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FOREST VEGETATION OF THE LOWER ALABAMA PIEDMONT[1]

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Abstract. Forest community types were distinguished for the lower Alabama Piedmont using a combination of two agglomerative clustering algorithms with a similarity sorting technique. All stands classified in 8 of the resulting 10 community types had within-type similarity values of at least 45%. Ordination by reciprocal averaging using tree basal areas indicated that community types can be segregated into three topographically defined groups: streambottom communities (Sweetgum–Water Oak–Red Maple and Small Streambottoms), mesic upland communities (White Oak, Chestnut Oak, Pine-Hardwoods, Mixed Oak–Hickory, and Loblolly Pine), and xeric upland communities (Oak-Pine, Blackjack Oak–Pine, and Longleaf Pine). A reciprocal averaging ordination using understory plants successfully separated most of the same community types.

The combined clustering-similarity sorting procedure identified "core" stands that provide a clearer representation of definable forest community types than would have resulted from inclusion of atypical or transitional stands. The combination of classification for description of vegetation and ordination for definition of vegetation-site relationships proved complementary and useful.

The highest tree species diversities were in mesic upland hardwood and pine-hardwood communities; the lowest were in pine communities. Diameter size class distributions revealed general underrepresentation in the seedling/sapling size classes for all important canopy species, even the climax *Quercus* and *Carya*. Underrepresentation was most severe in wet-to-mesic stands. Natural succession from pine toward hardwood dominance is more rapid on bottomlands, stream terraces, and other moist sites than on drier, more fire-prone uplands. Forest cutting practices of many nonindustrial owners accelerate the trend toward dominance of hardwoods, even on uplands.

Key words: Alabama; classification; forests; ordination; Piedmont; reciprocal averaging; vegetation; diversity; succession.

INTRODUCTION

This study was designed to examine the forest vegetation of the southern end of the Alabama Piedmont and its relationships to environment. This was accomplished by obtaining quantitative and qualitative data on the composition, structure, distribution, and environment of forest communities of a specific area within the region. The study was undertaken primarily because of the paucity of quantitative vegetation-site information for this part of the southeastern United States.

The Piedmont extends from New Jersey to Alabama (Fenneman 1938). Braun (1950) placed the bulk of the Piedmont in the Atlantic and Gulf slope sections of the "Oak-Pine Forest Region," with the dividing line between the two sections in central Georgia. She characterized the Alabama Piedmont, in which she included the Blue Ridge, as "the most representative part of the Oak-Pine region of the Gulf Slope." Some easily observed differences between the Alabama Piedmont and the North Carolina Piedmont as described by Oosting (1942) include the abundance of *Pinus palustris* (nomenclature follows Radford et al. 1968) in Alabama and the much more common occurrence of communities dominated by *Quercus alba* or *Q. rubra* in North Carolina.

Mohr (1901) and Harper (1943) published early qualitative descriptions of the vegetation of the Alabama Piedmont. The upland oak-hickory component of forest communities is the subject of recent study (Golden 1976). Johnson and Sellmann (1974) have developed a photo-interpretation key for broad forest types of the region which includes a description of forest cover as related to geology and topography.

Part of the challenge of the present study was to obtain a reasonable definition of vegetation-site relationships in an area where disturbance and uncertain successional status of the forest communities greatly complicate the task. Almost all Piedmont forests have been cleared or cut over at some time. Probably only small areas of rough or steep land have not been cleared at some time for crops or pasture. Early in this century Mohr (1901) stated, "Wherever ridges spread into wider expanses forming broad uplands, these now are denuded of their original forest growth and mostly subjected to cultivation." Poor conservation practices have resulted in land degradation and subsequent general abandonment of large-scale cropping, leaving most of the area in pasture or woodland. Much of the gentler terrain presently in woodland was planted to pines (typically *Pinus taeda*) or was reforested through old-field succession within the past 50 years.

Cutting practices vary widely. Most of the land is held in small tracts by private landowners and "high grading" is common. Extensive tracts are also managed by large corporations, usually for even-aged production of pines.

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METHODS

The study area

The study area is at latitude 33°N, longitude 86°W, and includes the western two-thirds of Tallapoosa County and part of eastern Elmore County, in east-central Alabama (Fig. 1), a total area of 83 920 ha. Elevation ranges from about 120 to 250 m above mean sea level.

This area was selected partly because it includes a cross-section of the geologic, topographic, and soil conditions encountered in the lower Piedmont. Large tracts are owned by corporate landowners and most of it is easily accessible. At least three physiographic regions are recognized (Johnston 1930). The Opelika Plateau (Fig. 1) is gently rolling, with local relief usually less than 20 m. Geologic substrata are predominantly igneous schists and gneisses. The Ashland Plateau is considerably rougher, with local relief sometimes up to 70 m. Substrata include mica schists, phyllites, quartzites, granites, and various schists and gneisses. A narrow belt of resistant quartzite and phyllite along the Brevard Fault is locally termed the "Devil's Backbone" (O'Neill and Valley 1970) or "Piedmont Ridge" (Hodgkins et al. 1976). Topography is steep with local relief 20 to 100 m.

Soils are predominantly Ultisols, with scattered Inceptisols. The most common soil series are Madison, Tallapoosa, Gwinnett, Cecil, Appling and Hiwassee.

The climate can be characterized as warm and humid. Summers are long and hot, winters are short and usually mild. The frost-free period averages 229 days. Mean annual precipitation is about 137 cm, almost all falling as rain. A period of soil moisture deficiency frequently occurs in the late summer and fall.

Stand selection

Before field sampling began and again in later stages of the field work, a number of line transects were placed on topographic maps of the study area. Placement was designed to sample the complete range of geologic, soil and topographic conditions. I then moved along these lines on the ground, sampling forest stands which were at least 0.5 ha, relatively homogeneous, and free from strong recent disturbance. Unavoidably, almost every stand sampled had some evidence of past cuttings or else appeared to have developed on an old field. Eighty-four stands were sampled, 16 in stream or river bottoms and 68 on upland sites.

Sampling methods

A 20 × 50 m quadrat (0.1 ha) was centrally located in each stand. On sloping sites the long axis was placed perpendicular to the slope direction. LaFrance (1972) demonstrated with artificial populations that such an orientation of rectangular plots is more efficient for extracting species groupings in ordination analysis than are plots parallel to the slope gradient. Trees ≥10 cm dbh were tallied by species and diameter in the 0.1 ha quadrat. Trees 2–9.9 cm dbh were tallied by diameter and species in a 10 × 50 m strip down the center of the plot. Tree seedlings taller than 15 cm but less than 2 cm dbh were counted by species in 10 systematically-placed 2 × 2 m quadrats. Presence of herb and shrub species (but not grasses, sedges or bryophytes) was recorded for each 0.1-ha plot.

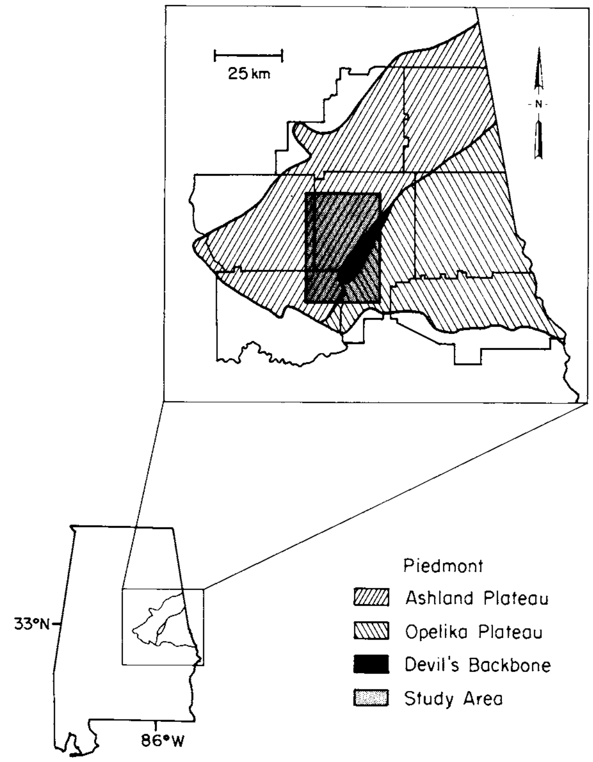

FIG. 1. Location and physiographic divisions of the study area.

Tree cover was measured by a line-intercept approach, using the vertical projection of tree parts from the canopy stratum onto a 50-m tape placed along the center of the 0.1-ha quadrat. Evidence of fire was noted and the number of stumps and apparent time since cutting were recorded within the large plot. The dispersed and varied ownerships precluded any realistic evaluation of stand histories from written or oral records.

At one or more locations within each stand, a soil pit was dug to bedrock or 1.5 m. Soil horizons were measured, described, and a sample taken from each. Soil samples were later analyzed for pH and nutrients at the Alabama State Soils Laboratory. A weak acid extraction solution was used for nutrient analyses. Slope steepness and direction were measured and the topographic position was classified as streambottom, lower slope, midslope, upper slope, broad ridge or narrow ridge.

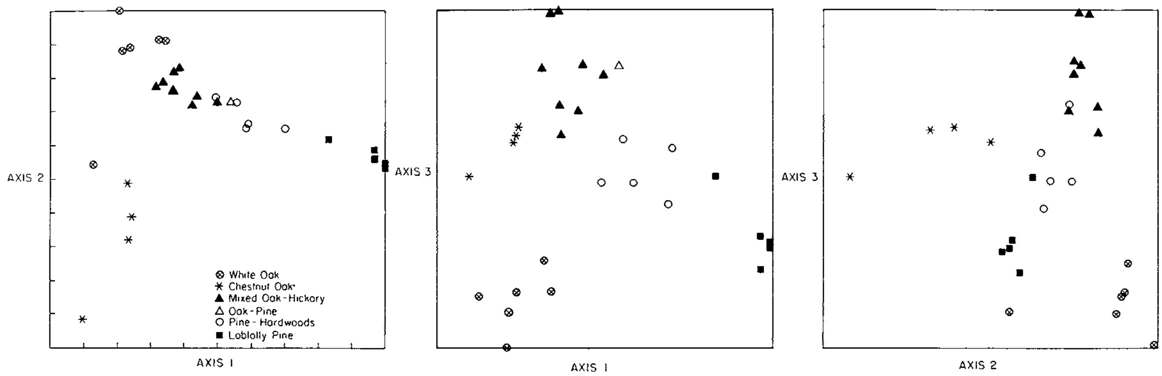

FIG. 2. Axes 1, 2, and 3 of the ordination of mesic upland stands. All 49 stands of the central cluster of the 82-stand ordination were used but only stands classified into types are shown here.

Classification

The process of classifying stands into types was begun with application of two polythetic agglomerative clustering algorithms (Williams 1971): minimum within-group dispersion using standard distance (Orloci 1967), and mutual information (Orloci 1969). Several studies (Grigal and Goldstein 1971, Grigal and Ohmann 1975, Robertson 1978) have reported these two approaches to be superior to other clustering techniques examined. Computations were performed using the programs MINDISP and MINFO of Goldstein and Grigal (1972). Tree species basal areas were used as input data. Dendrograms were constructed from the two analyses and convergent stand groups (dendrogram stems) were determined.

A problem common to all clustering procedures arises in deciding at what level to terminate each stem and treat the resulting groups as community types or associations. An assumed objective of vegetation classification is to identify groups with some reasonably high level of homogeneity. It consequently seems desirable that some homogeneity criterion should be used in determining or evaluating the final classification units. To provide a measure of the homogeneity of tentative stand groups, percentage similarities (Goodall 1973) based on species basal areas were computed for all stand pairs using Cornell Ecology Program CEP-5 (Gauch 1973).

Stand groups were desired which (1) were distinguished by both clustering algorithms (convergent), (2) were as large as possible, and (3) had no two stands with a pairwise similarity of less than 45%, an arbitrary level which provided groups of reasonable homogeneity and size. To accomplish these objectives, the matrices of pairwise similarity values within convergent groups were examined in steps at successively higher levels of the dendrograms. At each step, the minimum number of stands was removed which left the resulting similarity matrix free of low values (less than 45%). At low levels, this was commonly two or fewer stands (often none). This process was repeated for each dendrogram stem until further upward movement resulted in no net increase in group size.

One significant problem arose. Most of the streambottom stands were in two convergent groups. However, no combination of more than two of these stands could be grouped and still meet the 45% minimum similarity criterion. Rather than delete all of these stands from further classification, or use only two stands as representative of a community type, two streambottom types having lower internal similarities were recognized. These were designated the "Sweetgum (*Liquidambar styraciflua*)–Water Oak (*Quercus nigra*)–Red Maple (*Acer rubrum*)" and "Small Streambottom" community types, and had minimum internal similarities of 31 and 19%, respectively.

The procedure of dropping low-similarity stands in effect removes those which are intermediate or transitional between community types. Those remaining are viewed as "core" stands (Grigal and Goldstein 1971, Grigal and Ohmann 1975), clearly representative of a community type.

Seventy-one stands were included in the convergent groups. After the similarity sorting procedure, 53 stands remained as core representatives of 10 community types. Besides the two streambottom types previously mentioned, these were: White Oak (*Quercus alba*), Chestnut Oak (*Quercus prinus*), Pine (*Pinus*)-Hardwoods, Mixed Oak–Hickory (*Carya*), Loblolly Pine (*Pinus taeda*), Oak-Pine, Blackjack Oak (*Quercus marilandica*)–Pine, and Longleaf Pine (*Pinus palustris*).

Ordinations

Reciprocal averaging (RA), or "correspondence analysis" (Hill 1973, 1974), was used to ordinate stands and species (computer program CEP-25A, Gauch 1973). Basal areas (BA), computed using all stems ≥2 cm dbh of 49 tree species (those present in three or more stands), were used as species importance values. In the first ordination two outlier stands dominated the first axis and were deleted from subsequent ordinations.

The remaining 82 stands were again ordinated by the RA procedure. The first axis of this second ordination was readily interpretable, but a large cluster of stands and species appeared in the upper middle of the two-axis space. Additional axes did not meaningfully separate the stands or species of this cluster. To attain additional resolution within this group, the data set was partitioned and the 49 stands of the central cluster were ordinated separately (Fig. 2). Polar ordinations (Bray and Curtis 1957) of the same data sets gave similar results.

To explore further relationships among the hardwood stands of the central cluster, those with less than 25% *Pinus* basal areas (34 stands) were ordinated separately by reciprocal averaging. However, this ordination provided no significant additional information. It appeared to be an expansion of the pattern shown by the hardwood stands in Fig. 2.

To provide insight into the nature of the nontree portion of the communities, an RA ordination of the community types based on the presence of common shrubs, vines, pteridophytes, and herbs was obtained (Fig. 3). Community types were treated as individuals and species (measured by presence) as attributes. Both to concentrate on the typical, more constant species and to avoid a high number of zeros, only species present in more than 25% of the stands of at least one type were included in this analysis.

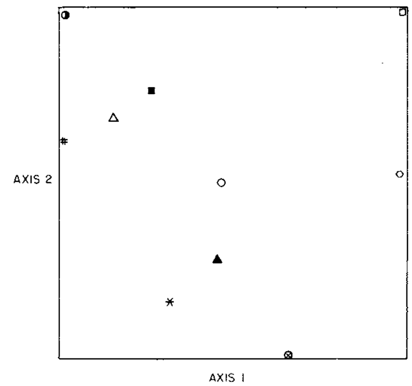

FIG. 3. Axes 1 and 2 of the reciprocal averaging ordination of forest communities computed using common shrub, vine, pteridophyte, and herb presence (percent) as community attributes. Community type symbols for mesic upland communities are the same used in Fig. 2. The other community type symbols are: ○ = Small Streambottoms, □ = Sweetgum–Water Oak–Red Maple, ◑ = Blackjack Oak–Pine, and # = Longleaf Pine.

RESULTS

Community types were named using tree species with the highest average relative basal area (RBA) which were present in all stands of the type. Species presence and average stand RBA of common tree species in each of the 10 types are presented in Table 1. The types and species are arranged in order of their average first-axis position in the 82-stand RA ordination.

The first two axes of this ordination, both of stands and of species, showed the "horseshoe" or arch configuration (Gauch et al. 1977) typical of RA with sample sets having a dominant gradient. The order of stands and species along the two-axis arch reflects a moisture complex-gradient characterized by changing topographic position, soil moisture regime, and microclimate. The two ends of the stand ordination are clearly defined by topography. The stands and tree species can be loosely grouped into three general, site-defined classes, as reflected in the ordination: streambottoms, mesic (in the sense of "medium") uplands, and xeric uplands.

Streambottom communities

Only two community types, Sweetgum–Water Oak–Red Maple and Small Stream bottoms, were identified among the stands from bottomland sites (Table 2). A greater variety of bottomland communities exists in the lower Piedmont, but thorough description of these would require a much larger number of samples. The extent of large river bottom sites in the study area is limited. Most of the bottomlands of the Tallapoosa River are inundated by a large impoundment. Tributary and small-stream bottomlands are frequent, but seldom exceed 100 m width and are usually much narrower.

Soil water drainage, bottomland width, and disturbance history appear to be the most significant factors affecting species composition of bottomland stands. Except for beaver ponds, extensive areas of poor drainage are rare. Most of the natural poorly drained sites within the bottoms are localized and quite narrow. While none of the stands sampled in the bottoms can be characterized as a swamp, several have small swampy areas included within them.

The two bottomland communities have different drainage characteristics: Sweetgum–Water Oak–Red Maple stands are found on sites with moderate to poor internal drainage and in both wide and narrow bottoms; Small Streambottom communities are typically in narrow, moderately well-drained floodplains and sheltered coves which have had no severe recent disturbance. The narrow width and generally good drainage result in a variable mixture of tree species, including those characteristic of large bottomlands (e.g., *Liquidambar styraciflua, Fraxinus pennsylvanica, Acer rubrum,* and *Quercus nigra*), moist coves (e.g., *Fagus grandifolia* and *Liriodendron tulipifera*), and mesic uplands (e.g., *Diospyros virginiana, Quercus alba, Carya ovalis,* and *Oxydendrum arboreum*). Commonly the presence of small, low, swampy areas results in an increase in *Magnolia virginiana, Liquid-*

TABLE 1. Species presence and average relative basal area (RBA) in each community type. Number of stands of each type is shown in parentheses under each type name.

	Community types									
Species*	Sweet-gum–Water Oak–Red Maple (4)	Small stream-bottoms (4)	White Oak (6)	Chest-nut Oak (4)	Pine-hard-woods (5)	Mixed Oak–Hickory (8)	Lob-lolly Pine (6)	Oak-Pine (4)	Black-jack Oak–Pine (6)	Long-leaf Pine (6)
	Presence (% × 0.1): Average RBA (%)									
Carya cordiformis	2:+									
Halesia spp.	2:+		2:+							
Betula nigra	5:+									
Quercus nigra	10:25	5:3	3:+			1:+	3:+	2:+		
Morus rubra	5:+	2:+			4:+	5:+				2:+
Ulmus americana	2:+									
Carpinus caroliniana	10:+	8:8				1:+				
Magnolia virginiana	2:+	8:10								
Fraxinus spp.†	5:+	5:9	3:+	2:+		1:+				
Ulmus alata	8:+	2:+			2:+					
Acer rubrum	10:15	10:3	7:+	2:+	2:+	2:+	3:+		3:+	
Ilex opaca		8:+								
Fagus grandifolia		10:19	7:+		2:+	1:+				2:+
Alnus serrulata	2:+	5:+								
Liquidambar styraciflua	10:27	5:7	8:+	2:+	8:5	5:+	8:+	2:+		2:+
Magnolia acuminata		2:2	2:+			2:+				
Ostrya virginiana		2:1	5:+							
Acer spp.‡	2:+				4:+	1:+				
Liriodendron tulipifera	8:6	10:14	8:+	2:+	6:+	8:+	5:+	2:+		3:+
Cercis canadensis	2:+				2:+					
Tilia spp.			2:+		2:+					
Diospyros virginiana	5:+	8:+	2:+	2:+		6:+	5:+	8:+	5:+	3:+
Quercus alba	2:+	5:1	10:47	8:+	10:+	8:5	2:+		5:+	2:+
Quercus rubra	2:+	8:1	5:+	2:+	2:+	2:+		2:+		
Quercus prinus		2:6	2:+	10:32	2:+	1:+		2:+		
Prunus serotina	2:+	5:+	7:+		6:+	2:+	3:+	2:+	3:+	
Carya ovalis	2:+	5:2	10:+	2:+	10:+	5:+		5:+	2:+	
C. carolinae-septentrionalis						2:+				
Oxydendrum arboreum		8:2	10:+	10:+	4:+	8:+	5:+	5:+		3:+
Juniperus virginiana					2:+		2:+			
Carya glabra		2:+	3:+	10:+	8:+	6:+	2:+	5:+	7:+	
Cornus florida	5:+	8:1	8:+	10:7	10:+	10:7	7:+	5:+	3:+	5:+
Carya pallida								2:+	2:+	
Quercus velutina			7:+	10:12	6:+	9:8		8:6	5:+	3:+
Carya tomentosa	5:+	2:1	10:5	10:13	8:9	10:26		10:+	7:+	2:+
Quercus coccinea			3:+	5:+	4:+	1:+		5:+		2:+
Nyssa sylvatica	8:+	8:5	8:+	10:+	10:+	9:+	3:+	10:+	2:+	7:+
Pinus taeda	2:6	5:2	5:+		10:33	8:5	10:72	10:6	7:9	2:+
Quercus stellata			5:+	8:+	10:5	10:20	3:+	10:12	10:+	2:+
Celtis occidentalis								2:+		
Quercus falcata		2:1	7:+	10:6	10:13	9:8	3:+	10:35	8:+	3:+
Pinus echinata	2:+	2:1	8:+	8:5	10:7	10:6	8:13	10:12	10:16	2:+
Sassafras albidum			2:+			2:+		5:+		8:+
Rhus copallina							2:+	2:+	2:+	
Quercus marilandica				2:+		4:+		10:7	10:42	3:+
Pinus palustris				2:+	2:+		3:+	8:13	8:21	10:86
Quercus incana									2:+	3:+

* Only tree species present in at least 3 of the 82 stands are included. Species absent in types or occurring in only one or two stands are *Acer negundo, Amelanchier arborea, Carya illinoiensis, Carya ovata, Catalpa speciosa, Castanea dentata, Gleditsia triacanthos, Juglans nigra, Magnolia macrophylla, Magnolia tripetala, Pinus virginiana, Quercus michauxii, Rhus glabra, Salix nigra*.

† Primarily *Fraxinus americana* and *F. pennsylvanica*.

‡ *Acer saccharum* subsp. *floridanum* and *Acer saccharum* subsp. *leucoderme*.

ambar styraciflua, and sometimes *Alnus serrulata*. Similar species-site relationships occur for *Alnus serrulata, Liquidambar styraciflua, Magnolia virginiana*, and *Q. nigra* in the small streambottoms of the southwestern Alabama Coastal Plain (Gemborys and Hodgkins 1971). However, there *Acer rubrum* is typically associated with wetter sites than is the case in the Piedmont.

TABLE 2. Vegetation, soil and site characteristics of the forest community types. Number of stands of each community type is shown in parentheses under the type name.

	Community types									
	Sweetgum–Water Oak–Red Maple (4)	Small stream-bottoms (4)	White Oak (6)	Chestnut Oak (4)	Pine-hardwoods (5)	Mixed Oak–Hickory (8)	Loblolly Pine (6)	Oak-Pine (4)	Blackjack Oak–Pine (6)	Longleaf Pine (6)
	Mean and Standard Deviation									
Canopy cover (%)	95 ± 2	96 ± 2	88 ± 5	84 ± 9	86 ± 7	85 ± 8	46 ± 19	70 ± 8	44 ± 9	49 ± 23
Shrub cover (%)	1 ± 1	38 ± 28	10 ± 9	28 ± 15	4 ± 5	9 ± 6	5 ± 5	12 ± 10	23 ± 19	27 ± 19
Slope position*	0 ± 0	0 ± 0	15 ± 8	18 ± 1	30 ± 14	24 ± 5	23 ± 8	35 ± 13	35 ± 12	38 ± 13
Slope steepness (%)	3 ± 2	3 ± 1	27 ± 19	42 ± 15	11 ± 7	33 ± 21	18 ± 26	16 ± 14	22 ± 16	29 ± 27
Slope direction†	5 ± 5	18 ± 2	11 ± 7	19 ± 1	12 ± 8	10 ± 5	5 ± 6	5 ± 6	8 ± 8	13 ± 6
Depth to bedrock (cm)	200+	200+	163 ± 41	156 ± 49	183 ± 23	183 ± 37	161 ± 57	150 ± 66	162 ± 35	85 ± 62
Soil A horizon										
Depth (cm)	28 ± 13	21 ± 8	19 ± 5	27 ± 11	18 ± 4	25 ± 12	17 ± 12	19 ± 6	23 ± 10	24 ± 30
pH (median)	4.7	4.7	4.9	5.2	5.6	5.4	5.0	4.9	5.1	5.0
Phosphorus (μg/g)	1 ± 1	2 ± 2	2 ± 1	1 ± 1	7 ± 13	22 ± 61	1 ± 1	1 ± 1	‡	2 ± 2
Potassium (μg/g)	22 ± 16	45 ± 27	54 ± 11	29 ± 4	60 ± 15	50 ± 20	36 ± 11	42 ± 24	20 ± 12	37 ± 15
Magnesium (μg/g)	44 ± 31	71 ± 40	41 ± 14	20 ± 7	113 ± 54	64 ± 59	30 ± 13	25 ± 18	45 ± 59	41 ± 28
Calcium (μg/g)	215 ± 159	253 ± 249	129 ± 102	68 ± 44	335 ± 190	251 ± 329	154 ± 95	94 ± 73	126 ± 118	191 ± 171
Soil B horizon										
pH (median)	5.5	5.3	5.3	5.4	5.5	5.5	5.5	5.4	5.4	5.5
Phosphorus (μg/g)	3 ± 2	3 ± 2	+	+	1 ± 2	14 ± 40	+	+	+	+
Potassium (μg/g)	19 ± 13	29 ± 10	45 ± 18	45 ± 22	42 ± 29	64 ± 28	36 ± 35	60 ± 52	28 ± 19	41 ± 28
Magnesium (μg/g)	98 ± 143	57 ± 24	76 ± 40	72 ± 35	92 ± 46	138 ± 85	108 ± 56	68 ± 18	126 ± 98	56 ± 48
Calcium (μg/g)	271 ± 196	443 ± 526	83 ± 74	55 ± 35	56 ± 22	310 ± 543	82 ± 51	45 ± 15	169 ± 226	157 ± 181
	Frequency of occurrence (%)									
Geologic region										
Opelika Plateau	25	25	0	0	20	12	17	25	17	0
Ashland Plateau	75	50	67	25	80	75	83	75	33	17
Devil's Backbone	0	25	33	75	0	12	17	0	50	83
Substrate type										
Phyllite	0	0	17	50	0	25	33	25	33	50
Mica schist	0	0	33	0	60	38	33	75	0	17
Granitic	0	0	33	25	40	38	33	0	50	0
Quartzite	0	0	0	25	0	0	0	0	17	33
Alluvium	100	100	17	0	0	0	0	0	0	0

* 0 = streambottom or cove, 10 = lower slope, 20 = midslope, 30 = upper slope, 40 = broad ridge, 50 = narrow ridge (less than 30 m crest width).
† Azimuth cosine transformation multiplied by 10, so that 215° (SW) = 0 and 45° (NE) = 20 (Beers et al. 1966).
‡ Less than 0.5 μg/g.

TABLE 3. Common shrubs, vines, pteridophytes and herbs present in the forest community types. Only species with >25% presence in at least one type are listed.

Species	Community types									
	Sweetgum Water Oak–Red Maple	Small stream-bottoms	White Oak	Chestnut Oak	Pine-hardwoods	Mixed Oak–Hickory	Loblolly Pine	Oak-Pine	Blackjack Oak–Pine	Longleaf Pine
	% presence									
Shrubs and woody vines										
Sambucus canadensis	50	50								
Decumaria barbara	50	100	17							
Itea virginica	25	50	17							
Arundinaria gigantea	25	50	17							
Anisostichus capreolata	100	50			20					
Cornus stricta	75	25				25				
Euonymus americanus	75	100	67	25		25				
Campsis radicans	100	25				25	33			
Lonicera japonica	75	100	17		20		50	25		
Rhododendron canescens	25	100	67	50		38		25		
Calycanthus floridus			33							
Aesculus pavia	25	25	50	25	20	25				
Aralia spinosa	25		17		40	12				
Hydrangea quercifolia	25	50	83	75		50				
Rhus radicans	100	100	100	75	60	63	83	50	17	
Smilax rotundifolia	75	50	83	25	60	12	33	50		33
Hypericum hypericoides	50		17			12	33	25	17	
Vaccinium elliottii	25	25	50	50	40	25	33			17
Parthenocissus quinquefolia	50	50	67	75	40	75	33	50	17	33
Vitis rotundifolia	75	100	100	100	80	88	83	100	50	33
Callicarpa americana		25			80	12	33		17	
Smilax glauca	50	75	67	100	80	75	67	100	67	67
Asimina parviflora	25	0	50	75	60	38	33	75	50	17
Vaccinium vacillans			67	75	20	38	67	25	50	33
Ceanothus americanus				50	20	50	17	75		17
Rhus toxicodendron			17	50		38	17	50	50	
Vaccinium arboreum				100	40	25	60	50	67	67
Vaccinium stamineum			17	50	20	38	67	75	50	100
Symplocos tinctoria				50			17		17	67
Epigaea repens				25				25		33
Gaylussacia dumosa				25				25	17	67
Gelsemium sempervirens							17		17	50
Ilex ambigua										50
Herbs and pteridophytes										
Arisaema dracontium	50	0								
Athyrium asplenioides	75	100	17							
Woodwardia areolata	50	100	17							
Arisaema triphyllum	50	75	17							
Osmunda cinnamomea	25	75	17							
Agrimonia pubescens	25	25	33							
Thalictrum thalictroides		25	33							
Polystichum acrostichoides	50	100	66	25	20	12				
Mitchella repens	50	100	50	25	20	25			17	
Dioscorea villosa	50	50	66	25	20	25				
Asplenium platyneuron		25	33			38				
Smilicina racemosa		25	50	25						
Hexastylis arifolia	25	75	100	50	40	38				17
Passiflora lutea	25				40	12				
Sanicula canadensis	25	25			40	12			33	
Smilax ecirrhata		25	33			25	17		17	
Elephantopus tomentosus	25		66	25	80	25	50			
Uvularia perfoliata		25	33	25	20	25		25		
Desmodium nudiflorum			33	50	20	25				17
Iris verna		25	17	100		12		25		50
Hypoxis hirsuta			17			12		50		
Coreopsis major			33	50	80	25	50	75	100	66
Silphium compositum			17	50		50	17	75	66	17
Pteridium aquilinum			17	75	40	38	33	75	83	83
Euphorbia corollata							33	25	17	
Schrankia microphylla				25		12		25	33	17
Houstonia longifolia					20				66	
Tephrosia virginiana				25		12	33	75	83	83
Eupatorium album							17	50	50	17

Although the two bottomland community types are separated somewhat by the second axis of the ordination using understory plants (Fig. 3), their relatively close similarity is revealed by axis one and in the understory species presence table (Table 3). Both communities are distinct from the upland stands in two-axis space. This distinctiveness arises primarily from the characteristic presence of a group of moist-site species in the bottomland stands.

Mesic upland communities

Overstories are characterized by a mixture of upland hardwoods and pines. The mesic upland communities are generally well-defined by the RA ordination (Fig. 2), particularly in the 1-and-3 axis space.

Axis 1 reflects a species composition gradient from hardwood to pine dominance. It shows no clear relationship to soil or site factors (Table 2), and can be interpreted as probably reflecting a general disturbance/successional trend. *Pinus taeda* and *P. echinata* are light-seeded intolerants and where seed sources are present, they are aggressive invaders of old fields and heavily disturbed forests. In comparison, the dominant mesic upland *Quercus* and *Carya* species are heavy-seeded, more tolerant, and are quite slow in invading new areas. However, once established, their ability to sprout usually assures their continued presence unless drastic perturbations, such as land clearing or extremely hot fires, occur. Some mixture of oaks and hickories is generally accepted as the climax forest composition in the Piedmont (Oosting 1942).

Axis 3 orders the hardwood communities from strong dominance by *Q. alba* to dominance by a mixture of *Quercus stellata, Q. falcata* and *Carya tomentosa*. This reflects a general trend from topographically moister to drier sites. White Oak stands, which form a distinct cluster at the lower end of axis 3, are located topographically no higher than midslope and the average slope position is well below midslope (Table 2). One of the White Oak communities is in a small cove. Conversely, all of the Mixed Oak–Hickory communities sampled are on middle or higher slope positions.

Chestnut Oak communities are on steep slopes with a north to northeasterly aspect. Slope angles ranged from 25 to 55% and the slope azimuths from 10° to 35°. All six stands with *Q. prinus* as the leading dominant (two were not typed) are on steep north-facing slopes.

The mesic upland communities, as characterized by understory species, occupy broadly the central 2-axis ordination space of Fig. 3. They exhibit a clear pattern of more xeric and open (upper left) to more mesic and closed communities (lower right).

Xeric upland communities

Longleaf Pine communities are generally quite distinctive. They are characterized by the strong dominance of *P. palustris* in an open canopy (Table 2). In five of the six stands its RBA was >85%. Subcanopy and understory species typically include *Symplocos tinctoria* (a small tree), one or more ericaceous shrubs (*Vaccinium arboreum, V. stamineum, V. vacillans, Gaylussacia dumosa, Kalmia latifolia*), and xeric herbaceous species such as *Tephrosia virginiana* and *Pteridium aquilinum* (Table 3). The seedling/herb stratum is usually poorly developed, due to a thick layer of pine needles and frequent fires. Most of the sites were found on ridges or upper slopes in the "Devil's Backbone" area (Fig. 1) and have shallow soils over phyllite or quartzite bedrock. Longleaf Pine communities also occur in the Ashland Plateau area, usually on ridges and upper slopes with shallow soils over mica schist bedrock.

The Blackjack Oak–Pine stands have *Q. marilandica* dominant in the canopy, along with either *Pinus palustris* or *P. echinata* as a second dominant. As with the Longleaf Pine communities, the canopy is typically open, but a slightly higher diversity of tree species is usually present. *Vaccinium arboreum, Tephrosia virginiana* and *Pteridium aquilinum* are commonly prominent in the shrub/herb layer. The stands are usually on upper slopes and ridges with shallow soils, or in one case with a deeper soil, a convex midslope with abundant quartzite fragments in the solum.

Soil and site characteristics

Trends among the stand, soil, and site characteristics are related most directly to topographic factors, but topography and typical soil depth are related in turn to the geologic substrata (Table 2). The highly resistant phyllites and quartzites of the Devil's Backbone result in steep terrain and narrow ridges, with predominantly shallow soils. The typical mica schist substrata of the Ashland Plateau are also fairly resistant. However, the Plateau has extensive areas of granites and less resistant schists which have gentler slopes with deeper soils (although a smaller proportion of these are forested). In contrast to this topography, the predominantly granitic schists and gneisses of the Opelika Plateau have weathered to a gently rolling terrain with deep soils. Consequently, xeric sites are more abundant in the Devil's Backbone and Ashland Plateau.

Contrasts between the streambottom and upper slope or ridge sites are evident for canopy cover, total soil depth, A horizon depth and B horizon phosphorus. Nutrient levels on most sites are low when compared to many temperate humid region soils (Buckman and Brady 1969). Low base levels are, however, usual for Ultisols of the southeastern U.S. (Perkins et al. 1973). The streambottom sites generally have higher levels of calcium and phosphorus than on uplands due to periodic deposition of sediment and lower levels of leaching.

A horizons are shallow on most uplands and shal-

TABLE 4. Mean numbers of species of trees, shrubs, woody vines, herbs, and pteridophytes in lower Piedmont forest community types.*

Community type	Trees†	Shrubs†	Woody vines	Herbs‡	Pteri-dophytes	Mean no. vascular taxa/plot‡	No. plots
Sweetgum–Water Oak–Red Maple	12 ± 1.7	8 ± 2.1	8 ± 1.7	8 ± 1.5	2 ± 1.7	38 ± 6.4	4
Small streambottoms	14 ± 2.5	12 ± 3.0	5 ± 0.5	11 ± 6.9	4 ± 0.8	45 ± 7.1	4
White Oak	17 ± 2.2	8 ± 1.6	4 ± 0.8	10 ± 2.2	2 ± 1.6	41 ± 6.3	6
Chestnut Oak	13 ± 1.0	11 ± 2.4	4 ± 1.0	8 ± 3.3	1 ± 0.8	37 ± 5.0	4
Pine-hardwoods	17 ± 1.3	8 ± 1.9	4 ± 1.2	7 ± 3.1	1 ± 0.8	37 ± 4.6	5
Mixed Oak–Hickory	16 ± 3.1	10 ± 5.8	4 ± 1.1	8 ± 4.2	1 ± 0.7	37 ± 12.2	8
Loblolly Pine	9 ± 5.3	8 ± 2.3	4 ± 1.0	6 ± 0.9	1 ± 0.5	29 ± 3.0	6
Oak-Pine	14 ± 1.5	9 ± 1.7	4 ± 1.3	10 ± 4.7	1 ± 0.5	37 ± 4.5	4
Blackjack Oak–Pine	12 ± 3.4	7 ± 2.0	2 ± 1.0	9 ± 3.7	1 ± 0.4	30 ± 7.8	6
Longleaf Pine	8 ± 4.5	9 ± 2.6	2 ± 0.5	5 ± 3.7	1 ± 0.4	25 ± 7.0	6

* Data for all categories are from 20 × 50 m plots (0.1 ha).
† Sub-canopy species are included with shrubs; e.g., *Cornus florida, Halesia* spp., *Cercis canadensis,* and others.
‡ Species and genera identifiable in the summer. Does not include grasses, sedges, or aquatics.

lowest on the Loblolly Pine, Pine-Hardwoods, Oak-Pine, and White Oak sites, due probably to erosion from past cultivation. Consistent with this hypothesis, the Chestnut Oak, Blackjack Oak–Pine, and Longleaf Pine sites, which are typically unsuitable for cultivation, have deeper A horizons and less evidence of accelerated erosion.

Species diversity

Average numbers of tree, shrub, woody vine, herb, and pteridophyte species found in stands of each community type were determined (Table 4). For comparison with species numbers compiled by Marks and Harcombe (1975) for various forest types, trees were defined as only species which are normally capable of reaching the canopy. All other woody species, including subcanopy species such as *Carpinus carolina, Cornus florida,* and *Ostrya virginiana,* were classed as shrubs.

The largest numbers of tree species per 0.1 ha plot were found in mesic upland hardwood and pine-hardwood communities—White Oak (17), Pine-Hardwoods (17), and Mixed Oak–Hickory (16). These numbers compare closely to the highest tree species average (16) reported by Marks and Harcombe (1975) for both cove transition forests of the Great Smoky Mountains (Whittaker 1965) and mixed mesophytic forests of the Cumberlands (Braun 1942).

The lowest numbers of tree species were in the two pine types, Loblolly Pine (9) and Longleaf Pine (8). These two types also had the lowest average number of herb species (6 and 5, respectively) and lowest average total vascular plant species (29 and 25, respectively) per stand. These low values are probably due to a combination of factors: the early to midsuccessional nature of most of the Loblolly Pine communities; the heavy litter layers and regime of frequent fires in both types; the xeric conditions and sometimes heavy ericaceous shrub layer of the Longleaf Pine communities.

In all 84 stands (including those not classified into community types), 220 vascular plant taxa were noted (excluding grasses, sedges, and aquatics): 51 tree species (those normally reaching the canopy), 52 shrubs, 14 woody vines, 93 herbs, and 10 pteridophytes.

Diameter distributions

To examine stand structure and replacement processes, diameter size class distributions per 0.1 ha were tabulated for important species in each of the 53 core stands of the community types. "Important" species were arbitrarily defined as overstory species with >10% relative basal area in a stand. Nineteen species met this criterion. Each stand had 1–5 such species. In the 53 stands, 137 cases of a population achieving importance occurred. The two stands from each community type with total basal areas closest to the type mean were selected, and diameter distributions (including seedlings) of important species in 4-cm size classes are presented in Table 5.

Underrepresentation (where there are fewer individuals in a size class than in subsequent larger classes) in the smaller size classes is widespread. One or more of the three smallest size classes (seedlings, 2 ≤ 6 cm, 6 ≤ 10 cm) are poorly represented or absent in 117 (85%) of the 135 cases where a population achieved importance. All individual species were underrepresented in half or more of stands where they were important.

In Coastal Plain forests of southeast Texas, Harcombe and Marks (1978) found a strong tendency for underrepresentation in the sapling classes to be most severe in wet and moist stands. Although not conclusive, the same tendency is evident here, with underrepresentation in the smallest size classes occurring in

TABLE 5. Diameter size class distributions of important tree species (>10% relative basal area of each stand) of two representative stands from each community type.* Stands shown are those with total basal areas closest to the mean basal area of the type. Underlining indicates underrepresentation (see text).

Community type	Stand no.	Species	SDL†	Diameter size class (cm) 2 ≤ 6	6 ≤ 10	10 ≤ 14	14 ≤ 18	18 ≤ 22	22 ≤ 26	26 ≤ 30	≥30
Sweetgum–Water Oak–Red Maple	45	*Quercus nigra*	225	0	2	0	0	1	0	0	3
		Liquidambar styraciflua	25	18	0	3	2	2	1	3	1
		Acer rubrum	125	12	8	6	4	0	0	0	3
		Fraxinus spp.	150	2	12	12	0	3	2	0	0
	49	*Pinus taeda*	0	0	0	0	1	0	1	0	4
		Liquidambar styraciflua	25	4	2	3	0	1	1	0	3
		Acer rubrum	250	2	0	1	1	0	0	1	3
		Liriodendron tulipifera	0	0	0	0	1	0	0	0	2
		Quercus nigra	75	0	6	4	0	0	0	1	2
Small streambottoms	26	*Fagus grandifolia*	0	0	2	1	0	0	1	0	5
		Quercus prinus	25	0	0	0	0	0	1	0	3
		Magnolia virginiana	50	0	6	3	2	1	4	1	2
	42	*Fagus grandifolia*	75	18	2	0	2	1	1	0	4
		Nyssa sylvatica	0	0	0	0	0	0	1	1	2
		Quercus nigra	75	2	4	0	2	0	0	1	2
White Oak	71	*Quercus alba*	475	0	4	2	5	3	4	1	10
	74	*Quercus alba*	425	0	0	0	0	0	1	1	9
		Quercus stellata	50	0	0	0	4	2	0	0	2
Chestnut Oak	14	*Quercus prinus*	100	6	8	3	6	5	0	2	1
		Quercus velutina	75	6	8	2	5	1	0	0	2
	72	*Carya tomentosa*	100	0	2	2	2	2	3	1	2
		Quercus prinus	150	12	0	1	1	1	0	0	4
		Quercus alba	100	2	0	0	0	0	0	0	1
Pine-hardwoods	20	*Pinus taeda*	0	0	6	1	4	5	5	5	3
		Liquidambar styraciflua	0	16	30	10	5	1	0	0	0
		Quercus falcata	100	4	0	1	0	2	1	0	1
	29	*Pinus taeda*	0	2	14	4	3	4	5	0	0
		Carya ovalis	200	8	12	1	0	0	0	1	1
Mixed Oak–Hickory	37	*Quercus stellata*	100	10	22	6	1	1	1	4	3
		Carya tomentosa	150	2	4	2	4	4	1	6	0
		Quercus velutina	50	6	18	4	1	3	1	0	0
	68	*Carya tomentosa*	200	28	2	0	1	0	2	1	4
		Quercus falcata	250	26	14	3	2	3	2	1	0
		Pinus echinata	0	6	6	10	3	3	1	0	0
Loblolly Pine	17	*Pinus taeda*	75	10	14	4	7	10	4	1	7
		Pinus echinata	25	8	10	11	6	3	2	0	0
	75	*Pinus taeda*	525	26	0	0	0	0	2	1	13
Oak-Pine	66	*Quercus falcata*	100	16	28	7	2	0	1	0	3
		Pinus palustris	‡	2	0	4	2	3	1	1	1
		Pinus echinata	25	16	14	4	7	0	0	1	0
	78	*Quercus falcata*	75	6	4	1	1	0	2	2	5
		Pinus palustris	‡	2	2	7	2	1	2	0	1
		Quercus marilandica	0	4	0	1	0	3	2	0	1
		Quercus stellata	25	30	12	3	2	2	2	0	0
Blackjack Oak–Pine	34	*Pinus palustris*	‡	33	6	3	1	0	0	1	4
		Quercus marilandica	200	12	2	3	3	2	1	2	0
		Pinus taeda	125	2	2	0	1	2	1	2	1
		Pinus echinata	0	4	2	5	2	1	2	0	1

TABLE 5. Continued.

Community type	Stand no.	Species	SDL†	Diameter size class (cm) 2 ≤ 6	6 ≤ 10	10 ≤ 14	14 ≤ 18	18 ≤ 22	22 ≤ 26	26 ≤ 30	≥30
	61	*Quercus marilandica*	150	4	18	6	4	1	3	1	3
		Pinus echinata	0	76	56	15	1	0	0	0	0
		Quercus stellata	0	8	2	0	0	0	0	2	2
Longleaf Pine	15	*Pinus palustris*	‡	350	6	3	7	7	9	9	4
	22	*Pinus palustris*	‡	10	24	13	10	19	12	10	2

* All numbers are stems per 0.1 ha.
† SDL = seedlings, all stems smaller than 2 cm dbh.
‡ Seedling age of *Pinus palustris* is not comparable to that of other tree species, since it typically remains in the "grass stage" for 3–7 yr. Therefore, all *P. palustris* stems smaller than 6 cm dbh were treated as one class.

23 of 25 cases (92%) in streambottom stands, 64 of 76 cases (84%) in mesic upland stands, and 29 of 36 cases (81%) in xeric upland stands.

This tendency is clearer when severity of underrepresentation is considered. Absence of individuals in a small size class would seem to constitute more severe underrepresentation than the case where a small number are present. It follows that absence in two or more smaller size classes is more severe than absence in only one size class. With degrees of severity thus distinguished, underrepresentation clearly increases along the moisture gradient from xeric to moist stands. Populations were severely or very severely underrepresented in 34% of the cases in xeric upland stands, compared to 63% and 72% in the mesic upland and streambottom stands, respectively.

DISCUSSION

Methodology

The objective of the combined clustering-similarity sorting procedure was to identify core stands that are clearly representative of repeating assemblages of forest canopy species. The resulting stand groups provide a clearer picture of definable community types than would be possible if transitional, disturbed, or manipulated stands were "forced" to fit into types. This is particularly valuable in an area where disturbance and successional history of the stands are generally quite uncertain and highly variable.

Combined use of numerical classification and ordination techniques provided a useful approach to definition and description of vegetation patterns and simplified identification of major trends of vegetation-site relationships. The inherent values of ordination for detecting and describing gradients and of classification for detecting and describing recurring species assemblages or "noda" (Poore 1962) along these gradients are logically complementary.

Vegetation-environment relationships

In general terms the vegetation pattern on the lower Piedmont in Alabama is most directly related to topographic characteristics and disturbance history. However, both of these major influences are complex. The strong relationship to topography is probably due in turn to its interrelationships with soil depth and drainage, degree of erosion, and microclimate. Topography and soil characteristics are strongly influenced by geologic substrata. Disturbance history is as complex as the varied landowner objectives and circumstances, with chance disturbances (e.g., fire, storms, insects and disease damage) superimposed.

Except where old-field succession has resulted in a pine overstory, the streambottom communities are quite distinctive compared to those on uplands. Mesic upland sites may support any of a variety of species mixtures, ranging from pure pine to oak-hickory overstories. Disturbance history and successional processes largely determine the present composition. *Quercus marilandica, P. palustris,* or both, are favored wherever topographic or soil characteristics result in a drier soil moisture regime. Fire gives the latter a distinct advantage on such sites.

Pinus palustris is abundant in the Devil's Backbone, common in the Ashland Plateau and rare in the Opelika Plateau (Table 2). *Pinus taeda* is conspicuously less common in the Devil's Backbone than in the other two areas. Most of the natural range of *P. palustris* is in the Coastal Plain of the southern United States, from North Carolina to Texas. It is typically most abundant on deep sandy soils, a result of its competitive advantage on dry, infertile sites subject to frequent fires (Chapman 1932, Wahlenberg 1946). Although the shallow, rocky, and clayey soils of the Devil's Backbone and Ashland Plateau ridges sharply contrast with deep sands in physical nature, they provide dry, infertile conditions and are indeed subject to frequent fires.

Wildfire has been a common occurrence in most of the Piedmont and has been especially frequent in the Devil's Backbone area. Definite evidence of fire was observed in 48 of the 68 upland stands of this study and in 18 of 21 in the Devil's Backbone area.

Quercus prinus is near the southern limit of its natural range (Fowells 1965). In the study area it is limited almost exclusively to steep northerly slopes in the Ashland Plateau and Devil's Backbone. These slopes are cooler than average, and this probably accounts for the presence of the more northern *Q. prinus*. Its scarcity on the Opelika Plateau may be due to the gentler terrain, which provides few steep northerly slopes. Elevation probably has little effect on its distribution here. Elevations of the Chestnut Oak stands varied from 150 to 190 m, a range which includes a large portion of the Opelika Plateau.

Succession and disturbance history

Succession and disturbance history are extremely important in determining the actual species composition and relative abundances in any particular community. Due to their rapid invasion capabilities, fast growth, and wide site adaptability, *Pinus taeda, P. echinata,* or both may predominate on almost any well-drained site. The widespread cropland abandonment which began in the 1930's and 1940's continued until recently. After abandonment, most of these old fields were soon dominated by pines. Many pine and pine-hardwood communities have old terraces in evidence. Most of these stands originating from earlier field abandonment have been cut over at least once.

The effect of this cutting on present composition varies. If, due to sufficient local seed sources and enough time, hardwoods (primarily *Quercus* and *Carya* species) had become established in the understory, subsequent cutting generally has increased their importance on the site, since they are usually left uncut due to small size or unmerchantability and stumps of cut individuals resprout readily.

Most of the present upland hardwood stands were originally farm woodlots (usually on rocky or steep sites) which have been selectively cut over. Such cutting has usually removed pines which had previously invaded openings. Scattered individuals or small groups of pines have become established where disturbance was drastic, such as at log loading decks and in skid trails. Even where commercially "clearcut," these stands remain dominated by sprout origin hardwoods unless drastic machine clearing or chemical treatment removes the rootstocks.

Although generally accepted as climax dominants for the southern Piedmont (Oosting 1942), *Quercus* and *Carya* species exhibit underrepresentation in smaller size classes as severe as that for the mid-successional, more intolerant pines (Table 5). Oak and hickory species found here are generally rated no more than intermediate in shade tolerance (Baker 1949, Fowells 1965). Hence low seedling/sapling survival under dense overstory-midstory strata of moist and mesic forest stands might be expected. In the absence of man-induced disturbances, the development and maintenance of an oak-hickory climax would seem to be dependent upon the regular occurrence of small-to-intermediate sized gaps in the canopy, as was postulated for southeast Texas forests by Harcombe and Marks (1978).

In the Alabama Piedmont, however, manipulation is the rule, and the natural trend toward oak-hickory dominance is quickened by certain land management practices which are common on nonindustrial lands. Seedlings of *Quercus* and *Carya* are generally more tolerant than saplings or larger trees (Fowells 1965), particularly in terms of survival under low light levels. Shaded seedlings and small saplings characteristically grow very slowly or not at all and frequently die back to ground level, but then commonly resprout. Hence, once established, individuals tend to persist as long as intensive clearing (such as site preparation for pine plantations) or very hot fires do not occur. These sprouts and many seedlings will respond quickly to increased light. Therefore, the relatively frequent partial cutting (usually involving removal of all merchantable pines) of many stands under nonindustrial ownership results in a steady increase in *Quercus-Carya* dominance in both understories and overstories.

Interaction between site characteristics and disturbance-successional processes is evident. One example of such interaction is the generally later abandonment of fields on well-drained bottomlands, stream terraces, lower slopes, and those gentle uplands where erosion was slight. Indeed, many of these sites are still in pasture or small agricultural fields.

In spite of this more recent field abandonment, which might seem to favor present dominance of the early-successional pines, a distinct trend toward hardwood dominance is quickly evident on bottomlands and stream terraces. Light-seeded hardwoods, particularly *Liquidambar styraciflua, Liriodendron tulipifera,* and *Acer rubrum,* aggressively invade openings on such sites. Seed sources for these species, as well as for moist-site oaks (primarily *Quercus nigra*), have usually been readily available near streams, where uncut strips were commonly left even after clearing for agriculture. Such hardwood species grow much more rapidly on these moist, fertile sites than on the uplands. Pines generally have fewer seed-producing individuals readily available to such sites, and have little or no competitive advantage in growth rate, an advantage *P. taeda* does have on most uplands. Thus it is not surprising that succession from pine to hardwood dominance usually proceeds more rapidly in the moist-to-wet environments. Consequently, pine-dominated stands are generally less common on bottomland and stream terrace sites than on uplands.

Conversely, in the drier environments pine-dominated communities are abundant and the trend toward hardwood dominance resulting from natural succession processes generally proceeds more slowly. This is due to both the slower growth rate of most hardwoods on uplands and the greater frequency of fire there; both factors favor the faster-growing and more fire-resistant pines. However, the commonly practiced selective removal of pines from mixed or midsuccessional stands (those with significant hardwoods in the understory) generally accelerates the trend toward hardwoods, even on drier uplands.

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