United States
Department of
Agriculture

Forest Service

**Southern
Research Station**

General Technical
Report SRS-23

An Old-Growth Definition for Dry and Dry-Mesic Oak-Pine Forests

David L. White and F. Thomas Lloyd

A Section of the Old-Growth Definition Series

The Authors:

David L. White, Ecologist, Southern Research Station, U.S. Department of Agriculture, Forest Service, Clemson, SC 29634-1003; and F. Thomas Lloyd, Research Forester, Southern Research Station, U.S. Department of Agriculture, Forest Service, Bent Creek, NC 28806.

Preface

Old growth is widely acknowledged today as an essential part of managed forests, particularly on public lands. However, this concept is relatively new, evolving since the 1970's when a grassroots movement in the Pacific Northwest began in earnest to define old growth. In response to changes in public attitude, the U.S. Department of Agriculture, Forest Service, began reevaluating its policy regarding old-growth forests in the 1980's. Indeed, the ecological significance of old growth and its contribution to biodiversity were apparent. It was also evident that definitions were needed to adequately assess and manage the old-growth resource. However, definitions of old growth varied widely among scientists. To address this discrepancy and other old-growth issues, the National Old-Growth Task Group was formed in 1988. At the recommendation of this committee, old growth was officially recognized as a distinct resource by the Forest Service, greatly enhancing its status in forest management planning. The committee devised "The Generic Definition and Description of Old-Growth Forests" to serve as a basis for further work and to ensure uniformity among Forest Service Stations and Regions. Emphasis was placed on the quantification of old-growth attributes.

At the urging of the Chief of the Forest Service, all Forest Service Stations and Regions began developing old-growth definitions for specific forest types. Because the Southern and Eastern Regions share many forest communities (together they encompass the entire Eastern United States), their efforts were combined, and a cooperative agreement was established with The Nature Conservancy for technical support. The resulting project represents the first large-scale effort to define old growth for all forests in the Eastern United States. This project helped bring the old-growth issue to public attention in the East.

Definitions will first be developed for broad forest types and based mainly on published information and so must be viewed accordingly. Refinements will be made by the Forest Service as new information becomes available. This document represents 1 of 35 forest types for which old-growth definitions will be drafted.

In preparing individual old-growth definitions, authors followed National Old-Growth Task Group guidelines, which differ from the standard General Technical Report format in two ways—the abstract (missing in this report) and the literature citations (listed in Southern Journal of Applied Forestry style). Allowing for these deviations will ensure consistency across organizational and geographic boundaries.

September 1998

Southern Research Station
P.O. Box 2680
Asheville, NC 28802

Table of Contents

Page

Introduction 1

Description of Forest-Type Group 1
Piedmont 2
Distribution and composition 2
Old-growth forest examples 3
Presettlement forests and disturbance 3

Coastal Plain: Atlantic Section 5
Distribution and composition 5
Old-growth forest examples 6
Presettlement forests and disturbance 6

Coastal Plain: Gulf Coast Section 6
Distribution and composition 6
Old-growth forest examples 6
Presettlement forests and disturbance 7

Interior Highlands 7
Distribution and composition 7
Old-growth forest examples 7
Presettlement forests and disturbance 8

Appalachian Mountains: Blue Ridge 8
Distribution and composition 8
Old-growth forest examples 10
Presettlement forests and disturbance 10

Appalachian Mountains: Plateau 11
Distribution and composition 11
Old-growth forest examples 12
Presettlement forests and disturbance 12

Appalachian Mountains: Valley and Ridge 13
Distribution and composition 13
Old-growth forest examples 13
Presettlement forests and disturbance 13

Forest Composition: Synthesis across Regions .. 14

Page

Narrative of Old-Growth Conditions 14
Living Tree Component 23
Size structure 23
Age structure 23
Canopy structure 24

Dead Tree Component: Coarse Woody Debris .. 26

Forest Dynamics and Ecosystem Function 27
Presettlement Disturbance Regimes 27
Disturbance continuum 27
Fire frequency 27
Patch size 27

Ecological Processes 28
Postsettlement changes 28

When Does Old Growth Begin? 29

Information Gaps 29

Representative Old-Growth Forests 30

Acknowledgment 30

Literature Cited 30

Appendix A 35

Appendix B 42

An Old-Growth Definition for Dry and Dry-Mesic Oak-Pine Forests

David L. White and F. Thomas Lloyd

Introduction

Dry and dry-mesic oak-pine forests are widely distributed throughout the Eastern and Southern United States from New Jersey to Texas. Shortleaf pine is the predominant pine species of this forest type in the Piedmont, Gulf Coastal Plain, and Interior Highlands, while pitch pine is the predominant pine species in the Appalachians. White oak is the predominant oak species across the range of old-growth oak-pine sites, although scarlet, chestnut, and other hardwood species share dominance on some sites.

Oak and pine species associated with this type have been prevalent in the Eastern United States for thousands of years (Delcourt and Delcourt 1987). The oak-pine type has been described as ephemeral on a given site and is maintained in a changing landscape mosaic by fire and other disturbance (Buckner 1989). Forests of this type do not adhere to the steady state or equilibrium concept of forest dynamics historically associated with "virgin" or old-growth forests. In addition, in defining old growth, we acknowledge that multiple ecological outcomes are possible for comparable sites (Oliver 1981, Sprugel 1991). The type, intensity, and frequency of disturbance and its interaction with the biotic and abiotic components of a specific site determine the "outcome." A greater understanding of these interactions should clarify management options for recognizing, creating, and maintaining old-growth types on the landscape.

Due to extensive postsettlement land clearing and soil disturbance in the Eastern United States, examples of old-growth forests are rare. To characterize the dry and dry-mesic oak pine type, we used recent studies and historical accounts of composition. In addition, we compiled information from existing descriptions of representative old-growth stands of this type. Across these old-growth sites, information was sparse. Therefore, one site in the South Carolina Piedmont was sampled intensively to obtain one full set of old-growth attribute data (White and Lloyd 1995). Additional data from this site will be presented here for the first time.

In this paper we describe the dry and dry-mesic oak-pine old-growth type for each of six physiographic provinces with an emphasis on composition, distribution (including presettlement), old-growth examples, and disturbance regimes. Specific attributes from a range of old-growth sites are presented in a standardized table and discussed; then, presettlement disturbance regimes and ecological processes associated with this type are discussed. Finally, we address the following questions regarding this oak-pine forest type: (1) when is a forest considered old growth, and (2) what is the minimum area needed to maintain old-growth forests?

Description of Forest-Type Group

The starting point for defining the dry and dry-mesic oak-pine type relates to soil moisture and the relative composition of oaks and pines. The soil moisture class for this type is defined as dry and dry-mesic, corresponding to soils that are somewhat excessively drained to well drained. Regarding the relative composition of oak and pine, we currently define the upper limit of pine composition to be >50 percent. Our reason for this is because the original old-growth classification for the Eastern United States (35 types) does not include a "pine-oak" forest type (pine composition >50 percent) that occurs on dry-mesic sites. To exclude a pine-oak type presumes that pine-dominated forest types were not represented on dry-mesic sites within the Eastern United States under presettlement disturbance. We do not consider this a sound assumption, especially considering that pine dominance on these sites has been described or implied for the southern Piedmont (Nelson 1957, Plummer 1975), upper section of the Atlantic Coastal Plain (Sargent 1884), portions of the Gulf Coastal Plain (Mohr 1901, Harper 1943, Delcourt 1976, Schafale and Harcombe 1983, Martin and Smith 1991), and portions of the Ozarks and Ouachitas (Foti and Glenn 1991, Tucker 1991). Defining an upper limit for pine composition (or a lower limit for oak) is somewhat arbitrary. From the Society of American Foresters (SAF) forest cover-type descriptions (Eyre 1980), "A species must comprise at least 20 percent of the total basal area to be used in the type name." Interpreting "species" broadly as either pines or oaks, we define the composition of the dry and dry-mesic oak-pine type as containing at least 20 percent pine basal area and at least 20 percent oak basal area. Using this designation, the upper limit for pine composition is 79 percent.

Dry and dry-mesic oak-pine forests constitute a large part of the eastern deciduous forest, extending from southern

Missouri to east Texas in the West across to the Atlantic coast from southern New York to northern Florida. This type occurs in the following physiographic provinces: Coastal Plain, Piedmont, Blue Ridge, Valley and Ridge, Appalachian Plateau, Ozark Plateau, and the Ouachitas. Most forests occur on coarse textured soils on ridges and south-facing slopes in the mountains and droughty uplands of the Piedmont and Coastal Plain. The inherent dryness of these sites makes them particularly prone to fire.

Principal species[1] vary widely depending on latitude, topography, geography, and disturbance. On dry sites, forests can include shortleaf pine, Virginia pine, Table Mountain pine, pitch pine, post oak, chestnut oak, scarlet oak, and blackjack oak. On dry-mesic sites, loblolly pine, white oak, southern red oak, black oak, mockernut hickory, pignut hickory, red maple, and blackgum are more prominent. Since most of the above species are restricted to certain physiographic regions, not all of these species necessarily co-occur.

Dry and dry-mesic oak-pine forests are similar to the following SAF cover types: shortleaf pine (75), shortleaf pine-oak (76), Virginia pine-oak (78), Virginia pine (79), loblolly pine-shortleaf pine (80), loblolly pine (81), and loblolly pine-hardwood (82).

The composition of the dry and dry-mesic oak-pine type (type 25) is similar to that of two other old-growth forest types—xeric pine and pine-oak forests and woodlands (type 24) and dry-mesic oak forests (type 21). Types 24 and 25 may occur adjacent to each other along a moisture gradient, with type 24 occupying more xeric sites along ridges. Types 21 and 25 may develop on some of the same site types depending on the type and intensity of disturbance.

Since few old-growth examples of dry and dry-mesic oak-pine forests exist, both recent studies and historical accounts of composition were used to describe this forest type. Recent studies consist of descriptions of "natural" vegetation within a region. Extensive postsettlement land clearing and soil disturbance in the East make it necessary to use historical documents and original land survey records to reconstruct pre- or early-settlement composition even though the reliability of these approaches is somewhat variable.[2] It is also important to acknowledge the dynamic nature of presettlement forests, which makes their assessment somewhat arbitrary. Furthermore, descriptions of forests at the time of settlement may describe forests significantly impacted by Native American population decline (i.e., less fire) as related to exposure to diseases introduced by explorers 200 years before settlement (DeVivo 1991).

Given the broad distribution of the dry and dry-mesic oak-pine type, we have chosen to describe this forest type by physiographic regions. For each physiographic region given below, we describe the old-growth type in the context of (1) distribution and composition, (2) old-growth forest examples (composition and location), and (3) presettlement forests and disturbance.

Piedmont

Distribution and composition—The Piedmont extends from the palisades of the Hudson River to Alabama. Few descriptions of vegetation composition exist for the entire Piedmont region. Although Godfrey's (1980) work was purely descriptive and did not consider pine as a mature forest species, his description of initial woody succession provided insight into the distribution of yellow pine species across the region. Pines share dominance with hardwoods during early succession from Maryland to northern South Carolina but dominate from South Carolina southward. Virginia pine is predominant in the northern Piedmont, sharing dominance with shortleaf pine in Virginia. Virginia pine decreases in importance from Virginia southward, occupying only the upper Piedmont in South Carolina. Shortleaf pine is dominant from North Carolina southward, with loblolly pine increasing in importance from the fall line westward where it becomes dominant in the Alabama Piedmont.

Braun (1950) considered most of the Piedmont a part of the oak-pine region with the exception of monadnocks, which were considered "Blue Ridge outliers," and more vegetationally similar to oak-chestnut forests. Within the Virginia Piedmont, a shift from the oak-pine to the oak-chestnut region is related to a shift from red and yellow soils (Cecil Series) to gray-brown forest soils (Chester Series) (Braun 1950). The oak-chestnut section in southern Virginia starts as a narrow, hilly belt adjacent to the Blue Ridge and contains an abundance of monadnocks (Fenneman 1938). North of the Potomac River is the Piedmont Lowland. Here, American chestnut, oaks, and hickories once dominated this area as well as the narrow, hilly belt, with pitch and Virginia pines as occasional associates. The intensity of postsettlement disturbance precludes a clear picture of early vegetation in the northern Piedmont.

[1] See appendix A for a list of scientific and common plant names as well as their presence in old-growth and non-old-growth forest stands. Scientific names are given in the text only if they were not included in appendix A or if used in reference to a number of species within one genus as in *Vaccinium* species. Nomenclature is from Kartesz and Kartesz (1980).

[2] Frost, C.C. 1997. Presettlement vegetation and natural fire regimes of the Savannah River Site. 179 p. Unpublished report. On file with: Savannah River Natural Resource Management and Research Institute, USDA Forest Service, New Ellenton, SC 29809.

In the southeastern Piedmont, we refer to site or vegetation studies, or both, from North Carolina[3] and South Carolina (Jones 1988) to provide insight into the distribution of the dry and dry-mesic oak-pine type. Peet compiled a tabulation of synonymous communities for the North Carolina Piedmont from various sources. This tabulation and the original studies allow us to infer which oak communities occupied sites where the dry and dry-mesic oak-pine type could develop, given sufficient disturbance (e.g., fire, wind and ice storms, and insects). The following tabulation shows similar community types that occupy sites where old-growth oak-pine may occur:

Community synonymy for North Carolina Piedmont

Peet and Christensen 1980	Oosting 1942	Schafale and Weakley 1990
Dry mesotrophic Clayey phase Sandy phase	White oak-black oak-red oak	Dry-mesic oak-hickory
Dry oligotrophic	White oak	Dry oak-hickory
Dry eutrophic	White oak-post oak	Basic oak-hickory

In South Carolina, Jones (1988) developed a predictive landscape ecosystem classification that integrates landform, soil, and late successional vegetation. While Jones' system predicts the late successional hardwood vegetation type from soil and landform variables, it is important to acknowledge that multiple ecological outcomes are possible on a given site unit. Different forest types will develop for each combination of soil type, landform, and disturbance regime. Based on Jones' descriptions, literature information, and our sampling, old-growth dry and dry-mesic oak-pine could develop on xeric, subxeric, and intermediate sites with the center of distribution on subxeric sites (table 1).

Old-growth forest examples—Few old-growth oak-pine stands have been documented in the Piedmont. Oosting (1942) described a relatively undisturbed white oak-post oak type in the Duke Forest of North Carolina that contained shortleaf pine (appendices A and B). He considered this type a variant of the oak-hickory climax. Shortleaf pine was the next most important species (basal area) in stands dominated by white and post oaks, followed by hickory species, scarlet and northern red oaks with dogwood prominent in the understory. Minor associates included black and blackjack oaks, sourwood, blackgum, and red maple. Shrubs included deerberry, black-haw, rusty black-haw, other *Viburnum* and *Vaccinium* species, wild azalea, strawberry bush, and fringe tree. Vines included muscadine, greenbrier, trumpet honeysuckle, and Virginia creeper. Herbs included broom-sedge, *Panicum* species, *Carex* species, wild ginger, five-finger, hawkweed, pipsissewa, bedstraw, and dwarf Dutchman's-pipe.

In South Carolina, we sampled the John de la Howe (JDLH) tract—a relatively undisturbed 200-year-old oak-pine stand on subxeric and intermediate sites where insects had sporadically killed pines (White and Lloyd 1995, appendices A and B). Shortleaf and loblolly pines and white oak were the dominant species followed by various hickory species, yellow-poplar, post oak, southern red oak, red maple, sourwood, black oak, and elm. Dogwood was the most important understory species. Others included eastern hophornbeam and Florida or southern sugar maple. Vine, shrub, and herb species given in order of decreasing frequency included muscadine, *Smilax* species, partridge-berry, bedstraw, wild ginger, strawberry bush, Virginia creeper, *Carex* species, miscellaneous grasses, perfoliate bellwort, dwarf Dutchman's-pipe, pipsissewa, *Viburnum* species, Solomon's-seal, deerberry, wild yam, sparkleberry, and others. Red maple was the most abundant tree seedling, followed by eastern hophornbeam, dogwood, pines (shortleaf and loblolly), black cherry, white oak, chalk maple (*Acer leucoderme* Small.), pignut hickory, black oak, and blackgum. The pine component in these stands is declining, and, even though seedling abundance was moderately high, no pines were represented in the 0.8- to 3.9-inch [1.8- 9.9 centimeter (cm)] diameter at breast height (d.b.h.) class, suggesting successful recruitment is unlikely. Lack of fire in this stand has likely resulted in the predominance of mesic understory species such as red and southern sugar maple, eastern hophornbeam, and others (Orwig and Abrams 1994).

Presettlement forests and disturbance—The composition of southeastern Piedmont forests before European settlement has been described (Nelson 1957, Brender 1974, Plummer 1975, Skeen et al. 1980, Peet and Christensen 1987, Skeen et al. 1993, Barden 1997), but no clear agreement exists. From these papers and several historical accounts of the Georgia, North Carolina, and South Carolina Piedmont [Drayton 1784, Mills 1826, Ruffin 1843, Logan 1859, Hammond 1883, Schoepf 1911, Bartram 1958, Lawson 1967, Clark 1973 (as cited in Michaux 1802)], the landscape consisted of relatively open, hardwood- dominated forests with scattered pines, extensive prairies and savannahs, and large stretches of cane brakes along streams and lowlands. Burning by Native Americans was credited for the

[3] Peet, Robert K. 1994. Community synonymy tables and data. 5 p. Unpublished report. On file with: University of North Carolina, Chapel Hill, NC 27514.

Table 1—Late successional community type, soil, and landform characteristics from the South Carolina Piedmont Landform Ecosystem Classification (Jones 1988) corresponding to potential sites for old-growth dry and dry-mesic oak pine

Site unit and community type	Distinguishing soil characteristics	Landform description
Xeric Post oak, black oak, and lowbush blueberry[a]	Heavy clay subsurface horizon 12 in. (31 cm) from surface or bedrock within 24 to 36 in. (61 to 91 cm)	Exposed ridge flats, upper slopes of any aspect
Subxeric White oak-scarlet oak-deerberry	Clay or sandy clay subsurface horizons at 12 to 24 in. (31 to 61 cm)	Ridge flats, upper slopes of any aspect or midslope with a southern aspect
	Or:	
	Heavy clay horizons within 12 in. (31 cm) of surface or bedrock within 24 to 36 in. (61 to 91 cm)	Less exposed midslopes with north or east aspects
Intermediate White oak-northern red oak-false Solomon's- seal	Sandy clay loam or clay loam at 12 to 24 in. (61 to 91 cm)	Midslopes with north or east aspects or mid to lower slopes with southern aspects

[a] *Vaccinium vacillans* Torr.; other species are given in appendix A.

maintenance of this early landscape (Rostlund 1957, Barden 1997). A case could be made, at least for parts of the South Carolina Piedmont, that pines became more abundant in the Piedmont after the mid-1700's by establishing on the more open areas after the Cherokees sold much of their land to the British (compare mid-1700's accounts by Logan 1859 and 1980 in reference to pine by Drayton 1784, Mills 1826, and Ruffin 1843). Pine establishment on abandoned agricultural land started in the late 1700's.

The Piedmont, as described by Peet and Christensen (1987), was dominated by oaks, hickories, and other hardwoods with loblolly and shortleaf pines found only occasionally, usually on exceptionally poor sites or where some disturbance (windfall, fire, or aboriginal cultivation) had created suitable conditions for pine. Skeen et al. (1980) suggested that oak-hickory-yellow-poplar was the "typal" forest climax in the southeastern Piedmont, with oak-hickory and oak-hickory-pine as edaphic and moisture-controlled variants of this type. Brender (1974) describes the "original" forest in the lower Piedmont as the "oak-hickory climax type" with other associated hardwoods and a "scattering of shortleaf and loblolly pines." The presumption that pine was only found occasionally in the Piedmont contrasts with the descriptions for the Georgia and Alabama Piedmont.

Nelson (1957) described the "original" forest of the Georgia Piedmont as ranging from pure pine to pure hardwoods. Oak-hickory types were more abundant in the "red lands" (35 to 40 percent of the Georgia Piedmont), whereas shortleaf pine and post, white, and red oaks occupied the "gray sandy lands" (45 percent of the region). These latter soils are generally described as gray sand and gravelly and probably are the uneroded Cecil, Appling, and Durham soils. Pine dominated the remaining 15 percent of the Piedmont, which is the Elberton granitic formation. Nelson indicated that pines were more prevalent west of the Atlantic-Gulf divide and generally decreased from the sandhills to the mountains. Plummer (1975) used survey records of the Georgia Piedmont and Blue Ridge from 1733 to 1832 to provide more specific information. Pine was especially abundant on steep slopes and upland soils of micaceous origin. Soils with higher clay content supported more post oak. The ratio of oak:pine:hickory was 53:23:8 on over one-half million acres surveyed.

Pine species were also a significant component of the "original" forests of the Alabama Piedmont (Mohr 1901, Harper 1943), with shortleaf occurring in "dry woods" along with southern red oak, post oak, hickory species, and black oak. Dogwood, black-haw, and hawthorne were common understory species. Longleaf pine and loblolly pine were also significant components of this region in Alabama. Mohr (1901) also described a mountainous area where longleaf pine dominated in open pine woodland along rocky ridges mostly below 2,000 feet [610 meters (m)]. Blackjack oak was an important associate, being replaced by chestnut oak,

American chestnut, and pignut hickory. On the deeper soils of slopes and ridges, hardwoods predominated with shortleaf pine as an occasional associate. This mountainous section, including Rebecca and Talladega Mountains, consists of both slate and quartzite rocks. Due to its location and parent material, there is disagreement as to which physiographic province this section belongs—Valley and Ridge, Blue Ridge, or Piedmont[4] (Fenneman 1938, Hodgkins et al. 1979). Braun (1950) described this section as an area where American chestnut, chestnut oak, and longleaf pine intergrade.

Whereas fire or other disturbances likely maintained pine as a component of forests in the Piedmont, we understand little of the spatial and temporal aspects of presettlement disturbance (human and nonhuman) in the Piedmont. Such understanding would provide insight into the relative abundance of the oak-pine type in this region. Frost (1995) estimated the presettlement fire frequency to be 4 to 6 years. He suggested that the influence of Native American fire was greater in the Piedmont than in the Coastal Plain (where lightning ignitions predominate) because of differences in fire compartment size.[5]

Differences in fuel moisture between the two regions also contribute to variations in fire occurrence. Fuel moisture is generally higher in the Piedmont, largely due to clay soils that retain water near the surface (Christensen 1981). It seems safe to deduce that the oak-pine type has been a component of the Piedmont for millennia. More research is needed, however, to characterize the extent of its presettlement distribution.

Coastal Plain: Atlantic Section

Distribution and composition—The Atlantic Coastal Plain extends from Florida to New Jersey. Specific information on the dry and dry-mesic oak-pine type's occurrence in this section is sparse. Most of the Coastal Plain north of the James River in Virginia was considered by Braun (1950) to be part of the oak-pine forest region, whereas that area south of the James River was considered southeastern evergreen forest. The upland forests of the eastern and western shores of Maryland resembled those of the Piedmont further south, according to Braun, with loblolly pine in association with Virginia pine or deciduous species.

On the Coastal Plain of New Jersey, pine-oak and oak-pine types are prevalent and include pitch and shortleaf pines, several oaks, and understory ericaceous species. The dry and dry-mesic oak-pine type corresponds to the pine-oak type described by Lutz (1934). This type is somewhat similar to the pitch pine forests of Southern Appalachian ridges (Whittaker 1979), but it also has species common to the southern Atlantic Coastal Plain (Christensen 1988a). Breden (1989) describes a dry oak-pine forest of the outer Coastal Plain of New Jersey as a closed canopy community where dominant tree heights range from 36 to 50 feet (11 to 15 m) to 75 to 102 feet (23 to 31 m) depending on fire history. The dominant oak species are black, chestnut, scarlet, post, and white, with pitch and shortleaf pines as important associates. Huckleberry, dangleberry, bear oak (*Quercus ilicifolia* Wang.), and lowbush blueberry occur in some of these stands. Breden further noted a scarlet oak-shortleaf pine subtype of the dry oak-pine forest as occurring on the eastern half of the Pine Barrens where scarlet and black oaks and shortleaf pine dominate. Little and Moore (1949) described the New Jersey pine region as consisting of "subclimax" stands of hardwoods and pine that have resulted from heavy cuttings and severe fires, the latter occurring at intervals of 15 to 40 years.

The dry and dry-mesic oak-pine type is uncommon on the southeastern Coastal Plain but fire suppression, the degree of postsettlement disturbance, and the scarcity of literature information precludes conclusive determination on this subject. Barry (1980) refers to scrubby oak barrens occupying the most xeric sites in the South Carolina sandhills and xeric pine-hardwoods in somewhat more mesic areas where sands are not as deep. In the latter, loblolly pine occurs with post, southern red, dwarf post, black, water (*Q. nigra* L.), and blackjack oaks and pignut and mockernut hickories. Barry describes similar communities for other sections of the Coastal Plain, but their occurrence appears infrequent.

Vegetation descriptions from Georgia (Pehl and Brim 1985), South Carolina (Barry 1980, Nelson 1986), and North Carolina (Schafale and Weakley 1990) are not clear on the occurrence of this type in the middle and lower Coastal Plain sections. In a synthesis of vegetation studies of the southeastern Coastal Plain by Christensen (1988a), there is no mention of a type corresponding to dry and dry-mesic oak-pine, except for a statement that mid-Atlantic flatwoods are roughly similar to the upper slope pine-oak forests described by Marks and Harcombe (1981) for east Texas (see Coastal Plain: Gulf Coast Section). The latter is considered to be similar to the dry and dry-mesic oak-pine type.

[4] Personal communication. 1994. Henry McNab, Research Forester, Southern Research Station, USDA Forest Service, Bent Creek Research and Demonstration Forest, 1577 Brevard Road, Asheville, NC 28806.

[5] Frost (1995) defines "fire compartment" as a unit of the landscape with no natural firebreaks, such that a lightning ignition in one part would be likely to burn the whole unit unless there were a change in weather or fuel conditions.

Old-growth forest examples—No documented examples of old-growth oak-pine exist to our knowledge.

Presettlement forests and disturbance—Historical references to this type are limited. In the Coastal Plain of southern Delaware, pine was considered an insignificant component of the "original" forest (Sterrett 1908). In the southeastern Coastal Plain, Bartram (1958) lists shortleaf and loblolly pines occurring with various Coastal Plain and Piedmont oaks approximately 50 miles [80 kilometers (km)] inland from Savannah, GA, but shortleaf is rarely encountered in the middle and lower Coastal Plain today. The most definitive early reference is from Sargent (1884), who described a transition area corresponding to the sandhills and upper Coastal Plain region as "shortleaved and loblolly pine intermixed with hardwoods in about equal proportion and scattered long leaved pine." Frost (1993) views these transitional types as rare remnants of savanna and woodland fire types with a species-rich herb layer, in contrast to the postlogging, fire-suppressed, successional, mixed pine-hardwood forests prevalent today. From Frost's (see footnote 2) descriptions of presettlement forests of the South Carolina sandhills, the dry and dry-mesic oak-pine type is likely best represented in the fire tension zones between upland longleaf and nonpyrophytic woodland below. Although sometimes relatively narrow in the sandhills, these fire tension zones can be much broader in other parts of the Coastal Plain (see footnote 2). These pyrophytic woodlands include shortleaf pine as a key species along with longleaf, white and post oaks, and, occasionally, loblolly. Shortleaf pine is rarely mentioned in more recent descriptions of these areas.

Sargent's (1884) description of a transition area in the upper Coastal Plain and sandhills is the most significant evidence for the occurrence of the dry and dry-mesic oak-pine type in the region. The disturbance dynamics that maintained this type on the landscape might be more similar to that prevailing in certain parts of the Gulf Coastal Plain, which will be discussed in more detail later. The extent of the dry and dry-mesic oak-pine type's distribution in the mid- and lower Coastal Plain sections is unknown.

Coastal Plain: Gulf Coast Section

Distribution and composition—The dry and dry-mesic oak-pine type is a more significant component of the Gulf Coastal Plain than the Atlantic Coastal Plain, occurring from Florida to Texas. The belted character of this region in the form of inner lowlands and cuestas and other low-ridge landforms (Bowman 1911, Fenneman 1938), the associated diversity of soil types, and differences in settlement history account for much of the difference in this type's distribution in the two Coastal Plain regions. Cuestas and other hills create strong environmental gradients which, coupled with soil characteristics, result in highly pyrogenic longleaf stands on sandy or sandy loam ridges, shortleaf pine-hardwood stands on upper to midslopes on clay soils, whereas loblolly pine-hardwood occupy lowland silt loam soils (Mohr 1901, Martin and Smith 1991). Wide variation in composition across this gradient is related to fire frequency and intensity (Martin and Smith 1991). Primarily, the shortleaf-hardwood type represents the dry and dry-mesic oak-pine type. Unlike most of the Atlantic Coastal Plain, shortleaf pine is an important species across much of the Gulf Coastal Plain, both presently and historically (Mohr 1901; Harper 1920, 1943; Delcourt 1976; Martin and Smith 1991).

Marks and Harcombe (1981) described composition in the Big Thicket of Texas. Stands on moderate to well-drained sandy loams on upper and midslopes of low ridges were described as dry to dry-mesic. The upper slope pine-oak forests were dominated by shortleaf, loblolly, southern red oak with longleaf, post oak, blackjack oak, and sweetgum (*Liquidambar styraciflua* L.) as associates. Midslope oak-pine forests were dominated by loblolly pine, white oak, southern red oak, shortleaf pine, with equal representation of red maple, sweetgum, blackgum, and American holly (*Ilex opaca* Ait.). Sweetgum was also present on upper slopes. Shortleaf and loblolly were more prevalent on the upper and midslope, respectively. Ridgetops of deep sands were dominated by longleaf pine-scrub oak. The authors note the similarity of the upper and midslope communities described above to previous descriptions of oak-pine and pine-hardwood types of the upper Coastal Plain and Piedmont (Braun 1950, Nelson 1957, Kuchler 1964, Delcourt 1976, Golden 1979). A similar moisture gradient with associated plant communities has been described for the Louisiana Coastal Plain (Martin and Smith 1991).

Old-growth forest examples—In the belted section of the Louisiana Coastal Plain on the Kisatchie National Forest, Martin and Smith (1991) described two old-growth shortleaf pine-oak-hickory stands (appendices A and B). Shortleaf pine; post, southern red, and white oaks; loblolly pine; and mockernut hickory dominated these stands. The midstory dominants were eastern hophornbeam and dogwood with red maple, blackgum, and hawthorne. Understory shrubs include yaupon, horse-sugar, and wild azalea. Blueberry was the dominant shrub in one of the stands. The most abundant herbs were partridge-berry, *Carex* species, *Panicum* species, *Uniola* species with lesser amounts of goldenrod, *Desmodium* species, *Aster* species, elephant's-foot, and little bluestem. Martin and Smith also described the composition of the "shortleaf pine-oak-hickory natural community type" based on historical and current information, which included species not found in the old-growth stands (see appendix A). They noted the shortleaf pine-oak understory was not as species rich as the adjacent longleaf pine community.

Presettlement forests and disturbance—Descriptions of "original" or early settlement forests (before extensive European disturbance) for Alabama (Mohr 1901, Harper 1943) and Mississippi (Hilgard 1860) report the widespread occurrence of shortleaf pine-mixed oak throughout the middle and upper Coastal Plain. This community was commonly found on dry uplands with sandy clay to sandy soils and prevalent in the upper or hilly Coastal Plain, post oak flatwoods, red hills, and upper portion of the longleaf pine belt of the middle Coastal Plain (pine hills). Shortleaf was associated with southern red and post oaks and loblolly pine, along with dogwood in the understory. Scarlet oak, blackjack oak, mockernut hickory, and white and black oaks were also common. Longleaf pine communities, occurring on dry, sandy ridges, were commonly adjacent to shortleaf pine-oak communities in this region.

Hilgard (1860) described shortleaf pine and associated hardwood species as being significant components of the northeast pine hills, flatwoods, yellow loam region (includes red hills), central prairie, and upper section of the longleaf pine region (pine hills) in Mississippi. Longleaf pine was largely confined to the pine hills region of the middle Coastal Plain, which contrasts with its more widespread distribution in Alabama. Hilgard mentions American chestnut as an occasional associate of the oak-shortleaf pine type in addition to the associated species mentioned above for Alabama. Shortleaf pine and associated hardwoods were generally found on sandy ridges or uplands between drainages. In areas with less topographic relief or with more clayey soils, hardwoods increased in importance.

Braun (1950) described the oak-pine region of the Coastal Plain of Texas, Louisiana, and Arkansas as rolling to hilly with shortleaf as the dominant pine in the northern section "originally" and loblolly as the dominant in the southern section where longleaf is also prevalent. Associated oaks were post, blackjack, and southern red. Braun also described a transition area between the oak-pine and oak-hickory forest regions in southern Arkansas where pine is a component of oak-hickory forests that contain white, chestnut, southern red, and Shumard oaks (*Q. shumardii* Buckl.), as well as pignut, mockernut, and bitternut hickory [*Carya cordiformis* (Wangenh.) K. Koch].

Studies of presettlement forest composition in northern Louisiana (Delcourt 1976) and east Texas (Schafale and Harcombe 1983) suggest where longleaf, shortleaf, and loblolly pines likely occurred on the landscape. Shortleaf pine probably dominated the northern part of the hilly Coastal Plain section north of the Red River in Louisiana whereas longleaf dominated the southern part. The abundance of pine in this region was attributed to natural fires and Indian activities (Delcourt 1976). In the presettlement landscape of the Big Thicket area of east Texas, prairies were more extensive than they are today, and pine species were prevalent in most community types, including mesic hardwood forests (Schafale and Harcombe 1983). An upland pine type (95 percent pine) was likely longleaf dominated, whereas the intermediate pine-hardwood (57 percent pine) and white oak-red oak-pin oak (*Q. palustris* Muenchh.) types (32 percent pine) probably contained loblolly and shortleaf. The authors acknowledged fire and other disturbances as favoring pine abundance in the more mesic forests, but the scale of disturbance was not discussed. Since the Big Thicket experiences many tropical storms, it is conceivable that the 1800's presettlement pine composition was high because of storm-related damage followed by intense fires due to heavy fuel loads.

Frequency of lightning fire was estimated to be 5 to 15 years in shortleaf pine-oak forests in Louisiana and 5 years or less in adjacent longleaf pine communities (Martin and Smith 1991). Canopy level disturbances (blowdowns) in the shortleaf-oak stands were likely small to moderate in size based on the uneven-aged structure of these stands. The authors estimated that over one-half of the "original" shortleaf pine-oak-hickory forest was now in mixed hardwood-loblolly, whereas approximately one-third of the "original" longleaf pine forest was now in shortleaf-oak-hickory. Marks and Harcombe's (1981) study describing the Big Thicket of Texas supports Martin and Smith's concept that the pyrogenic longleaf pine community functions as a fire source for adjacent, somewhat less flammable, communities. With more frequent fire, longleaf pine increases on upper slopes, whereas shortleaf pine increases on midslopes with a decline in mesic hardwood species. With less fire, loblolly and other mesic species move or "creep" upslope, a phenomenon observed in the Piedmont and other regions where loblolly is present.

Interior Highlands

Distribution and composition—This region includes the Ouachita Mountains and the Ozark Plateau that Braun (1950) characterized as the oak-hickory forest region. The Ozark Plateau consists of a dissected plateau and the higher, more rugged Boston Mountains on the southern end. Limestones, cherts, and dolomites are the predominant parent materials of the plateau, whereas sandstones and shale are common in the Boston Mountains. The Ouachitas consist of shales, sandstones, quartzites, and cherts. Although Braun viewed oak-hickory as the prevailing type, pine and pine-oak communities occurred on southern slopes and ridges. Shortleaf was more abundant in the Ouachitas than in the Ozark Plateau. Species associated with shortleaf include post, blackjack, white, black, and southern red oaks and hickory species on upland sites.

Old-growth forest examples—Several old-growth stands have been characterized for the Interior Highlands (Dale and Watts 1980, Fountain and Sweeney 1985, Fountain 1991)

(appendices A and B). Most of the Ouachita Mountains are oriented east-west, resulting in distinct vegetation types on the north- and south-facing slopes. In the Roaring Branch Research Natural Area (Roaring Branch RNA), north- and lower south-facing slopes were dominated by white oak, northern red oak, mockernut hickory, and other hardwoods (Fountain and Sweeney 1985). South slopes, at mid and upper slope positions, were dominated by shortleaf pine, oaks (northern red, white, and black), and mockernut hickory with shortleaf more abundant on midslopes. Blackjack oak and black hickory were associates on south-facing ridges. Understory species included lowbush blueberry, sparkleberry, and eastern hophornbeam on mid and upper slopes, while *Smilax* species, Virginia creeper, and sassafras were found on upper south-facing slopes only.

In the Hot Springs National Park (Hot Springs NP), the dry and dry-mesic oak-pine type is best exemplified by the oak-hickory-pine type (mesic and xeric subtypes) as described by Dale and Watts (1980). The mesic subtype occurs on lower north-facing slopes and flats where shortleaf and white oak share dominance. Other species include mockernut hickory, blackgum, and southern red, post, and black oaks. The xeric subtype occupies south and southeast slopes and occasionally steep, northern exposures and is dominated by shortleaf followed by post and blackjack oaks, black and mockernut hickory, and white oak.

The Lake Winona Research Natural Area (Lake Winona RNA) is an example of an uneven-aged, old-growth, shortleaf pine stand in the Ouachita Mountains (Fountain and Sweeney 1987, Fountain 1991). Unlike most of the Ouachitas, ridges in this area are north-south oriented. Vegetation was similar on east and west ridges, with shortleaf dominant. Uplands consisted of mostly clayey soils over shale where white oak was the dominant hardwood. Hardwood composition is similar to that reported for Hot Springs NP and Roaring Branch RNA. Lowbush blueberry was the most important shrub species.

Presettlement forests and disturbance—The Ouachita Mountain landscape at the time of settlement contained an abundance of shortleaf pine, which tended to dominate on sandstone substrates, whereas oaks dominated on shale (Foti and Glenn 1991). Shortleaf dominated southerly aspects and intermediate slopes and, unlike today, was common on northwest aspects. Black oak dominated west slopes and white oak on north and east aspects. Post oak was more important on gentle slopes and flats, whereas it is currently found on steep slopes. Forests were generally more open then than today, presumably due to more frequent fire (Foti and Glenn 1991).

According to historical accounts and General Land Office surveys at the time of settlement, the vegetation mosaic of the Ozark Mountains is relatively unchanged with the exception of prairies, which have declined dramatically (Tucker 1991). While the amount of pine in the "original" forest is still open to question, it is generally agreed that pine was widespread in the region and increased southward. Early surveyors described tornado damage but did not mention fire and insect outbreaks. Tucker indicates that understory vegetation is greater now than in the past, and that mesic species [e.g., *Acer saccharinum* L.–*A. floridanum* (Chapm.) Pax complex] have expanded to drier areas in more recent times, which may be related to reduced fire frequency.

Based on fire scars from the period 1780–1938, mean fire frequency across all sites in the Hot Springs NP was estimated to be about 32 years and less on south and west slopes (Johnson and Schnell 1985). Low-intensity fires often fail to produce fire scars, which means that fire may have occurred more often than these scars indicate. For the period 1788–1817, Foti and Glenn (1991) estimated a mean fire interval of 7.25 years, also based on fire scars. Fire is required for the maintenance of pine and oak-pine types in the Ouachitas (Fountain and Sweeney 1985, Johnson and Schnell 1985, Fountain 1991).

Appalachian Mountains: Blue Ridge

Distribution and composition—The Blue Ridge Mountains extend from southern Pennsylvania to northern Georgia. Braun (1950) describes the Southern Appalachian oak-chestnut forest region as composed of oak-chestnut forests on the slopes, mixed mesophytic forests in the coves, and pine or oak-pine communities on dry slopes and ridges. The demise of American chestnut earlier this century greatly influenced forest structure and composition in this region. Chestnut was dominant on intermediate to dry sites at a wide range of elevations from 1,500 to 4,500 feet (457 to 1372 m) (Braun 1950). The most common replacement species are chestnut oak, red maple, and northern red oak (Woods and Shanks 1959, Golden 1974); and on drier sites, pitch pine and scarlet oak. Historically, chestnut was a component of the dry and dry-mesic oak-pine type.

The principal yellow pines of the Appalachians are variously tolerant of fire. Cone serotiny in Table Mountain pine gives it an advantage over shortleaf, pitch, and Virginia pines when subjected to crown fires.[6] Pitch pine has some degree of cone serotiny (Fowells 1968), a characteristic shared, in part, by shortleaf, and is more fire resistant than Virginia or Table Mountain pine due to thicker bark and dormant buds along the bole (Zobel 1969). Pitch and shortleaf pines develop a basal crook in seedlings, which also may protect them from fire (Little and Mergen 1966). Pitch pine is

[6] Sanders, G., and E. Buckner. 1988. Fire: is it an essential component in Table Mountain pine ecosystems? Poster session at 1988 National Society of American Forestry Meeting, Rochester, NY.

typical of ecosystems that experience high-intensity fires at intervals of 10 to 30 years (Christensen 1981).

White pine is not considered a principal pine species of the dry and dry-mesic oak-pine type in this region, even though it is a common associate of the oak-pine type. White pine differs from the fire resilient yellow pine species mentioned above in that it is somewhat more shade tolerant and is commonly found on mesic sites (McCune 1988). White pine distribution has expanded to upland sites in the Southern Appalachians, likely as a result of forest disturbances in the late 1800's and early 1900's (logging, farm abandonment, severe fires), followed by a period of little or no fire. This species may be a component of old-growth oak-pine forests in the future since relatively old trees (>70 years) are common on a variety of sites in the Southern Appalachians.[7] [8] It is likely that the fire regime before 1900, including fires associated with Native Americans, had a frequency that largely restricted white pine to more mesic sites in the Appalachians, but this is not certain.

In the Great Smoky Mountains National Park (Great Smoky Mountains NP), the oak-pine type is found in the ecotone between xeric pine forests and intermediate oak forests and often occurs on soils with a relatively high clay content, i.e., 30 percent (Golden 1974, 1981; Callaway et al. 1987). Topography and elevation were found to be the most important factors affecting distribution of plant communities (Whittaker 1956, Golden 1981, Callaway et al. 1987). Whittaker (1956) described xeric pine forests and intermediate oak forests of the Great Smoky Mountains NP but did not describe the ecotonal "oak-pine" as a distinct type. Descriptions for xeric pine forests and chestnut oak-chestnut heath provide insight into the composition of oak-pine forests (below and appendix A).

Southwest slopes and ridges in the Great Smoky Mountains NP were occupied by Virginia pine below 2,500 feet (762 m), pitch pine heath between 2,200 and 3,200 feet (671 and 976 m), and Table Mountain pine heath between 3,500 and 4,500 feet (1067 and 1372 m). Intermediate oak forests found adjacent to the xeric pine stands included red oak-chestnut forests and the subxeric, chestnut oak-chestnut heath. The latter occurs on open slopes under 3,700 feet (1128 m), except south and southwest slopes. The red oak-chestnut type occupies sheltered south slopes and open slopes above 3,700 feet (1128 m). Chestnut oak, American chestnut, blackgum, sourwood, and red maple were important associates in all three pine types, whereas scarlet oak was an associate in the Virginia and pitch pine types. Black, blackjack, and white oaks were important in the Virginia pine community, whereas black locust and sassafras were common in the Table Mountain pine heath.

Shrub importance was greater in the pitch and Table Mountain pine types. Mountain laurel, trailing arbutus, blueberry, deerberry, and huckleberry were common to all three types. Of the lowbush blueberry species, *Vaccinium vacillans* Torr. was common in Virginia and pitch pine types, *V. hirsutum* Buckley in the pitch and Table Mountain pine types (along with male blueberry) and *V. pallidum* Aiton in the Table Mountain pine type. Highbush blueberry (*V. constablaei* Gray), flame azalea, and fetterbush were also common in the Table Mountain type. Herb species common to all three types were little bluestem, galax, and bracken fern. Wintergreen was common to the two higher elevation forest types. Composition of xeric pine and oak-heath forests is similar to oak-pine communities elsewhere in the Southern Appalachians (appendix A).

In the Nantahala National Forest in North Carolina, McNab and Browning (1993) identified a xeric, pine-oak heath on steep, narrow, convex ridges with shallow soils, centered around 3,500 feet (106 km). Scarlet and chestnut oaks with sourwood and pitch pine dominated these relatively exposed sites. Mountain laurel dominated the understory, whereas low, deciduous heath (blueberry, huckleberry, and male blueberry) was abundant on slightly more mesic sites. A dry community of chestnut oak and red maple was adjacent to the xeric community and occurred on steep sideslopes with variable aspects and deeper soils. Low, deciduous heath or tree seedlings comprised the understory.

Other studies clarifying the distribution of the oak-pine type in the Appalachians include several that are descriptive of river gorges found on the southeastern edge of the Appalachians along the Blue Ridge Escarpment (Cooper 1963, Rodgers 1965, Mowbray 1966, Racine 1966, Mowbray and Oosting 1968, Dumond 1970, Tobe et al. 1992). From many of these studies, Mowbray and Oosting (1968) identified three intermediate to xeric types: (1) chestnut oak-mixed oak on cool, moist slopes dominated by chestnut, black, and northern red oaks; (2) oak-hickory on drier west- and south-facing slopes dominated by scarlet and chestnut oaks and several hickories; and (3) ridgetop communities ranging from pure oak (scarlet and chestnut) to pure pine (shortleaf, Virginia, pitch, and Table Mountain). Associated with scarlet and chestnut oaks and pitch pine were sourwood and red maple with a dense cover of mountain laurel, lowbush blueberry, deerberry, and bear

[7] Carlson, P.J. 1995. An assessment of the old-growth forest resource on National Forest System lands in the Chattooga River Watershed. Report to Chattooga Ecosystem Demonstration Management Project, U.S. Department of Agriculture, Forest Service, Region 8, Atlanta, GA. 83 p. On file with: USDA Forest Service, Southern Region, 1720 Peachtree Road, NW, Atlanta, GA 30367.

[8] Continuous Inventory of Stand Condition (CISC) data files from the following national forests: Pisgah, Nantahala, Chattahoochee, Sumter, and Cherokee. On file with: USDA Forest Service, Southern Region, 1720 Peachtree Road, NW, Atlanta, GA 30367.

huckleberry. Mountain laurel cover decreased and blueberry cover increased along the gradient from chestnut oak-heath to pine leads and ridges.

Southern red, post, and blackjack oaks—typical Piedmont species—and Virginia pine were described by Mowbray (1966) as reaching their thermal limit at 1,800 to 1,900 feet (549 to 579 m) in the Bearwallow Gorge, whereas Dumond (1970) described the same three oak species as occurring below 3,000 feet (915 m) in the Chattooga River Gorge. Racine (1966) described the altitudinal limit of Virginia and shortleaf pines as 2,800 feet (854 m), an elevation where the pitch pine and scarlet oak association develops. Species composition described for the Thompson River Gorge (Racine 1966) is representative of most of the other escarpment sites and is included in appendix A.

Shortleaf pine is an important species at lower elevations of the Appalachians. In the Chauga River Gorge, shortleaf pine dominates the ridges below 2,000 feet (610 m), whereas a rare Table Mountain pine-Virginia pine association is found above 2,000 feet (610 m) (Tobe et al. 1992). Shortleaf type associates include red maple, dogwood, blackgum, sourwood, Table Mountain pine, Virginia pine, pitch pine, scarlet and southern red oaks, with lowbush blueberry and storax in the shrub layer (appendix A). The chestnut oak type, the most common in this gorge, merges with pine types on north and east aspects of the upper slopes. Scarlet oak is a consistent codominant in the chestnut oak and pine-dominated forests of the upper gorge slopes.

In a central Appalachian gorge in Virginia, Ramsey et al. (1993) described an oak-pine heath on thin, acid soils on south and west slopes, dominated by Virginia, pitch, and Table Mountain pines, and northern red, chestnut, and scarlet oaks. The understory included bear oak, serviceberry [*Amelanchier arborea* (Michx. f.) Fern.], mountain laurel, chestnut sprouts, sweet-fern [*Comptonia peregrina* (L.) Coult.], lowbush blueberry, deerberry, huckleberry, minnie-bush [*Menziesia pilosa* (Michx.) Juss.], wild azalea, Catawba rhododendron, spirea (*Spirea betulifolia* Pallas), buffalo nut, hawthorne, and sassafras.

Old-growth forest examples—Few old-growth oak-pine stands have been studied or documented in this region. At 2,200 to 3,000 feet (671 to 915 m) in the Scarlet Oak Natural Area of the Pisgah National Forest in North Carolina, oak-pine stands considered high in "virgin attributes" were described by Delapp and Wentworth[9] (appendix A). Scarlet and chestnut oaks, sourwood, pitch pine, and red maple dominated on broad, south-facing leads and knobs. Other species included mountain laurel, huckleberry, lowbush blueberry, deerberry, *Smilax* species, pipsissewa, and bracken fern. Pitch pine increased in importance on drier sites in these scarlet oak-dominated stands. Scarlet oak was considered the "climax" species on these sites.

The remaining descriptions of old growth are more general and do not provide detailed, stand-level information. Carlson (see footnote 7) assessed old growth across parts of three national forests. The oak-pine type was underrepresented as old growth as compared to its current relative abundance in younger age classes. Carlson described stands containing pitch and shortleaf pines; white, black, and scarlet oaks; and large red maple and white pine. The yellow pine species exceeded 200 years in age. Although some of these stands approximated old-growth conditions, the effects of chestnut blight, early logging and fire, and 20th-century fire suppression greatly influenced current stand composition and structure.

Zahner[10] described dry oak and oak-pine old-growth types for the Highlands Ranger District on the Nantahala National Forest in North Carolina as occurring on high ridges and upper, south-facing slopes. Species included white oak, scarlet oak, black oak, chestnut oak, pitch pine, white pine, witch-hazel (*Hamamelis virginiana* L.), black locust, Table Mountain pine with Catawba rhododendron, mountain laurel, and mountain myrtle [*Leiphyllum buxifolium* (Berg.) Ell.] in the understory.

Yost et al. (1994) used five forest types to delineate old growth in the Great Smoky Mountains NP. Their subxeric and xeric oak types contained yellow pine species and corresponded closely with the dry and dry-mesic oak-pine type. Scarlet, chestnut, and black oaks dominated the subxeric type, with an understory dominated by mountain laurel, huckleberry, and *Rhododendron* species. Xeric sites were dominated by blackjack, scarlet, and chestnut oaks, with Virginia, pitch, and Table Mountain pine, sourwood, blackgum, and red maple as associates and mountain laurel and blueberry species in the understory. Their assessment of these dry types for the Great Smoky Mountains NP is incomplete at this time.

Presettlement forests and disturbance—The abundance of the oak-pine type in the Appalachians at the time of European settlement is not clear. Bartram (1958) described the vegetation in the Carolina mountains but makes only one reference to pines. He mentioned white pine, Scotch pine

[9] Delapp, J.A., and T.R. Wentworth. 1977. Proposed research natural areas in the Southern Appalachian Mountains. 117 p. Unpublished report. On file with: Highlands Biological Station, Highlands, NC 28741.

[10] Zahner, R. 1990. Upland hardwood and pine-hardwood forest of the Southern Appalachian Mountains—old-growth stands: definitions and characteristics for identification, inventory, and restoration on the Highlands Ranger District, Nantahala National Forest. 13 p. Unpublished report. On file with: USDA Forest Service, Highlands Ranger District, Highlands, NC 28741.

(*Pinus sylvestris* L.), and other species at a South Carolina site. His reference to Scotch pine may be an incorrect identification of Virginia or Table Mountain pine since Scotch pine is not native to the area. Sargent (1884) describes the North Carolina and Virginia mountains as containing "northern pines" but focused generally on the "great body of relatively undisturbed hardwood forest" of that region. Malter (1977) quotes a 1901 article describing the forests of the Citico Creek in Tennessee before the extensive logging of the early 1900's: "the finest timber lands he has ever seen, barring none. Pine, oak, poplar and hemlock abound . . . and the forest affords uniformly good timber throughout its entire length and breadth, speaking with respect to the 43,000 acres of land owned or controlled by the company."

The pollen record indicates the group of southern yellow pine species expanded northward into the Southern Appalachians approximately 10,000 years ago as glaciers retreated (Delcourt and Delcourt 1987) at approximately the same time Native Americans entered the region. Wind and ice storm damage and insect outbreaks, coupled with fire, could have resulted in large burns in the Appalachians. Use of fire by Native Americans (Buckner 1989, Van Lear and Waldrop 1989), coupled with lightning fire and other natural disturbances, probably enhanced and maintained the oak-pine type in presettlement times.

Although it is widely acknowledged that Native American land use strongly impacted southeastern landscapes, the magnitude and frequency of their disturbances across large regions is uncertain. It is our view that natural disturbances (wind and ice storms, insects, pathogens, and lightning fire) may have been sufficient to maintain the oak-pine type in the Appalachians. The assessment by Barden and Woods (1974, 1976) that lightning-caused crown fires are extremely uncommon in the Appalachians should be interpreted cautiously. The short duration of their study and the fact that the lightning fires they investigated were successfully extinguished (except those that went out on their own) rather than having been allowed to burn unhindered or to smolder until burning conditions improved, allow other interpretations. Frost (1995) suggests the importance of lightning fire on exposed ridges and upper slopes in the Appalachians in maintaining pine and pine-oak types. Frost estimated presettlement fire frequency (for the most exposed parts of landscape) to be 7 to 12 years in the lower mountains [≤3,000 feet (915 m)] and more than 12 years in higher mountains. Frost suggests the Indian fires were of greater impact in more topographically diverse areas such as the mountains, upper Piedmont, and sandhills compared to the less dissected Piedmont and Coastal Plain. Whittaker (1956) viewed pine stands and oak-chestnut heaths as self-maintaining, whereas more recent studies have shown that this is not the case, except possibly on extremely dry sites (Barden 1976, Williams and Johnson 1992).

Old-growth representatives of the dry and dry-mesic oak-pine type are uncommon in the Appalachians. However, younger stands are common and often exist in the ecotone between xeric pine and intermediate to dry oak-dominated forests. The prevalence of this type is due to fire and other disturbances. Scarlet oak and chestnut oak are the most common oak species of this type, whereas the relative dominance of the four yellow pine species is determined by elevation, exposure, and the type and magnitude of disturbance.

Appalachian Mountains: Plateau

Distribution and composition—The Appalachian Plateau extends from central New York to southwestern Alabama. We describe the vegetation in the unglaciated sections from central Pennsylvania southward. Shimer (1972) described this region's appearance from the air as a choppy sea of small mountains oriented randomly, regionally appearing as a basin-type structure with cuesta scarps along its border. On its eastern front are the Allegheny and Cumberland Mountains, with the majority of the region consisting of the Allegheny and Cumberland Plateaus. Braun (1950) described four sections within these plateaus: (1) rugged eastern area—occurring mostly between the Allegheny and Cumberland Mountains; (2) low hills belt—comprising most of West Virginia, northeastern Kentucky, and southern Ohio; (3) knobs border area—consisting of a series of conical hills at the western edge of the Allegheny Plateau in northern Kentucky and southern Ohio; and (4) cliff section—extending from Berea, KY, to Alabama, initially along the western plateau border as a distinct escarpment but widening in Tennessee and Alabama where it forms most of the plateau.

Although Braun (1950) described the overall area as the mixed mesophytic forest region, other types such as oak, oak-pine, and pine types were represented on exposed areas throughout the region. In the Cumberland Mountains (Braun 1935, 1942, 1950), dry pine and oak forests occupied dry ridges and upper south slopes. Virginia, pitch, and shortleaf pines occurred with chestnut; black, white, and scarlet oaks; blackgum; American chestnut; red maple; yellow-poplar; dogwood; sassafras; and sourwood. The oak-pine forests were small in stature on the shallow soils, increasing in size as soil became deeper, grading into chestnut oak and American chestnut communities.

Braun (1935) described several oak-pine to pine heath stands that she considered representative of "primary" forests on Pine Mountain in Kentucky. Overstory composition was described as above. Understory shrubs included mountain laurel, lowbush blueberry, deerberry, and others. See appendix A for additional species.

Yellow pines were apparently not as prevalent in the Allegheny Mountains as they were in the Cumberland Mountains based on Braun's (1950) descriptions but were components of the oak-chestnut type on upper slopes and ridges. Braun cites Jennings' (1927) description of a chestnut-chestnut oak-black oak association occurring with pitch pine on the upper slopes and "undisturbed top" of Chestnut Ridge in Pennsylvania. Understory species included mountain laurel, azalea, blueberry, trailing arbutus, and wintergreen.

Within the rugged eastern area of the Cumberland and Allegheny Plateau region, several observers have described the oak-pine type. Braun (1950) describes pitch and shortleaf pines as scattered along ridges and occasionally in small groups in oak-chestnut and oak-hickory communities. Martin and Shepherd (1973) described upland tree and shrub species in the "virgin" portion of the Lilley Cornett Woods in Kentucky that included pitch, Virginia, and shortleaf occurring occasionally. In the nearby Robinson Forest, shortleaf and pitch pines were minor components of upper slope, second-growth forests (Phillippi and Boebinger 1986).

In the low hills section, Braun cites Crandall's (1876) description of the "original" vegetation of an area in eastern Kentucky where pine species accounted for 11 percent of the composition on hilltops dominated by chestnut oak. Overall, pine was likely a minor component of the oak- and oak-hickory-dominated slopes and ridges of the low hills section.

The conical hills of the narrow knobs border area are underlain by shales, limestones, and sandstones. Oak, chestnut, oak-hickory, and pine types predominated near the summit of ridges or knobs (Braun 1950). Pines capped the knobs and extended down the steep, southwestern slopes. The heath layer is similar to that described for the Cumberland and Allegheny Mountains. The pine-oak and chestnut heath type communities dominated on noncalcareous soils (sandstone or shale), whereas oak-hickory was more common on limestone ridgetops.

The cliff section of the Cumberland Plateau in southern Kentucky is flat to rolling with shallower drainages and gorges than the area farther south. The plateau supports oak-hickory and oak-pine forests of white, black, and post oaks; mockernut and shagbark hickories [*C. ovata* (P. Mill.) K. Koch]; yellow-poplar; dogwood; shortleaf and pitch pines; and often blackgum, red maple, and Virginia pine (Braun 1950). Lowbush blueberry, wild azalea, sawbrier, grape, and box huckleberry [*Gaylussacia brachycera* (Michx.) Gray] make up the understory. Toward the western margin of the plateau along the western escarpment, sandstone cliffs become prominent. Forests there vary from open pine woods with grassy understories to pine and pine-oak heath with scarlet and chestnut oaks and an understory dominated by mountain laurel, lowbush blueberry, huckleberry, or occasionally, box huckleberry (Braun 1950).

The southern part of the cliff section in Alabama and Tennessee consists of oak, oak-hickory, and oak-pine communities (Braun 1950). At the plateau's margin above the gorges, pine heath communities dominate. Hinkle (1989) noted Virginia pine occupying the dry ridges and cliff edges and, on deeper soils, identified a shortleaf pine-white oak type that he viewed as succeeding white oak. He refers to this section in Tennessee as the plateau uplands.

Schmalzer (1988) described three moderately xeric oak-pine or pine communities of the Obed River Gorge in Tennessee as white pine-white oak-chestnut oak, white oak-scarlet oak, and Virginia pine. Virginia pine was common and persistent on shallow siliceous soils of cliff edges and on upland sites following logging and fire. Shortleaf, Virginia, and white pines were significant components of the white oak-scarlet oak type. Unlike other areas of the Appalachian Plateau, chestnut and hickory were not significant components of oak-dominated upland plateau communities in Tennessee. The prevalence of fire may explain the scarcity of hickory. Schmalzer (1988) and Hinkle (1989) acknowledge the role of fire in affecting the composition of these upland types.

Old-growth forest examples—No documented examples of old-growth oak-pine exist to our knowledge.

Presettlement forests and disturbance—Little information is available on presettlement distribution of the oak-pine type in the region other than that described above. In the plateau region of Alabama, Harper (1943) described shortleaf pine and mixed oaks as occurring in dry woods around Little Mountain in the Tennessee Valley and coal region. Both loblolly and shortleaf were significant components of the "original" forest of the latter, occurring with post, southern red, and white oaks. In the Tennessee River Valley as a whole, pine was a minor component (Mohr 1901, Harper 1943).

On the Alabama tablelands of the Warrior and Coosa Basins, Mohr (1901) described chestnut oak as a dominant species, occurring with post and southern red oaks, or, rarely, blackjack, black, white, and scarlet oaks. Shortleaf was more prevalent on lower elevation ridges with thinner soils and was rare when chestnut oak was dominant. He found dense groves of loblolly pine growing in poorly drained depressions and Virginia pine, on the poorest sites, mostly above 1,200 feet (366 m). Lowbush blueberry, deerberry, and wild azalea were important understory species associated with the drier oak and pine types.

In summary, mixed oak and pine communities containing pitch, shortleaf and Virginia pines, or both, are prevalent in

the Cumberland Mountains and southern portion of the Appalachian Plateau, often growing on sandstone or shale-derived soils on exposed sites. Composition of these communities does not vary significantly across the region. Historically, fire has been an important factor in maintaining the pine and oak-pine types on these droughty uplands.

Appalachian Mountains: Valley and Ridge

Distribution and composition—The Valley and Ridge province extends from the St. Lawrence River lowland to northeast Alabama (Shimer 1972). The section in northern Pennsylvania and from New Jersey northward was glaciated and is mostly beyond the range of the dry and dry-mesic oak-pine type. This province consists of long ridges, mostly oriented southwest to northeast, predominately sandstone and conglomerate, with the intervening valleys or lowlands underlain by shale and limestone. The Great Valley or Appalachian Valley, a series of large valleys, occurs between the easternmost ridge of the province and the Blue Ridge. Braun (1950) noted that most of these ridges were not high enough to have well-defined altitudinal variations in vegetation. Because ridge forests are easily accessible, most have been logged heavily by the charcoal, railroad, and chemical industries.

In the glaciated areas of the Valley and Ridge region, dry to xeric pitch pine-oak communities with heath understories have been found in northern New Jersey (Niering 1953) and southeastern New York (McIntosh 1959). These communities were similar to those of the New Jersey Pine Barrens (Buell and Cantlon 1950), except for different species of *Gaylussacia* and *Vaccinium*. Many of these forests are stunted and considered too xeric for the dry and dry-mesic oak-pine type, although Niering does describe 17- to 19-inch (43- to 48-cm) d.b.h. pitch pines 140 years old in a pine-oak stand.

Braun (1950) considered the unglaciated parts of the Valley and Ridge to be in the oak-chestnut region except for the southern end that includes the Coosa Valley in Alabama, which she considered part of the oak-pine region. She described forests of the ridges and mountain ranges for three areas. The northern area, in Pennsylvania, included a scarlet oak or scarlet oak-pine community on dry, south, and west slopes. The second area, from Spruce Knob, WV, south 100 miles (160 km), had chestnut oak dominating dry, upper slopes with pines common on the cliff margins. Chestnut oak, northern red oak, and Virginia pine occupied open shale barrens. The third area, in southern Virginia and Tennessee, was primarily hardwood. The region from Knoxville, TN, south was discussed by Braun in the context of valley floor vegetation and lacked mountain ranges. White oak was dominant in the valley, whereas on low shale ridges, oak communities (white, black, scarlet, and chestnut) were prevalent. White, pitch, and Virginia pines were associates in the north, although southern pines occurred in the south with blackjack and southern red oaks. Martin (1971) also describes the prevalence of white oak communities in eastern Tennessee, where white oak is often codominant with other oaks and Virginia and shortleaf pines.

In the oak-pine forests of southwest Virginia, scarlet, chestnut, and black oaks were dominant on side slopes, whereas pitch and pitch pine-scarlet oak were dominant on convex sites (McEvoy et al. 1980). Lowbush blueberry, huckleberry, and mountain laurel were common on these sites. Tree cover declined as shrub cover increased from mesic to xeric sites, as was found in the Great Smoky Mountains NP (Whittaker 1956). Elsewhere in southwest Virginia, relatively undisturbed Table Mountain pine stands occupied southwest slopes at 2,500 feet (762 m) and contained scarlet and chestnut oaks, sassafras, and blackgum (Williams and Johnson 1992). Within the Valley and Ridge, Table Mountain pine typically occupies steep, lower, and middle slopes, often on shale outcroppings (Zobel 1969) or ridge-capping sandstones at higher elevations.

Old-growth forest examples—No documented examples of old-growth oak-pine exist to our knowledge.

Presettlement forests and disturbance—Little is known about the "original" forests of the Valley and Ridge province (Clarkson 1966). Clarkson grouped the "original" forest of the Monongahela National Forest, WV, into four types. Mixed oak-chestnut was the only type that contained yellow pines (primarily pitch, but also Table Mountain, shortleaf, and Virginia). Pines were abundant on southern and eastern slopes on thin soils derived from shale or sandstone. Early forests of West Virginia were described by Sargent (1884), who quotes a report from a Mr. Pringle, who described the long mountain chains of West Virginia after leaving Pennsylvania: " . . . fewer evergreens appeared than I had previously seen. A few slopes were principally occupied by pine variety, but the mountains of this region were covered with a growth of deciduous trees, white, black, red, Spanish, and chestnut oaks, hickories, butternuts, black walnuts, yellow-poplars, locusts, elms, sugar maples . . . ."

The presettlement forests in Pennsylvania were comprised of oak (42 percent), pine (27 percent), and American chestnut (13 percent) on ridges and oak (56 percent), pine (13 percent), and hickory (12 percent) in the valleys (Nowacki and Abrams 1992). Fire and other disturbances are thought to be required to maintain oak and yellow pine in these forests. The pine component of these forests has been drastically reduced by past logging activities. Repetitive harvesting for charcoal production greatly fostered vegetative species (i.e., oak, chestnut) at the expense of pine. Due to recent fire suppression, composition is shifting toward greater maples, black cherry, and black

birch (*Betula lenta* L.). Dry sites are currently dominated by blueberry and huckleberry species with mountain laurel confined to ridge sites. Northern red oak is an important associate of chestnut oak on drier ridge sites, whereas scarlet oak is an important associate of white oak on coarse textured soils in the valley. The authors suggest that the increased presence of scarlet oak in valleys more so than on ridges may be a local phenomenon. They propose that the abundance of northern red oak on ridges may have been due to more presettlement fires in the valleys where most Native Americans resided because northern red oak is less tolerant of fire than most oaks (Lorimer 1985).

In the southern part of the Valley and Ridge province, surveys of northwest Georgia from the early 1800's indicate that the oaks-to-pines-to-hickories ratio was 50:18:8 (Plummer 1975). Post oak was the most abundant oak with hickories and American chestnut on ridges. Elevation of this section ranged from 600 to 1,700 feet (183 to 518 m). In the Coosa Valley of Alabama, many of the chert hills and sandstone ridges supported longleaf pine on sandy and gravelly soil (Harper 1943). On dry soils, shortleaf pine and southern red and post oaks were dominant, with dogwood, rusty black-haw, and hawthorne in the understory. Loblolly was widely distributed. About 40 percent of the "original" forest was estimated to have been evergreen (mostly pine).

An assessment of age structure and factors affecting recruitment in relatively undisturbed Table Mountain pine-oak communities of the Jefferson National Forest indicated that Table Mountain pine was not self-maintaining and that successful seedling recruitment and establishment were unlikely without fire (Williams and Johnson 1992). In general, without fire, pines become less abundant in these forests and, in some cases, oaks eventually decrease as well (Nowacki and Abrams 1992). The intensity of postsettlement disturbance in this area conceals the "original" abundance of pine or oak-pine types in the region, since much of this disturbance has decreased pine abundance.

Forest Composition: Synthesis across Regions

Species composition of the oak-pine forest type described above is shown for several old-growth and other representative stands in appendix A. *Pinus, Quercus, Carya,* and *Vaccinium* were represented in all seven old-growth stands. Herb and vine species found in most stands included *Carex, Panicum*, broom-sedge, and other grasses, pipsissewa, *Desmodium*, bracken fern, *Smilax*, Virginia creeper, and *Vitis*. Shortleaf pine and white oak were the most widely distributed trees across all stands (appendix A).

Shortleaf was the primary pine species of the dry and dry-mesic oak-pine type in the Piedmont, Coastal Plain, and Interior Highlands, whereas pitch was predominant in the mountainous regions. Other widely distributed oaks include black, post, southern red, and blackjack. Scarlet and chestnut oaks were more prevalent in the Appalachian stands. Red maple, blackgum, and sourwood were common across most sites shown in appendix A and may be increasing on most sites due to fire suppression. Dogwood was common except in some of the mountain stands. *Vaccinium* species (*V. vacillans* and *V. stamineum* primarily) were the most common shrubs across regions, whereas mountain laurel was common on mountain sites. *Gaylussacia* species [primarily *G. baccata* (Wang.) K. Koch] were common on half the sites.

Narrative of Old-Growth Conditions

In this section, we describe characteristics of the living and dead components of old-growth stands found in the Piedmont, Blue Ridge, Ouachita Mountains, and Gulf Coastal Plain (table 2). See appendix B for additional information on each of the old-growth stands presented in table 2. The most complete old-growth attribute information available for the dry and dry-mesic oak-pine type is from the John de la Howe (JDLH) forest tract in the South Carolina Piedmont. Since this stand will be frequently referred to in this section, a short description of it follows.

The JDLH stand is an approximately 120-acre [48.6-hectare (ha)], 200-year-old stand that in recent years has suffered significant pine mortality. Prior to settlement, the general area was subjected to aboriginal fires and likely consisted of open woods with scattered prairie-like openings (Logan 1859, 1980). It is located in an area that was settled by French Huguenots around 1770, abandoned in the 1790's, and has been generally protected since. From current soil and vegetation conditions (age, composition) and from archeological evidence (Steen 1993), site disturbance likely included some land clearing for crops and timber as well as woodland livestock grazing. The disturbances that preceded abandonment in the late 1700's resemble, in terms of their effect on the landscape, relatively large-scale natural disturbance (disease, wind, ice, tornados) followed by fire. Scattered cutting in the periphery of the stand and pine salvage in a few areas has taken place in recent years. These areas were avoided when sampled. Data was collected at four levels of mortality, which will be described later.

Table 2 (English units)—Standardized table of old-growth attributes for dry and dry-mesic oak-pine forests

Quantifiable attribute	Range[a]	Mean	Number of stands[b]	References
Stand density (no./acre)				
John de la Howe tract			1	This study
—all species ≥4 in. d.b.h.	130–183	171		
Shortleaf and loblolly pines	1–42	25		
Oak species	31–51	42		
—all species ≥20 in. d.b.h.	7–22	15		
Shortleaf and loblolly pines	1–15	9		
Oak species	1–5	4		
Duke Forest			1	Oosting 1942
—all species ≥1 in. d.b.h.[c]		134		
Shortleaf pine		32		
Oak species		93		
Scarlet Oak Natural Area			2	Delapp and Wentworth[d]
—all species ≥3 in. d.b.h.	312–328	320		
Pitch pine	20–134	77		
Oak species	117–200	160		
Lake Winona Research Natural Area			1	Fountain 1991
—all species ≥4 in. d.b.h.		209		
Shortleaf pine		138		
Hardwoods		71		
—shortleaf pine ≥20 in. d.b.h.		3		
Roaring Branch Research Natural Area			2	Fountain and Sweeney 1985
—all species ≥4 in. d.b.h.	223–225	224		
Shortleaf pine	30–56	42		
Oak species	115–156	137		
—shortleaf pine ≥20 in. d.b.h.	0–3	2		
Hot Springs National Park			12	Dale and Watts 1980
—all species ≥3.5 in. d.b.h.	313–618	496		
Shortleaf pine	67–367	212		
Oak species	117–367	202		
Kisatchie National Forest			2	Martin and Smith 1991
—all species ≥5 in. d.b.h.	61–107	84		
Shortleaf and loblolly pines	14–24	18		
Oak species	38–75	57		
—all species ≥20 in. d.b.h.	10–16	13		
Shortleaf and loblolly pines	6–10	8		
Oak species	4–6	5		
Stand basal area (ft^2/acre)				
John de la Howe tract			1	This study
—all species ≥4 in. d.b.h.	64–150	118		
Shortleaf and loblolly pines	5–80	47		
Oak species	20–43	35		
—all species ≥20 in. d.b.h.	22–71	47		
Shortleaf and loblolly pines	5–55	28		
Oak species	4–18	13		
Duke Forest			1	Oosting 1942
—all species ≥1 in. d.b.h.[c]		128		
Shortleaf pine		38		
Oak species		76		

Table 2 (English units)—Standardized table of old-growth attributes for dry and dry-mesic oak-pine forests (continued)

Quantifiable attribute	Range[a]	Mean	Number of stands[b]	References
Stand basal area (ft^2/acre) (cont.)				
Scarlet Oak Natural Area			2	Delapp and Wentworth[d]
—all species ≥3 in. d.b.h.	90–110	100		
Pitch pine	10–57	33		
Oak species	36–68	52		
Lake Winona Research Natural Area			1	Fountain 1991
—all species ≥4 in. d.b.h.		112		
Shortleaf pine		101		
Hardwoods		11		
—shortleaf pine ≥20 in. d.b.h.		2		
Roaring Branch Research Natural Area			2	Fountain and Sweeney 1985
—all species ≥4 in. d.b.h.	80–81	81		
Shortleaf pine	24–30	27		
Oak species	42–46	44		
—shortleaf pine ≥20 in. d.b.h.	0–9	5		
Hot Springs National Park			12	Dale and Watts 1980
—all species ≥3.5 in. d.b.h.	57–112	79		
Shortleaf pine	18–60	34		
Oak species	20–55	34		
Kisatchie National Forest			2	Martin and Smith 1991
—all species ≥5 in. d.b.h.	59–128	94		
Shortleaf and loblolly pines	27–45	36		
Oak species	30–81	56		
—all species ≥20 in. d.b.h.	33–50	42		
Shortleaf and loblolly pines	22–33	28		
Oak species	11–17	14		
Age of large trees (yrs)[e]				
John de la Howe tract			1	This study
Shortleaf pine	89–205	144		
Loblolly pine	79–189	117		
White oak	82–207	149		
Hickory species[f]	142–207	179		
Post oak	101–216	144		
Southern red oak	64–190	124		
Yellow-poplar	94–194	160		
Scarlet Oak Natural Area			1	This study
Pitch pine	117–163			
Scarlet oak	73–123			
Chestnut oak	66–170			
Great Smoky Mountains National Park (max. age)			--	Blozan 1994
Chestnut oak	347			
White oak	344			
Scarlet oak	165			
Black oak	180			
Pignut hickory	327			
Pitch pine	148			
Table Mountain pine	204			
Virginia pine	135			

Table 2 (English units)—Standardized table of old-growth attributes for dry and dry-mesic oak-pine forests (continued)

Quantifiable attribute	Range[a]	Mean	Number of stands[b]	References
Age of large trees (yrs)[e] (cont.)				
Chattooga River Watershed				
(max. age)			--	Carlson 1995[g]
Chestnut oak	362			
White oak	348			
Scarlet oak	190			
Black oak	211			
Mockernut hickory	335			
Pitch pine	235			
Shortleaf pine	300			
Virginia pine	108			
Lake Winona Research Natural Area			--	Stahle et al. 1985
Shortleaf pine	108–314			
Roaring Branch Research Natural Area			--	Stahle et al. 1985
Shortleaf pine	133–275			
Hot Springs National Park			--	Stahle et al. 1985
Shortleaf pine	124–247			
Number of 4-in size classes[h]				
John de la Howe tract			1	This study
Shortleaf pine	8			
Hardwoods	7			
Scarlet Oak Natural Area			2	Delapp and Wentworth[d]
Pitch pine	4			
Hardwoods	4			
Lake Winona Research Natural Area	5		1	Fountain 1991
Roaring Branch Research Natural Area			2	Fountain and Sweeney 1985
Shortleaf pine	6			
Hardwoods	4			
Kisatchie National Forest			2	Martin and Smith 1991
Shortleaf and loblolly pines	7			
Hardwoods	5			
D.b.h. of large trees (in.)[e]				
John de la Howe tract			1	This study
Shortleaf pine	11–32	19		
Loblolly pine	12–39	21		
White oak	12–33	20		
Hickory species[g]	10–23	16		
Post oak	8–19	14		
Southern red oak	12–32	22		
Yellow-poplar	12–31	22		
Roaring Branch Research Natural Area			1	Stahle et al. 1985
Shortleaf pine	14–26	19		
Standing coarse woody debris (no./acre)				
John de la Howe tract			1	This study
Snags ≥4 in. d.b.h.	15–69	33		
Snags ≥20 in. d.b.h.	2–16	8		

Table 2 (English units)—Standardized table of old-growth attributes for dry and dry-mesic oak-pine forests (continued)

Quantifiable attribute	Range[a]	Mean	Number of stands[b]	References
Standing coarse woody debris (no./acre) (cont.)				
Hot Springs National Park[i]			3	Johnson and Schnell 1985
(mass only—tons/acre)				
Snags ≥3 in. d.b.h.	1.9–13.1	8.7		
Downed coarse woody debris				
John de la Howe tract			1	This study
Volume (ft^3/acre)	747–2528	1545		
Mass (tons/acre)	7.4–25.4	15.4		
Hot Springs National Park[i]			3	Johnson and Schnell 1985
Mass (tons/acre)	.9–4.2	3.1		
Tree canopy structure				
John de la Howe tract			1	This study
Number of canopy layers (1–3)	2–3			
Percent canopy in gaps	24–80	37		
Mean gap size[j] (acres)	.002–.503	.06		

[a] For the John de la Howe tract, this represents the range of means from areas showing different degrees of mortality, and applies to all attribute data except age, diameter, and gap size.

[b] Number of stands included (may not equal number of citations).

[c] Oosting did not define the diameter limit for overstory. Density values are for overstory only. If understory is included, density of trees ≥1 in. in d.b.h. is 687, 89, and 154 for all trees, pines, and oaks, respectively. Basal area values are given for all trees ≥1 in. in d.b.h.

[d] Delapp, J.A., and T.R. Wentworth. 1977. Proposed research natural areas in the Southern Appalachian Mountains. 117 p. Unpublished report. On file with: Highlands Biological Station, Highlands, NC 28741.

[e] Includes dominant and codominant trees that comprise the upper canopy. Mean diameter for trees from the John de la Howe tract is the quadratic mean.

[f] Includes mockernut, shagbark [*Carya ovata* (Mill.) K. Koch], and pignut hickory species.

[g] Carlson, P.J. 1995. An assessment of the old-growth forest resource on National Forest System lands in the Chattooga River Watershed. Report to Chattooga Ecosystem Demonstration Management Project, U.S. Department of Agriculture, Forest Service, Region 8, Atlanta, GA. 83 p. On file with: USDA Forest Service, Southern Region, 1720 Peachtree Road, NW, Atlanta, GA 30367.

[h] For inclusion, 1 percent of all trees must be present within a size class—size classes start at 4 in.

[i] Average across three stands: (1) stand dominated by medium to large, actively growing shortleaf, (2) a "decadent" old-growth shortleaf-dominated stand, and (3) an old-growth oak-hickory stand with a few large shortleaf pines.

[j] Refers to canopy gaps ≤1 acre in size. Gaps exceeding 1 acre were variable sized patches of extensive pine mortality that accounted for 58 percent of the total gap area.

Table 2 (metric units)—Standardized table of old-growth attributes for dry and dry-mesic oak-pine forests

Quantifiable attribute	Range[a]	Mean	Number of stands[b]	References
Stand density (no./acre)				
John de la Howe tract			1	This study
—all species ≥10 cm d.b.h.	321–452	422		
Shortleaf and loblolly pines	2–104	62		
Oak species	77–126	104		
—all species ≥50.8 cm d.b.h.	17–54	37		
Shortleaf and loblolly pines	2–37	22		
Oak species	2–12	10		
Duke Forest			1	Oosting 1942
—all species ≥2.5 cm d.b.h.[c]		331		
Shortleaf pine		79		
Oak species		230		
Scarlet Oak Natural Area			2	Delapp and Wentworth[d]
—all species ≥7.6 cm d.b.h.	771–810	790		
Pitch pine	50–330	190		
Oak species	289–494	395		
Lake Winona Research Natural Area			1	Fountain 1991
—all species ≥10 cm d.b.h.		516		
Shortleaf pine		341		
Hardwoods		175		
—shortleaf pine ≥50.8 cm d.b.h.		7		
Roaring Branch Research Natural Area			2	Fountain and Sweeney 1985
—all species ≥10 cm d.b.h.	551–556	553		
Shortleaf pine	74–138	104		
Oak species	284–385	338		
—shortleaf pine ≥50.8 cm d.b.h.	0–7	5		
Hot Springs National Park			12	Dale and Watts 1980
—all species ≥8.9 cm d.b.h.	773–1526	1225		
Shortleaf pine	165–906	524		
Oak species	289–906	499		
Kisatchie National Forest			2	Martin and Smith 1991
—all species ≥12.7 cm d.b.h.	151–264	207		
Shortleaf and loblolly pines	35–59	44		
Oak species	94–185	141		
—all species ≥50.8 cm d.b.h.	25–40	32		
Shortleaf and loblolly pines	15–25	20		
Oak species	10–15	12		
Stand basal area (m^2/ha)				
John de la Howe tract			1	This study
—all species ≥10 cm d.b.h.	15–34	27		
Shortleaf and loblolly pines	1–18	11		
Oak species	5–10	8		
—all species ≥50.8 cm d.b.h.	5–16	11		
Shortleaf and loblolly pines	1–13	6		
Oak species	1–4	3		
Duke Forest			1	Oosting 1942
—all species ≥2.5 cm d.b.h.[c]		29		
Shortleaf pine		9		
Oak species		17		

Table 2 (metric units)—Standardized table of old-growth attributes for dry and dry-mesic oak-pine forests (continued)

Quantifiable attribute	Range[a]	Mean	Number of stands[b]	References
Stand basal area (m^2/ha) (cont.)				
Scarlet Oak Natural Area			2	Delapp and Wentworth[d]
—all species ≥7.6 cm d.b.h.	21–25	23		
Pitch pine	2–13	8		
Oak species	8–16	12		
Lake Winona Research Natural Area			1	Fountain 1991
—all species ≥10 cm d.b.h.		26		
Shortleaf pine		23		
Hardwoods		3		
—shortleaf pine ≥50.8 cm d.b.h.		0		
Roaring Branch Research Natural Area			2	Fountain and Sweeney 1985
—all species ≥10 cm d.b.h.	18–19	19		
Shortleaf pine	6–7	6		
Oak species	10–11	10		
—shortleaf pine ≥50.8 cm d.b.h.	0–2	1		
Hot Springs National Park			12	Dale and Watts 1980
—all species ≥7.6 cm d.b.h.	13–26	18		
Shortleaf pine	4–14	8		
Oak species	5–13	8		
Kisatchie National Forest			2	Martin and Smith 1991
—all species ≥12.7 cm d.b.h.	14–29	22		
Shortleaf and loblolly pines	6–10	8		
Oak species	7–19	13		
—all species ≥50.8 cm d.b.h.	8–11	10		
Shortleaf and loblolly pines	5–8	6		
Oak species	3–4	3		
Age of large trees (yrs)[e]				
John de la Howe tract			1	This study
Shortleaf pine	89–205	144		
Loblolly pine	79–189	117		
White oak	82–207	149		
Hickory species[f]	142–207	179		
Post oak	101–216	144		
Southern red oak	64–190	124		
Yellow-poplar	94–194	160		
Scarlet Oak Natural Area			1	This study
Pitch pine	117–163			
Scarlet oak	73–123			
Chestnut oak	66–170			
Great Smoky Mountains National Park (max. age)			--	Blozan 1994
Chestnut oak	347			
White oak	344			
Scarlet oak	165			
Black oak	180			
Pignut hickory	327			
Pitch pine	148			
Table Mountain pine	204			
Virginia pine	135			

Table 2 (metric units)—Standardized table of old-growth attributes for dry and dry-mesic oak-pine forests (continued)

Quantifiable attribute	Range[a]	Mean	Number of stands[b]	References
Age of large trees (yrs)[e] (cont.)				
Chattooga River Watershed				
(max. age)			--	Carlson 1995[g]
Chestnut oak	362			
White oak	348			
Scarlet oak	190			
Black oak	211			
Mockernut hickory	335			
Pitch pine	235			
Shortleaf pine	300			
Virginia pine	108			
Lake Winona Research Natural Area			--	Stahle et al. 1985
Shortleaf pine	108–314			
Roaring Branch Research Natural Area			--	Stahle et al. 1985
Shortleaf pine	133–275			
Hot Springs National Park			--	Stahle et al. 1985
Shortleaf pine	124–247			
Number of 10-cm size classes[h]				
John de la Howe tract			1	This study
Shortleaf pine	8			
Hardwoods	7			
Scarlet Oak Natural Area			2	Delapp and Wentworth[d]
Pitch pine	4			
Hardwoods	4			
Lake Winona Research Natural Area	5		1	Fountain 1991
Roaring Branch Research Natural Area			2	Fountain and Sweeney 1985
Shortleaf pine	6			
Hardwoods	4			
Kisatchie National Forest			2	Martin and Smith 1991
Shortleaf and loblolly pines	7			
Hardwoods	5			
D.b.h. of large trees (cm)[e]				
John de la Howe tract			1	This study
Shortleaf pine	28	81		
Loblolly pine	30	99		
White oak	30	84		
Hickory species[g]	25	58		
Post oak	20	48		
Southern red oak	30	81		
Yellow-poplar	30	79		
Roaring Branch Research Natural Area			1	Stahle et al. 1985
Shortleaf pine	36	66		
Standing coarse woody debris (no./ha)				
John de la Howe tract			1	This study
Snags ≥10 cm d.b.h.	37	170		
Snags ≥50.8 cm d.b.h.	5	40		

Table 2 (metric units)—Standardized table of old-growth attributes for dry and dry-mesic oak-pine forests (continued)

Quantifiable attribute	Range[a]	Mean	Number of stands[b]	References
Standing coarse woody debris (no./ha) (continued)				
Hot Springs National Park[i]			3	Johnson and Schnell 1985
(mass only—metric tons/ha)				
Snags ≥7.6 cm d.b.h.	4.3	29.3		
Downed coarse woody debris				
John de la Howe tract			1	This study
Volume (m^3/ha)	52	177		
Mass (metric tons/ha)	16.6	56.9		
Hot Springs National Park[i]	2.0	9.4		
Tree canopy structure				
John de la Howe tract			1	This study
Number of canopy layers (1–3)	2–3			
Percent canopy in gaps	24–80	37		
Mean gap size[j] (hectares)	.001–.204	.024		

[a] For the John de la Howe tract, this represents the range of means from areas showing different degrees of mortality, and applies to all attribute data except age, diameter, and gap size.

[b] Number of stands included (may not equal number of citations).

[c] Oosting did not define the diameter limit for overstory. Density values are for overstory only. If understory is included, density of trees ≥2.5 cm in d.b.h. is 1697, 220, and 380 per hectare for all trees, pines, and oaks, respectively. Basal area values are given for all trees ≥2.5 cm in d.b.h.

[d] Delapp, J.A., and T.R. Wentworth. 1977. Proposed research natural areas in the Southern Appalachian Mountains. 117 p. Unpublished report. On file with: Highlands Biological Station, Highlands, NC 28741.

[e] Includes dominant and codominant trees that comprise the upper canopy. Mean diameter for trees from the John de la Howe tract is the quadratic mean.

[f] Includes mockernut, shagbark [*Carya ovata* (Mill.) K. Koch], and pignut hickory species.

[g] Carlson, P.J. 1995. An assessment of the old-growth forest resource on National Forest System lands in the Chattooga River Watershed. Report to Chattooga Ecosystem Demonstration Management Project, U.S. Department of Agriculture, Forest Service, Region 8, Atlanta, GA. 83 p. On file with: USDA Forest Service, Southern Region, 1720 Peachtree Road, NW, Atlanta, GA 30367.

[h] For inclusion, 1 percent of all trees must be present within a size class—size classes start at 10 cm.

[i] Average across three stands: (1) stand dominated by medium to large, actively growing shortleaf, (2) a "decadent" old-growth shortleaf-dominated stand, and (3) an old-growth oak-hickory stand with a few large shortleaf pines.

[j] Refers to canopy gaps ≤.4 ha in size. Gaps exceeding .4 ha were variable sized patches of extensive pine mortality that accounted for 58 percent of the total gap area.

Living Tree Component

Size structure—Density of trees ≥4 inches (10 cm) in d.b.h. was similar for JDLH and two Ouachita Mountain sites but varied greatly across the range of sites given in table 2. Differences in density may be related to disturbance history and age, as well as differences in diameter classes used to describe the stands. Highest values were found in the Hot Springs NP in Arkansas and lowest in the Kisatchie National Forest of the Gulf Coastal Plain. The proportion of yellow pines also varied greatly. The Lake Winona Research Natural Area contained the highest density of pines and comprised 90 percent of stand basal area and, therefore, can't be considered "oak-pine." It is included here because it is unique and includes dry and dry-mesic sites. Density of large oaks and pines [≥20 inches (51 cm) in d.b.h.] was similar for the JDLH and Kisatchie National Forest and exceeded values from two of the Ouachita Mountain sites.

Basal area was greater than 100 feet^2 per acre (23 m^2 per hectare) for JDLH, Duke Forest, Scarlet Oak Natural Area, and Lake Winona Research Natural Area (table 2). As with density, basal area of large trees was almost identical for JDLH and Kisatchie National Forest. The proportion of basal area in species other than pine or oak was highest for JDLH. Here, hickories accounted for 10 percent of the basal area, followed by yellow-poplar, red maple, and sourwood. The high end of the range for JDLH [150 feet^2 per acre (34 m^2 per hectare)] actually reflects stand-wide basal area before significant pine mortality. This finding resulted when recently dead pines were included in (live) basal area calculations from an area of high pine mortality where values exceeded 150. The high basal area may be due to relatively mesic conditions at JDLH compared to typical dry and dry-mesic sites, since just over half the JDLH was classified intermediate, and the remainder, subxeric.

Maximum diameter-at-breast-height values of dominant and codominant trees is limited to JDLH and Roaring Branch Research Natural Area (table 2). Mean "large tree" diameter at breast height for shortleaf was the same for both sites, but Stahle et al. (1985) sampled trees to obtain long tree ring chronologies, and, hence, these data may overestimate mean diameter at breast height. The largest tree sampled at JDLH was a 39-inch (99-cm) d.b.h. loblolly pine. The largest shortleaf was 32 inches (81 cm) [shortleaf trees exceeding 32 inches (81 cm) were present in the stand but not in sample plots]. The largest hardwoods were white oak [33 inches (84 cm)], southern red oak [32 inches (81 cm)], and yellow-poplar [31 inches (79 cm)].

Detailed diameter-at-breast-height distributions were available for JDLH and Lake Winona Research Natural Area. Total stem distribution at Lake Winona Research Natural Area was reverse-J (q = 1.1), typical of a balanced uneven-aged system (Fountain 1991). However, distribution of pines did not follow a normal or reverse-J distribution, which Fountain suggested resulted from major disturbances. Total stem diameter-at-breast-height distribution for JDLH also followed a reverse-J curve (q = 1.6). Since the idealized reverse-J distribution approximates a negative exponential series, a straight line results when the logarithm of density is plotted against diameter class (DeLiocourt 1898, Meyer 1952, Leak 1964). Implicit in this relationship is a constant percentage loss with each increase in diameter. Diameter distributions in many old or old-growth forests more closely fit the form of the rotated sigmoid curve than the more commonly expected negative exponential form (Goff and West 1975, Schmalzer 1988). When plotted with log (10) of density, the diameter-at-breast-height distribution of total stems on JDLH approximates the rotated sigmoid curve (fig. 1). This pattern typically indicates high mortality for both understory and oldest overstory trees, with little mortality in actively growing canopy trees, which results in the flat portion of the curve (Goff and West 1975). This curve may shift to a straight line as more pines die (see "hardwoods only" in figure 1).

Regardless of the specific form of the reverse-J distribution, the single curve is the result of a combination of species curves. Peak density of individual species curves is expressed at different points along the diameter range (Hough 1932), which, in turn, is determined by a number of factors. Spatial and temporal variation in disturbance are two of those factors. The result is patches of different size and age, which support species with different light and space requirements.

Hardwood-dominated forests, examples of the uneven-aged, "steady state" phase, have been described by Peet and Christensen (1987) as a mosaic of even-aged patches of various sizes and ages. Within each gap or patch, the early phases of forest development (establishment, thinning, and transition) take place. This process of maintaining the composition and uneven-aged condition through time is applicable to oak-pine types only if sufficient canopy and forest floor disturbance occurs periodically to establish patches of oak and pine species. The development stage exemplified by JDLH could be described as the transition phase (Peet and Christensen 1987) or "understory reinitiation" phase (Oliver 1981), which precedes the "old growth" phase, respectively. An alternative view is that the JDLH stand, where pines and hardwoods have persisted for 200 years, represents an ephemeral old-growth stage. The change in composition and structure of the JDLH stand discussed above and shown in figure 1 illustrates the temporal nature of old-growth oak-pine. Although it may be temporal on a given site, it is maintained on the broader landscape by disturbances distributed over space and time.

Age structure—Age ranges or maximum ages, or both, are presented for several areas in table 2. In the Great Smoky

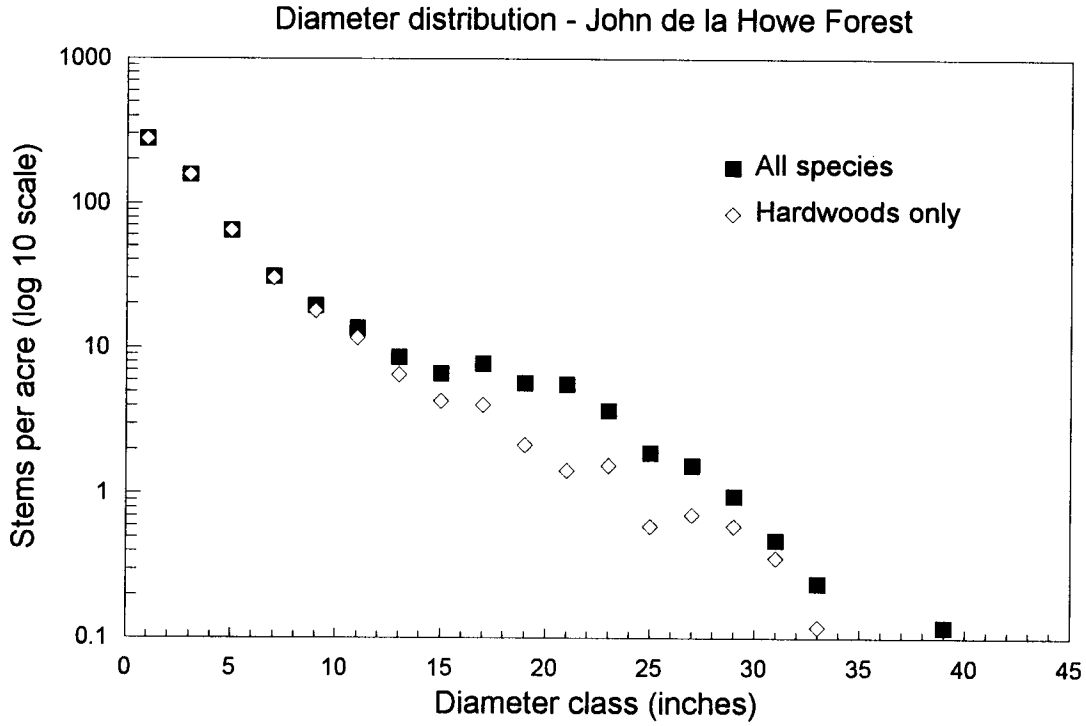

Figure 1—Diameter distribution for hardwoods and all species (hardwood and pines). Data is from the John de la Howe Tract, McCormick County, South Carolina. Stems per acre (log 10 transformation) versus diameter [2-inch (5-cm) diameter classes].

Mountains NP, white and chestnut oaks and pignut hickory were the oldest oak-pine species exceeding 300 years, whereas pitch and Table Mountain pines exceeded 200 years. Shortleaf pine exceeded 300 years in the Ouachita Mountains (Stahle et al. 1985) and shortleaf, white oak, post oak, and hickories exceeded 200 years at JDLH. It is noteworthy that shortleaf and several oaks (especially white oak) have been observed to respond to crown release at 180 years old and that the maximum age of black and scarlet oaks in the Southern Appalachians exceeds that commonly observed for these species (see footnote 7).

The uneven-aged structure of stands at JDLH and the Ouachita Mountains, described in the previous section, is also supported by age class distributions (Stahle et al. 1985). Three Ouachita Mountain old-growth forests contained shortleaf pine in several age classes of 100 years or greater. Similar observations were made for this species at JDLH (fig. 2). White and post oaks, shortleaf and loblolly pines, and hickories were found in most age classes, and there were also a few old southern red oak and yellow-poplar.

Loblolly was more common than shortleaf in age classes <150 years at JDLH. Two distinct groups of white oak were observed. The youngest group ranged from 75 to 100 years and varied in size from 5 to 20 inches (12.7 to 50.8 cm) in d.b.h., whereas the older group ranged from 140 to 200 years and 17 to 33 inches (43.2 to 83.8 cm) in d.b.h. Most other species, including red maple, red oaks, and most yellow-poplar sampled, were generally less than 100 years old. With the exception of pines, very few individuals were in the 100- to 140-age class. The presence of more mesic and fire-sensitive species like red maple ≤ 100 years in age suggests that fire may have affected this stand before the late 1800's. Age distributions of other species suggest scattered disturbance of sufficient size to result in regeneration of pine and other intolerant species over the past 200 years.

Canopy structure—In most old-growth oak-pine forests, there are two to three distinct canopy layers, in addition to an herbaceous layer (table 2). Typically, there is an ericaceous shrub layer dominated by mountain laurel, blueberry, or huckleberry; a midstory layer with variable amounts of blackgum, dogwood, sourwood, Florida maple, and eastern hophornbeam; and the dominant canopy layer.

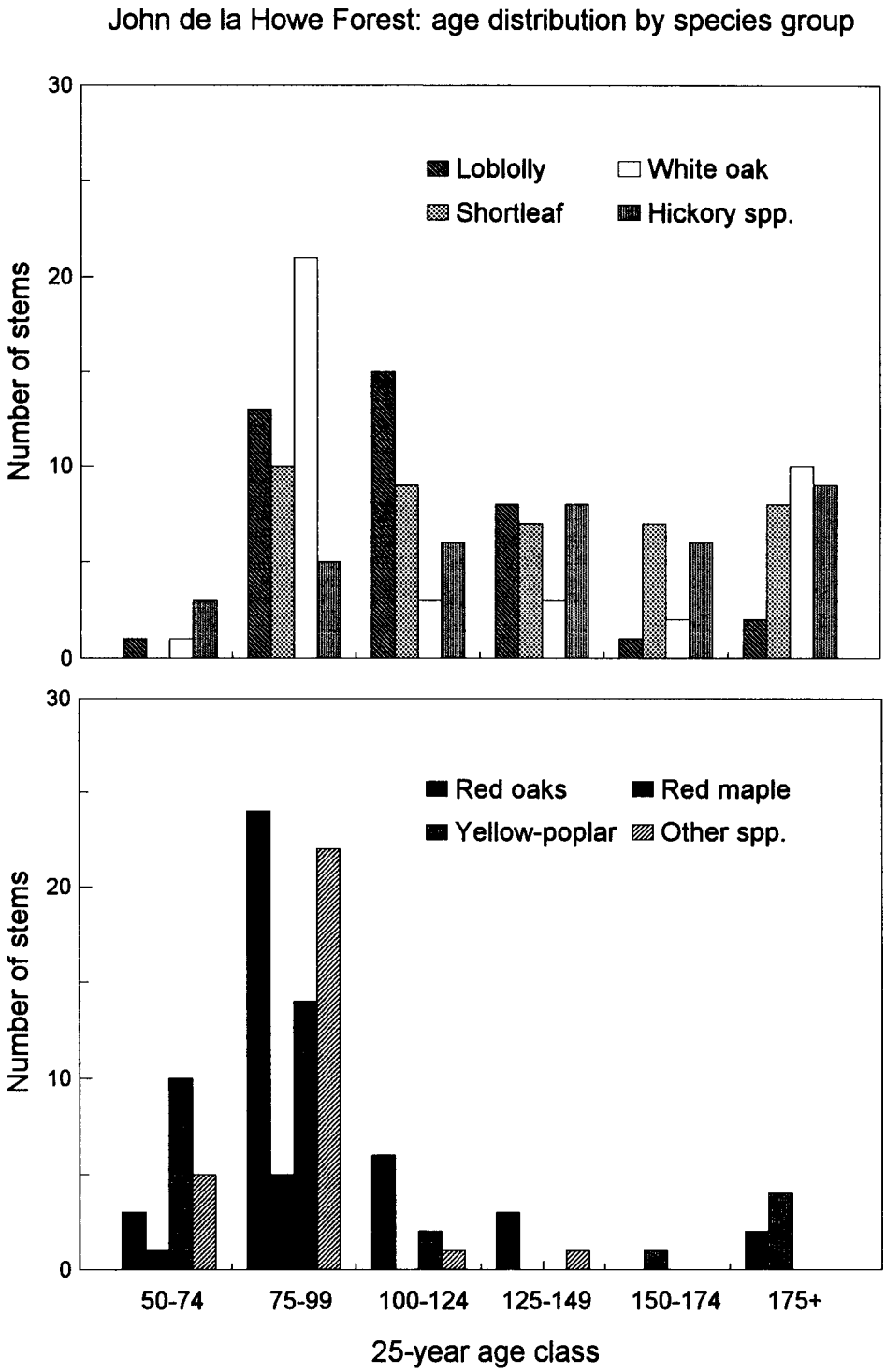

Figure 2—Age class distribution for major species from the John de la Howe Tract, McCormick County, South Carolina.

Height information is lacking. The mean height of dominant hardwoods and pines in the JDLH stand was 100 and 110 feet (30.5 and 34.4 m), respectively. The mean height of midstory species (hardwoods only) was 48 feet (14.6 m). The understory structure and composition in old-growth oak-pine have likely been impacted by 20th-century fire suppression as evidenced by a greater presence of mesic species (Tucker 1991).

The age structure of trees in a forest is the sum of the age structures in the mosaic of patches of the forest, and descriptions of the mosaic may provide more information about the dynamics of the system than an overall forest assessment (Harper 1977). Information on canopy gaps is available only for JDLH (table 2). Mortality patterns or distribution of canopy gaps has been described previously by White and Lloyd (1995). They collected data at four levels of mortality defined as canopy openness or percent of canopy in gaps: (1) low, <25 percent canopy gaps; (2) intermediate, 25 to 50 percent canopy gaps; (3) high-old, >50 percent canopy gaps formed 3 or more years prior; and (4) high-recent, >50 percent in canopy gaps occurring within the past 1 to 2 years. In the areas of low and medium mortality, the canopy is characterized as relatively continuous, broken by various sized canopy gaps, and generally <0.3 acres (.12 ha), averaging 0.06 per acre (.024 per hectare) [58 feet (17.7 m) in diameter]. Most mortality is in pine; 23 percent is in hardwoods, and 15 percent is in pines and hardwoods combined. The range and mean gap size found at JDLH on low-to-medium mortality areas was similar to that found by Clinton et al. (1993) in a mature Southern Appalachian mixed oak forest. In the high-mortality areas (recent and old), overstory canopy openness ranged from 60 to 80 percent, with open patches from 0.5 to 10 acres (.2 to 4.0 ha). Almost all mortality was due to shortleaf and loblolly pines. Because pine mortality occurred at different times in the life of the stand and because variable amounts of hardwoods were present during pine mortality, the size and age structure within gaps varies across the stand.

Dead Tree Component: Coarse Woody Debris

Across the gradient of canopy openness (mortality) described for JDLH, certain old-growth characteristics vary greatly. Density of standing coarse woody debris (CWD) or snags ≥4 inches (10 cm) in d.b.h. ranged from about 15 per acre (37 per hectare) in the areas of low-to-medium mortality to 70 per acre (170 per hectare) in the areas of high-recent mortality (table 2). In Kentucky, McComb and Muller (1983) reported 14 to 32 snags [≥4 inches (10 cm) in d.b.h.] per acre (35 to 79 per hectare) in old-growth beech (*Fagus grandifolia* Ehrh.) and chestnut oak forests, respectively. Sabin (1991) reported 11 snags per acre (27 per hectare) across a range of 20- to 60-year-old South Carolina Piedmont forest types. The density of large snags [≥20 inches (50.8 cm) in d.b.h.] averaged 8 per acre (20 per hectare) at JDLH, exceeding that described for old-growth and second-growth mixed mesophytic forests in Kentucky (McComb and Muller 1983). The only other snag data for old-growth oak-pine is in terms of mass rather than density (Hot Springs NP) (Johnson and Schnell 1985) and, therefore, are not comparable to those reported for JDLH.

The pattern for JDLH snags also applies to downed CWD, except that the high-recent mortality area currently has relatively low quantities. In the high-recent mortality area, most of the dead pine is still standing in contrast to high-old mortality areas. Values of 25 tons per acre (57 metric tons per hectare) in the high-old mortality class are higher than the 8 to 11 tons per acre (18 to 25 metric tons per hectare) in old-growth mixed oak-hardwood forests of the Eastern United States (Lang and Forman 1978, MacMillan 1981, Harmon et al. 1986, Muller and Liu 1991), but less than half of that reported for mature uneven-aged pine on the South Carolina Coastal Plain following Hurricane Hugo (Myers et al. 1993). Coarse woody debris mass for Hot Springs NP (Johnson and Schnell 1985) is much smaller than that for JDLH. Inputs of CWD from broad-scale disturbances, such as insect-related mortality and hurricanes, represent large but infrequent pulsed inputs.

Coarse woody debris in the low-to-medium mortality areas correspond to the range for eastern old-growth oak forests listed above. This information, coupled with gap information described earlier, implies that disturbance patterns and associated effects that predominate in low-to-medium mortality areas are similar to those found in other mature or old-growth forests in the East. This is temporary, however, given that additional pine mortality is expected in these areas in the future. As pines succumb to southern pine beetle, littleleaf disease, and pathogens, a further shift to oaks and other hardwoods will occur. Without forest floor disturbance such as fire, pines will become minor components of this stand in the future.

In the Southern Appalachians, snags, downed CWD, and other old-growth characteristics, such as pit and mound microtopography, may be reduced or lacking in the drier, upland old-growth types (see footnote 7). The deviation from the classic old-growth characteristics attributed to cove hardwood stands is most evident on xeric and subxeric sites where disturbances (especially fire) are more frequent and intense.

Forest Dynamics and Ecosystem Function

Presettlement Disturbance Regimes

A review of paleoecological and other literature pertinent to the history of the oak-pine forest type (White and Lloyd 1995) revealed three important points: (1) oaks and pines have been components of the eastern deciduous forest for thousands of years, (2) shifts in their relative abundance have been related to climate changes and to fire used by aboriginal people in the past 10,000 years, and (3) oaks and pines that dominate the dry and dry-mesic oak-pine type require disturbance to maintain their dominance. Buckner (1989) described the pine-hardwood type as a "mid-seral stage that is ephemeral on a given site and is maintained in a changing landscape mosaic where scattered disturbances reinitiate succession in a stochastic manner." In this paper, we have referred to the old-growth oak-pine type as resembling the transition or understory reinitiation phase of forest development or the mid-to-late phase of plant succession. It is, indeed, ephemeral on a given site unless sufficient disturbance occurs. It is important to acknowledge, however, that multiple ecological outcomes are possible for comparable sites (Oliver 1981, Sprugel 1991). The "outcome" depends on the nature of the disturbance and its interaction with the biotic and abiotic components of a given site.

Disturbance continuum—A greater understanding of presettlement disturbance and species response to disturbance should clarify management options for recognizing, creating, and maintaining old-growth types on the landscape. Our understanding of these factors, however, is limited. Natural forest disturbance in the form of hurricanes, tornadoes, ice and wind storms, drought, insect- and pathogen-induced mortality, and lightning fire represent the low end of a disturbance continuum. The presettlement human disturbance regime superimposed on the natural disturbance regime represents the upper end of this continuum in which eastern forests have developed. Although presettlement disturbance dynamics are much more complex than the above description implies, distinguishing endpoints of a disturbance continuum may represent a starting point for improving our understanding. With increased urbanization in the Eastern United States, accompanied by increased demands on Federal land, management options are more limited (e.g., restrictions on burning to minimize smoke). However, if we know more about the endpoints of this disturbance continuum, managers, decision-makers, and the public will be in a better position to make decisions as to the assemblage of vegetation types we seek to manage or restore.

The relative impact of nonhuman and human disturbances varies across regions. Lightning fires are more prevalent in the Coastal Plain and Ozark region (Komarek 1964, 1968). Hurricanes are more common in the Coastal Plain than in inland areas, whereas tornadoes are common events in the Ouachitas and Ozarks (Turner 1935, Foti and Glenn 1991, Tucker 1991). The impact of early human disturbance was likely greater in regions where the frequency and impact of lightning fires were less such as the mountains and Piedmont (Frost 1995). Earlier, we described pyrogenic patches in parts of the Coastal Plain functioning as ignition sources for adjacent communities. Although this situation may apply to other regions (e.g., mountainous regions:xeric ridgetops), it may be less relevant for the Piedmont where moisture gradients are less extreme than in areas with greater topographic relief or areas with more coarse textured soils, or both. Compared to other regions, we have little understanding of the spatial and temporal aspects of presettlement disturbance in the Piedmont.

Fire frequency—Various estimates of fire frequency have been given for different physiographic regions earlier in this paper, but the variability associated with these estimates is often large (Christensen 1988b). Christensen suggests that this variability is an essential component in maintaining fire-prone ecosystems by citing the importance of chance variations in determining structure, composition, and distribution of different ecosystems. In the Ouachitas, fire-return intervals varied from 7.25 to 32 years depending on site and period of time examined (Johnson and Schnell 1985, Foti and Glenn 1991). Fire-return intervals were estimated to be 5 to 15 years for shortleaf pine-oak-hickory of the Louisiana Coastal Plain (Martin and Smith 1991). Frost (1995) describes presettlement fire frequency for the Southeastern United States as being 1 to 3 years for the southern part of the Atlantic Coastal Plain and lower Gulf Coastal Plain; 4 to 6 years for the Coastal Plain of Virginia and upper North Carolina, the Piedmont, and the middle and upper parts of the Gulf Coastal Plain; 7 to 12 years in northern Alabama and part of the Appalachians, foothills, and upper Piedmont [300 to 3,000 feet (92 to 915 m) in elevation]; and 12 or more in the high mountains (6,000 feet or 1829 m) and wet swamps. Nowacki (1995) estimated the presettlement disturbance frequency (includes fire, storms, drought, disease) in the Valley and Ridge province of Pennsylvania to be 21 years.

Patch size—Successful establishment of pines, and to a lesser degree oaks, depends on ground fires (Christensen 1981, Abrams 1992, Van Lear and Watt 1993). Establishment of these species as canopy dominants, however, depends on the amount of canopy disturbance. In the Gulf Coastal Plain, small-to-intermediate-sized gaps are thought to be required for maintaining oak-pine and related types (Harcombe and Marks 1978, Golden 1979, Martin and Smith 1991). In the Ouachitas, large-scale disturbances were found to be the origin of three "virgin" shortleaf pine stands (Turner 1935). Turner suggested tornadoes were responsible, but it could have been a combination of other

canopy disturbance and fire as well. Carlson (see footnote 7) described canopy-age classes exceeding 150 years across the Southern Appalachians, suggesting region-wide, prelogging disturbances. These were common on upper slopes and ridges currently occupied by oaks or pines, or both, and were assessed as relatively large-scale disturbances.[11] At JDLH, a range of canopy gap sizes resulted from mostly pine mortality, but pine regeneration was considered unlikely without fire or other forest floor disturbance (White and Lloyd 1995). If pine regeneration is present, canopy disturbances resulting in 0.1 acre (.04 ha) or larger openings [74 feet (22.6 m) in diameter] are sufficient for establishment of yellow pines in the Piedmont (Waldrop 1991, Perry and Waldrop 1995). Beyond a certain minimum gap size, fire is crucial for oak-pine maintenance. Consequently, a wide range of disturbance patch sizes may result in pine establishment if forest floor disturbance is sufficient.

Ecological Processes

Early concepts of old-growth forests were based on the steady-state, equilibrium view of forest dynamics, but several authors have presented alternative views of forest succession or have acknowledged the role of a wide range of disturbances in forest development (Egler 1954, Spurr and Barnes 1973, Harper 1977, Oliver 1981, Denslow 1985, Pickett and White 1985, Glitzenstein et al. 1986, Christensen 1988b, Platt and Schwartz 1990, Sprugel 1991). The dry and dry-mesic oak-pine type and some other old-growth types do not adhere to steady-state dynamics; rather, disturbance by fire or other agents is required for its maintenance on the landscape. Various sized patches of various ages need to be reestablished on the landscape to allow forests to continually recruit into oak-pine old growth. If not, oak-pine old growth will be lost over much of its former range.

Wind, fire, insects, and plant pathogens commonly impact ecological processes in old-growth oak-pine forests, and they often interact adding to ecosystem complexity (Jackson 1968). Broad-scale wind and insect disturbance can produce large, pulsed inputs of CWD. If ignition occurs when fuel loads are high and conditions are conducive to fire, severe fires can occur. This can significantly impact future composition of the forest and affect both short- and long-term quantities of nutrients and organic matter on the site even though fires rarely consume all CWD. In the absence of fire, decay proceeds, rendering CWD less conducive to supporting fire. This large-pulsed input of CWD may represent habitat for many organisms and contributes much organic matter to the site. Coarse woody debris retains water and serves as both nutrient source and sink during the decomposition process, playing a critical role in water and nutrient cycles. With relatively frequent ground fires, CWD may have been a much less significant component of old-growth dry and dry-mesic oak-pine during presettlement times.

The dynamics of CWD inputs and the long-term effects on various ecosystem processes are not well understood (Van Lear 1996, Waldrop 1996). We have provided an example of large-pulsed inputs of CWD due to stand-wide pine mortality. In simulation studies of CWD dynamics for mixed hardwood stands growing on xeric and mesic sites in Tennessee, CWD loads increased from age 32 to 90 followed by a gradual decrease through age 200 (Waldrop 1996). Waldrop demonstrated that whereas CWD inputs were much higher on the mesic site than on the xeric site, CWD loads were similar when a slightly slower decomposition rate was simulated for the xeric site. Inputs from natural disturbance, such as insect-related pine mortality, was not included in the simulation but might have a significant impact on long-term CWD dynamics.

If a management objective is to maintain an old-growth forest type that contains a significant pine component, it is important to consider the effect of insects and pathogens on the composition and structure of old growth (Haack and Byler 1993), as well as the interaction of old growth with surrounding stands. In the Southeastern United States, the impact from southern pine beetle is less in mixed pine-hardwood stands than in pure pine stands because pine continuity is interrupted by hardwoods (Belanger et al. 1986, Showalter and Turchin 1993). The management challenge is to allow natural disturbance in old-growth forests, while minimizing losses in surrounding stands. Separating intensively managed stands (high pine component, disease risk dependent on stand conditions) from old-growth oak-pine stands (moderate pine component, moderate-to-high disease risk) with pure hardwood stands or with mixed pine-hardwood stands may reduce disease-caused losses (White and Lloyd 1995).

Postsettlement changes—The most dramatic postsettlement change to eastern landscapes was conversion of forests to agricultural fields, especially widespread in the Piedmont and Coastal Plain. Few areas were untouched by the plow, and soil erosion was extensive in some areas, resulting in significant changes to site productivity and biological potential. Other major postsettlement changes included the shift to woodland grazing by cattle and hogs at the time of settlement (shift from native grazers such as bison and elk), the cessation of woodland grazing by 1900, and 20th-century fire suppression. These changes likely contribute to differences in composition and structure between presettlement and current old-growth forests (White and White 1996). It is important to acknowledge the impact of

[11] Personal communication. 1995. Paul J. Carlson, Forester, 162 Goshen Road, Franklin, NC 28734.

these disturbances on the distribution and composition of current and future old-growth forests.

Without fire, species less tolerant of fire, such as red maple, Florida maple, and eastern hophornbeam, increase in abundance. Loblolly pine and other mesic species have been described as "creeping" upslope due to lack of fire. This may also apply to white pine in the mountains. Plant diversity in most dry and dry-mesic oak-pine forests is relatively low, especially since many of these types have understories dominated by one or two layers of ericaceous species. Understory diversity in presettlement oak-pine types may have been greater than current stands (Harper 1943, Frost 1993). Frost described presettlement oak-pine types of the upper Coastal Plain as woodland fire types with a species-rich herb layer. Harper described the shortleaf pine-oak forests of the dry uplands of Alabama as having lightning fires every 10 years and having a "good deal of grassy undergrowth," suggesting a potentially more diverse herbaceous layer than is currently seen. How prevalent this condition was in other regions is unknown. Logging disturbance may result in oak- and pine-dominated forests, but will not create the diverse, pyrogenic understories Frost refers to.

When Does Old Growth Begin?

Defining old growth demands the following questions be addressed: (1) when is a forest considered old growth, and (2) what is the minimum area needed to maintain old-growth forests? The first question is partially clarified by the generic definition of old growth, as drafted by the National Old-Growth Task Group in 1989:

> Old-growth forests are ecosystems distinguished by old trees and related structural attributes. Old-growth encompasses the later stages of stand development that typically differ from earlier stages in a variety of characteristics which may include tree size, accumulations of large dead woody material, number of canopy layers, species composition, and ecosystem function.

No single characteristic, such as age or size, can define old growth. To illustrate this, consider a 125- to 150-year-old oak-shortleaf pine stand that contains many of the structural and compositional features of old growth but may not exhibit accumulation of dead woody material. The first significant CWD accumulation in this stand could have resulted from a severe southern pine beetle/littleleaf epidemic that essentially eliminated the pine component. How does this disturbance impact the old-growth status of this stand? Can it be defined as old growth because snags and downed CWD are "suddenly" present in the stand, or is it no longer old growth because it lost the old pine component? We might consider that it was old growth before and after the disturbance, depending on other stand factors, and that we have witnessed an abrupt compositional change in the old-growth stand from oak-pine to oak.

We consider oak-pine stands that have minimal evidence of postsettlement human disturbance and contain pines exceeding 100 to 125 years to be approaching, if not already functioning as, old growth. For Virginia pine on most sites, 100 years represents old age. For shortleaf pine on good sites, this may be too young to be considered old growth. Hepting (1971) specifies 80 years for maturity of Virginia pine, 100 years for loblolly and pitch pines, and 120 years for shortleaf pine. In general, we recommend that most stands with pines and oaks that exceed 100 to 125 years and have experienced little recent human disturbance, be considered to be in the early stages of old growth. Impacts from disturbance, site quality, growth form of the oldest cohort, age and size structure, composition, and accumulation of dead woody material must all be considered when characterizing the old-growth status of forests.

Addressing the second question regarding the area required to maintain old growth is more complex. When large-scale disturbances are associated with a forest type, the area of land required to maintain that type on the landscape increases accordingly (Shugart 1984, Busing and White 1993). Also, the probability that a stand will be subjected to natural catastrophes increases with stand age (Oliver 1981). Rather than focusing on the size of a stand, the entire landscape should be emphasized, especially with ephemeral forest types. Whether an old-growth oak-pine stand is 5 or 100 acres (2 or 40 ha), it matters little if it is the only old-growth patch within some larger area [e.g., 5,000 to 20,000 acres (2000 to 9000 ha)]. To ensure that old-growth forests are maintained on the landscape, a mosaic of relatively large, contiguous blocks of old-growth forests among blocks of younger forests are needed. Managing for this mosaic better ensures that the structural, functional, and compositional diversity of forested ecosystems will be maintained (Harris 1984, Franklin and Forman 1987, Franklin 1988). Since many public land managers manage forests for multiple values, strategies to maintain old-growth forests and to produce other sustainable commodities should be integrated.

Information Gaps

Gaps in our knowledge about old-growth oak-pine result from the fact that few of these stands exist and even fewer have been studied. There is a need to locate, document, and describe existing stands and their old-growth characteristics. In addition, more work is needed to document threatened, endangered, and sensitive plant and animal species that are associated (currently or historically) with this forest type. Information is also lacking on presettlement forest conditions, spatial and temporal scales of nonhuman disturbances, and the distribution of Native American

populations and their impact on presettlement landscapes. The availability of information varies with the region. In some cases, information on Native American populations and activities may be well known, but this information has not been put into a larger spatial and temporal context.

Representative Old-Growth Forests

Dry and dry-mesic old-growth oak-pine forests verified directly or indirectly by the authors

- Hot Springs National Park, Arkansas
- Lake Winona Scenic Area, Ouachita National Forest, Arkansas
- Roaring Branch Research Natural Area, Ouachita National Forest, Arkansas
- Bobs Creek Shortleaf and Old Shortleaf Slope on the Kisatchie National Forest, Louisiana
- Great Smoky Mountains National Park, North Carolina and Tennessee
- Linville Gorge, Pisgah National Forest, North Carolina
- Scarlet Oak Natural Area, Pisgah National Forest, North Carolina
- John de la Howe Tract, McCormick County, South Carolina

Other dry and dry-mesic old-growth oak-pine forests not verified by the authors

- Magazine Mountain, Logan County, Arkansas
- Marshall Forest Preserve, west of Rome, Georgia
- Ack Tract, along Piney River, Texas County, Missouri
- Big Spring Towering Pines, Carter County, Missouri
- Hickory Canyons Natural Area, Ste. Genevieve County, Missouri
- Meramec Upland Forest Natural Area, Meramec State Park, Missouri
- Mudlick Mountain Natural Area, Sam A. Baker State Park, Missouri
- Bienville Pines Scenic Area, Bienville National Forest, Mississippi
- McCurtain County Wilderness Area, McCurtain County, Oklahoma
- Martins Hill, Buchanan State Forest, Bedford County, Pennsylvania
- Lennox Woods Preserve, Red River County, Texas

Acknowledgment

We would like to thank John Haney, Carol Perry, Shawna Reid, and Jane Thompson for field assistance at John de la Howe. We would also like to thank the John de la Howe staff for their cooperation. Critical reviews of the manuscript were provided by Peter Kapeluck, Greg Nowacki, Jane Thompson, Joan Walker, Tom Waldrop, and Peter White.

Literature Cited

Abrams, Marc D. 1992. Fire and the development of oak forests. Bioscience 42(5):346–353.

Barden, L.S. 1976. Pine reproduction in the Thompson River watershed, North Carolina. J. Elisha Mitchell Soc. 92:110–113.

Barden, L.S. 1997. Historic prairies in the Piedmont of North and South Carolina, USA. Nat. Areas J. 17(2):149–152.

Barden, L.S., and F.W. Woods. 1974. Characteristics of lightning fires in Southern Appalachian forests. P. 345-361 *in* Proc. Tall Timbers Fire Ecology Conf. 13. Tall Timbers Research Station, Tallahassee, FL.

Barden, L.S., and F.W. Woods. 1976. Effects of fire on pine and pine-hardwood forests in the Southern Appalachians. For. Sci. 22(4):399–403.

Barry, J.M. 1980. Natural vegetation of South Carolina. Univ. of South Carolina Press, Columbia, SC. 214 p.

Bartram, William. 1958. Travels. Francis Harper (ed.). Yale Univ. Press, New Haven, CT. 727 p. [First published in 1791]

Belanger, R.P., R.L. Hedden, and F.H. Tainter. 1986. Managing Piedmont forests to reduce losses from the littleleaf disease-southern pine beetle complex. U.S. Dep. Agric. Handb. 649. 19 p.

Blozan, W. 1994. The importance of increment core samples and disturbance history in the evaluation of old growth forests in Great Smoky Mountains National Park. Nat. Areas J. 114(2):141–142.

Bowman, I. 1911. Forest physiography. Wiley, New York. 759 p.

Braun, E.L. 1935. The vegetation of Pine Mountain, Kentucky: an analysis of the influence of soils and slope exposure as determined by geologic structure. Am. Midl. Nat. 16:517–565.

Braun, E.L. 1942. Forests of the Cumberland Mountains. Ecol. Monogr. 12(4):415–447.

Braun, E.L. 1950. Deciduous forests of Eastern North America. Blakiston Co., Philadelphia. 596 p.

Breden, T.F. 1989. A preliminary natural community classification for New Jersey. *In* New Jersey's rare and endangered plants and animals, Karlin, E.F. (ed.). Inst. Environ. Stud., Ramapo Coll., Mahwah, NJ. 280 p.

Brender, E.V. 1974. Impact of past land use on the lower Piedmont forest. J. For. 72:34–36.

Buckner, E. 1989. Evolution of forest types in the Southeast. P. 27-33 *in* Proc. pine-hardwood mixtures: a symp. of management and ecology of the type, Waldrop, T.A. (ed.). U.S. Dep. Agric. For. Serv. Gen. Tech. Rep. SE-58.

Buell, M.F., and J.E. Cantlon. 1950. A study of two communities of the New Jersey Pine Barrens and a comparison of methods. Ecology 31:567–586.

Busing, R.T., and P.S. White. 1993. Effects of area on old growth forest attributes: implications for the equilibrium landscape concept. Landscape Ecol. 8(2):119–126.

Callaway, R.M., E.C. Clebsch, and P.S. White. 1987. A multivariate analysis of forest communities in the western Great Smoky Mountains National Park. Am. Midl. Nat. 118(1):107–120.

Christensen, N.L. 1981. Fire regimes in southeastern ecosystems. P. 112-136 *in* Fire regimes and ecosystem properties, Mooney, H.A., T.M. Bonicksen, N.L. Christensen, J.E. Lotan, and W.A. Reiners (eds.). U.S. Dep. Agric. For. Serv. Gen. Tech. Rep. WO-26.

Christensen, N.L. 1988a. Vegetation of the southeastern Coastal Plain. P. 315-363 *in* North American terrestrial vegetation, Barbour, M.G., and W.D. Billings (eds.). Cambridge Univ. Press, Cambridge.

Christensen, N.L. 1988b. Succession and natural disturbance: paradigms, problems, and preservation of natural ecosystems. P. 62-86 *in* Ecosystem management for parks and wilderness, Agee, J.K., and D.R. Johnson (eds.). Univ. of Washington Press, Seattle, WA.

Clark, Thomas D. 1973. South Carolina: the grand tour, 1780-1865. Univ. of South Carolina Press, Columbia, SC. 342 p.

Clarkson, R.B. 1966. The vascular flora of the Monongahela National Forest, West Virginia. Castanea 31(1):1–119.

Clinton, B.D., L.R. Boring, and W.T. Swank. 1993. Canopy gap characteristics and drought influences in oak forests of the Coweeta Basin. Ecology 74(5):1551–1558.

Cooper, A.W. 1963. A survey of the vegetation of the Toxaway River Gorge with some remarks about early botanical explorations and an annotated list of the vascular plants of the gorge area. J. Elisha Mitchell Soc. 79(1):1–21.

Crandall, A.R. 1876. Report on the timber growth of Greenup, Carter, Boyd and Lawrence counties in eastern Kentucky. Kentucky Geol. Surv. 1:9–26.

Dale, E.F., and M.R. Watts. 1980. Vegetation of Hot Springs National Park, Arkansas: final report for the southwest region, National Park Service. U.S. Dep. Inter. CX-70299001. 85 p.

Delcourt, H.R. 1976. Presettlement vegetation of the north of Red River land district, Louisiana. Castanea 41:122–139.

Delcourt, P.A., and H.R. Delcourt. 1987. Long-term forest dynamics of the temperate zone. Ecol. Stud. 63. Springer-Verlag, New York. 450 p.

DeLiocourt, F. 1898. De l'amenagement des sapinieres. P. 346–409 *in* Bull. Soc. Forest Franch-Fonte Belforet, Besancon.

Denslow, J.S. 1985. Disturbance-mediated coexistence of species. P. 307-321 *in* The ecology of natural disturbance and patch dynamics, Pickett, S.T.A., and P.S. White (eds.). Academic Press, Orlando, FL.

DeVivo, M.S. 1991. Indian use of fire and land clearance in the Southern Appalachians. P. 306-310 *in* Fire and the environment: ecological and cultured perspectives: Proc. int. symp., Nodvin, S.C., and T.A. Waldrop (eds.). U.S. Dep. Agric. For. Serv. Gen. Tech. Rep. SE-69.

Drayton, William. 1784. William Drayton's journal of a 1784 tour of the South Carolina backcountry. Krawczynski, Keith (ed.). South Carolina Hist. Mag. 97(3):183–205.

Dumond, D.M. 1970. Floristic and vegetational survey of the Chattooga River Gorge. Castanea 35:201–244.

Egler, F. E. 1954. Vegetation science concepts. I. Initial floristic composition - a factor in old-field vegetation development. Vegetatio. 4:412–417.

Eyre, F.H. (ed.). 1980. Forest cover types of the United States and Canada. Soc. Am. For., Washington, DC. 148 p.

Fenneman, N.M. 1938. Physiography of Eastern United States. McGraw Hill, New York. 714 p.

Foti, T.L., and S.M. Glenn. 1991. The Ouachita Mountain landscape at the time of settlement. P. 49-66 *in* Restoration of old-growth forests in the Interior Highlands of Arkansas and Oklahoma: Proc. Conf., Henderson, D., and L.D. Hedrick (eds.). Winrock Int., Morrilton, AR.

Fountain, M.S. 1991. Tree and non-tree dimensions of an old-growth shortleaf pine stands: Lake Winona Research Natural Area. P. 139-146 *in* Restoration of old-growth forests in the Interior Highlands of Arkansas and Oklahoma: Proc. Conf., Henderson, D., and L.D. Hedrick (eds.). Winrock Int., Morrilton, AR.

Fountain, M.S., and J.M. Sweeney. 1985. Ecological assessment of the Roaring Branch Research Natural Area. U.S. Dep. Agric. For. Serv. Res. Pap. SO-213. 15 p.

Fountain, M.S., and J.M. Sweeney. 1987. Ecological assessment of the Lake Winona Research Natural Area. U.S. Dep. Agric. For. Serv. Res. Pap. SO-235. 14 p.

Fowells, H.A. 1968. Silvics of forest trees of the United States. U.S. Dep. Agric. Handb. 271. 762 p.

Franklin, J.F. 1988. Structural and functional diversity in temperate forests. P. 166-175 *in* Biodiversity, Wilson, E.O. (ed.). Natl. Acad. Press, Washington, DC. 521 p.

Franklin, J.F., and R.T.T. Forman. 1987. Creating landscape patterns by forest cutting: ecological consequences and principles. Landscape Ecol. 1(1):5–18.

Frost, C.C. 1993. Four centuries of changing landscape patterns in the longleaf pine ecosystem. P. 17-44 *in* Proc. 18th Tall Timbers Fire Ecol. Conf., the longleaf pine ecosystem: ecology, restoration, and management, Hermann, S.M. (ed.). Tall Timbers Research Station, Tallahassee, FL.

Frost, C.C. 1995. Presettlement fire regimes in southeastern marshes, peatlands, and swamps. P. 39-60 *in* Proc. 19th Tall Timbers Fire Ecol. Conf., fire in wetlands: a management perspective, Cerulean, S.I., and R.T. Engstrom (eds.). Tall Timbers Research Station, Tallahassee, FL.

Glitzenstein, J.S., P.A. Harcombe, and D.R. Streng. 1986. Disturbance, succession, and maintenance of species diversity in an east Texas forest. Ecol. Monogr. 56:243–258.

Godfrey, M.A. 1980. A Sierra Club naturalists guide to the Piedmont. Sierra Club Books, San Francisco. 498 p.

Goff, F.G., and D. West. 1975. Canopy-understory interaction effects on forest population structure. For. Sci. 21:98–108.

Golden, M.S. 1974. Forest vegetation and site relationships in the central portion of the Great Smoky Mountains National Park. Ph.D. Diss., Univ. of Tennessee, Knoxville, TN. 275 p.

Golden, M.S. 1979. Forest vegetation of the lower Alabama Piedmont. Ecology 60:770–782.

Golden, M.S. 1981. An integrated multivariate analysis of forest communities of the central Great Smoky Mountains. Am. Midl. Nat. 106(1):37–53.

Haack, Robert A., and James W. Byler. 1993. Insects and pathogens: regulators of forest ecosystems. J. For. 91(9):32–37.

Hammond, H. 1883. South Carolina: resources and population, institutions, and industries. State Board of Agric. of South Carolina. Walker, Evans, and Cogswell Print., Charleston, SC. 726 p.

Harcombe, P.A., and P.L. Marks. 1978. The diameter distribution and replacement processes in southeast Texas forests. For. Sci. 24:153–166.

Harmon, M.E., et al. 1986. Ecology of coarse woody debris in temperate ecosystems. Adv. Ecol. Res. 15:133–302.

Harper, J.L. 1977. Population biology of plants. Academic Press, New York. 892 p.

Harper, R.M. 1920. Resources of southern Alabama. Spec. Rep. 11. Geol. Surv. [Location of publisher unknown], AL. 152 p.

Harper, R.M. 1943. Forests of Alabama. Monogr. 10. Univ. of Alabama, Geol. Surv. Wetumpka Printing Co., Wetumpka, AL. 230 p.

Harris, L.D. 1984. The fragmented forest. Univ. of Chicago Press, Chicago. 211 p.

Hepting, G.H. 1971. Diseases of forest and shade trees of the United States. U.S. Dep. Agric. Handb. 386. 656 p.

Hilgard, E.W. 1860. Report of geology and agriculture of the State of Mississippi. Publ. Mississippi Geol. Surv. E. Barksdale, State Printer, Jackson, MS. 391 p.

Hinkle, C.R. 1989. Forest communities of the Cumberland Plateau of Tennessee. J. Tennessee Acad. Sci. 64(3):123–129.

Hodgkins, E.J., M.S. Golden, and W.F. Miller. 1979. Forest habitat regions and types on a photomorphic-physiographic basis: a guide to forest site classification in Alabama and Mississippi. South. Coop Ser. 210. Alabama Agric. Exp. Stn., Auburn, AL. 64 p.

Hough, A.F. 1932. Some diameter distributions in forest stands of northwestern Pennsylvania. Ecology 17:9–28.

Jackson, W.D. 1968. Fire, air, water and earth - an elemental ecology of Tasmania. Proc. Ecol. Soc. Australia 3:9–16.

Jennings, O.E. 1927. Classification of the plant societies of central and western Pennsylvania. Proc. Pennsylvania Acad. Sci. 1:23–55.

Johnson, F.L., and G.D. Schnell. 1985. Wildland fire history and the effect of fire on vegetative communities at Hot Springs National Park, Arkansas: final report, National Park Service. U.S. Dep. Inter. CX-702930034. [Publisher unknown]: Santa Fe, NM. 49 p.

Jones, S.M. 1988. Old-growth forests within the Piedmont of South Carolina. Nat. Areas J. 8(1):31–37.

Kartesz, J.T., and R. Kartesz. 1980. A synonymized checklist of the vascular flora of the United States, Canada, and Greenland. Vol. II: the biota of North America. Univ. of North Carolina Press, Chapel Hill, NC. 498 p.

Komarek, E.V. 1964. The natural history of lightning. P. 139-183 *in* Proc. 3rd Tall Timbers Fire Ecol. Conf., Tall Timbers Research Station, Tallahassee, FL.

Komarek, E.V. 1968. Lightning and lightning fires as ecological forces. P. 169-197 *in* Proc. 8th Tall Timbers Fire Ecol. Conf., Tall Timbers Research Station, Tallahassee, FL.

Kuchler, A.W. 1964. Potential natural vegetation of the conterminous United States. Spec. Publ. 36, Am. Geogr. Soc., New York. 116 p.

Lang, G.E., and R.T.T. Forman. 1978. Detrital dynamics in a mature oak forest: Hutcheson Memorial Forest, New Jersey. Ecology 59:580–595.

Lawson, John. 1967. A new voyage to Carolina. Univ. of North Carolina Press, Chapel Hill, NC. 305 p. [Originally published in 1709]

Leak, W.B. 1964. An expression of diameter distribution for unbalanced unevenaged stands and forests. For. Sci. 10:39–50.

Little, S., and E.B. Moore. 1949. The ecological role of prescribed burns in pine oak forests of southern New Jersey. Ecology 30:223–233.

Little, S., and F. Mergen. 1966. External and internal changes associated with basal-cook formation in pitch and shortleaf pines. For. Sci. 12:268–275.

Logan, John H. 1980. A history of the upper country of South Carolina from the earliest periods to the close of the War of Independence. Vol. 2. Southern Historical Press, Easley, SC. 121 p.

Logan, John H. 1859. A history of the upper country of South Carolina. Vol. 1. S.G. and Courtney and Co., Charleston, SC. 522 p.

Lorimer, C.G. 1985. The role of fire in the perpetuation of oak forests. P. 8-25 *in* Challenges in oak management and utilization, Johnson, J. E. (ed.). Univ. of Wisconsin Ext., Madison, WI.

Lutz, H.J. 1934. Ecological relations in the pitch pine plains of southern New Jersey. Yale Univ. Sch. For. Bull. 38. Yale Univ. Press, New Haven, CT. 80 p.

MacMillan, P.C. 1981. Log decomposition in Donaldson Woods, Spring Mill State Park, Indiana. Am. Midl. Nat. 106:335–344.

Malter, J.L. 1977. The flora of Citico Creek Wilderness Area, Cherokee National Forest, Monroe County, Tennessee. MS Thesis. Univ. of Tennessee, Knoxville, TN. 117 p.

Marks, P.L., and P.A. Harcombe. 1981. Forest vegetation of the Big Thicket, southeast Texas. Ecology 51:287–305.

Martin, D.L., and L.M. Smith. 1991. A survey and description of the natural communities of the Kisatchie NF Winn and Kisatchie districts. Louisiana Dep. Wildl. Fish., Baton Rouge, LA. 372 p.

Martin, W.H. 1971. Forest communities of the Great Valley of east Tennessee and their relationship to soil and topographic properties. Ph.D. Diss., Univ. of Tennessee, Knoxville, TN. 366 p.

Martin, W.H., and C. Shepherd. 1973. Trees and shrubs of Lilly Cornett Woods. Letcher County Kentucky. Castanea 38:327–335.

McComb, W.C., and R.M. Muller. 1983. Snag densities in old-growth and second growth Appalachian forests. J. Wildl. Manage. 47(2):376-382.

McCune, B. 1988. Ecological diversity in North American pines. Am. J. Bot. 75(3):353–368.

McEvoy, T.J., T.L. Sharik, and D.W. Smith. 1980. Vegetation structure of an Appalachian oak forest in southwest Virginia. Am. Midl. Nat. 103(1):96–105.

McIntosh, R.P. 1959. Presence and cover in pitch pine oak stands of the Shawangunk Mountains, New York. Ecology 40(3):482–485.

McNab, W.H., and S.A. Browning. 1993. Preliminary ecological classification of arborescent communities on the Wine Spring Watershed, Nantahala National Forest. P. 213-221 *in* Proc. seventh bienn. south. silvic. res. conf., Brissette, John C. (ed.). U.S. Dep. Agric. For. Serv. Gen. Tech. Rep. SO-93.

Meyer, H.A. 1952. Structure, growth and drain in balanced, unevenaged forests. J. For. 50:85–92.

Mills, Robert. 1826. Statistics of South Carolina. The Reprint Co., Spartanburg, SC. 42 p.

Mohr, C. 1901. Plant life of Alabama. Vol VI. Brown Printing Co., Montgomery, AL. 921 p.

Mowbray, T.B. 1966. Vegetational gradients in the Bearwallow Gorge of the Blue Ridge escarpment. J. Elisha Mitchell Soc. 82:138–149.

Mowbray, T.B., and H.J. Oosting. 1968. Vegetation gradients in relation to environment and phenology in a southern Blue Ridge Gorge. Ecol. Monogr. 38(4):309–343.

Muller, R.N., and Y. Liu. 1991. Coarse woody debris in an old-growth deciduous forest on the Cumberland Plateau, southeastern Kentucky. Canadian J. For. Res. 21:1567–1572.

Myers, R.K., D.H. Van Lear, and F.T. Lloyd. 1993. Estimation of above-ground biomass in a hurricane-impacted Coastal Plain forest. P. 189-196 *in* Proc. seventh bienn. south. silvic. res. conf., Brissette, John C. (ed.). U.S. Dep. Agric. For. Serv. Gen. Tech. Rep. SO-93.

Nelson, J.B. 1986. The natural communities of South Carolina, initial classification and description. South Carolina Wildl. Mar. Resour. Dep., Div. Wildl. Freshwater Fish, Columbia, SC. 55 p.

Nelson, T.C. 1957. The original forest of the Georgia Piedmont. Ecology 38(3):390–397.

Niering, W.A. 1953. The past and present vegetation of High Point State Park, New Jersey. Ecol. Monogr. 23(2):127–148.

Nowacki, G.J. 1995. Historical development, disturbance dynamics, and community ecology of oak-dominated forests of central Pennsylvania. Ph.D. Diss. Pennsylvania State Univ., University Park, PA. 193 p.

Nowacki, G.J, and M.D. Abrams. 1992. Community, edaphic, and historical analysis of mixed oak forests of the Ridge and Valley Province of central Pennsylvania. Canadian J. For. Res. 22:790–800.

Oliver, C.D. 1981. Forest development in North America following major disturbance. For. Ecol. Manage. 3:153–168.

Oosting, H.J. 1942. An ecological analysis of the plant communities of Piedmont, North Carolina. Am. Midl. Nat. 28(1):1–126.

Orwig, D.A., and M.D. Abrams. 1994. Land-use history (1720–1992), composition, and dynamics of oak-pine forests within the Piedmont and Coastal Plain of northern Virginia. Canadian J. For. Res. 24:1216–1225.

Peet, R.K., and N.L. Christensen. 1980. Hardwood forest vegetation of the North Carolina Piedmont. Veröffentlichungen des Geobotanischen Inst., Stiftung Rubel, Zurich. 69:14–39.

Peet, R.K., and N.L. Christensen. 1987. Competition and tree death. Bioscience 37(8):586–595.

Pehl, C.E., and R.L. Brim. 1985. Forest habitat regions of Georgia, Landsat IV imagery. Spec. Publ. 31. Georgia Agric. Exp. Stn., Coll. Agric., Univ. of Georgia, Athens, GA. 12 p.

Perry, C.J., and T.A. Waldrop. 1995. Opening size and site preparation techniques affect regeneration success for uneven-aged pine-hardwood mixtures. P.401-405 *in* Proc. eighth bienn. south. silvic. res. conf., Edwards, M. Boyd (comp.). U.S. Dep. Agric. For. Serv. Gen. Tech. Rep. SRS-1.

Phillippi, M.A., and A. Boebinger. 1986. A vegetational analysis of three small watersheds in Robinson Forest, eastern Kentucky, USA. Castanea 51(1):11–30.

Pickett, S.T.A., and P.S. White (eds.). 1985. The ecology of natural disturbance and patch dynamics. Academic Press, Orlando, FL. 472 p.

Platt, W.J., and M.W. Schwartz. 1990. Temperate hardwood forests. P. 194-229 *in* Ecosystems of Florida, Meyers, R., and J. Ewel (eds.). Univ. of Central Florida Press, Orlando, FL.

Plummer, G.L. 1975. Eighteenth century forests in Georgia. Bull. Georgia Acad. Sci. 33:1–19.

Racine, C.H. 1966. Pine communities and their site characteristics in the Blue Ridge escarpment. J. Elisha Mitchell Soc. 82:172–181.

Ramsey, G.W., et al. 1993. Vascular flora of the James River Gorge in the central Blue Ridge Mountains of Virginia. Castanea 58(4):260–300.

Rodgers, C.L. 1965. The vegetation of Horsepasture Gorge. J. Elisha Mitchell Soc. 81:103–111.

Rostlund, E. 1957. The myth of a natural prairie belt in Alabama: an interpretation of historical records. Ann. Assoc. Am. Geogr. 47:392–411.

Ruffin, Edmund. 1843. Agriculture, geology, and society in antebellum South Carolina: the private diary of Edmund Ruffin, 1843. Matthew, W.M. (ed.). Univ. of Georgia Press, Athens, GA. 368 p.

Sabin, G.R. 1991. Snag dynamics and utilization by wildlife in the upper Piedmont of South Carolina. M.S. Thesis. Clemson Univ., Clemson, SC. 48 p.

Sargent, C.S. 1884. Report on forests of North America. Vol. 9. U.S. Dep. Inter. Census Off., Washington, DC. 612 p.

Schafale, M.P., and P.A. Harcombe. 1983. Presettlement vegetation of Hardin County, Texas. Am. Midl. Nat. 109(2):355–366.

Schafale, M.P., and A.S. Weakley. 1990. Classification of the natural communities of North Carolina: third approximation. North Carolina Nat. Heritage Program, Div. Parks Recreation, North Carolina Dep. Environ., Health Nat. Resour., Raleigh, NC. 325 p.

Schmalzer, P.A. 1988. Vegetation of the Obed River Gorge system, Cumberland Plateau, Tennessee. Castanea 53(1):1–32.

Schoepf, Johann David. 1911. Travels in the confederation, 1783-1784. Morrison, A.J. (ed. and transl.). William J. Campbell, Pub., Philadelphia. 344 p.

Shimer, J.A. 1972. Field guide to landforms in the United States. Macmillan Co., New York. 172 p.

Showalter, T.D., and P. Turchin. 1993. Southern pine beetle infestation development: interaction between pine and hardwood basal areas. For. Sci. 39(2):201–210.

Shugart, H.H. 1984. A theory of forest dynamics: the ecological implications of forest succession models. Springer Verlag, New York. 278 p.

Skeen, J.N., M.E.B. Carter, and H.C. Ragsdale. 1980. Yellow-poplar: the Piedmont case. Bull. of the Torrey Bot. Club. 107:1–6.

Skeen, J.N., P.D. Doerr, and D.H. Van Lear. 1993. Oak-hickory-pine forests. P. 1-33 *in* Biodiversity of the southeastern United States: upland terrestrial communities, Martin, William H., Stephen G. Boyce, and Arthur C. Echternacht (eds.). Wiley, New York.

Sprugel, D.G. 1991. Disturbance equilibrium and environmental variability: what is "natural" vegetation in a changing environment? Biol. Conserv. 58:1–18.

Spurr, S.H., and B.V. Barnes. 1973. Forest ecology. The Ronald Press, New York. 571 p.

Stahle, D.W., et al. 1985. Tree ring chronologies for the south central United States. Tree Ring Lab., Univ. of Arkansas, Fayetteville, AR. 135 p.

Steen, C. 1993. Draft preliminary report on the 1992 excavations at John de la Howe's Lethe Farm. Diachronic Res. Found., Columbia, SC. 72 p.

Sterrett, W.D. 1908. Report on forest conditions in Delaware. Delaware Coll. Agric. Exp. Stn. Bull. 82. Newark, DE. 58 p.

Tobe, J.D., J.T. Fairey, and L.L. Gaddy. 1992. Vascular flora of the Chauga River Gorge. Castanea 57(2):77–109.

Tucker, G.E. 1991. Presettlement vegetation of the Ozark National Forest. P. 67-76 *in* Restoration of old-growth forests in the Interior Highlands of Arkansas and Oklahoma: Proc. conf., Henderson, D., and L.D. Hedrick (eds.). Winrock Int., Morrilton, AR.

Turner, L.M. 1935. Catastrophes and southern shortleaf pine. Ecology 16(2):213–215.

Van Lear, D.H. 1996. Dynamics of coarse woody debris in southern forest ecosystems. P. 10-17 *in* Biodiversity and coarse woody debris in southern forests, proceedings of the workshop on coarse woody debris in southern forests: effects on biodiversity, McMinn, J.W., and D.A. Crossley, Jr. (eds.). U.S. Dep. Agric. For. Serv. Gen. Tech. Rep. SE-94.

Van Lear, D.H., and T.A. Waldrop. 1989. History, uses, and effects of fire in the Appalachians. U.S. Dep. Agric. For. Serv. Gen. Tech. Rep. SE-54. 20 p.

Van Lear, D.H., and J. Watt. 1993. The role of fire in oak regeneration. P. 66-78 *in* Proc., oak regeneration: serious problems, practical recommendations, Loftis, David L., and Charles McGee (eds.). U.S. Dep. Agric. For. Serv. Gen. Tech. Rep. SE-84.

Waldrop, T.A. 1991. Pine-hardwood regeneration in small openings for uneven-aged management. P. 398-408 *in* Proc. sixth bienn. south. silvic. res. conf., Coleman, Sandra S., and Daniel G. Neary (comps., eds.). U.S. Dep. Agric. For. Serv. Gen. Tech. Rep. SE-70.

Waldrop, T.A. 1996. Dynamics of coarse woody debris-a simulation study for two southeastern forest ecosystems. P. 18-24 *in* Biodiversity and coarse woody debris in southern forests, proceedings of the workshop on coarse woody debris in southern forests: effects on biodiversity, McMinn, J.W., and D.A. Crossley, Jr. (eds.). U.S. Dep. Agric. For. Serv. Gen. Tech. Rep. SE-94.

White, D.L., and F.T. Lloyd. 1995. Defining old growth: implications for management. P. 51-62 *in* Proc. eighth bienn. south. silvic. res. conf., Edwards, M. Boyd. (comp.). U.S. Dep. Agric. For. Serv. Gen. Tech. Rep. SRS-1.

White, P.S., and R.D. White. 1996. Old-growth oak and oak-hickory forests. P. 178-198 *in* Eastern old-growth forests: prospects for rediscovery and recovery, Davis, M.B. (ed.). Island Press, Washington, DC.

Whittaker, R.H. 1956. Vegetation of the Great Smoky Mountains. Ecol. Monogr. 26(1):1–69.

Whittaker, R.H. 1979. Vegetational relationships of the Pine Barrens. P. 315-352 *in* Pine Barrens: ecosystem and landscape, Formann, R.T.T. (ed.). Academic Press, New York.

Williams, C.E., and W.C. Johnson. 1992. Factors affecting recruitment of *Pinus pungens* in the Southern Appalachian Mountains. Canadian J. For. Res. 22:878–887.

Woods, F.W., and R.E. Shanks. 1959. Natural replacement of chestnut by other species. Ecology 40:349–361.

Yost, E.C., K.S. Johnson, and W. Blozan. 1994. Delineation of old-growth oak and eastern hemlock in the Great Smoky Mountains National Park. Park Sci. (fall):14–16.

Zobel, D.B. 1969. Factors affecting the distribution of *Pinus pungens,* an Appalachian endemic. Ecol. Monogr. 39(3):303–333.

Appendix A

List of common trees, shrubs, and herbaceous species[a] occurring in old-growth and non-old-growth forest stands representative of the oak-pine type in the Eastern United States, with scientific and common names given. Nomenclature is from Kartesz and Kartesz (1980).

		Old-growth stands[b]						Non-old-growth stands[b]							
		Piedmont		Gulf CP	Ouachita Mountains			Southern Appalachian Mountains							Plateau
Common name	Scientific name	1 JDLH	2 Duke	3 KNF	4 RBRNA	5 HSNP	6 LWRNA	7 SCONA	8 ESCARP	9 Chauga	10 SM:VP	11 SM:PP	12 SM:TMP	13 SM:C-H	14 Pine Mt.
Trees: *Pinus* species															
Pines		X	X	X	X	X	X	X	X	X	X	X	X	X	X
Shortleaf pine	*Pinus echinata* Mill.	X	X	X	X	X	X	-	X	X	-	-	-	-	X
Loblolly pine	*P. taeda* L.	X	-	X	-	-	-	-	-	-	-	-	-	-	-
Longleaf pine	*P. palustris* Mill.	-	-	X[c]	-	-	-	-	-	-	-	-	-	-	-
Pitch pine	*P. rigida* Mill.	-	-	-	-	-	-	X	X	X	X	X	X	-	X
Table Mountain pine	*P. pungens* Lamb.	-	-	-	-	-	-	-	-	X	-	-	X	-	-
Eastern white pine	*P. strobus* L.	-	-	-	-	-	-	-	-	-	X	-	-	X	-
Virginia pine	*P. virginiana* Mill.	-	-	-	-	-	-	-	X	X	X	-	-	-	X
Trees: *Quercus* species		X	X	X	X	X	X	X	X	X	X	X	X	X	X
White oak	*Quercus alba* L.	X	X	X	X	X	X	-	X	-	X	-	-	X	X
Black oak	*Q. velutina* Lam.	X	X	X[c]	X	X	X	-	-	-	X	-	-	X	X
Blackjack oak	*Q. marilandica* Muenchh.	-	X	X[c]	X	X	X	-	-	-	X	-	-	-	-
Post oak	*Q. stellata* Wangenh.	X	X	X	-	X	X	-	-	-	-	-	-	-	-
Southern red oak	*Q. falcata* Michx.	X	-	X	-	X	X	-	-	X	-	-	-	-	-
Scarlet oak	*Q. coccinea* Muenchh.	-	X	-	-	-	-	X	X	X	X	X	X	X	X
Northern red oak	*Q. rubra* L.	-	X	-	X	-	-	-	-	-	-	-	-	-	-
Chestnut oak	*Q. prinus* L.	-	-	-	-	-	--	X	X	-	X	X	X	X	X
Trees: *Carya* species		X	X	X	X	X	X	X	-	-	X	X	X	X	X
Mockernut hickory	*Carya tomentosa* (Poir.) Nutt.	X	-	X	X	X	-	-	-	-	-	-	-	-	-
Black hickory	*C. texana* Buckl.	-	-	X[c]	X	X	-	-	-	-	-	-	-	-	-
Pignut hickory	*C. glabra* (Mill.) Sweet	X	-	-	-	-	-	-	-	-	-	-	-	-	-
Red hickory	*C. glabra* var. *odorata* (Marsh.) Little	-	-	-	X	-	-	-	-	-	-	-	-	-	-
Trees: others															
Red maple	*Acer rubrum* L.	X	X	X	-	X	X	X	X	X	X	X	X	X	X
Blackgum	*Nyssa sylvatica* Marsh.	X	X	X	-	X	X	X	X	X	X	X	X	X	X
Flowering dogwood	*Cornus florida* L.	X	X	X	-	X	X	-	-	X	-	-	-	-	X
Eastern hophornbeam	*Ostrya virginiana* (Mill.) K. Koch	X	-	X	X	-	-	-	-	-	-	-	-	-	-
Sourwood	*Oxydendron arboreum* (L.) DC.	X	X	-	-	-	-	X	X	X	X	X	X	X	X

(continued)

Appendix A

List of common trees, shrubs, and herbaceous species[a] occurring in old-growth and non-old-growth forest stands representative of the oak-pine type in the Eastern United States, with scientific and common names given. Nomenclature is from Kartesz and Kartesz (1980).

		Old-growth stands[b]							Non-old-growth stands[b]							
		Piedmont		Gulf CP	Ouachita Mountains				Southern Appalachian Mountains						Plateau	
Common name	Scientific name	1 JDLH	2 Duke	3 KNF	4 RBRNA	5 HSNP	6 LWRNA	7 SCONA	8 ESCARP	9 Chauga	10 SM:VP	11 SM:PP	12 SM:TMP	13 SM:C-H	14 Pine Mt.
Trees: others (cont.)															
Winged elm	*Ulmus alata* Michx.	X	-	X[c]	-	-	-	-	-	-	-	-	-	-	-
Southern sugar maple	*A. floridanum* (Chapman) Pax	X	-	-	-	-	-	-	-	-	-	-	-	-	-
Persimmon	*Diospyrus virginiana* L.	-	-	X[c]	-	-	-	-	-	-	-	-	-	-	-
Yellow-poplar	*Liriodendron tulipifera* L.	X	-	-	-	-	-	-	-	-	-	-	-	-	X
Black cherry	*Prunus serotina* Ehrh.	-	-	X[c]	-	-	-	-	-	-	-	-	-	-	-
Sassafras	*Sassafras albidum* (Nutt.) Nees	-	-	-	X	-	-	-	-	-	-	-	X	X	X
American elm	*U. americana* L.	X	-	-	-	-	-	-	-	-	-	-	-	-	-
American chestnut	*Castanea dentata* (Marsh.) Borkh.	-	-	-	-	-	-	-	-	-	X	X	X	X	-
Black locust	*Robinia pseudoacacia* L.	-	-	-	-	-	-	-	-	-	-	-	-	X	-
Shrubs: *Ericaceae*															
Blueberry	*Vaccinium* spp.	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Deerberry	*V. stamineum* L.	X	X	X[c]	-	X	-	X	X	-	X	-	X	-	X
Lowbush blueberry	*V. vacillans* Torr.	-	-	X[c]	X	X	X	X	X	-	X	X	-	X	X
Sparkleberry	*V. arboreum* Marsh.	X	-	X[c]	X	-	-	-	-	-	-	-	-	-	-
Huckleberry	*Gaylussacia baccata* (Wang.) K. Koch	-	-	X[c]	-	-	-	X	-	-	X	X	X	-	X
Dangleberry	*G. frondosa* (L.) T.&G.	-	-	X[c]	-	-	-	-	-	-	-	-	-	-	-
Mountain laurel	*Kalmia latifolia* L.	-	-	-	-	-	-	X	X	-	X	X	X	X	X
Wild azalea	*Rhododendron canescens* (Michx.) Sweet	-	-	X	-	-	-	-	-	-	-	-	-	-	-
Wild azalea	*R. periclymenoides* (Michx.) Shinners	-	X	-	-	-	-	-	-	-	-	-	-	-	-
Highbush blueberry	*V. elliottii* Chapman	-	-	X[c]	-	-	-	-	-	-	-	-	-	-	-
Trailing arbutus	*Epigaea repens* L.	-	-	-	-	-	-	-	-	-	X	X	X	X	X
Wintergreen	*Gaultheria procumbens* L.	-	-	-	-	-	-	-	X	-	-	X	X	X	X
Bear huckleberry	*Gaylussacia ursina* (M.A. Curtis) T.&G.	-	-	-	-	-	-	-	X	-	-	-	-	X	-
Male blueberry	*Lyonia ligustrina* (L.) DC.	-	-	-	-	-	-	-	-	-	-	X	X	X	-
Fetterbush	*Pieris floribunda* (Pursh) B. & H.	-	-	-	-	-	-	-	-	-	-	-	X	-	-

(continued)

Appendix A

List of common trees, shrubs, and herbaceous species[a] occurring in old-growth and non-old-growth forest stands representative of the oak-pine type in the Eastern United States, with scientific and common names given. Nomenclature is from Kartesz and Kartesz (1980).

		Old-growth stands[b]							Non-old-growth stands[b]						
		Piedmont		Gulf CP	Ouachita Mountains			Southern Appalachian Mountains						Plateau	
Common name	Scientific name	1 JDLH	2 Duke	3 KNF	4 RBRNA	5 HSNP	6 LWRNA	7 SCONA	8 ESCARP	9 Chauga	10 SM:VP	11 SM:PP	12 SM:TMP	13 SM:C-H	14 Pine Mt.
Shrubs: *Ericaceae* (cont.)															
Flame azalea	*R. calendulaceum* (Michx.) Torr.	-	-	-	-	-	-	-	-	-	-	-	X	-	X
Catawba rhododendron	*R. catawbiense* Michx.	-	-	-	-	-	-	-	-	-	-	-	X	-	-
Mountain rosebay	*R. maximum* L.	-	-	-	-	-	-	-	-	-	-	-	-	X	-
Highbush blueberry	*V. constablaei* Gray	-	-	-	-	-	-	-	-	-	-	-	X	X	-
Lowbush blueberry	*V. hirsutum* Buckley	-	-	-	-	-	-	-	-	-	-	X	X	-	-
Lowbush blueberry	*V. pallidum* Aiton	-	-	-	-	-	-	-	-	X	-	-	X	-	-
Shrubs: others															
Fringe tree	*Chionanthus virginicus* L.	-	X	X[c]	-	-	-	-	-	-	-	-	-	-	-
Strawberry bush	*Euonymous americanus* L.	X	X	-	-	-	-	-	-	-	-	-	-	-	-
Poison ivy	*Toxicodendron radicans* (L.) Kuntze	X	-	X[c]	-	-	-	-	-	-	-	-	-	-	-
Viburnum	*Viburnum* spp.	X	X	-	-	-	-	-	-	-	-	-	-	-	-
Black-haw	*V. prunifolium* L.	-	X	X[c]	-	-	-	-	-	-	-	-	-	-	-
Rusty black-haw	*V. rufidulum* Raf.	-	X	X[c]	-	-	-	-	-	-	-	-	-	-	-
Red buckeye	*Aesculus Pavia* L.	-	-	X[c]	-	-	-	-	-	-	-	-	-	-	-
False buckthorn	*Bumelia lanuginosa* (Michx.) Pers.	-	-	X[c]	-	-	-	-	-	-	-	-	-	-	-
American beauty-berry	*Callicarpa americana* L.	-	-	X[c]	-	-	-	-	-	-	-	-	-	-	-
New Jersey tea	*Ceanothus americanus* L.	-	-	-	-	X	-	-	-	-	-	-	-	-	-
Hawthorne	*Crataegus* spp.	-	-	X	-	-	-	-	-	-	-	-	-	-	-
Yaupon	*Ilex vomitoria* Ait.	-	-	X	-	-	-	-	-	-	-	-	-	-	-
Hop-tree	*Ptelea trifoliata* L.	-	-	-	X	-	-	-	-	-	-	-	-	-	-
Fragrant sumac	*Rhus aromatica* Ait.	-	-	-	X	-	-	-	-	-	-	-	-	-	-
Winged sumac	*R. copallina* L.	-	-	X[c]	-	-	-	-	-	-	-	-	-	-	-
Horse-sugar	*Symplocos tinctoria* (L.) L'Her.	-	-	X	-	-	-	-	-	-	-	-	-	-	-
Southern arrow-wood	*V. dentatum* L.	-	-	X[c]	-	-	-	-	-	-	-	-	-	-	-
St. Andrew's cross	*Ascyrum Hypericoides* L.	-	-	-	-	-	-	-	-	-	-	-	-	-	X
Sweet pepperbush	*Clethra acuminata* Michx.	-	-	-	-	-	-	-	-	-	-	-	-	X	-
Buffalo nut	*Pyrularia pubera* Michx.	-	-	-	-	-	-	-	-	-	-	-	-	X	-
Storax	*Styrax grandifolia* Ait.	-	-	-	-	-	-	-	-	X	-	-	-	-	-

(continued)

Appendix A

List of common trees, shrubs, and herbaceous species[a] occurring in old-growth and non-old-growth forest stands representative of the oak-pine type in the Eastern United States, with scientific and common names given. Nomenclature is from Kartesz and Kartesz (1980).

		Old-growth stands[b]						Non-old-growth stands[b]							
		Piedmont		Gulf CP	Ouachita Mountains			Southern Appalachian Mountains							Plateau
Common name	Scientific name	1 JDLH	2 Duke	3 KNF	4 RBRNA	5 HSNP	6 LWRNA	7 SCONA	8 ESCARP	9 Chauga	10 SM:VP	11 SM:PP	12 SM:TMP	13 SM:C-H	14 Pine Mt.
Vines															
Smilax	*Smilax* spp.	X	X	X[c]	X	X	-	-	-	-	-	-	-	-	-
Virginia creeper	*Parthenocissus quinquefolia* (L.) Planch.	X	X	X[c]	X	-	-	-	-	-	-	-	-	-	-
Grape	*Vitis* spp.	X	X	X[c]	-	X	-	-	-	-	-	-	-	-	-
Muscadine	*V. rotundifolia* Michx.	X	X	-	-	X	-	-	-	-	-	-	-	-	-
Yellow jessamine	*Gelsemium sempervirens* (L.) St. Hill.	-	-	X[c]	-	-	-	-	-	-	-	-	-	-	-
Trumpet honeysuckle	*Lonicera sempervirens* L.	-	X	-	-	-	-	-	-	-	-	-	-	-	-
Sawbrier	*S. glauca* Walt.	-	-	-	-	-	-	X	-	-	X	-	-	-	-
Greenbrier	*S. rotundifolia* L.	-	X	-	-	-	-	-	-	-	X	-	-	-	-
Herbs: *Asteraceae*															
Sunflower	*Helianthus* spp.	-	X	X[c]	X	X	-	-	-	-	-	-	-	-	-
Pussytoes	*Antennaria plantaginifolia* L. Richards.	-	-	X[c]	-	X	X	-	-	-	X	-	-	-	-
Aster	*Aster* spp.	-	-	X	-	-	X	-	X	-	X	-	-	-	X
Hawkweed	*Hieracium gronovil* L.	-	X	-	-	-	-	X	-	-	-	-	-	-	-
Hawkweed	*H. venosum* L.	-	X	X[c]	-	-	-	-	X	-	-	-	-	-	-
Goldenrod	*Solidago* spp.	-	-	X	-	-	X	-	X	-	X	-	-	-	X
Anomalous aster	*A. anomalus* Engelm.	-	-	-	-	-	X	-	-	-	-	-	-	-	-
Elephant's-foot	*Elephantopus tomentosus* L.	-	-	X	-	-	-	-	-	-	-	-	-	-	-
Daisy fleabane	*Erigeron strigosus* Muhl. ex Willd.	-	-	-	-	X	-	-	-	-	-	-	-	-	-
Prairie sunflower	*H. laetiflorus* Pers.	-	-	-	X	-	-	-	-	-	-	-	-	-	-
Stiff sunflower	*H. divaricatus* L.	-	-	-	-	X	-	-	-	-	-	-	-	-	-
Blazing star	*Liatris* spp.	-	-	X[c]	-	-	-	-	-	-	-	-	-	-	-
Gumweed	*Silphium* spp.	-	-	X[c]	-	-	-	-	-	-	-	-	-	-	-
Goldenrod	*Solidago caesia* L.	-	-	X	-	-	-	-	-	-	-	-	-	-	-
Hispid goldenrod	*S. hispida* Muhl.	-	-	-	-	-	X	-	-	-	-	-	-	-	-
Ironweed	*Vernonia* spp.	-	-	X[c]	-	-	-	-	-	-	-	-	-	-	-
Tickseed	*Coreopsis major* Walt.	-	-	-	-	-	-	-	X	-	X	X	-	-	X

(continued)

Appendix A

List of common trees, shrubs, and herbaceous species[a] occurring in old-growth and non-old-growth forest stands representative of the oak-pine type in the Eastern United States, with scientific and common names given. Nomenclature is from Kartesz and Kartesz (1980).

		Old-growth stands[b]							Non-old-growth stands[b]						
		Piedmont		Gulf CP	Ouachita Mountains				Southern Appalachian Mountains						Plateau
Common name	Scientific name	1 JDLH	2 Duke	3 KNF	4 RBRNA	5 HSNP	6 LWRNA	7 SCONA	8 ESCARP	9 Chauga	10 SM:VP	11 SM:PP	12 SM:TMP	13 SM:C-H	14 Pine Mt.
Herbs: *Asteraceae* (cont.)															
Golden aster	*Pityopsis graminifolia* (Michx.) Nutt.	-	-	-	-	-	-	-	X	-	-	-	-	-	X
Goldenrod	*S. bicolor* L.	-	-	-	-	-	-	-	-	-	X	-	-	-	X
Goldenrod	*S. oroda* Ait.	-	-	-	-	-	-	-	-	-	-	-	-	-	X
Herbs: *Fabaceae*															
Beggar's-lice	*Desmodium* spp.	-	-	X	X	-	X	-	-	-	-	-	-	-	X
Tephrosia	*Tephrosia* spp.	-	-	X[c]	-	-	-	-	-	X	X	-	-	-	X
Baptista	*Baptisia* spp.	-	-	X[c]	-	-	-	-	-	-	X	-	-	-	X
Partridge pea	*Cassia fasciculata* Michx.	-	-	X[c]	-	-	-	-	-	-	-	-	-	-	-
Butterfly-pea	*Centrosema virginianum* (L.) Benth.	-	-	X[c]	-	-	-	-	-	-	-	-	-	-	-
Beggar's-lice	*D. laevigatum* (Nutt.) DC.	-	-	-	-	-	X	-	-	-	-	-	-	-	X
Lespedeza	*Lespedeza* spp.	-	-	X[c]	-	-	-	-	-	-	-	-	-	-	X
Wild indigo	*B. tintoria* (L.) R. Br.	-	-	-	-	-	-	-	-	-	X	-	-	-	X
Butterfly-pea	*Clitoria mariana* L.	-	-	-	-	-	-	-	X	-	-	-	-	-	X
Dollar leaf	*D. rotundifolium* DC.	-	-	-	-	-	-	-	-	-	-	-	-	-	X
Herbs: grasses and sedges															
All grass species		X	X	X	X	X	X	X	X	-	X	X	X	X	X
Panic-grass	*Panicum* spp.	X	X	X	X	X	X	X	X	-	X	-	-	X	-
Broom-straw	*Andropogon* spp.	-	X	-	-	X	X	-	X	-	X	-	-	-	-
Broom-sedge	*A. virginicus* L.	-	X	-	-	X	X	-	-	-	X	-	-	-	-
Sedge	*Carex* spp.	X	X	X	-	-	-	-	-	-	-	-	-	-	-
Triple-awned grass	*Aristida* spp.	-	-	X[c]	-	-	-	-	-	-	-	-	-	-	-
	Danthonium spp.	-	-	-	X	-	-	-	-	-	-	-	-	-	X
Poverty-grass	*D. spicata* (L.) Beauv. ex. Roemer & Schul.	-	-	-	X	-	-	-	-	-	-	-	-	-	-
	Paspalum spp.	-	-	X[c]	-	-	-	-	-	-	-	-	-	-	-
Little bluestem	*Schizachyrium scoparium* (Michs.) Nash	-	-	X	-	-	-	-	-	-	X	X	X	-	X
Nutrush	*Scleria* spp.	-	-	-	-	-	X	-	-	X	-	-	-	-	-
	Uniola spp.	-	-	X	-	-	-	-	-	-	-	-	-	-	-
Indian grass	*Sorghastrum nutans* (L.) Nash	-	-	-	-	-	-	-	-	-	-	-	-	-	X

(continued)

Appendix A

List of common trees, shrubs, and herbaceous species[a] occurring in old-growth and non-old-growth forest stands representative of the oak-pine type in the Eastern United States, with scientific and common names given. Nomenclature is from Kartesz and Kartesz (1980).

		Old-growth stands[b]							Non-old-growth stands[b]						
		Piedmont		Gulf CP	Ouachita Mountains				Southern Appalachian Mountains						Plateau
Common name	Scientific name	1 JDLH	2 Duke	3 KNF	4 RBRNA	5 HSNP	6 LWRNA	7 SCONA	8 ESCARP	9 Chauga	10 SM:VP	11 SM:PP	12 SM:TMP	13 SM:C-H	14 Pine Mt.
Herbs: others															
Pipsissewa	*Chimaphila maculata* (L.) Pursh	X	X	-	-	-	-	X	X	X	-	-	-	-	-
Bracken fern	*Pteridium aquillinum* (L.) Kuhn	-	-	-	-	X	X	X	X	X	X	X	X	-	X
Dwarf Dutchman's-pipe	*Aristolochia serpentaria* L.	X	X	-	-	-	-	-	-	-	-	-	-	-	-
Wild yam	*Dioscorea villosa* L.	X	-	-	-	X	-	-	-	-	-	-	-	-	-
Bedstraw	*Galium* spp.	X	X	-	-	-	-	-	-	-	-	-	-	-	-
Wild ginger	*Hexastylus* spp.	X	X	-	-	-	-	-	-	-	-	-	-	-	-
Milkweed	*Asclepias* spp.	-	-	X[c]	-	-	-	-	-	-	-	-	-	-	-
Prairie spurge	*Euphorbia corollata* L.	-	-	-	-	X	-	-	-	-	-	-	-	-	-
Wild ginger	*H. virginica* (L.) Small	-	X	-	-	-	-	-	-	-	-	-	-	-	-
Partridge-berry	*Mitchella repens* L.	X	-	-	-	-	-	-	-	-	-	-	-	-	-
Solomon's-seal	*Polygonatum biflorum* (Walt.) Ell.	X	-	-	-	-	-	-	-	-	-	-	-	-	-
Five-finger	*Potentilla canadensis* L.	-	X	-	-	-	-	-	-	-	-	-	-	-	-
False Solomon's-seal	*Smilacena racemosa* (L.) Desf.	X	-	-	-	-	-	-	-	-	-	-	-	-	-
Purple cress	*Streptanthus maculatus* Nutt.	-	-	-	X	-	-	-	-	-	-	-	-	-	-
Perfoliate bellwort	*Uvularia perfoliata* L.	X	-	-	-	-	-	-	-	-	-	-	-	-	-
Colicroot	*Aletris farinosa* L.	-	-	-	-	-	-	-	-	-	-	-	-	-	X
False foxglove	*Aureolaria laevigata* (Raf.) Raf.	-	-	-	-	-	-	-	-	-	-	-	-	X	-
Bellflower	*Campanula divaricata* Michx.	-	-	-	-	-	-	-	-	-	-	-	-	X	-
Galax	*Galax urceolata* (Poir.) Brummitt	-	-	-	-	-	-	-	X	-	X	X	X	X	X
Gentian	*Gentiana villosa* L.	-	-	-	-	-	-	-	-	-	-	-	-	-	X

(continued)

Appendix A

List of common trees, shrubs, and herbaceous species[a] occurring in old-growth and non-old-growth forest stands representative of the oak-pine type in the Eastern United States, with scientific and common names given. Nomenclature is from Kartesz and Kartesz (1980).

		Old-growth stands[b]							Non-old-growth stands[b]						
		Piedmont		Gulf CP	Ouachita Mountains				Southern Appalachian Mountains						Plateau
Common name	Scientific name	1 JDLH	2 Duke	3 KNF	4 RBRNA	5 HSNP	6 LWRNA	7 SCONA	8 ESCARP	9 Chauga	10 SM:VP	11 SM:PP	12 SM:TMP	13 SM:C-H	14 Pine Mt.
Herbs: others (cont.)															
Stargrass	*Hypoxis hirsuta* (L.) Coville	-	-	-	-	-	-	-	-	-	-	-	-	-	X
Violet	*Viola* spp.	-	-	-	-	-	-	-	-	-	-	-	-	-	X
Birdfoot-Violet	*V. pedata* L.	-	-	-	-	-	-	-	X	-	-	-	-	-	X
Violet	*V. sagittala* Ait.	-	-	-	-	-	-	-	-	-	-	-	-	-	X

[a] Species are listed by species group in the order of their abundance across old-growth stands.
[b] Stands 1 through 14 are: JDLH = John de la Howe, mixed oak-shortleaf/loblolly pine forest (this study); Duke = Duke Forest, white oak-post oak-shortleaf pine (Oosting 1942); KNF = Kisatchie National Forest, shortleaf pine-oak-hickory forest (Martin and Smith 1991); RBRNA = Roaring Branch Research Natural Area, oak-shortleaf pine forest (Fountain and Sweeney 1985); HSNP = Hot Springs National Park, oak-hickory-shortleaf pine (Dale and Watts 1980); LWRNA = Lake Winona Research Natural Area, shortleaf pine forest (Fountain and Sweeney 1987, Fountain 1991); SCONA = Scarlet Oak Natural Area, scarlet oak-pitch pine forest (Delapp and Wentworth 1977); ESCARP = Blue Ridge Escarpment, Thompson River Gorge, pitch pine-scarlet oak/oak-pitch pine (Racine 1966); Chauga = Chauga River Gorge, shortleaf pine forest (Tobe et al. 1992); SM:VP = Great Smoky Mountains National Park, Virginia pine forest (Whittaker 1956); SM:PP = Great Smoky Mountains National Park, pitch pine forest (Whittaker 1956); SM:TMP = Great Smoky Mountains National Park, Table Mountain pine forest (Whittaker 1956); SM:C-H = Great Smoky Mountains National Park, chestnut oak-chestnut-heath forest (Whittaker 1956); Pine Mt. = Pine Mountain, Kentucky, pine-oak to oak-pine forests (Braun 1935).
[c] Species not sampled in old-growth stands within the Kisatchie National Forest (KNF) but were described as part of the KNF shortleaf pine oak-hickory natural community type by Martin and Smith (1991).

Appendix B

Descriptions of old-growth stands and data used in table 2 by physiographic region:

Piedmont

(1) John de la Howe tract, a mixed oak-shortleaf-loblolly stand near McCormick, SC, has been described in part by White and Lloyd (1995) (see text for additional information); (2) a white oak-post oak stand on the Duke Forest, NC (Oosting 1942). This stand, which contained a significant shortleaf pine component, was one of three that Oosting sampled to characterize the white oak-post oak type that he considered a variant of the oak-hickory climax. Oosting described the oak-hickory stands as having 200- to 300-year-old trees and showing little evidence of recent disturbance.

Ouachita Mountains

Three stands from this region were described previously as old growth in the literature: (1) Roaring Branch Research Natural Area (Fountain and Sweeney 1985), (2) Lake Winona Research Natural Area (Fountain 1991), and (3) Hot Springs National Park—composition and structure (Dale and Watts 1980) and coarse woody debris (Johnson and Schnell 1985). Age data were derived from Stahle et al. (1985) for these areas.

Gulf Coastal Plain

Shortleaf pine-oak-hickory stands in the Kisatchie National Forest, LA, were described as old growth by Martin and Smith (1991). The two stands used in table 2 are referred to as Bobs Creek Shortleaf and Old Shortleaf Slope. They are 113 and 127 years old, respectively.

Southern Appalachians

Two stands in the Scarlet Oak Natural Area were characterized in the disturbance class as "virgin, undisturbed" (see footnote 8). The report contained composition and structure data for each stand. We relocated one of these stands and obtained increment cores from chestnut oak, scarlet oak, and pitch pine. Pitch pine and chestnut oak exceeded 150 years old, but younger age classes of all species were present. Age data in table 2 for the Southern Appalachians were obtained from the Great Smoky Mountains National Park (Blozan 1994) and the Chattooga River Gorge watershed (see footnote 7) that encompasses the national forests in Georgia, North Carolina, and South Carolina.

White, David L.; Lloyd, F. Thomas. 1998. An old-growth definition for dry and dry-mesic oak-pine forests. Gen. Tech. Rep. SRS-23. Asheville, NC: U.S. Department of Agriculture, Forest Service, Southern Research Station. 42 p.

Dry and dry-mesic oak-pine forests are widely distributed from New Jersey to Texas, but representative old-growth stands are rare. Historical accounts of composition, along with information from existing old-growth stands, were used to characterize this type. Shortleaf pine and white oak were the most widely distributed trees across all old-growth stands. Shortleaf was the primary pine species of the oak-pine type in the Piedmont, Gulf Coastal Plain, and Interior Highlands, while pitch pine was predominant in the mountainous regions. Scarlet and chestnut oaks were more prevalent in the Appalachians. Maximum age for pitch and shortleaf pines exceeded 200 and 300 years, respectively. Forests of this type do not adhere to the steady state or equilibrium concept of forest dynamics; rather old-growth oak-pine may be ephemeral on a given site. Disturbance by fire or other agents distributed through space and time is required for its maintenance on the broader landscape. Characteristics of the living and dead components of old-growth oak-pine are presented.

Keywords: Disturbance, dry-mesic, fire, oak-pine, old growth, presettlement.

The Forest Service, United States Department of Agriculture (USDA), is dedicated to the principle of multiple use management of the Nation's forest resources for sustained yields of wood, water, forage, wildlife, and recreation. Through forestry research, cooperation with the States and private forest owners, and management of the National Forests and National Grasslands, it strives—as directed by Congress—to provide increasingly greater service to a growing Nation.

The USDA prohibits discrimination in all its programs and activities on the basis of race, color, national origin, gender, religion, age, disability, political beliefs, sexual orientation, and marital or family status. (Not all prohibited bases apply to all programs.) Persons with disabilities who require alternative means for communication of program information (Braille, large print, audiotape, etc.) should contact USDA's TARGET Center at 202-720-2600 (voice and TDD).

To file a complaint of discrimination, write USDA, Director, Office of Civil Rights, Room 326-W, Whitten Building, 14th and Independence Avenue, SW, Washington, DC 20250-9410 or call 202-720-5964 (voice or TDD). USDA is an equal opportunity provider and employer.