribution to the total for all species.

IV were used to calculate diversity of the woody understory components according to Simpson's and Shannon's indices (Odum 1975) and to calculate percent similarity between the years of inventory (Monk 1967). Goff and Cottam (1967) noted that a combination of properties (i.e., basal area, density, frequency, and height) is amenable to various forms of arithmetic combinations to yield a single IV that provides a better expression of overall biotic influence than the use of a single property. Simpson's index was expressed as percent diversity so that the higher the value, the greater the diversity. For percent similarity, the possible range between years was 0 (having no species in common) to 100 (exactly identical).

**Fig. 1.** Overstory–midstory density and basal area in a 32-ha pine–oak forest during 38 years without catastrophic disturbance.




Linear regression was used to determine the association ($p \leq 0.05$) between initial height in 1954 and subsequent years of survival for understory woody species having >10 rootstocks at the time of the 1954 inventory.

## Results

### Dynamics of the overstory and midstory component

Temporal trends in the character of overstory and midstory trees are briefly presented to support the interpretation of understory dynamics. Between 1952 and 1993, four inventories recorded the number of trees ≥9 cm DBH (Fig. 1). Density of these trees averaged between 350 and 450 stems/ha. During that 41-year interval, pine density declined by 58%, while hardwood density increased by 50%. Hardwoods other than oaks had the greatest gain in numbers. Although total density of these overstory trees remained relatively constant, basal area increased by 26% (Fig. 1). Pines were the dominant species during the entire 41 years of study (64% of basal area in 1952 and 63% of basal area in 1993). Gains in pine basal area were only 6% during the last 30 years, whereas basal area for the oak component increased by 72%. Dominant pines and oaks (>50 cm DBH) ranged in age from 80 to 140 years. In midsummer of 1993, canopy coverage was 97.0% (86–100%) at a height of 3 m above the 52 understory sample points

**Table 1.** Descriptive variables for woody understory species at the beginning (1954) and end (1992) of 38 years without catastrophic disturbance.

| Species, by potential canopy position* | Density (no./ha) | | Mean height (m) | | Frequency (%)[†] | |
|---|---|---|---|---|---|---|
| | 1954 | 1992 | 1954 | 1992 | 1954 | 1992 |
| **Overstory species** | | | | | | |
| *Carya* spp. | 0.0 | 47.5 | — | 0.17 | 0.00 | 3.33 |
| *Fraxinus* spp. | 332.5 | 237.5 | 1.63 | 0.96 | 13.33 | 10.00 |
| *Liquidambar styraciflua* | 1377.5 | 190.0 | 2.75 | 4.09 | 31.67 | 11.67 |
| *Nyssa sylvatica* | 950.0 | 427.5 | 1.82 | 2.32 | 36.67 | 23.33 |
| *Pinus echinata* – *Pinus taeda* | 142.5 | 2707.5 | 2.70 | 0.26 | 3.33 | 41.67 |
| *Quercus alba* | 641.2 | 2208.8 | 1.67 | 0.62 | 18.33 | 55.00 |
| *Quercus falcata* | 570.0 | 498.8 | 1.27 | 0.44 | 25.00 | 16.67 |
| *Quercus nigra* | 332.5 | 166.2 | 1.93 | 0.33 | 15.00 | 10.00 |
| *Quercus phellos* | 71.2 | 451.2 | 0.99 | 0.25 | 1.67 | 23.33 |
| *Quercus stellata* | 71.2 | 118.8 | 3.38 | 0.65 | 5.00 | 8.33 |
| **Midstory species** | | | | | | |
| *Acer rubrum* | 522.5 | 1781.2 | 1.28 | 0.69 | 25.00 | 43.33 |
| *Cornus florida* | 665.0 | 1235.0 | 2.32 | 1.70 | 23.33 | 38.33 |
| *Diospyros virginiana* | 23.8 | 0.0 | 2.20 | — | 1.67 | 0.00 |
| *Ilex opaca* | 190.0 | 332.5 | 2.08 | 2.49 | 6.67 | 15.00 |
| *Morus rubra* | 0.0 | 23.8 | — | 0.27 | 0.00 | 1.67 |
| *Ostrya virginiana* | 688.8 | 736.2 | 3.26 | 2.53 | 20.00 | 26.67 |
| *Prunus serotina* | 71.2 | 71.2 | 3.74 | 2.12 | 5.00 | 5.00 |
| *Quercus marilandica* | 0.0 | 23.8 | — | 0.46 | 0.00 | 1.67 |
| *Sassafras albidum* | 95.0 | 190.0 | 1.69 | 0.28 | 6.67 | 6.67 |
| *Ulmus* spp. | 1781.2 | 570.0 | 1.87 | 3.70 | 53.33 | 26.67 |
| **Understory species** | | | | | | |
| *Aralia spinosa* | 118.8 | 0.0 | 5.02 | — | 6.67 | 0.00 |
| *Cercis canadensis* | 23.8 | 0.0 | 3.51 | — | 1.67 | 0.00 |
| *Crataegus* spp. | 926.2 | 190.0 | 1.57 | 0.93 | 40.00 | 10.00 |
| *Hamamelis virginiana* | 95.0 | 261.2 | 3.01 | 2.52 | 1.67 | 1.67 |
| *Ilex decidua* – *Ilex vomitoria* | 47.5 | 237.5 | 2.33 | 0.79 | 1.67 | 11.67 |
| *Prunus* spp. | 47.5 | 0.0 | 1.69 | — | 1.67 | 0.00 |
| **Shrub species** | | | | | | |
| *Callicarpa americana* | 546.2 | 665.0 | 1.34 | 0.78 | 21.67 | 28.33 |
| *Ligustrum* spp. | 0.0 | 23.8 | — | 0.27 | 0.00 | 1.67 |
| *Rhus* spp. | 0.0 | 23.8 | — | 0.15 | 0.00 | 1.67 |
| *Symplocos tinctoria* | 0.0 | 166.2 | — | 0.53 | 0.00 | 3.33 |
| *Viburnum* spp. | 0.0 | 23.8 | — | 0.27 | 0.00 | 1.67 |

*Includes all woody understory species that were identified during any inventory.
[†]Frequency = (number of quadrats occupied by individual species/total number of quadrats) × 100.

and 97.4% (94–100%) when taken at a height of 1.37 m, indicating a closed canopy.

## Dynamics of the understory component

*Species importance values*
No woody species was consistently dominant when ranked by individual importance criterion (Table 1). In 1954, for example, *Ulmus* spp. had the highest density and were also the most frequently occurring species; whereas *Aralia spinosa* L. had the tallest stems. By 1992, *Pinus* spp. had the highest density, *L. styraciflua* had the greatest mean height, and *Q. alba* was the most frequently occurring species.

One overstory species (*Carya* spp.), two midstory species (*Morus rubra* L. and *Quercus marilandica* Muenchh.), and four shrubs (*Ligustrum* spp., *Rhus* spp., *Symplocos tinctoria* (L.) L'Her., and *Viburnum* spp.) were not present in 1954 but had appeared by 1992 (Table 1). Concomitantly,

**Table 2.** Shade tolerance and importance values (IV) for woody understory species during 38 years without catastrophic disturbance.

| Species, by potential canopy position* | Shade tolerance | IV, by year of inventory (%) | | | |
|---|---|---|---|---|---|
| | | 1954 | 1963 | 1982 | 1992 |
| | **Overstory species** | | | | |
| *Carya* spp. | Intermediate† | 0 | 0.27 | 0 | 0.39 |
| *Fraxinus* spp. | Intermediate† | 3.14 | 4.33 | 2.41 | 1.88 |
| *Liquidambar styraciflua* | Intolerant | 13.28 | 11.37 | 6.17 | 3.16 |
| *Nyssa sylvatica* | Tolerant† | 9.12 | 8.06 | 6.21 | 5.14 |
| *Pinus echinata – Pinus taeda* | Intolerant | 1.37 | 1.44 | 0 | 11.48 |
| *Quercus alba* | Intermediate† | 5.42 | 6.79 | 11.03 | 12.82 |
| *Quercus falcata* | Intermediate | 5.25 | 4.05 | 4.41 | 3.02 |
| *Quercus nigra* | Moderately intolerant | 3.44 | 3.15 | 1.75 | 1.31 |
| *Quercus phellos* | Moderately intolerant | 0.49 | 0 | 2.99 | 3.18 |
| *Quercus stellata* | Moderately intolerant | 1.06 | 0.63 | 0.25 | 1.12 |
| | **Midstory species** | | | | |
| *Acer rubrum* | Tolerant | 5.01 | 7.35 | 12.94 | 10.55 |
| *Cornus florida* | Very tolerant | 6.69 | 7.25 | 15.19 | 10.84 |
| *Diospyros virginiana* | Tolerant† | 0.31 | 0.34 | 0.38 | 0 |
| *Ilex opaca* | Very tolerant | 1.84 | 2.24 | 3.15 | 3.88 |
| *Morus rubra* | Tolerant | 0 | 0 | 0 | 0.20 |
| *Ostrya virginiana* | Very tolerant | 7.57 | 8.64 | 6.91 | 8.15 |
| *Prunus serotina* | Intolerant† | 1.10 | 1.33 | 1.63 | 0.91 |
| *Quercus marilandica* | Moderately intolerant | 0 | 0 | 0 | 0.21 |
| *Sassafras albidum* | Intolerant† | 1.17 | 0.68 | 0.22 | 1.11 |
| *Ulmus* spp. | Moderately tolerant | 15.82 | 14.40 | 9.91 | 8.31 |
| | **Understory species** | | | | |
| *Aralia spinosa* | Intolerant | 1.93 | 2.25 | 0 | 0 |
| *Cercis canadensis* | Tolerant | 0.36 | 0.40 | 0 | 0 |
| *Crataegus* spp. | Intermediate† | 8.92 | 8.22 | 2.36 | 1.65 |
| *Hamamelis virginiana* | Intermediate† | 0.91 | 1.58 | 2.37 | 2.28 |
| *Ilex decidua – Ilex vomitoria* | Tolerant | 0.48 | 0.55 | 2.96 | 1.92 |
| *Prunus* spp. | Intolerant | 0.43 | 0 | 0.22 | 0 |
| | **Shrub species** | | | | |
| *Callicarpa americana* | Intermediate† | 4.89 | 4.68 | 5.78 | 5.02 |
| *Ligustrum* spp. | Intermediate† | 0 | 0 | 0 | 0.20 |
| *Rhus* spp. | Intolerant | 0 | 0 | 0 | 0.20 |
| *Symplocos tinctoria* | Tolerant | 0 | 0 | 0.76 | 0.87 |
| *Viburnum* spp. | Intermediate† | 0 | 0 | 0 | 0.20 |
| Yearly total | | 100.00 | 100.00 | 100.00 | 100.00 |

**Note**: Species IV = (relative density + relative height + relative frequency)/3.

*Includes all woody understory species that were identified during any inventory.

†Cases where shade-tolerance classifications are uncertain (i.e., inconsistent classification in published references) or shade tolerance varies with ontogeny.

**Table 3.** Diversity of woody understory plants during 38 years without catastrophic disturbance.

| Descriptive variable | 1954 | 1963 | 1982 | 1992 |
|---|---|---|---|---|
| | Year of inventory | | | |
| Diversity index* | | | | |
| Simpson's (%) | 91.66 | 92.19 | 91.53 | 92.22 |
| Shannon's index | 2.72 | 2.74 | 2.68 | 2.78 |
| Richness (no. of species) | 24 | 23 | 22 | 27 |
| Density (rootstocks/ha) | 10 331 | 9 025 | 11 234 | 13 609 |

*Simpson's index = $[1 - \Sigma(n_i/N)^2] \times 100$; Shannon's index = $-\Sigma(n_i/N)\log_e(n_i/N)$; where $N$ is the total of importance values per year and $n_i$ is the importance value for each species.

**Table 4.** Percent similarity (by year of inventory) of woody understory plant communities during 38 years without catastrophic disturbance.

| | 1963 | 1982 | 1992 |
|---|---|---|---|
| 1954 | 91.4 | 68.0 | 62.2 |
| 1963 | | 72.3 | 67.0 |
| 1982 | | | 81.3 |

**Note:** Percent similarity = $[2w/(a + b)] \times 100$; where $w$ is the sum of lower importance value for each species being compared between two years. $a + b$ = sums of the species importance values in the two years being compared.

other species could not be relocated in 1992 even though they were present in 1954. These species that disappeared included one shade-tolerant midstory species (*Diospyrus virginiana* L.), two shade-intolerant understory species (*Aralia spinosa* L. and *Prunus* spp.), and one shade-tolerant understory species (*Cercis canadensis* L.).

For trees with overstory potential, *Quercus* spp., as a group, generally had the highest relative IVs, ranging from 15% to 22% of the total throughout 38 years (Table 2). Between 1954 and 1963, *L. styraciflua* and *Ulmus* spp. contributed another 26–29% to total IVs. By 1982, *Acer rubrum* L. and *Quercus alba* L. achieved the highest relative IV's (24% of total), and these two species were still the most important midstory and overstory hardwoods 10 years later (23% of total IV's). Understory *Pinus* spp. accounted for less than 2% of relative importance values from 1954 to 1982, but the relative importance for understory pine seedlings exceeded 10% of total in the 1992 inventory.

Out of the 10 species categorized as midstory, only the five shade tolerants (*A. rubrum*, *Cornus florida* L., *Ilex opaca* Ait., *Morus rubra* L., and *Ostrya virginiana* (Mill.) K. Koch) exhibited gains in relative importance through time (Table 2). During the first 28 years of monitoring, *Cornus* doubled in relative IV, then declined slightly to about 11% of total. The shrub *Callicarpa americana* L. was one of the most stable species in terms of relative IV, changing by little more than 1% in 38 years.

**Table 5.** Survival of woody understory plants during 38 years without catastrophic disturbance.

| Species, by potential canopy position* | No. in 1954[†] | Survival, by year of inventory (%) 1963 | 1982 | 1992 |
|---|---|---|---|---|
| **Overstory species** | | | | |
| *Fraxinus* spp. | 14 | 100 | 57 | 29 |
| *Liquidambar styraciflua* | 58 | 72 | 24 | 12 |
| *Nyssa sylvatica* | 40 | 70 | 38 | 25 |
| *Pinus echinata* – *Pinus taeda* | 6 | 50 | 0 | 0 |
| *Quercus alba* | 27 | 82 | 41 | 22 |
| *Quercus falcata* | 24 | 67 | 4 | 4 |
| *Quercus nigra* | 14 | 57 | 21 | 7 |
| *Quercus phellos* | 3 | 0 | 0 | 0 |
| *Quercus stellata* | 3 | 67 | 0 | 0 |
| **Midstory species** | | | | |
| *Acer rubrum* | 22 | 77 | 36 | 27 |
| *Cornus florida* | 28 | 54 | 21 | 21 |
| *Diospyros virginiana* | 1 | 100 | 100 | 0 |
| *Ilex opaca* | 8 | 88 | 88 | 88 |
| *Ostrya virginiana* | 29 | 79 | 45 | 31 |
| *Prunus serotina* | 3 | 100 | 100 | 33 |
| *Sassafras albidum* | 4 | 50 | 0 | 0 |
| *Ulmus* spp. | 75 | 71 | 39 | 29 |
| **Understory species** | | | | |
| *Aralia spinosa* | 5 | 80 | 0 | 0 |
| *Cercis canadensis* | 1 | 100 | 0 | 0 |
| *Crataegus* spp. | 39 | 77 | 13 | 3 |
| *Hamamelis virginiana* | 4 | 100 | 75 | 75 |
| *Ilex decidua* – *Ilex vomitoria* | 2 | 100 | 100 | 50 |
| *Prunus* spp. | 2 | 0 | 0 | 0 |
| **Shrub species** | | | | |
| *Callicarpa americana* | 23 | 61 | 26 | 26 |

*Includes only those species that were identified in the 1954 inventory.
[†]Number of rootstocks on fifty-two 8-$m^2$ quadrats.

*Species diversity*

During 38 years without catastrophic disturbances, species richness ranged from 16 to 19 woody plants that had the potential of attaining overstory or midstory stature (Table 2). At least 31 different woody species or species groups were identified within sample quadrats during 38 years (Table 2). However, during any one inventory, no more than 27 and no fewer than 22 species groups were observed (Table 3).

Over a period of 38 years and during each of four inventories, Simpson's index of dominance for understory species exceeded 90% (Table 3). Throughout 38 years, Shannon's index averaged about 2.7. Mean density ranged from 9000 to 14 000 rootstocks/ha, with the higher numbers occurring at the end of 38 years.

Although the plots did not exhibit radical changes in species richness, dominance, or density of understory stems, similarity of woody understory composition declined by almost 38% between 1954 and 1992 (Table 4). Between

**Table 6.** Linear relationship of survival years to initial height in 1954 for woody understory species.

| Species, by potential canopy position* | $n$ | Regression coefficients† $a$ | $b$ | $r^2$ | Root MSE | $p>F$ |
|---|---|---|---|---|---|---|
| **Overstory species** | | | | | | |
| *Fraxinus* spp. | 14 | 27.56 | 0.40 | 0.01 | 9.27 | 0.743 |
| *Liquidambar styraciflua* | 58 | 11.09 | 2.64 | 0.16 | 10.95 | 0.002 |
| *Nyssa sylvatica* | 40 | 14.19 | 3.60 | 0.21 | 12.35 | 0.003 |
| *Quercus alba* | 27 | 20.60 | 1.32 | 0.02 | 12.34 | 0.433 |
| *Quercus falcata* | 24 | 15.05 | −0.32 | 0.01 | 8.56 | 0.714 |
| *Quercus nigra* | 14 | 12.32 | 1.78 | 0.14 | 11.91 | 0.182 |
| **Midstory species** | | | | | | |
| *Acer rubrum* | 22 | 14.27 | 6.07 | 0.25 | 11.25 | 0.018 |
| *Cornus florida* | 28 | 10.56 | 2.47 | 0.13 | 12.53 | 0.062 |
| *Ostrya virginiana* | 29 | 15.09 | 2.66 | 0.34 | 10.60 | 0.001 |
| *Ulmus* spp. | 75 | 9.55 | 6.58 | 0.44 | 9.88 | <0.001 |
| **Understory species** | | | | | | |
| *Crataegus* spp. | 39 | 14.16 | 2.13 | 0.06 | 8.30 | 0.130 |
| **Shrub species** | | | | | | |
| *Callicarpa americana* | 23 | 15.31 | 1.57 | 0.01 | 13.62 | 0.639 |

*Includes only those species that had >10 rootstocks in 1954.
†$y = a + bx$; where $y$ is the number of years the species survived and $x$ is the initial height.

any successive inventories the change in percent similarity was less than 20%.

*Survival*

Only two species, *I. opaca* and *Hamamelis virginiana* L., had better than 50% survival during the 38-year sampling period (Table 5). At least 7 of 24 species groups that were identified in 1954 had disappeared by 1982, and an eighth species was no longer present in 1992. Three of those species had canopy potential, and the other five were small trees or shrubs. Although rootstocks from eight of the original species were unable to survive in the understory for 38 years, four of these original species reappeared by 1992 (Table 2): *Pinus* spp., *Quercus phellos* L., *Q. stellata*, and *Sassafras albidum* (Nutt.) Nees.

The linear relationship of survival to initial height was positive and statistically significant ($p \leq 0.05$) for 5 of 12 species groups with enough data for analysis (Table 6). With the exception of *L. styraciflua*, these significant correlations were for shade-tolerant species. Given the same initial height for understory species with significant correlations and using the appropriate regression coefficients in the equation, *A. rubrum* could be expected to survive the longest, *L. styraciflua* would have the shortest survival time, and *O. virginiana*, *N. sylvatica*, and *Ulmus* spp. would fall between these extremes. Because of the low $r^2$ values associated with these regressions, the equations indicate apparent trends but would not be useful as precise estimates of species survival.

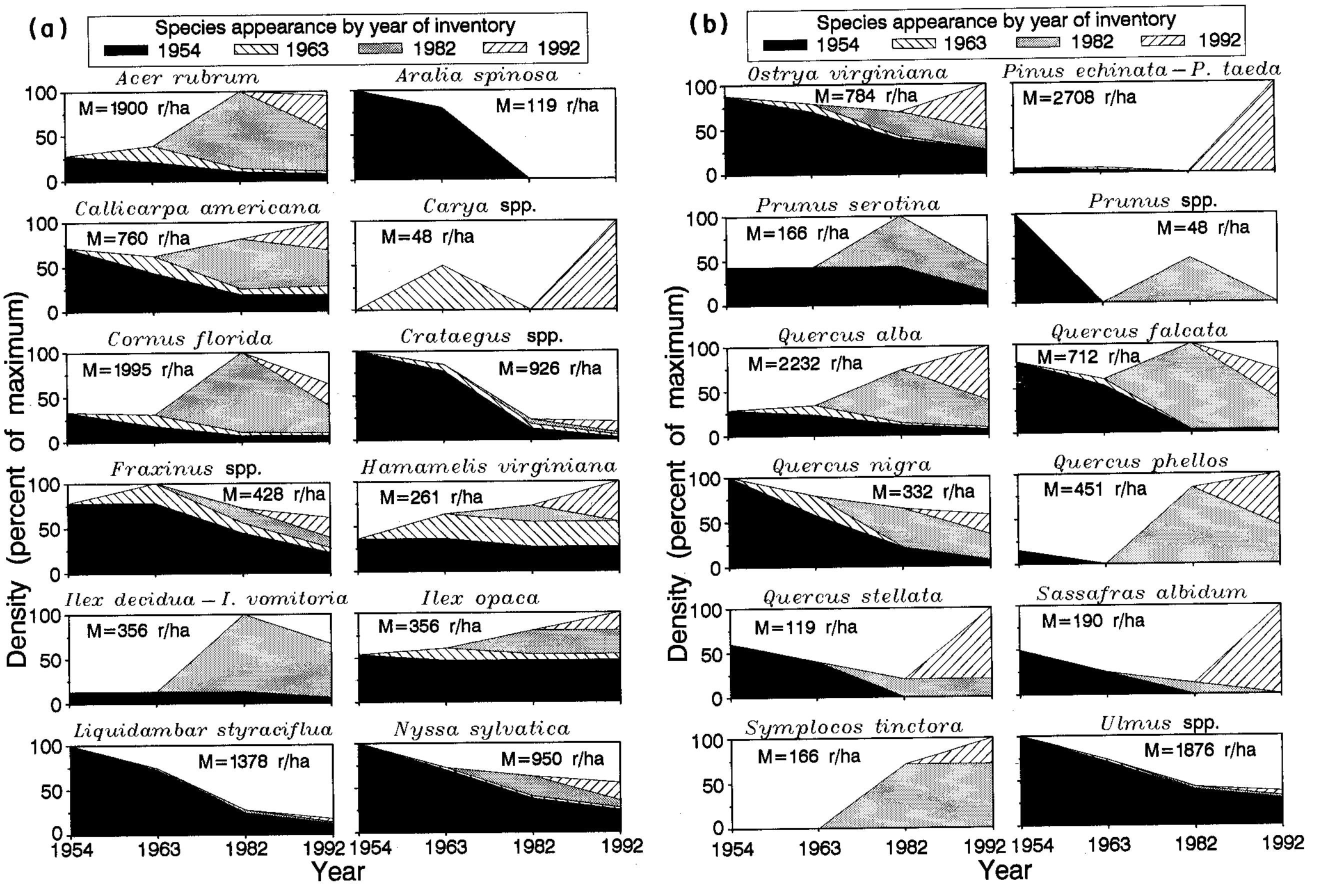
*Species recruitment and decline*

There were 24 woody understory species or groups where two or more rootstocks (48 rootstocks/ha) were counted during any inventory. Temporal trends in relative density for these species are illustrated in Fig. 2. Only 6 of these 24 species averaged more than 1000 rootstocks/ha during any one inventory.

After the 1954 inventory, the greatest gains in rootstock numbers were achieved by *A. rubrum*, *C. florida*, *Q. alba*, and *Pinus* spp. In contrast, *L. styraciflua* and *Ulmus* spp. exhibited the greatest loss in numbers, while *Aralia spinosa* L., an early successional species, disappeared completely by 1982.

One anomaly appeared to be consistent among several species, but only in the 1982 inventory. There was a substantial gain in rootstock density for 12 of these 24 species between 1963 and 1982. *Acer rubrum*, *C. florida*, *Ilex decidua* Walt. – *Ilex vomitoria* Ait., *Prunus serotina* Ehrh., and *Q. falcata* Michx. attained maximum densities in 1982. However, during the next 10 years, rootstock gains that were achieved by 1982 had declined for 10 of these 12 species. Only 2 species (*I. opaca* and *S. tinctoria*) were able to maintain their 1982 rootstock densities. This decline in species density between 1982 and 1992 was attributed to a drought that occurred during May through June of 1985, when only 4.8 cm of precipitation was recorded on the experimental forest. That precipitation was 78% less than the May through June average that was recorded during 65 years of weather measurements.

**Fig. 2.** Recruitment and decline of woody understory species in a 32-ha pine–oak forest during 38 years without catastrophic disturbance. Density is expressed as a percent of maximum (*M*) rootstocks per hectare (r/ha) for each species having at least 48 rootstocks/ha.




*Growth*

Annual height growth was computed for those woody understory species having more than five rootstocks (119 rootstocks/ha) that survived for 38 years. Overall, height growth was <0.1 m/year when averaged across all species (Table 7). Of the eight species with positive height growth, all but two (*Q. alba* and *L. styraciflua*) are classified as tolerant of shade. The shrub *Callicarpa americana* was the only long-term survivor whose average growth was negative. This result would be expected because shrub species are relegated to the understory, with a high probability of dieback in a closed-canopy stand. Height growth relative to initial size in 1954 averaged less than 10% for all surviving species (Table 7). Although *I. opaca* ranked near the bottom in absolute height growth, relative height growth for this shade-tolerant species was second only to *Q. alba*. Compared with the other long-term survivors, only *Q. alba*, *N. sylvatica*, and *L. styraciflua* had overstory potential. Two shade-tolerant species (*N. sylvatica* and *Ulmus alata* Michx.) had the greatest number of survivors (Table 7).

Height growth dynamics are presented for 24 woody understory species groups where two or more rootstocks (48 rootstocks/ha) were counted during any inventory (Fig. 3). Of those 24 species, only two groups, *Carya* spp. and *Prunus* spp., had no rootstocks that survived from one inventory to the next. For most survivors, the general trend was little or no height growth. Even for *Q. alba*, with the greatest average height growth, only one rootstock exhibited a substantial gain in total height; it was also the tallest tree developing from the understory and was >20 m in 1992. A similar trend was apparent for a singular rootstock of *A. rubrum* and *Fraxinus* spp. Shade-tolerant species exhibited the most consistent height gains for survivors: *A. rubrum*, *C. florida*, *Ilex* spp., *N. sylvatica*, *O. virginiana*, and *Ulmus* spp. With the exception of *Q. phellos*, most recruits that appeared in 1982 tended to have positive rather than negative height growth during the next 10 years.

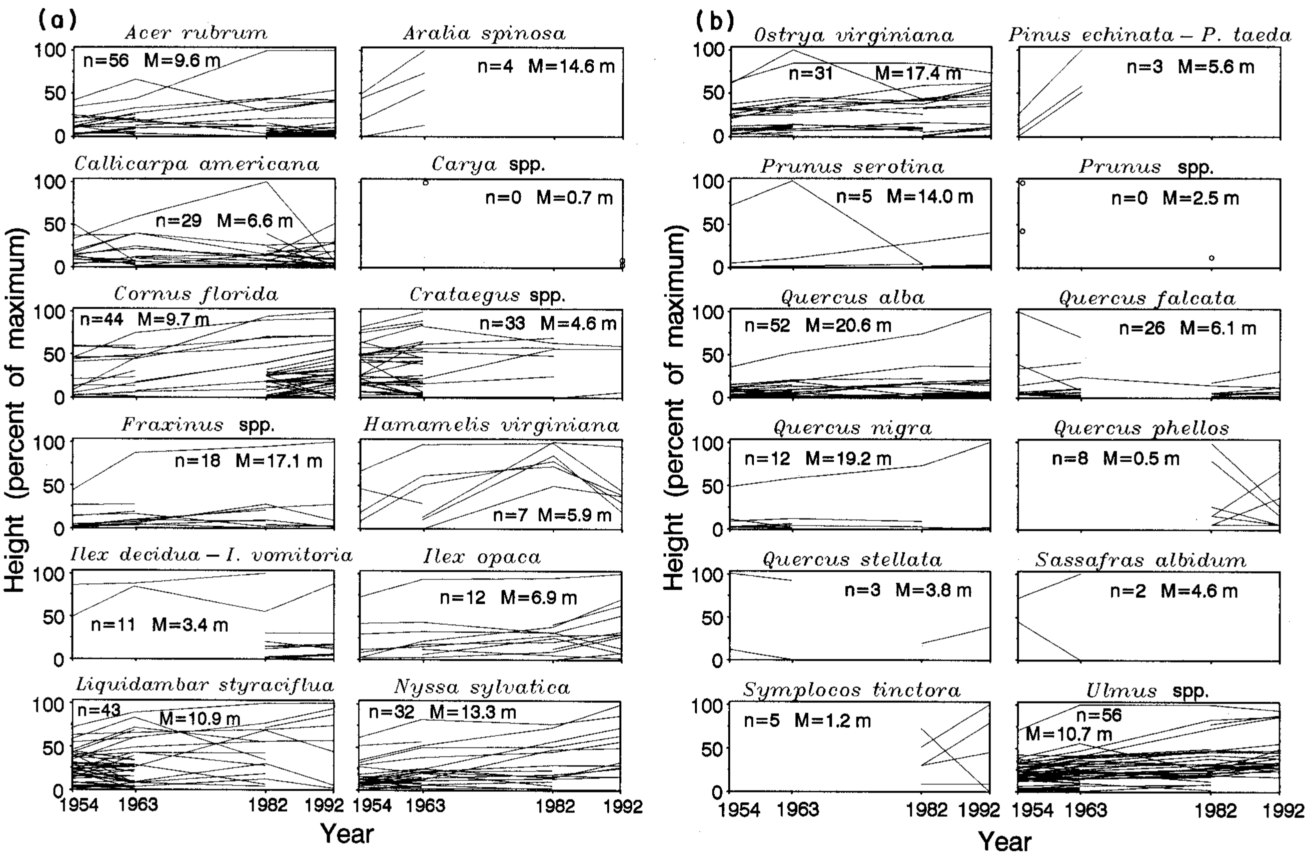
Nine woody species had rootstocks that grew large enough to be classified as part of the midstory component (trees ≥9 cm DBH). Of the original rootstocks that were identified on sample quadrats before 1982, 214/ha had achieved midstory stature by 1982. Between 1982 and 1992, an additional 166 rootstocks/ha grew out of the understory, thereby yielding 380 rootstocks/ha as midstory recruits: five shade-tolerants (*A. rubrum*, *C. florida*, *N. sylvatica*, *O. virginiana*, and *U. alata*); two inter-mediate in tolerance (*Fraxinus* spp. and *Q. alba*); one moderately intolerant (*Q. nigra*); and one intolerant (*L. styraciflua*). *Nyssa sylvatica* had the most recruits, at 95 rootstocks/ha.

## Discussion

### Understory dynamics

The density of survivors by year of inventory suggests a dynamic population of woody understory vegetation, with

**Fig. 3.** Height growth trends for woody understory species in a 32-ha pine–oak forest during 38 years without catastrophic disturbance. Height is expressed as a percent of maximum height (*M*) for each species having at least 48 rootstocks/ha. *n*, number of rootstocks that survived between at least two inventories on fifty-two 8-$m^2$ quadrats. *Carya* spp. and *Prunus* spp. had no rootstock survival between years of inventory.




individuals appearing, persisting, or declining in numbers relative to shade tolerance. Most of these understory plants could be categorized as transgressives, i.e., 0.3 to 3 m tall (Quarterman and Keever 1962).

In midsummer of 1993, only 3% of the canopy above sample quadrats was judged to be open by densiometer readings, which is consistent with earlier assessments of canopy cover in this forest (Cain 1987). In that earlier evaluation, it was found that between 1954 and 1982, the percent of sample quadrats overtopped by hardwood or pine–hardwood cover increased from 60% to 74%, with a concomitant decrease in pine or open overtopping conditions (40% in 1954 to 26% in 1982). These temporal trends suggest a closed canopy with a corresponding decrease in photosynthetically active radiation at the understory level. The narrow range in canopy coverage (86–100%) indicated that canopy gaps created by overstory mortality were too small to be detected, or the gaps have been obscured by the midstory and upper portion of the understory canopy. As mature pines died, they remained vertical and gradually decayed into snags; there was no evidence of windthrow during the 1982 or 1992 surveys.

Increasing density and basal area for overstory and midstory hardwoods created an understory environment generally unfavorable for the survival, growth, and development of shade-intolerant species. Shade-tolerant trees (*A. rubrum*, *C. florida*, and *Ilex* spp.) and those intermediate in tolerance (*H. virginiana* and *Q. alba*) tended to increase in importance throughout 38 years. In contrast, the shade-intolerant *L. styraciflua* had a distinct proclivity to decline during the same interval. One intolerant (*Aralia spinosa*) and one tolerant (*Cercis canadensis*) species disappeared completely after 1963.

Between 1982 and 1992, four of five species that grew out of the understory (<9 cm DBH) and into the midstory (≥9 cm DBH) were classified as shade tolerant. The tolerants included *A. rubrum*, *C. florida*, *N. sylvatica*, and *U. alata*. One intolerant species, *L. styraciflua*, also achieved midstory status during the previous 10 years. Although *N. sylvatica* had the most recruits to midstory status and had a survival rate of 25% during 38 years, this shade-tolerant species declined in relative importance mainly because of a 55% decline in rootstock density between 1954 and 1992. Concomitantly, Blair and Brunett (1976) found that *N. sylvatica* ranked second to all other species in relative density within a pine–hardwood ecosystem in central Louisiana, but noted that the species rarely attains dominance in a stand of mixed species. Another shade-tolerant group, *Ulmus* spp., had 29% survival of established rootstocks during 38 years, but relative importance declined because there were 68% fewer stems in 1992 than in 1954. Toumey (1929) concluded that failure of plants

**Table 7.** Mean annual height growth among woody understory species that survived for 38 years.

| Species* | *n* | Annual height growth | |
|---|---|---|---|
| | | Absolute (m) | Relative† (%) |
| *Quercus alba* | 6 | 0.116 | 9.53 |
| *Cornus florida* | 6 | 0.106 | 7.99 |
| *Nyssa sylvatica* | 10 | 0.105 | 4.57 |
| *Ostrya virginiana* | 9 | 0.062 | 1.34 |
| *Acer rubrum* | 6 | 0.055 | 2.92 |
| *Liquidambar styraciflua* | 7 | 0.050 | 1.01 |
| *Ulmus alata* | 22 | 0.040 | 1.27 |
| *Ilex opaca* | 7 | 0.040 | 9.16 |
| *Callicarpa americana* | 6 | −0.001 | 0.23 |

*Includes only those species having more than five rootstocks in 1992.

†Relative height growth = (annual height growth/total height in 1954) × 100.

to survive under a closed forest canopy was as much the result of root competition for soil moisture as it was the result of the shade from the overstory.

*Pinus* spp. were the only woody understory species to vanish after 1963 then rebound to become one of the more important understory plants in 1992. At least two events facilitated pine recruitment: better than average pine seed crops in southern Arkansas during the winters of 1990–1991 and 1991–1992 (Cain 1993) and adequate soil moisture during the growing seasons. In that respect, *Pinus* spp. are probably the most opportunistic of all species recorded in this 32-ha forest. This redivivus anomaly for pine is consistent with observations made in other investigations. For example, 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 efficiently and die out.

These data suggest that regardless of shade-tolerance characteristics, individual stems are able to subsist in the understory of this closed-canopy stand. Although the understory environment was most favorable for shade-tolerant species, microsite variation appeared to benefit some shade-intolerant species as well.

The relative importance of *Quercus* spp., as a group (15–22%), made a substantial contribution to the understory community for 38 years. Nevertheless, long-term persistence of individual rootstocks was poor at best for all *Quercus* spp., except *Q. alba*, which averaged 22% survival during 38 years. Because of its ability to become established, survive, and grow beneath this closed canopy, *Q. alba* should probably be classified as moderately tolerant of shade rather than intermediate in tolerance.

Because of the contribution that oaks make in this forest cover type, it is important to discuss their performance in the understory of this 32-ha forest and how that performance relates to published research. *Quercus alba* and *Q. nigra* were the only oaks with rootstocks (24/ha) that grew out of the understory and into the midstory by 1982, and no additional oaks achieved midstory stature during the next 10 years. These findings are consistent with those of Glitzenstein et al. (1986), who reported an abundance of oak seedlings in the understory of an east Texas, mixed pine–hardwood forest that also was devoid of large oak saplings. Similarly, Parker et al. (1985) reported that despite repeated dieback, oak seedlings persisted for 25 years beneath an old-growth, deciduous forest in Indiana. Lorimer (1984) noted that a striking feature of upland oak forests in central Massachusetts and southern New York was a dense understory of shade-tolerant species dominated by *A. rubrum* with a sparse representation of oak saplings.

According to Lorimer (1981), oak saplings that originate under shade are prone to repeated top kill when not receiving substantial direct solar radiation. This observation was substantiated by Abrams and Downs (1990), who surmised that the small number of hardwood saplings in a mixed mesophytic forest of Pennsylvania was due to the monopolization of resources and canopy closure. Viewed another way, understory plants may grow past a size that can be sustained, and when a stressful event occurs, the plants cannot maintain their size because of their inability to compete with canopy trees (Yeaton 1978).

Even though *Carya* spp. have been categorized as major components of the oak–hickory climax (Oosting 1956), few rootstocks from that group of species were identified in the present investigation. The lack of *Carya* spp. in the understory of this 32-ha forest suggests that this genus will not be a major component of the climax community. Similarly, McCarthy and Wistendahl (1988) predicted that *Carya* spp. would not be maintained in a southeastern Ohio second-growth oak–hickory forest if the forest was subjected only to small-scale gap disturbances. Other researchers have also concluded that *Carya* spp. are not important enough in eastern United States forests to justify the oak–hickory and oak–pine–hickory names that have been applied to some regions (Monk et al. 1990; Ware 1992).

Surprisingly, more woody understory species were identified in 1992 than in earlier inventories, but alpha diversity for the woody understory in this 32-ha forest was >90% according to Simpson's index, and about 2.7 when Shannon's index was used, regardless of the year of inventory. IV for understory woody species were likely to be most similar when inventories were closely spaced through time and least similar the greater the time that passed. Although diversity changed very little in 38 years, the relative importance of individual species was dynamic.

According to Monk (1967), high levels of tree species diversity are indicated when Shannon–Wiener values are ≥3.0. Concomitantly, Martin (1992) proposed that before a forest can be categorized as old-growth mixed mesophytic, one criterion is that the Shannon–Wiener index must exceed 3.0. At that level of diversity, Martin (1992) described the forests as species rich and structurally complex. According to the successional development of forest communities proposed for the Gulf Coastal Plain by Switzer et al. (1979), most of the vegetation within the present 32-ha forest is in the veteran period of late succession, which is a transitional phase when dominance shifts from pines to hardwoods.

Even in the absence of catastrophic natural or anthropogenic perturbations, forests are a network of complex interactions that result in continuous change. Long-term dynamics in this 32-ha forest suggest that smaller plants of shade-intolerant species within the understory will most likely die and be replaced by species that persist in the shade of overtopping vegetation. It is not unusual for an anthropogenically derived forest to be composed of overstory species that are shade intolerant or intermediate in tolerance, while the understory and midstory are populated with tolerant species. This phenomenon has often been observed in mature forests of widely different cover types, for example, mixed mesophytic hardwoods (Runkle 1981; Abrams and Downs 1990; Brothers 1993); *Pinus* spp. – *Quercus* spp. (Halls and Homesley 1966; Switzer et al. 1979); *Pinus strobus* L. (Peet 1984); *Quercus* spp. (Parker et al. 1985; McCarthy et al. 1987; Abrams and Nowacki 1992); *Quercus* spp. – *Carya* spp. (Pallardy et al. 1988; Shotola et al. 1992); southern mixed hardwood forest (Hartnett and Krofta 1989); *Tsuga canadensis* (L.) Carr. – *P. strobus* – northern hardwoods (Whitney 1984); and western Cascade conifers (Stewart 1989). The present 32-ha forest differs from most of these other forest cover types owing to its lack of shade-tolerant, late-successional species that have overstory potential.

Forests that are subjected to allogenic disturbances are not likely to follow the trends described in this paper. A classic example of such disturbance was the virtual elimination of *Castanea dentata* (Marsh.) Borkh. by the chestnut blight fungus (*Endothia parasitica* (Murr.) And.) during the first three decades of the 20th century (Stephenson 1986). Before the blight, American chestnut was a dominant or codominant species in upland forest communities throughout much of North America.

It is doubtful that the overstory of the present 32-ha forest will continue to be dominated by *P. taeda* and *P. echinata* in the absence of large-scale perturbations that would facilitate the development of younger cohorts from these shade-intolerant species (Oliver 1981). Since 32 ha would represent the upper limit of scale, 1-ha gaps would be considered as large-scale disturbances in this forest. These findings are generally consistent with those of Harcombe and Marks (1978), who reported that an underrepresentation of saplings of dominant overstory tree species (e.g., *P. echinata*, *P. taeda*, *Fagus grandifolia* Ehrh., *Magnolia grandiflora* L., *Q. nigra*, and *L. styraciflua*) was common in mesic and wet forests of southeast Texas. They considered the phenomenon to be geographically widespread and attributed sapling mortality to competition from both overstory and understory species.

**Relevance to forest development and succession**

Oliver and Larson (1990) described four stages of stand development: the stand initiation stage, the stem exclusion stage, the understory reinitiation stage, and the old-growth stage. However, developmental stages in the present 32-ha forest are not so straightforward because harvesting that occurred before 1915 was partial.

In the early interpretation of plant succession (Clements 1916), one or a few species invaded a disturbed area and predominated. As these plants altered the environment, other species invaded, became dominant, and further altered the environment. This replacement of one species by another (relay floristics) is often referred to as the "facilitation" model (Connell and Slatyer 1977). In this model, a single species or a group of species eventually predominates and replaces itself, creating a stable end point or climax (Oliver and Larson 1990).

Egler (1954) proposed a different path for plant succession based on "initial floristic composition." In this model, most plants are present at the time of disturbance or invade shortly after rather than throughout the life of a forest stand. Species that predominate later are thought to have been present since disturbance but are overlooked because of their small size, scarcity, slow growth, or suppression by other species (Drury and Nisbet 1973). The sequence of species in this model is determined solely by their life-history characteristics, and the climax forests are composed of the most shade-tolerant species (Connell and Slatyer 1977). Within this theory of plant succession, there are two subsidiary models, i.e., tolerance and inhibition (Finegan 1984). In the tolerance model, later species can become established and grow to maturity in the presence of other species because they adapt to lower levels of resources than earlier ones (Connell and Slatyer 1977). In the inhibition model, later species cannot grow to maturity in the presence of earlier ones, but their ultimate dominance occurs because they live longer and gradually accumulate as they replace the earlier species (Connell and Slatyer 1977).

Finegan (1984) proposed that facilitation, tolerance, and inhibition are interdependent mechanisms in succession and may affect the same individual successively or simultaneously during its life cycle. The long-term development of understory woody species in the present 32-ha forest was most likely influenced by all three mechanisms. The stand initiation stage began after the diameter-limit cut in the 1910s, in accordance with the model of initial floristic composition. After available growing space was reoccupied, new individuals could not become established, thus the forest entered the stem exclusion stage.

In 1954, when plots were first established to monitor woody understory development, the forest was still in the stem exclusion stage. At that time, overstory and midstory trees consisted of remnants of the virgin forest plus cohorts, most likely dominated by pines, that became established after the diameter-limit cut. Although new shrubs and trees appeared in the understory during the most recent inventory, the lack of subsequent growth and development suggests no strong trend toward the understory reinitiation stage, when regeneration becomes established and develops as overstory trees die and create canopy gaps. The periodic increase in overstory basal area throughout the 38-year investigation lends credence to this hypothesis.

In general, the predominant understory species are shade tolerant, they tend to appear and survive under a dense canopy, but they grow very little. Examples of species that were excluded from the understory without significant recruitment over 38 years of monitoring include *A. spinosa*, *Crataegus* spp., *L. styraciflua*, *N. sylvatica*, and *Ulmus* spp. (Fig. 2). The later development of shade-tolerant species in the understory followed the facilitation, tolerance, and inhibition models. Examples of species displaying an increasing density over 38 years of monitoring include the following intermediate and shade-tolerant species: *A. rubrum*, *Callicarpa americana*, *C. florida*, *H. virginiana*, *I. opaca*, *O. virginiana*, *Q. alba*, and *S. tinctoria* (Fig. 2).

The study of forest succession is difficult because of the long time scale involved (Hibbs 1983). Nevertheless, the brief 38-year results of understory dynamics presented in this study contribute to our understanding of forest succession in a 32-ha, temperate pine–oak forest that has not undergone catastrophic disturbance. During the described period of succession, the pattern of understory dynamics was dominated by a closed midstory and overstory, which prevented light penetration to the understory. Consequently, shade-tolerant understory species increased in importance, while shade-intolerant species declined. Monitoring of stand dynamics will continue in the present forest to validate current trends.

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