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Characteristics of Dry-Mesic Old-Growth Oak Forests in the Eastern United States

Martin A. Spetich [1,*], Michael A. Jenkins [2], Stephen R. Shifley [3], Robert F. Wittwer [4,†] and David L. Graney [5,†]

[1] Arkansas Forestry Sciences Laboratory, USDA Forest Service, Southern Research Station, P.O. Box 1270, Hot Springs, AR 71902, USA
[2] Department of Forestry and Natural Resources, Purdue University, 715 West State Street, West Lafayette, IN 47907, USA
[3] School of Natural Resources, University of Missouri, Columbia, MO 65211, USA
[4] Department of Forestry, Room 008C, Ag Hall, Oklahoma State University, Stillwater, OK 74078, USA
[5] USDA Forest Service, Southern Research Station, P.O. Box 648, Jasper, AR 72641, USA
* Correspondence: martin.spetich@usda.gov
† These two authors have retired.

Abstract: Dry-mesic old-growth oak forests are widely distributed remnants across the eastern U.S. and are expected to increase in number and extent as second-growth forests mature. In this study, we synthesize published and unpublished information to better define the species, structure and extent of these forests. Mean site tree density for trees $\geq$10 cm dbh ranged from 341–620 trees ha^{-1}. In the eastern part of the region, most stand basal areas were >23 m^2 ha^{-1}, compared to $\leq$23 m^2 ha^{-1} in the westernmost stands. Overall, woody species diversity was relatively low compared to old-growth oak forests on moister sites, with tree species per forest ranging from 5–18. The most common species among the stands were white oak (*Quercus alba*), northern red oak (*Quercus rubra*), and black oak (*Quercus velutina*). Shrub and vine species per forest ranged from 1–10, with common species or genera including Virginia creeper (*Parthenocissus quinquefolia*), poison ivy (*Toxicodendron radicans*), *Vaccinium* spp., and grapevines (*Vitis* spp.). Within the southern Appalachian Mountains, rosebay rhododendron (*Rhododendron maximum*) and mountain laurel (*Kalmia latifolia* L.) were common. Herbaceous species per stand ranged from 4–51, with the highest richness occurring in a southern Appalachian oak-hickory forest. The maximum within-stand age of the large trees ranged from 170 to over 365 years. The mean density of standing dead trees $\geq$10 cm dbh ranged from 31–78 ha^{-1} and the volume of coarse woody debris $\geq$10 cm in diameter averaged 52 m^3 ha^{-1}. We more fully describe the characteristics of these forests and fill gaps in the collective knowledge of this increasingly important forest type. However, over the past 20 years, there has been scant research on these forests, and older research studies have used a variety of research plots and methods. A uniform approach to surveying these sites is needed to gain a better understanding of these forests before we are faced with caring for an increase in old-growth forest areas.

Keywords: forest structure; white oak; species composition; tree age; old growth; physiographic regions; forest dynamics; succession

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1. Introduction

Oak-dominated forests represent 53 percent of the biomass and cover 47 percent of the forest area in the eastern United States [1]. These forests are aging; a recent forest inventory and analysis report indicated that 67.8 percent of the oak-dominated forests in the eastern US were 40 to 99 years old [1]. With millions of hectares expected to grow into age classes >100 years old in the near future, more forests in the eastern U.S. are, or soon will be, entering an old-growth phase of development (minimal human manipulation over the past 40–100 years, mature trees >150 years old, large canopy gaps, uneven-aged, and a significant amount of coarse woody debris—standing and down). Dry-mesic oak forests are found in both the U.S. and Europe [2–4]. They occur across most physiographic regions of the eastern U.S. [5] and are typically situated on ridges or west-facing, south-facing, and, to a lesser extent, east-facing upper slopes.

Old-growth forests around the world are considered of biological importance due, in part, to their rarity. These forests represent the late seral stage of forest development and typically contain mature old trees, have experienced minimal human manipulation, contain canopy gaps where trees have succumbed to natural disturbance (e.g., wind, decay, old age and/or insect damage), and typically contain a substantially greater amount of standing and down coarse woody debris than would be found in earlier stages of forest development. Old growth is especially rare in the eastern United States, mainly due to past anthropogenic disturbances. Understanding these old-growth forests helps us better understand a forest's long-term dynamics. In the 1990s, there was an effort to expand that understanding by characterizing 35 old-growth forest types in the United States by physiographic region [5]. Research has been published on many of these forest types. However, research on the dry-mesic old-growth oak forest type has never been published. In this paper, we fill this research gap.

Additionally, in the southeastern U.S., the average annual temperature is expected to increase, while average annual precipitation decreases through 2060 [6], leading to dryer, hotter climatic conditions. Oaks have existed in this region since the Cretaceous period and is exceptionally well adapted to flourish under these conditions [7]. However, a thorough investigation of the characteristics of dry-mesic old-growth oak forests has never been published. In this manuscript, we synthesized the characteristics of dry-mesic old-growth oak forests of the eastern U.S., as described in the materials and methods below, helping to fill gaps in collective knowledge of this increasingly important forest type.

Dry-mesic oak forests are widely distributed across the eastern United States. These forests occur mainly in unglaciated uplands. Associated Society of American Foresters cover types include 44-chestnut oak, 52-white oak-black oak-northern red oak, 53-white oak, 55-northern red oak, and 110-black oak [8]. Dominant species include white oak (*Q. alba* L.), scarlet oak (*Q. coccinea* Muenchh), chestnut oak (*Quercus prinus* L.), black oak (*Q. velutina* Lam.) and northern red oak (*Q. rubra* L.).

2. Materials and Methods

We synthesized information to define the overall character of these forests, including species, structure and extent. Sources of information were identified through unpublished data, unpublished and published reports, unpublished surveys, personal communications with experts and a review of existing literature. Criteria to identify source information to be included in this study first included identifying old-growth sites that were classified as dry-mesic oak. For each physiographic region, we chose those sites that had quantified data on most of the following characteristics: contained mature trees >150 years old, contained canopy gaps, were uneven-aged, and included data on standing and/or down coarse woody debris. Studies that met these criteria and had a well-established study design over multiple years were included. Sites without data, location information or that otherwise did not meet the above criteria were excluded. Some regions had no sites that met these criteria. One of our objectives was to provide detailed information on these sites to provide an important consolidated baseline describing dry-mesic oak forests. We partitioned our summary of the character of these forests into two sections: (1) physiographic region and (2) old-growth forest conditions with a focus on structural features.

Both quantifiable and non-quantifiable characteristics are described in this paper. Many of the sources that reported quantifiable characteristics, such as stand densities, basal area, size class, tree diameters, number of snags and coarse woody debris, measured trees ≥10 cm in diameter. However, some sources reported these characteristics for trees with starting diameters of 2.5, 7.6, 9.0, 12.7 or 15.0 cm. For most summaries and comparisons among sites, we used 10 cm as the minimum tree dbh (diameter at breast height) and as the minimum diameter for coarse woody debris inventories. Old-growth sites for which the quantifiable character of the forests could not be computed and compared using the 10 cm minimum diameter are nevertheless included in our tables to provide additional sources of reference. Information was synthesized through detailed summaries, tables and comparisons

3. Results

3.1. Physiographic Region

3.1.1. Piedmont

Piedmont extends from southeastern New York and northern New Jersey to central Alabama (Figure 1). The oak-pine region described by Braun [9] generally coincides with the Piedmont region, especially in the Carolinas and adjacent Georgia. White, black, post (*Quercus stellata* Wangenh.), northern red and southern red (*Quercus falcata* Michx.) oaks and loblolly (*Pinus teada* L.), shortleaf (*Pinus echinate* Mill.) and Virginia pine (*Pinus virginiana* Mill.) characterize upland forests in the oak-pine region. In general, the successional sequence in old fields abandoned from agriculture is herbaceous and shrub cover succeeding to pine forest, which then succeeds in mixed pine-oak, oak or oak-hickory forest.

Old growth examples

The Hutcheson Memorial Forest is a 26 ha suburban forest surrounded by fields in the New Jersey Piedmont (Figure 1) that has had little human disturbance in the past three centuries [10]. The canopy cover percent for canopy dominants, white oak, black oak, and red hickory (*Carya ovalis* (Wangenh.) Sarg.) remained relatively unchanged for three decades. [It should be noted that the taxonomy of red hickory is controversial. The species has also been classified as pignut hickory (*C. glabra (Mill.) Sweet*), as a variety of *C. glabra* and as an inter-specific hybrid between pignut hickory and shagbark hickory (*C. ovata* (Mill.)K.Koch.)] [11]. Flowering dogwood (*Cornus florida* L.) was the only tree species to decrease canopy cover. Maple-leaf viburnum (*Viburnum acerifolium)* was the most common shrub and mayapple (*Podophyllum peltatum* L.) and Japanese honeysuckle (*Lonicera japonica* Thunb.) dominated the herbaceous layer [12]. Wind (hurricanes) and drought appeared to be the most important disturbance factors producing canopy gaps.

Oosting's [13] exhaustive study of plant communities in the North Carolina Piedmont (Duke Forest) included a "climax" white oak-post oak type with trees 200–300 years old and little evidence of disturbance. Besides white and post oak, several hickory species, scarlet oak (*Quercus coccinea* Münchh) and northern red oak were present in the overstory. Shortleaf pine was well represented, and some loblolly pines were noted. Associated species included black oak, sourwood (*Oxydendrum arboreum* [L.] DC.), flowering dogwood, black gum (*Nyssa sylvatica* Marsh.) and red maple (*Acer rubrum* L.). Common shrubs included viburnum (*Viburnum* spp. L.) and blueberry (*Vaccinium* spp. L.) species.

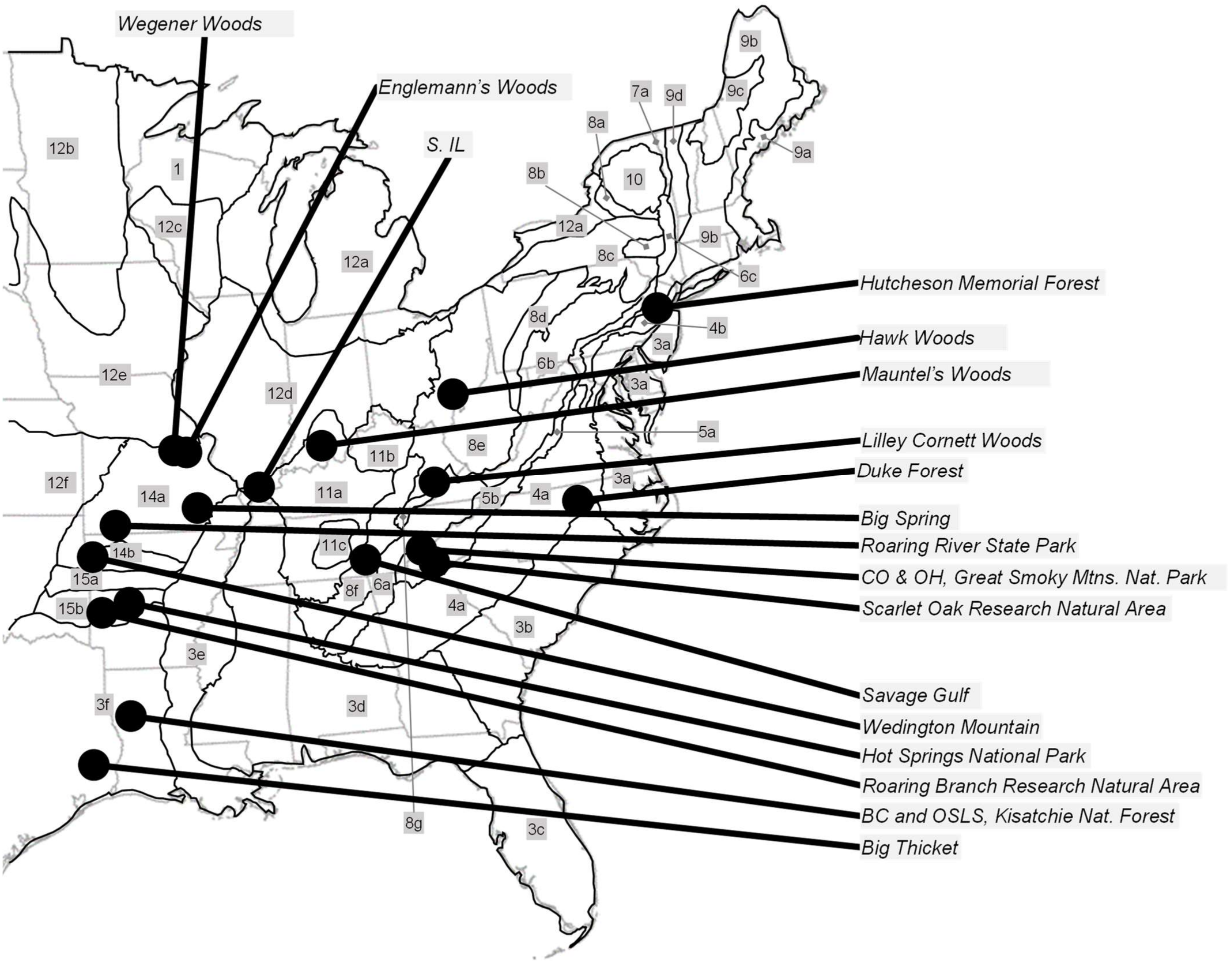

Figure 1. Map of the dry-mesic old-growth sites discussed in this manuscript by physiographic region. Grey lines are state boundaries and black lines are physiographic region boundaries. BC represents Bob's Creek and OSLS represents Old Shortleaf Slope stand. Physiographic Region codes (in gray boxes on map): 1—Superior Upland; 3a—Coastal Plain, embayed section; 3b—Coastal Plain, sea island section; 3c—Coastal Plain, Floridian section; 3d—Coastal Plain, east gulf coastal plain; 3e—Coastal Plain, Mississippi alluvial plain; 3f—Coastal Plain, west gulf coastal plain; 4a—Piedmont province, piedmont upland; 4b—Piedmont province, piedmont lowlands; 5a—Blue Ridge province, northern section; 5b—Blue Ridge province, southern section; 6a—Valley and Ridge province, Tennessee section; 6b—Valley and Ridge province, middle section; 6c—Valley and Ridge province, Hudson Valley; 7a—St. Lawrence Valley, Champlain section; 8a—Appalachian Plateaus province, Mohawk section; 8b—Appalachian Plateaus province, Catskill section; 8c—Appalachian Plateaus province, Southern New York section; 8d—Appalachian Plateaus province, Allegheny Mountain section; 8e—Appalachian Plateaus province, Kanawha section; 8f—Appalachian Plateaus province, Cumberland plateau section; 8g—Appalachian Plateaus province, Cumberland Mountain section; 9a—New England Province, Seabed Lowland section; 9b—New England Province, New England upland section; 9c—New England Province, White Mountain section; 9d—New England Province, Green Mountain section; 10—Adirondack province; 11a—Interior Low Plateaus, Highland Rim section; 11b—Interior Low Plateaus, Lexington Plain; 11c—Interior Low Plateaus, Nashville Basin; 12a—Central Lowland, Eastern Lake section; 12b—Central Lowland, Western Lake section; 12c—Central Lowland, Wisconsin Driftless section; 12d—Central Lowland, Till Plains; 12e—Central Lowland, Dissected Till Plains; 12f—Central Lowland, Osage Plains; 14a—Ozark Plateaus, Springfield-Salem plateaus; 14b—Ozark Plateaus, Boston "Mountains"; 15a—Ouachita province, Arkansas valley; 15b—Ouachita province, Ouachita Mountains.

3.1.2. Appalachian Plateaus

The Appalachian Plateaus Province extends from southern New York to northern Alabama [14]. Much of the area is underlain by nearly horizontal beds of sandstone [15]. Most of this region was included in Braun's [9] Mixed Mesophytic Forest. However, inclusions of oak-chestnut and oak-hickory communities develop on drier sites [9].

Old growth examples

Appalachian Plateaus: Allegheny Plateau

Located in the unglaciated section of the Allegheny Plateau within the Mixed Mesophytic Forest Region, Hawk Woods is a 35 ha privately owned forest near Athens, OH, that exhibits no evidence of human disturbance, such as stumps or road scars [16]. An abundance of large trees and a species-rich herbaceous layer were also cited as evidence of an old-growth forest. While mixed meosphytic or mixed oak-yellow poplar (*Liriodendron tulipifera* L.) types constituted 75 percent of the forest, white oak, oak-hickory and oak-heath types were recognized on upper slopes and ridge tops with westerly aspects. The latter types characterize dry-mesic oak forests. White, chestnut and scarlet oak predominated in one or more of these types; scarlet and chestnut oaks were especially important in the oak-heath type. Sugar maple (*Acer saccharum* L.), red and black oak, and white ash (*Fraxinus americana* L.) were associates. Sugar maple and dogwood predominated in the sapling size class beneath the oak overstory. There was little evidence of disturbance in Hawk Woods, leading McCarthy et al. [16] to conclude that oak-dominated stands would eventually succeed in sugar maple dominance.

Appalachian Plateaus: Cumberland Plateau

Lilley Cornett Woods is located in the Cumberland Plateau region in southeastern Kentucky. When acquired by the state in 1969, it was reported to contain approximately 106 ha of near-virgin forest [17]. Although centered within the Mixed Mesophytic Forest Region defined by Braun [9], the dissected landscape resulting in variations in microclimatic and soil conditions is associated with the distribution of diverse plant communities. Oak communities occupy the more xeric sites, i.e., steep south-facing slopes (>40 percent), and/or upper slopes and ridge crests [17]. White oak, chestnut oak and, to a lesser extent, black and scarlet oaks predominate [17,18]. Eastern hemlock (*Tsuga canadensis* L. [Carr.]) and American beech (*Fagus grandifolia* Ehrh.) are also major canopy species; the presence of hemlock on south slopes appears to be associated with finer-textured soils derived from shale and siltstone rather than adjacent sandstone, according to Martin [17]. Virginia pine, mockernut and pignut hickory, and red maple were also well represented. Muller [19] compared the stand structure for a portion of the old-growth at Lilley Cornett Woods with an adjacent second growth stand. This work identified three species groupings for old growth based on the distribution of American beech, sugar maple, red maple and chestnut oak. The chestnut oak-red maple type on upper slope positions is representative of dry-mesic oak forests. These sites exhibited lower soil fertility and moisture levels than adjacent sites, supporting mesophytic forests. McEwan and Muller [20] found that oak in the subcanopy was becoming limited to the driest areas of the forest, further emphasizing the importance of dry-meisc sites to maintaining oak successional durability.

The Savage Gulf on the western Cumberland Plateau (Grundy County, TN, USA) is reported to support one of the largest areas of virgin forest in the eastern US [21]. Sherman [21] identified six community types, many of which contained species typical of mesic conditions, such as white basswood (*Tilia heterophylla* Vent.), yellow poplar, sugar maple and hemlock. However, a chestnut oak type occurring on sandy shallow soils on steep upper south slopes is representative of the dry-mesic oak type. Fewer canopy species were present in this type relative to other community types that are representative of mesic conditions. In addition to chestnut oak, common species in the canopy were mockernut hickory (*Carya tomentosa*), shagbark hickory and northern red oak. Common tree species in the understory included red maple, dogwood and black gum. Disturbance from blowdowns, fire or boulder movement appears to provide gaps for the regeneration of the dry-mesic oak forest type. Data for Sherman's [21] mockernut hickory-northern red oak type are also included in Tables 1 and 2 and Appendices A and B. However, the greater species diversity including yellow poplar, cucumbertree (*Magnolia accuminata* L.), hemlock and others suggest that it contains inclusions that are more mesic than conditions that typify the dry-mesic oak type.

3.1.3. Ridge and Valley

The Ridge and Valley Province, lying parallel to and west of the Blue Ridge Mountains, extends from the Champlain-Hudson region of eastern New York to central Alabama. The ridge and valley topography results from differential weathering and erosion of folded, and sometimes faulted, sedimentary rocks [15]. This relatively narrow and long region reaches its maximum width in Pennsylvania. Braun [9] named the forest region predominating in the Ridge and Valley Province as oak-chestnut, although the American chestnut (*Castanea dentata*) was composed of dead or nearly dead trees at the time.

Old growth example

Nowacki and Abrams [22] reported on the relationships between relatively undisturbed oak stands and soil-site factors in central Pennsylvania. The focus of their work was not "old-growth" forests and results are not presented as ideal examples of old-growth stand attributes. However, species composition data for their ridge crest, upper north and south slopes, and coarse-textured valley floor physiographic divisions provide a useful description of dry-mesic oak forests in the Ridge and Valley.

Chestnut, northern red, black, white and scarlet oaks were dominant on these sites; species other than oaks were observed only in the canopy on mesic sites in the study area. Oak regeneration was well represented on all the sites; other understory species present on dry-mesic sites included red maple, striped maple (*A. pensylvanicum* L.), sweet birch (*Betula lenta* L.), and black cherry (*Prunus serotina* Ehrhart). The authors concluded that oak would decrease in the future, while red maple and sweet birch would increase on drier slopes and ridge crests.

Table 1. Stand density (# ha^{-1}) of representative dry-mesic old-growth oak forests.

Quantifiable Attribute	Range	Mean	No. of Stands	References
STAND DENSITY (# ha^{-1})				
Piedmont				
Hutcheson Memorial Forest (≥10 cm dbh)	556–564	560	1	[23] [24]
Duke Forest				
White oak (≥2.5 cm dbh)	1789–1853	1831	3	[13]
Post oak (≥2.5 cm dbh)	1460–2300	1826	3	
Appalachian Plateaus				
Allegheny Plateau				
Hawk Woods (≥10 cm dbh)	250–443	341	3	[16] [24]
Cumberland Plateau				
Lilley Cornett Woods (≥12.7 cm dbh)	289–395	346	5	[17]
Chestnut oak-R. maple (≥10 cm dbh)		450	1	[19]
Savage Gulf				
Chestnut oak (≥12.7 cm dbh)		398	1	[21]
Hickory-Red oak (≥12.7 cm dbh)		454	1	[21]
White oak (≥10 cm dbh)		620	12	[25]
Ridge and Valley				
South Central Pennsylvania				
Ridge and upper slopes (≥10 cm dbh)	408–714	521	9	[22] 1991 (Data)
Middle Slopes (≥10 cm dbh)	403–546	477	4	

Table 1. *Cont.*

Quantifiable Attribute	Range	Mean	No. of Stands	References
STAND DENSITY (# ha^{-1})				
Blue Ridge Mountains				
Great Smoky Mountain NP				
Oak-Hickory (≥10 cm dbh)		403	1	[26] (data)
Chestnut oak (≥10 cm dbh)		620	1	[26] (data)
Scarlet Oak (≥7.6 cm dbh)	620–991	783	4	[27]
Interior Low Plateau				
Shawnee Hills				
Southern Indiana—Mauntel's Woods (≥10 cm dbh)		430		[28]
Southern Illinois				
South Slope (≥10 cm dbh)		415	1	[29] p 300
Upper North Slope (≥10 cm dbh)		377	1	
Interior Highlands				
Ouachita Mountains				
Hot Springs N.P. (≥9 cm dbh)	536–1527	1206	4	[30]
Roaring Branch R.N.A.				
Upper & Mid N Slope (≥15 cm dbh)		368	1	[31]
Boston Mountains				
Upper West Slope (≥15 cm dbh)		600	1	[32]
Springfield Plateau				
Roaring River State Park				
1992				
North & East Slopes (≥10 cm dbh)	310–600	442	1	[33] (1992 Data)
Ridge + S & W Slopes (≥10 cm dbh)	300–580	443	1	[33] (1992 Data)
2011				
North & East Slopes (≥10 cm dbh)	240–590	390	1	[34] (2011 Data)
Ridge + S & W Slopes (≥10 cm dbh)	280–600	435	1	[34] (2011 Data)
Salem Plateau				
Big Spring (≥10 cm dbh)	310–770	469	1	[33] (1992 Data)
Big Spring (≥10 cm dbh)	280–560	402	1	[34] (2011 Data)
Missouri River Hills				
Englemann Woods				
Ridge + S & W Slopes (≥10 cm dbh)	460–670	535	1	[33] (1992 Data)
	277–530	407	1	[34] (2011 Data)
Wegener Woods (≥9 cm dbh)		376	1	[35]
Southern Coastal Plain				
Western Gulf				
Kisatchie Natl Forest (≥12.7 cm dbh)				
Old Shortleaf Slope		280	1	[36]
Bob's Creek		151	1	

3.1.4. Blue Ridge Mountains

The Blue Ridge Mountains range from southern Pennsylvania to northern Georgia, between the Piedmont to the east and the Ridge and Valleys to the west. Braun [9] placed the forests of the Blue Ridge Mountains into her oak-chestnut region while recognizing the great diversity in forest cover it encompassed. Principal types that she recognized at "moderate elevations," which presumably would represent a majority of the landscape, were (1) oak or oak-chestnut covering most of the slopes, (2) mixed mesophytic or cove hardwoods and hemlock or hemlock-hardwood in more mesic environments, and (3) oak and oak-pine on dry slopes and ridges.

Table 2. Basal area (m^2 ha^{-1}) of representative dry-mesic old-growth oak forests.

Quantifiable Attribute	Range	Mean	No. of Stands	References
BASAL AREA (m^2 ha^{-1})				
Piedmont				
Hutcheson Memorial Forest				
(≥10 cm dbh)	26–27	27	1	[24]
Duke Forest				
White oak (≥2.5 cm dbh)	37–44	40	3	[13]
Post oak (≥2.5 cm dbh)	27–38	32	3	
Appalachian Plateaus				
Allegheny and Cumberland Plateaus				
Hawk Woods				
(≥10 cm dbh)	22–41	29	3	[16]
Lilley Cornett Woods				
(≥12.7 cm dbh)	24–29	26	5	[17]
Chestnut oak-red maple (≥10 cm dbh)		26	1	[19]
Savage Gulf				
Chestnut oak (≥12.7 cm dbh)		37	1	[21]
Hickory-Red oak (≥12.7 cm dbh)		37	1	
White oak (≥10 cm dbh)		29	12	[25]
Ridge and Valley				
South Central Pennsylvania				
Ridge & upper slopes (≥10 cm dbh)	22–38	29	9	[22] 1991 (Data)
Middle Slopes (≥10 cm dbh)	31–42	36	4	
Blue Ridge Mountains				
Great Smoky Mountain NP				
Oak-Hickory (≥10 cm dbh)		28	1	[26]
Chestnut oak (≥10 cm dbh)		30	1	[26]
Scarlet Oak				
(≥7.6 cm dbh)	17–26	22	4	[27]
Interior Low Plateau				
Shawnee Hills				
Southern Indiana—mauntel's woods				
(≥10 cm dbh)		33	1	[28]
Southern Illinois				
South Slope (≥10 cm dbh)		21	1	[29]
Upper North Slope (≥10 cm dbh)		26	1	
Interior Highlands				
Ouachita Mountains				
Hot Springs N.P. (≥9 cm dbh)	13–23	19	4	[30]
Roaring Branch R.N.A. (≥10 cm dbh)				
Upper and Mid North Slope		18	1	[31]
Boston Mountains				
Upper West Slope (≥15 cm dbh)		25	1	[32]
Springfield Plateau				
Roaring River State Park				
1992				
North & East Slopes (≥10 cm dbh)	14–32	23	1	[33] (1992 Data)
Ridge + S & W Slopes (≥10 cm dbh)	12–28	20	1	
2011				
North & East Slopes (≥10 cm dbh)	15–33	23	1	[34] (2011 Data)
Ridge + S & W Slopes (≥10 cm dbh)	16–29	21	1	
Salem Plateau				
Big Spring (≥10 cm dbh)	17–28	22		[33] (1992 Data)
Big Spring (≥10 cm dbh)	15–32	22	1	[34] (2011 Data)
Missouri River Hills				
Englemann Woods				
1992				
Ridge + S & W Slopes (≥10 cm dbh)	16–29	22	1	[33] (1992 Data)
2011				
Ridge + S & W Slopes (≥10 cm dbh)	12–27	21	1	[34] (2011 Data)
Wegener Woods (≥10 cm dbh)		20	1	[35]
Southern Coastal Plain				
Western Gulf				
Kisatchie National Forest (≥12.7 cm dbh)				
Old Shortleaf Slope		32	1	[36]
Bob's Creek		14	1	
Big Thicket (≥1 cm dbh)				
Mid Slope Oak Pine Forest		32	1	[37]

Old growth examples

Scarlet Oak, a proposed research natural area in the Pisgah District, Pisgah National Forest, in Henderson County, North Carolina, has been reported to exhibit old-growth attributes [27]. Scarlet oak trees predominated, followed by chestnut oak and pitch pine (*Pinus rigida*) in terms of the relative basal area. Sourwood, white oak and red maple were also present (Appendix A). On the driest, most exposed sites, pitch pine sometimes achieved co-dominance with scarlet oak. Dominant shrubs were mountain laurel (*Kalmia latifolia* L.) and black huckleberry (*Gaylussacia baccata* [Wang.] K. Koch) and blueberry species (Appendix B). By 1983, the mature scarlet oaks had reached their physiological maturity and were beginning to die. Due to that mortality, the proposed area was not formally established as a research natural area but rather as a special use area (personal communication with W. Henry McNab 2020).

Great Smoky Mountains National Park contains over 64,500 ha of montane oak-hickory forests, comprising 31 percent of forest cover in the park [26]. Over 20 percent of the park was never logged or cleared for agriculture and includes areas of oak-dominated old-growth forest. According to Jenkins [26], an old-growth montane oak-hickory forest in the Cataloochee area of the park was dominated by northern red oak, chestnut oak, white oak, and red maple. Historically, American chestnut was a codominant species in this forest. The understory was relatively open and dominated by striped maple (*Acer pensylvanicum* L.), serviceberry (*Amelanchier laevis* Wiegand) and residual sprouts of American chestnut. The herbaceous layer of this forest contained 51 species with a smooth Solomon's seal [*Polygonatum biflorum* (Walter) Elliott], false Solomon's seal [*Maianthemum racemosum* (L.) Link ssp. *racemosum*] and white lettuce (*Prenanthes* spp. L.) (Appendix C). Located on a more exposed ridge, an old-growth chestnut oak forest in the Greenbrier area of the park was dominated by chestnut oak, with lesser components of northern red oak and red maple in the overstory and an understory heavily dominated by a dense shrub layer of rosebay rhododendron (*Rhododendron maximum* L.) and mountain laurel. The herbaceous layer was relatively depauperate, containing only 11 species with galax (*Galax urceolata* [Poir.] Brummitt) and greenbrier (*Smilax rotundifolia* L.), displaying the greatest cover (Appendix C).

3.1.5. Interior Low Plateaus

This province ranges from the Shawnee Hills of southern Indiana through the Nashville Basin of central Tennessee, which is surrounded by the Highland Rim, and into northern Alabama. The Bluegrass Region of central Kentucky is also included. Thus, it includes major rivers that facilitated early settlement and undisturbed forests are a rarity. This area essentially coincides with Braun's [9] Western Mesophytic Forest Region. See [38] for a definition of old-growth Western and Mixed Mesophytic forests. They reported Western Mesophytic Forests to be "oak-dominated" and lacking yellow buckeye (*Aesculus flava* Marshall) and basswood (*Tilia americana* L.), which are indicators for the mixed mesophytic type.

Old growth examples

<u>Interior Low Plateau: Shawnee Hills</u>

A 6 ha "virgin" forest in the Shawnee Hills of southwest Indiana, Mauntel's Woods, was described in 1934 by Potzger and Friesner [28] and the data were cited by Braun in 1950 [9]. White and black oaks and shagbark and pignut hickories dominated the main canopy. Flowering dogwood was the predominate species present below the main canopy—the authors thought the absence of sugar maple, American beech, American hornbeam (*Carpinus caroliniana* Walt.) and hophornbeam (*Ostrya virginiana* Mill.), to be noteworthy. Whereas most of the dry-mesic oak forests described in the eastern U.S. contained some pine species, Eastern redcedar (*Juniperus virginiana* L.) was the only conifer reported in this stand.

Fralish et al. [29] compared present-day "old-growth" forests with presettlement forests reconstructed from witness tree data in the General Land Office survey records from 1806–1807 in the Illinois Shawnee Hills region. They categorized six site types: rocky south slope, south slope, ridgetops, high north slope, low north slope and terrace. The rocky slopes are xeric and the north slopes and terraces are mesic. South slopes and ridgetop sites represent dry-mesic environments (Fralish, personal communication 2002). White oak and black oak were the most important species on these sites and the existing "old-growth" appeared representative of presettlement forests. Post oak and pignut hickory were also present. At mesic sites, differences in composition and structure between existing old-growth and presettlement forests were attributed to protection from fires. Presettlement forests on mesic sites were dominated by oaks but are rapidly shifting in composition to sugar maple and other mesic species.

3.1.6. Interior Highlands

The Interior Highlands include the Ouachita Mountains of eastern Oklahoma and western Arkansas, the Boston Mountains in northwest Arkansas, and the Ozark Plateau, including the Springfield and Salem Plateaus of northern Arkansas and southern Missouri. Forests here represent the westerly extent of the Eastern Deciduous Formation. Braun's [9] oak-hickory region is centered in this physiographic province and extends into glaciated areas to the north. The zone of forest–prairie transition, often called Cross Timbers, is composed of post and blackjack oak (*Quercus marilandica*) and lies to the west.

Old growth examples

Interior Highlands: Ouachita Mountains

A comprehensive survey of the vegetation of Hot Springs National Park in Arkansas provided information on oak forests in the Ouachita Mountains [30]. Four community types were identified: (1) a mixed forest type restricted to the most mesic environments in creek bottoms and ravines; (2) a xeric pine-oak hickory type on dry south slopes near ridgetops with shortleaf pine dominating the overstory; (3) an upland hardwood type along ridgetops and sloping or flat areas throughout the park; and (4) the oak hickory-pine type as the most extensive. The occurrence of these types correlates with exposure and slope, which influence soil moisture conditions.

In decreasing order, oak species represented in the upland hardwood type were white, southern red, black and northern red. Shortleaf pine, post oak, and bitternut hickory [*Carya cordiformis* (Wangenh.) K. Koch] was also present. Although shortleaf pine was the single most important species in the oak hickory-pine type, the combined oak and hickory basal area exceeded the shortleaf pine component; shortleaf pine represented 25 to 30 percent of the basal area, while the hardwood composition was similar to the upland hardwood type. Blueberry species and cypress panicgrass (*Panicum dichotomum* L.) were among the more prominent species on the forest floor.

While the Hot Springs National Park vegetation study provided valuable information on the distribution of trees, shrubs and herbaceous species, the Roaring Branch Research Natural Area (RBRNA) appears to provide the best source of information on the attributes of old-growth dry-mesic oak forests in the Ouachita Mountains. Established in 1969 on the Caddo Ranger District of the Ouachita National Forest [39], the RBRNA encompasses 121 ha, with no evidence of commercial timber harvest and limited access via foot trails. The topography is characterized by steep, parallel ridges with a southwest–northeast orientation. This orientation results in north- or south-facing slopes with wide differences in the microclimate.

White oak, northern red oak and mockernut hickory were the three most important species on both north and south slopes. However, there were some significant differences for the other species. While shortleaf pine was the next most important species on south slopes, measured by importance value, it was not found on north slopes where blackgum (*Nyssa sylvatica*) ranked fourth. Data from mid- and upper-north slopes are reported in the tables as representative of the dry-mesic oak type, as these sites rank intermediate between the xeric south slopes and the mesic lower-north slopes. Dominant shrubs for the mid- and upper-north slopes included witch hazel (*Hamamelis virginiana* L.), lowbush blueberry (*Vaccinium vacillans* Torr.), mountain azalea (*Rhodeodendron roseum* f. *albidum* Steyer), and poison ivy (*Toxicodendron radicans* L.).

Interior Highlands: Boston Mountains

The Boston Mountains are located mainly in northwest Arkansas, between the Arkansas river valley to the south and the Ozarks to the north. Although topography is generally similar to the Ozarks, soils are derived from interbedded sandstone and shale, while Ozark soils are derived from highly weathered limestone and dolomite. Soils across the region are generally low in productivity. The Boston Mountains also have generally higher elevations (max. 780 m) compared to the Ozarks (max. 549 m).

Old growth examples

The tree ring chronology work of Stahle et al. [32] provided information on remnants of old-growth forests in the Interior Highlands. An undisturbed post oak forest on the upper slopes of Wedington Mountain in northwest Arkansas serves as an example of the dry-mesic oak type in the Boston Mountains; however, site conditions trend toward a xeric environment. In addition to post oak, which constituted nearly one-half the basal area, northern red oak and mockernut hickory were also common canopy species. Other species present include blackjack, white, and black oak; serviceberry (*Amelanchier arborea* (Michx.f.) Fern.); white ash; persimmon (*Diospyros virginiana* L.); and ironwood (*Carpinus caroliniana* Walt.). Stahle et al. [32] reported that white and red oak increased in importance on the more mesic north slopes.

Interior Highlands: Springfield Plateau

The Springfield Plateau lies north of the Boston Mountains in northwest Arkansas and southwest Missouri. It includes that portion of the Ozarks mainly underlain by Mississippian-age rocks.

Old growth examples

Roaring River State Park in southwest Missouri contains a 49-ha old-growth tract with trees of 200 to 250 years old [40]. Forests are principally xeric to dry-mesic oak-hickory [34,41]. White, black, post and northern red oaks, mockernut hickory, black hickory (*Carya texana*) and black gums were present in the canopy. Flowering dogwood, serviceberry and hickory species were present in the understory. An endangered Ozark chinkapin (*Castenea ozarkensis* Ashe) was reported to occur here [42]. In the primarily dry-mesic old-growth portion, mean stand density was 442 trees ha^{-1} in 1992 and 390 in 2011, mean basal area was 23 m^2 ha^{-1} in both the 1992 and 2011 inventories on north and east slopes and 20 m^2 ha^{-1} in 1992 and 21 m^2 ha^{-1} in 2011 on ridge and south and west-facing slopes, maximum age of large trees was 330 years [40], the largest trees were 69 cm in 2011, number of 10 cm diameter classes was 7 in 2011, mean number of snags was 30.6 in 1992 and 34.7 in 2011, coarse woody debris ranged from 34.2 m^3 ha^{-1} in 1992 to 32.5 m^3 ha^{-1} in 2011.

Interior Highlands: Salem Plateau

The Salem Plateau includes much of southeastern and south-central Missouri west of the Mississippi Alluvial Plain. Underlying rocks are mainly of Ordovician age and older. Soils are cherty loams and silt loams that are well to excessively drained.

Old growth examples

The Big Spring site is a 134-ha tract in the Ozark Scenic Riverway in Carter County, MO. Forest associations are xero-mesic to xeric oak-hickory and oak-pine [34,41]. Prior examination classified the site as a mixture of old-growth and old second-growth oak and oak-pine [43]. The dominant overstory species are white and scarlet oak and shortleaf pine. Dogwood, white oak, and hickory spp. dominate the woody understory. According to Lowney [34], in the dry-mesic old-growth portion, mean stand density was 469 ha^{-1} in 1992 and 402 ha^{-1} in 2011, mean basal area was 22 m^2 ha^{-1} in both the 1992 and 2011 inventories, mean age of large trees was 141 years for post oak and 120 years for white oak in 1992, largest trees were 69 cm dbh in 2011, number of 10 cm diameter classes was 6 in 2011, mean number of standing snags was 38 ha^{-1} in 1992 and 43.3 ha^{-1} in 2013, mean volume of coarse woody debris ranged from 32.0 m^3 ha^{-1} in 1992 to 48.5 m^3 ha^{-1} in 2011.

Interior Highlands: Missouri River Hills

The Missouri River Hills are found between the glaciated Till Plains to the north and the unglaciated Ozarks to the south. A thick layer of deep loess distinguishes the soil characteristics of this area from adjacent physiographic provinces. Soil depth and fertility are favorable for tree growth. Oak-hickory forests occur on drier slopes and mesophytic species are located on northerly slopes and lower slope positions.

Old growth examples

Englemann Woods is a 60-ha forest located near the Missouri River in Franklin County, Missouri. This forest is designated as a natural area in the Missouri Department of Conservation system. The dry-mesic portion of the forest is located on ridge, south- and west-facing slopes, where dominant canopy species include chinkapin oak (*Quercus muehlenbergii* Engelm.). This is one of only three dry-mesic old-growth sites in the eastern U.S., in which we have data from repeated inventories using the same plots and measurement methods. The other two sites are the Big Spring site on the Salem Plateau and the Roaring River State Park on the Springfield Plateau (see previous paragraphs in this Interior Highlands section). In 1992, Englemann Woods basal area ranged from 16 to 29 m^2 ha^{-1} with a mean of 22 m^2 ha^{-1}. By 2011, basal area ranged from 12 to 27 m^2 ha^{-1} with a mean of 21 m^2 ha^{-1}. In 1992, the maximum age of large trees was 204 years for chinkapin oak. In 2011, the diameter of dominant and codominant trees ranged from 36 to 43 cm dbh with a mean diameter of 41 cm dbh for white oak and 23 to 69 cm dbh for chinkapin oak with a mean diameter of 36 cm dbh. The mean number of standing snags in this area was 43 ha^{-1} in 1992 and 32 in 2011. The mean volume of coarse woody debris increased over a 19-year period from 23 m^3 ha^{-1} in 1992 to 30.2 m^3 ha^{-1} by 2011.

Wegner's Woods, in Warren County, Missouri, is a 16-ha stand of upland hardwood forest preserved by the same family since 1853 [35]. Although the Missouri Natural Areas Inventory has classified this stand as dry-mesic, the relatively deep, fertile, silt loam soils likely make this a more productive site for tree growth than other dry-mesic sites. This site was designated by the Secretary of the Interior as a National Natural Landmark (a program administered by the National Park Service) in 1975. Programs like this one have played a key role in preserving old-growth forests across the eastern United States.

According to Government Land Office surveys from 1816–1817, forests in the region were composed primarily of white oak with black oak, sugar maple, and species of elms (*Ulmus* spp.), hickories and ash, as well as hackberry (*Celtis occidentalis* L.) and black walnut (*Juglans nigra* L.). Wuenscher [35] reported on the species composition and structure of Wegner's Woods. Based on sampling in 1966, large-diameter white oaks averaged 43 cm dbh, and white oak was the dominant species in terms of basal area. The mean number of 10 cm size classes was 9. Bitternut hickory was also well represented in the main canopy. Wuenscher [35] characterized this stand as consisting of large old white oak and bitternut hickory transforming into a sugar maple stand. Slippery elm (*Ulmus rubra* Muhl.) and white ash were also reported.

3.1.7. Southern Coastal Plain: Gulf Coast

The Southern Coastal Plain lies along the Atlantic and Gulf coasts from Virginia to Texas [9], varying in width from about 150 miles in the Atlantic section to 400 miles in the Gulf section. Braun [9] considered the Southeastern Evergreen Forest Region to coexist with the Coastal Plain except at the north end and in the Gulf States, where the Oak-Pine Forest Region is transitional between the central deciduous forest and the Southeastern Evergreen Forests. Deciduous trees do not predominate in the evergreen forests and cycles of clearing, cultivation and abandonment in much of the oak-pine region has maintained pine in much of the region [9]. Accessibility to coastal ports and gentle topography has also facilitated timber harvesting or land clearing so that examples of undisturbed old-growth hardwood forests are very rare.

Old-growth examples

The dry and dry-mesic oak-pine type is more significant in the Gulf section than in the Atlantic section of the Southern Coastal Plain [44]. A survey and classification of natural plant communities in the Kisatchie and Winn Districts, Kisatchie National Forest, in central Louisiana identified two stands that provide some insight into old-growth coastal plain forest with an oak component [36]. These two stands, both in the Kisatchie District, were characterized as old-growth shortleaf pine/oak-hickory forests, with a few stumps suggesting past selective harvests. Post oak, white oak, and southern red oak comprised

50 percent or more of the basal area. Shortleaf pine, lesser amounts of loblolly pine, and mockernut hickory were also present in the stand. Hophornbeam and dogwood dominated the mid-story. Numerous dead and fallen trees were observed. Low light levels limited the abundance of understory shrubs, but Elliott's blueberry (*Vaccinium elliottii* Chapman), yaupon (*Illex vomitoria* Aiton.) and azalea (*Rhodendron canescens* [Michaux] Sweet) were found.

Martin and Smith [36] believed the shortleaf/oak-hickory forests often occurred adjacent to longleaf pine forests (*P. palustris* Mill) during presettlement times. They estimated growing season burns, at frequencies of 5 to 15 years, burned through the shortleaf/pine-oak forests. They speculated that this regime tended to favor shortleaf pine because of its sprouting ability and the prevalent oaks over more "fire-tender" species such as American beech and sweet gum (*Liquidambar styraciflua* L.). They suggest that the fire-prone longleaf pine forests served as a fire source for adjacent communities such as shortleaf/pine-oak forests.

3.2. Old Growth Conditions

3.2.1. Ownership

Currently, these old-growth forests are protected through a range of ownerships, including public lands (such as state parks, natural areas, the National Natural Landmark program and university properties), as well as private landowners and conservancies. Historically, many of these forests received protection as part of privately owned family farms, ensuring their survival into the present day [45]. Conservation land trusts have played a role in the further protection of properties that previously were privately held. The few remnant old-growth forests that exist in the eastern U.S. today are the result of the combined actions of all of these private and public entities.

3.2.2. Living Tree Component

The range in density was quite large due to differences in degree of disturbance and site conditions resulting in mean site density among studies (for those that measured trees $\geq$10 cm at dbh) of 341–620 trees ha^{-1} (Table 1). Higher densities at Hot Springs National Park included a high density of shortleaf pine comprising approximately 50 percent of all stems; however, this inventory included trees down to 9 cm dbh. Mean stand basal areas for the studies that measured trees $\geq$10 cm at dbh were greater than 23 m^2 ha^{-1} in 78 percent of eastern U.S. stands, and less than or equal to 23 m^2 ha^{-1} in westernmost stands, which included all stands in physiographic regions 14a, 14b, 15a and 15b (Figure 1, Table 2).

Oak species associated with dry-mesic sites are intermediate in shade tolerance [46]. White oak, found at 91 percent of sites, was the most common tree species documented on these dry-mesic sites (Appendix A). Canopy disturbance is necessary to provide for the continued development of oak regeneration. However, the role of fire on dry-mesic sites is not as clear as it is for moister sites (see our disturbance section for details). Infrequent gap-creating disturbance events, as well as sporadic seed production, contribute to irregular age-class distributions in these old-growth stands. Therefore, some but not all trees in stands with old-growth attributes will be of advanced age. See Appendix A for a comprehensive list of tree species found on the dry-mesic old-growth sites discussed in this manuscript.

The maximum within-stand age for large trees ranged from 170 to 365 years old (Table 3). Species in the white oak group (white, chestnut and post oak) were generally older than those in the red oak group (northern and southern red, scarlet and black oak). In the stands examined in this paper, trees in the Piedmont and Appalachian Mountains stands were older than most of those in the western physiographic regions.

To the lay public, a large tree diameter is likely the single attribute most often associated with the concept of an old-growth forest. However, tree diameter is influenced by site productivity and stand density, as well as age. While Martin [47] suggested that at least 7 trees ha^{-1} >75 cm dbh indicated old-growth for mixed mesophytic forests, these forests typically occur on more productive sites within the Eastern Deciduous Forest. The maximum diameters for oak species in stands examined in this paper ranged from 34 to 102 cm (Table 4). Species in the white oak group exhibited some of the largest diameters; for example, both Wegner's Woods [35] and Hutcheson Memorial Forest [48] had white oaks with maximum tree diameters of 102 cm dbh.

Although tree diameter is not a reliable indication of actual age [49], the number of diameter classes may be related to the number of age classes. For instance, from four to nine 10 cm dbh classes were observed in the stands listed in Table 5. More refined data from two stands—(1) old-growth forest at Roaring River State Park in Missouri [34] (2013, 2011 data) and (2) Mauntel's Woods in southern Indiana [28]—exhibited a negative exponential relationship characteristic of a balanced uneven-aged stand (Figure 2). Other old-growth forest studies have reported the number of 10 cm dbh classes as 7–8 for dry and dry-mesic oak-pine forests [44], 8–11 for southern mixed hardwood forests [50] and 4–6 for xeric pine and pine-oak forests [51].

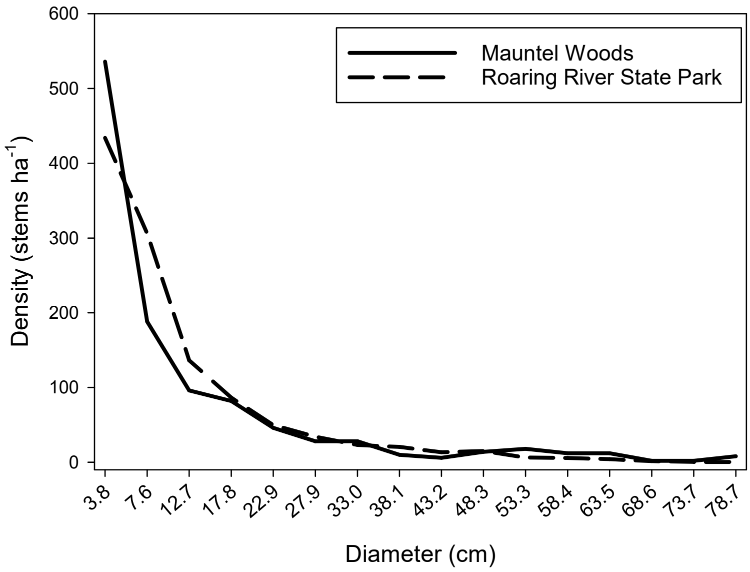

Figure 2. Comparison of the distribution of diameter classes on two dry-mesic old-growth forests, one at Roaring River State Park in Missouri and the other at Mauntel's Woods in southern Indiana.

Table 3. Age in years of large trees (dominant and codominant crown class) of representative dry-mesic old-growth oak forests.

Quantifiable Attribute	Range	Mean	No. of Stands	References
AGE OF LARGE TREES (years)				
Piedmont				
Hutcheson Memorial Forest				
White oak				
Red oak	200–324		1	[52]
Black oak				[53]
Ridge and Valley				
South Central Pennsylvania				
Ridge and Upper Slopes				
N. Red oak and black oak	84–196	119	9	[22] 1991 (Data)
Chestnut oak	84–365	170		
Sweet birch	102–230	129		
White pine	101–119	112		
Middle Slopes				
N. Red oak and black oak	80–236	123	4	[22] 1991 (Data)
Chestnut oak	80–324	159		
Mockernut hickory	133–197	171		

Table 3. *Cont.*

Quantifiable Attribute	Range	Mean	No. of Stands	References
AGE OF LARGE TREES (years)				
Blue Ridge Mountains				
Scarlet Oak				
Scarlet oak	73–123		2	[44]
Chestnut oak	66–170			
Pitch pine	117–163			
Chattooga Watershed	Max. Age (dbh-cm)			
Chestnut oak	362 (53)			[54]
White oak	348 (69)			
Northern Red oak	240 (66)			
Post oak	225 (36)			
Black oak	211 (46)			
Scarlet oak	190 (61)			
Blackgum	360 (61)			
Mockernut hickory	335 (66)			
Shortleaf pine	300 (71)			
Pitch pine	235 (69)			
Virginia pine	108 (46)			
Blue Ridge Mountains				
Great Smoky Mountain NP	Max. Age (dbh-cm)			
Chestnut oak	347 (56)			[49]
White oak	344 (69)			
Northern Red oak	270 (56)			
Black oak	180 (66)			
Scarlet oak	165 (41)			
Blackgum	319 (43)			
Red maple	220 (66)			
Pignut hickory	327 (46)			
Pitch pine	148			
Virginia pine	135 (64)			
Interior Highlands				
Ouachita Mountains				
Hot Springs N.P.				
Shortleaf pine	124–247		4	[40]
Roaring Branch RNA				
Northern Red oak	65–120	110	1	[39]
White oak	51–150	130	1	[31]
Shortleaf pine	121–300	150+	1	[40]
Boston Mountains				
Upper West Slope				
Post oak	140-253	192	1	[32]
Missouri River Hills				
Englemann Woods				
Ridge + S & W Slopes				
White oak		120	1	[33]
Black oak		103		
Chinkapin oak	139–204	172		
Wegener Woods				[40]
White oak	250-320		1	[35]
Springfield Plateau				
Roaring River State Park				
White oak	200–250		1	[40]
Post oak	200–300		1	
Salem Plateau				
Big Spring				
White oak	87–137	120	1	[33]
Black oak	107–135	120		
Post oak	(max >150)	141		
Shortleaf pine	106–116	112		

Table 4. DBH (cm) of large trees (dominant and codominant crown class) of representative dry-mesic old-growth oak forests.

Quantifiable Attribute	Value Range	Mean	No. of Stands	References
DBH OF LARGE TREES (cm)				
Piedmont				
Hutcheson Memorial Forest				
White oak	51–102		1	[48]
Black oak	51–102			
Northern Red oak & scarlet oak	51–76			
Red Hickory	38–64			
Ridge and Valley				
South Central Pennsylvania				
Ridge and Upper Slopes				
Northern Red oak & black oak	31–64	41	9	[22] 1991 (Data)
Chestnut oak	31–89	43	1	
Birch	31–46	38		
White pine		33		
Middle Slopes				
Northern Red oak & black oak	31–69	43	4	[22] 1991 (Data)
Chestnut oak	31–99	46		
Hickory	31–51	36		
Blue Ridge Mountains				
Great Smoky Mountain NP				
Oak-Hickory				
Northern Red oak	30–86	50	1	[26] (data)
White oak	37–83	60		
Chestnut oak	26–53	38		
Red maple	23–34	27		
Chestnut Oak				
Chestnut oak	18–78	47	1	[26] (data)
Scarlet oak	26–34	29		
Northern Red oak	26–41	32		
Red maple	23–34	27		
Scarlet Oak				
Scarlet oak	36–51		4	[27]
Chestnut oak	36–46			
White oak	36–46			
Pitch pine	46			
Mockernut and Pignut hickory	36–51			
Interior Low Plateau				
Shawnee Hills				
Southern Indiana—Mauntel's Woods				
White oak	51–81			[28]
Black oak	51–81			
Northern Red oak	38–51			
Shagbark hickory	25–38			
Mockernut hickory	25–38			
Pignut hickory	25–38			
Interior Highlands				
Ouachita Mountains				
Roaring Branch RNA				
Upper and Mid North Slope				
Northern Red oak	33–46	41	1	[31]
Black oak	33–46	36		
White oak	33–61	41		
Blackgum	31–46	38		
Boston Mountains				
Upper West Slope				
Post oak	28–61	41	1	[32]
Springfield Plateau				
Roaring River State Park				
White oak	33–79	51		[34] (2011 Data)
Black oak	33–69	46		
Post oak	31–51	41		
Northern Red oak	33–64	43		
Blackgum	31–61	41		
Mockernut hickory	31–48	38		
Black hickory	31–48	38		

Table 4. *Cont.*

Quantifiable Attribute	Value Range	Mean	No. of Stands	References
DBH OF LARGE TREES (cm)				
Salem Plateau				
Big Spring Natural Area				
White oak	31–69	46	1	[34] (2011 Data)
Black oak	36–69	48		
Post oak	36–53	43		
Scarlet oak	33–66	48		
Southern Red oak	31–61	46		
Northern Red oak	31–56	43		
Shortleaf pine	31–53	41		
Missouri River Hills				
Englemann Woods				
White oak	36–43	41	1	[34] (2011 Data)
Chinkapin oak	23–69	36		
Northern Red oak	28–61	43		
Shagbark hickory	31–46	36		
Sugar maple	28–41	31		
Eastern Red cedar	23–41	28		
Missouri River Hills				
Wegener Woods				
White oak	31–102	43	1	[35]
N. Red oak		41		
Shagbark hickory		33		
Sugar maple		18		
Southern Coastal Plain				
Western Gulf				
Kisatchie National Forest				
Old Shortleaf Slope	25–76	41	1	[36]
Bob's Creek	25–76	48	1	

Table 5. Number of 10 cm size classes of representative dry-mesic old-growth oak forests.

Quantifiable Attribute	Range	Mean	No. of Stands	References
NUMBER OF 10 CM. SIZE CLASSES (Starting at 10 cm)				
Piedmont				
Hutcheson Memorial Forest		9	1	[48]
Appalachian Plateaus				
Allegheny and Cumberland Plateaus				
Hawk Woods				
(≥10 cm dbh)		7	2	[16]
Ridge and Valley				
South Central Pennsylvania				
Ridge and upper slopes (≥10 cm dbh)	4–8	6	9	[22] (Data)
Middle Slopes (≥10 cm dbh)	4–9	6	4	
Blue Ridge Mountains				
Great Smoky Mountain NP				
Oak-Hickory (≥10 cm dbh)		7	1	[26] (data)
Chestnut oak (≥10 cm dbh)		7	1	[26] (data)
Scarlet Oak				
(≥10 cm dbh)	4–5	4	4	[27]
Interior Low Plateau				
Shawnee Hills				
Southern Indiana—Mauntel's Woods				
(≥10 cm dbh)		7	1	[28]
Interior Highlands				
Ouachita Mountains				
Roaring Branch RNA				
Upper & Mid North Slope				
(≥10 cm dbh)		5	1	[31]
Boston Mountains				
Upper West Slope (≥10 cm dbh)		6	1	[32]

Table 5. *Cont.*

Quantifiable Attribute	Range	Mean	No. of Stands	References
NUMBER OF 10 CM. SIZE CLASSES (Starting at 10 cm)				
Springfield Plateau				
Roaring River State Park (≥10 cm dbh)		7	1	[34] (2011 Data)
Salem Plateau				
Big Springs (≥10 cm dbh)		6	1	[34] (2011 data)
Missouri River Hills				
Englemann Woods				
Ridge + S & W Slopes (≥10 cm dbh)		8	1	[34] (2011 Data)
Wegener Woods (≥10 cm dbh)		9	1	[35]
Southern Coastal Plain				
Western Gulf				
Kisatchie National Forest				
Old Shortleaf Slope (≥12.7 cm dbh)		5 [1]	1	[36]
Bob's Creek (≥12.7 cm dbh)		5 [1]	1	

[1] Number of 12.7 cm size classes.

3.2.3. Dead Tree Component

The mean density of standing dead trees in the studies that measured snags ≥10 cm dbh ranged from 30.6 to 78 ha^{-1} (Table 6). The low number of 15 ha^{-1} at Hutcheson Memorial Forest in the New Jersey Piedmont may be due in part to the combined effects of a larger starting measurement diameter of ≥15 cm and wind—three hurricanes caused extensive damage between 1950 and 1955, 10 to 15 years prior to the inventory [55]. Investigation of natural mortality in this forest found stem breakage by wind to be the most significant cause of mortality [56]. This factor alone could account for the low number of standing snags by the time of the 1965 study.

McComb and Muller [57] found 78 snags ha^{-1} ≥ 10 cm dbh in the dry-mesic, chestnut oak-red maple type at Lilley Cornett Woods in southeastern Kentucky. Snag densities in mesic beech and sugar maple forest types were lower. While the ratio of standing snags to live trees was 1:12 on the dry-mesic site, it was 1:23 in mesic environments. In addition, the ratio of snags to standing trees averaged over the three forest types was 1:27 for species in the red oak group and 1:43 for the white oak group. Shifley et al. [58] found an average of 35 snags ha^{-1} in five old-growth stands in Missouri. The ratio of standing dead to standing live trees was 9 percent or approximately 1:11 (comparable to the Lilley Cornett Woods dry-mesic ratio above) and the frequency distribution by dbh class for snags showed the same trend as for live trees on a given site.

Accumulation of coarse woody debris (CWD) is the net product of production gains minus decomposition losses (Table 7). Production of CWD is a function of site productivity and mortality, while decomposition is influenced greatly by temperature, moisture and decomposer organisms. Thus, quantities of CWD might be expected to vary widely between stands and sites and temporally on a given site. In Spetich et al. [59], total deadwood increased with increasing productivity old-growth sites, and the relationship between stand age and down deadwood volume followed a pseudo-hyperbolic curve.

Decomposition rates also influence the lifespan and accumulation of CWD. At the regional scale, the quantity and distribution of precipitation associated with dry-mesic oak sites likely slows decomposition relative to mesophytic forests, especially in the Interior Highlands, where summer precipitation is erratic [60]. On a local scale, MacMillan [61] also found that CWD from oak and hickory species decayed more slowly than that from beech and maple in an old-growth southern Indiana forest.

Table 6. Standing snags (# ha^{-1}) of representative dry-mesic old-growth oak forests.

Quantifiable Attribute	Value Range	Mean	No. of Stands	References
STANDING SNAGS (# ha^{-1}) except as noted below				
Piedmont				
Hutcheson Memorial Forest				
(15 cm–86.4 cm dbh)		15	1	[56]
Appalachian Plateaus				
Allegheny and Cumberland Plateaus				
Lilley Cornett Woods				
(≥10 cm dbh)		78	1	[57]
Ridge and Valley				
Southwest Virginia				
(≥10 cm dbh)		64		[62]
Interior Highlands				
Ouachita Mountains				
Hot Springs N.P.				
Mass only (≥ 7.6 cm dbh) Mg ha^{-1}	14.4–25.1	19.8	2	[63]
Springfield Plateau				
Roaring River State Park				
North and East slopes (≥10 cm dbh)	0–70 0–80	30.6 34.7	1 1	[33] (1992 Data) [34] (2011 Data)
Ridge + S & W slopes (≥10 cm dbh)	10–130 0–80	53.8 37.7	1 1	[33] (1992 Data) [34] (2011 Data)
Salem Plateau				
Big Spring Natural Area (≥10 cm dbh)	0–110 0–130	38.0 43.3	1 1	[33] (1992 Data) [34] (2011 Data)
Missouri River Hills				
Englemann Woods				
Ridge + S & W Slopes (≥10 cm dbh # ha^{-1})	0–140 10–70	43.0 32.0	1 1	[33] (1992 Data) [34] (2011 Data)

Table 7. Downed coarse woody debris (either m^3 ha^{-1} or Mg ha^{-1} as noted below) of representative dry-mesic old-growth oak forests.

Quantifiable Attribute	Value Range	Mean	No. of Stands	References
DOWNED CWD (either m^3 ha^{-1} or Mg ha^{-1} as noted below)				
Piedmont				
Hutcheson Memorial Forest				
(≥10 cm–Mg ha^{-1})		21.8	1	[64]
Appalachian Plateaus				
Allegheny and Cumberland Plateaus				
Lilley Cornett Woods				
(≥20 cm) m^3 ha^{-1}	23–85	64.7	1	[65]
(≥20 cm) Mg ha^{-1}	4.5–24	20.6	1	
Blue Ridge Mountains				
Great Smokey Mountain NP				
Oak-Hickory (≥10 cm; m^3 ha^{-1})		182.5		[26]
Chestnut oak (≥10 cm; m^3 ha^{-1})		74.0		[26]
Interior Highlands				
Ouachita Mountains				
Hot Springs N.P.				
Mass only (≥7.6 cm.) Mg ha^{-1}	1.6–9.4	5.6	2	[63]
Springfield Plateau				
Roaring River State Park				
North and East Slopes (≥10 cm; m^3 ha^{-1})	6.5–87.1 9.4–67.4	34.2 32.5	1 1	[33] (1992 Data) [34] (2011 Data)
Ridge + South & West Slopes				
(≥ 10 cm; m^3 ha^{-1})	7.4–128.1 9.1–59.2	37.2 25.9	1	[33] (1992 Data) [34] (2011 Data)
Salem Plateau				
Big Spring Natural Area				
(≥10 cm; m^3 ha^{-1})	5.3–96.4 6.4–121.0	32.0 48.5	1 1	[33] (1992 Data) [34] (2011 Data)
Missouri River Hills				
Englemann Woods				
Ridge + South & West Slopes (≥10 cm dbh; m^3 ha^{-1})	2.5–94.6 6.3–62.5	23.0 30.2	1 1	[33] (1992 Data) [34] (2011 Data)

3.2.4. Other Components

Data on shrubs were not collected in every stand examined in this paper. In several stands, sparse understory vegetation was observed. In Mauntel's Woods, southern Indiana, "The floor of the forest was remarkably devoid of both herbaceous and woody species" [28]. However, 15 years prior to inventory of the site, a portion of the forest had been grazed, which could account, at least in part, for the sparse forest floor. Viburnum and blueberry shrubs were common among several stands (Appendix B). Poison ivy and Virginia creeper (*Parthenocissus quinquefolia*) are the two forest floor species most often found across the range of physiographic regions represented in the stands examined. See Appendix B for a more comprehensive list of shrub and vine species found on these dry-mesic old-growth sites.

Describing the herb layer for the dry-mesic oak type is complicated by the ephemeral occurrence of many important species. Herbaceous vegetation was only abundant in early spring before trees leafed out in Wegner's Woods in the Missouri River Hills [35]. At the Hutcheson Memorial Forest, Mayapple (*Podophyllum peltatum*) was a characteristic spring species and enchanter's nightshade (*Circaea quadrisulcata*) was a late summer species. Monk [48] found 61 percent of the space in the herb layer to be unoccupied in the Hutcheson Memorial Forest on the New Jersey Piedmont. Total unoccupied space was 32 percent lower in late summer than in other seasons [48]. Tick-trefoil (*Desmodium* spp.) were represented in stands across the various physiographic regions, while panic grasses (*Panicum* spp. L. and *Dichanthelium* spp. L.) were more common in stands from the western physiographic regions. See Appendix C for a more comprehensive list of herbaceous species found on these sites.

Trees reported to have at least one cavity >10 cm or otherwise hollow have been examined in three dry-mesic old-growth forests [33]. For trees ≥10 cm dbh, mean values for these were up to 8 trees ha^{-1} on an interior highland site on the Springfield Plateau in Missouri, 8 trees ha^{-1} on a site on the Salem Plateau and 13 trees ha^{-1} on a Missouri River Hills site (Table 8).

Table 8. Density (stems/ha) of dominant and co-dominant trees with at least one cavity >10 cm width.

Quantifiable Attribute	Value Range	Mean *	No. of Stands	References
TREES (# ha^{-1})				
Interior Highlands				
Springfield Plateau				
Roaring River St. Park				
N and E Slopes (≥10 cm dbh)	0–20	4	1	[33] (1992 Data)
Ridge + S & W Slopes (≥10 cm dbh)	0–40	8	1	
Salem Plateau				
Big Spring Natural Area (≥10 cm dbh)	0–30	8	1	[33] (1992 Data)
Missouri River Hills				
Englemann Woods				
Ridge + S & W slopes (≥10 cm dbh; #ha^{-1})	10–20	13	1	[33] (1992 Data)

* Means are among 30 plots per site. Each circular plot is 35.68 m in diameter.

Information on vegetation layering of dry-mesic old growth was available for only one site [66], which reported four distinct vegetation layers. They described the four vegetation layers as: (1) a maple-leaved viburnum layer (lowest layer), followed by (2) an understory tree layer, (3) a layer between the understory and main canopy and (4) the main forest canopy.

There are no known species of mammals, birds or herpetofauna that are restricted solely to old-growth dry-mesic oak forest habitats in the East. A list of species associated with the oak-hickory forest type has been compiled in Appendix D.

4. Discussion

4.1. Ownership

Many of the old-growth forests that exist today survive in part due to a history of protection on family farms. Most such sites are now in public ownership. For those forests that no longer exist, we are fortunate that early researchers had the foresight to inventory and describe them prior to their demise, e.g., [14,28]. Because of their work, and the work of others, we were able to elaborate the character of these forests, documenting differences, similarities and trends. For instance, eastern stands had a greater volume of coarse woody debris than western stands. On average, stands on less productive, dry-mesic sites might be expected to contribute less biomass to CWD than more productive mesophytic forests. Greenberg et al. [38] reported an average CWD volume of 155 m^3 ha^{-1} in old-growth western and mixed mesophytic forests. The dry-mesic oak stands that measured trees $\geq$ 10 cm in diameter in Table 7 average 52 m^3 ha^{-1}. However, while stands in the western part of the region averaged 32.9 m^3 ha^{-1}, the eastern stands (both in the Great Smoky Mountain National Park) averaged 128.3 m^3 ha^{-1} [26].

4.2. Forest Dynamics and Succession

4.2.1. Site

In the United States, more than 51 percent of the forest land that lies east of the 100th meridian is dominated by oak species [67]. In the eastern U.S., the ecoregion with the highest proportion of oak basal area, 63.5 percent, is the Ozark Highlands, a region characterized by dry uplands [68]. On the local scale, oak forests occur at the dryer end of the moisture gradient and are associated with topographic positions that experience greater solar radiation. The aridity of forested sites can be influenced by several factors that act at regional to local scales [69,70]: climate (decreased precipitation along the transition from eastern forests to Midwestern prairies and increased evapotranspiration demand with increasing temperatures in the southeast), soil water-holding capacity (influenced by depth, stoniness and texture), and topography (aspect, slope steepness, and slope shape).

Dry-mesic old-growth oak forests can also be found outside the U.S.; for instance, there are a total of 19 sites in Europe: 2 sites in Austria, 2 sites in Italy, 12 sites in Portugal and 3 in Slovakia [24]. Many of the characteristics of European and US sites are relatively similar. For example, stem densities of European sites ranged from 239–591 trees ha^{-1} (mean 471 trees ha^{-1}) compared to 341–620 trees ha^{-1} (mean 460 trees ha^{-1}) for the U.S. sites. European site basal areas ranged from 35.1–35.5 m^2 ha^{-1} (mean 35.3 m^2 ha^{-1}) compared to 18–36 m^2 ha^{-1} (mean 25 m^2 ha^{-1}) for U.S. sites. Down deadwood volume ranged from 17–55.1 m^3 ha^{-1} (mean 43.7 m^3/ha) compared to 23–183 m^3 ha^{-1} (mean 58 m^3 ha^{-1}). However, if we eliminate the eastern-most U.S. sites, then the range of down deadwood volume is 23–65 m^3 ha^{-1} with a mean of 38 m^3 ha^{-1}. Developing consistent inventory methods for both U.S. and European sites would allow for more direct comparisons of forest parameters.

4.2.2. Regeneration

Oak species commonly found on dry-mesic sites are shade intolerant, growing slowly under shade. Most oak stems do not remain as true seedlings (i.e., with the original main stem intact) for many years. Various biotic (deer, rodents, insects) and environmental factors (low light, drought, frost, fire) kill the tops but not the roots of these oak seedlings [71], allowing the stem to resprout from the root collar. Under moderate shading, the survival of understory oaks is relatively high, and, over time, strong root systems develop at the expense of the aboveground stem [72]. These well-developed, older root systems provide the potential for rapid height growth when favorable conditions occur, i.e., a canopy opening develops. Continued survival of oak regeneration after death or damage to the aboveground parts is enhanced by a large and vigorous root system [71,72]. These poorly formed, low vigor stems attached to a well-developed root system, up to 30 years old, are termed seedling-sprouts [71,72]. This ability to repeatedly resprout is an important adaptation of oaks to frequent low-intensity surface fire [73,74]. However, on moister sites oaks are often outcompeted due to more shade-tolerant species, such as maple.

4.2.3. Stand Development

Dry-mesic oak forests and dry-mesic oak-pine forests may develop at some of the same sites [44]. According to Braun [9], increasing aridity near the forest-prairie boundary and summer droughts in the southern Appalachians limit more mesic forest development [9]. However, oak forests on mesic sites often succeed toward dominance by more shade-tolerant species [16,29]. Fire suppression has allowed the development of these more shade-tolerant understory components [72,75], and the rate of succession toward mesophytic species is more rapid on more mesic sites.

Maintenance of oak forests requires periodic disturbances, if not for initial establishment of seedling sprouts, then certainly for their continued development in stature and recruitment into the overstory. Larson and Johnson's [76] review of the linkage between the ecology of natural oak regeneration and silviculture and the comprehensive study of oak forests by Johnson et al. [72] emphasized two phases of the regeneration process: (1) accumulation of oak seedling sprouts and (2) recruitment of reproduction from the understory into the overstory. However, abundant oak regeneration may not be a prerequisite for future stands with a significant oak component. Studies of stand development in central New England forests found that low red oak seedling numbers in relation to red maple and black birch did not preclude oak dominance in mature forests [77]. However, there are other examples where red oak regeneration is not expected to develop in closed canopy forests [72,78].

4.2.4. Disturbance

Several disturbances are important to oak establishment and recruitment in dry-mesic old-growth forests. As stated previously, fire or lack thereof, seems to be a pivotal factor in the development of oak forests on upland sites [73,79]. A significant effect of fire is the reduction of later successional species competing with oaks in the regeneration layer, particularly on more mesic sites. Major oak replacement species throughout the eastern United States include sugar maple, red maple, black cherry [73], and yellow poplar [75]. Abrams [73] suggested that the burning intervals of 30 to 50 years that occurred for centuries prior to European settlement promoted the dominance and stability of oak forests in southern New England and the mid-Atlantic region. More contemporary work indicates that the historic mean fire return interval was greater than 35 years in northern New England and generally decreased with decreasing latitude to less than 2 years in southeast Georgia [80]. While fire appears to have a significant role in reducing competing species on mesic sites, it may not be essential to the stability of oak forests on xeric sites [72,73]. In contrast to mesic sites, the necessity of periodic fires to maintain oaks as mature, dominant, overstory trees on dry-mesic sites is less clear. There are many examples where mature oak-dominated forests have been sustained on dry-mesic sites without periodic fire. However, that result has often been associated with the concurrent application of uneven-aged silviculture [72,81].

In addition to fire, White and White [69] reported grazing effects as the most cited reason for the late 20th century composition and structure of oak forests. Acorns and nuts produced in oak-hickory forests were utilized to fatten livestock and rooting by hogs may have damaged shallow-rooted competitors, while aboveground herbivory favored the success of resprouting oaks. Significant reduction in grazing and foraging by livestock (cattle, goats, sheep, hogs) in the early and mid-1900s allowed for an increase in non-oak understory stem densities in many areas.

The introduction of the chestnut blight (*Cryphonectria parasitica*) in the early 1900s was a significant disturbance factor in oak forests. Woods and Shanks [82] studied 2569 forest openings created by the death of American chestnuts in the Great Smoky Mountains and found chestnut oak and northern red oak were the two most common replacement species.

In mesic cove sites, replacements included eastern hemlock, yellow poplar, white basswood and sugar maple. While the most profound impacts of the chestnut blight are long past, the impact of another imported pest, the gypsy moth (*Lymantria dispar*), continues [83]. The moth has a preference for oaks over many of the commonly associated canopy species, and it continues to migrate south and westward from the Middle Atlantic States.

Intense weather events such as hurricanes, tornadoes and ice storms are disturbance factors that also affect the dynamics of these forests. Stress caused by less conspicuous insects, diseases, air pollution, or drought can cause slow decline, mortality and randomly spaced variable-sized canopy gaps. Clinton et al. [84] studied the impact of the 1985–1988 drought on mortality and the creation of canopy gaps in mixed oak forests. The gap area averaged 239 m^2 with a formation rate of 0.8 gaps·ha^{-1}. Scarlet, northern red, and black oaks were the most prevalent gap-forming species. Within mature, even-aged stands on dry-mesic sites, these red oak group species have been shown to be susceptible to stand-level decline and cohort senescence triggered by repeated drought [85–87].

Gap dynamics are complex. Runkle [88] stated that there are considerations other than size and distribution when evaluating the implications of canopy gap formation: (1) what is the rate of gap closure? and (2) is the occurrence of more than one gap necessary for understory species to reach the canopy? Investigation of gap dynamics in a mesic *Acer-Fagus* forest [88] found the optimal combinations of gap age and size for the four dominant species to be: small gaps of all ages for maples, old gaps of all sizes for beech, large young gaps for white ash, and large gaps of all ages for yellow poplar. A study examining white oak survival in canopy gaps formed through group selection in dry-mesic oak forests found that gaps as small as 5 m could result in seedling survival from 50 to 90 percent for large diameter seedlings and up to 55 percent for small diameter seedlings 12 years after gap formation [89].

Runkle [88] also emphasized the lack of information on disturbance regimes, most important for oaks. Some species, typically those tolerant of shade, dominate in forests characterized by small-scale disturbances, and other species, usually intolerant of shade, dominate in forests affected by large-scale disturbances. Runkle [88] suggested that crucial factors for oak success may involve understory disturbance in addition to or instead of canopy disturbance. This view is in agreement with Larson and Johnson's [76] emphasis on two phases of oak regeneration: (1) accumulation of advance regeneration, mostly seedling-sprouts, and (2) recruitment of the regeneration to the main canopy.

4.3. Other Characteristics and Suggestions for the Future of These Forests

Mean stand basal areas were generally greater in the eastern physiographic provinces (Piedmont, Allegheny Highlands, Interior Low Plateaus) than in the drier western stands. However, the number of herbaceous species within the dry-mesic, old-growth oak forests varied widely, ranging from 4 to 51 per forest. The number of tree species among these dry-mesic old-growth sites ranged from 5 to 18 and is relatively low compared to old-growth forests on moister sites such as Davis Research Forest [90] and Warren's Woods, [91], both with 34 species.

These sites occur principally in unglaciated uplands. In the east, dry-mesic oak forests are often found on the upper and south-facing aspects. As one moves along the gradient of decreasing precipitation and increasing evaporative demand (i.e., moves west and south), southern aspects become more xeric and dry-mesic oak stands gradually shift to more favorable topographic positions on north-facing slopes. In terms of productivity, dry-mesic old-growth oak forests commonly exist at the low end of the productivity range compared to oak-dominated old-growth forests on moister sites [59]. Studies of old-growth stands seldom report on-site index due to lack of suitable trees for direct measurement. However, the site index is related to site productivity. A 1999 study of old-growth forests across the Central Hardwood Region found that dryer forests were located in areas with low potential biomass productivity, starting at 3.5 m^3 ha^{-1} $year^{-1}$, while more mesic sites were located in areas with higher potential biomass productivity, up to 6 m^3 ha^{-1} $year^{-1}$ [59]. Dry-mesic old-growth forests exist at the low end of this productivity range.

The dry-mesic nature of these forests drives both the rate and direction of succession on these sites. However, within this general forest type, composition varies along environmental gradients. Within the range of dry-mesic forests, relatively mesic forests are composed of white, northern red, and black oaks and beech, while more xeric forests are composed of post, blackjack, chestnut and scarlet oak [69]. White and Lloyd [44] defined dry and dry-mesic types as corresponding to sites with soils that are somewhat excessively well-drained.

Pine species were a minor component across the eastern U.S. dry-mesic old-growth oak stands. Mockernut hickory was distributed widely across regions, while pignut hickory occurred in the eastern and central regions and black hickory was found in the western physiographic regions centered on the Ozark Mountains of Missouri and Arkansas. Red maple, black gum, white ash, and dogwood were widely occurring associates across a range of forest types.

Once established, tree species composition on many of these dry, edaphically poor sites are relatively stable since there are few replacement species that can tolerate these site conditions. However, on a few sites where site conditions are in the mesic portion of the dry-mesic gradient, red maple has the potential to be highly competitive with oak due to its much greater tolerance to shade than oaks. Regeneration and subcanopy species on dry-mesic sites are prone to be oak, leading to oak successional durability. Nonetheless, wide fluctuations in stand structure can occur over time and relatively little is known about fluctuations of other characteristics such as abundance and percent ground cover of herbaceous species, and the abundance and diversity of birds, mammals and herpetofauna. Moreover, there are no known species of mammals, birds, herbs or herpetofauna that are restricted to old-growth dry-mesic oak forests.

Over the past 20 years, there has been scant research on these forests, and older research studies have used a variety of research plots and methods. A uniform approach in surveying these sites is needed to gain a better understanding of these forests before we are faced with caring for the predicted increase in old-growth forest areas. An inventory of sites using consistent techniques (e.g., the study plan by Shifley et al. [33]) would allow for direct comparisons among sites, as we did for three such measured sites in the Interior Highlands section of this paper: Roaring River, Big Spring and Engelman Woods. It would be useful if future studies reported comparable structural forest data, e.g., Figure 2; for example, in this paper it was valuable to be able to compare tree structure for trees $\geq$ 10 cm DBH. Where structure refers to stand density, basal area, diameter distribution, standing and down coarse woody debris, as well as species distribution by diameter. In this way, these forests can be directly compared through time in a meaningful way. For instance, the distribution of species by diameter class may help predict successional trends. Useful characteristics to incorporate into future inventories include ground cover, herbaceous species, birds, mammals and herpetofauna.

There is a tendency among managers to avoid disturbances in old-growth forests, including dry-mesic old-growth oak forests. However, on sites with competing regeneration that can be controlled by fire, periodic application of prescribed fire may be a viable option to maintain future oak dominance in the canopy.

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Appendix A. Tree Species Characteristic of Old-Growth Dry Mesic Oak Forests

	Piedmont		Appalachian Mts.								Interior Low Plateaus			Interior Highlands							Coastal Plain			Percent of Sites where This Species Occurred
			Allegheny/ Cumberland Pl.			Ridge & Valley		Blue Ridge			S. IN	S. ILL		Ouachita Mts.		Bost. Mts.	Springfield Pl.	Salem Pl.	Missouri River Hills		Western Gulf			
SPECIES	HMF [a]	DF	HW	LCW	SG	Upper Slope	Mid-Slope	SO	CO	OH	MW	S. Slope	Upper N. Slope	HSPNP	RBRNA	WM	RRSP	BS	EW	WW	BC	OSLS	BT	
Acer saccharum	X		X	X	X						X		X						X	X				35
Acer rubrum	X	X	X	X	X	X	X	X	X	X	X			X	X								X	61
Carya cordiformis			X											X						X				13
Carya glabra			X		X		X				X	X	X											26
Carya ovalis	X		X	X	X																			17
Carya ovata	X				X						X		X						X	X				26
Carya texana												X		X	X		X	X	X					26
Carya tomentosa				X	X		X							X	X	X	X	X			X	X	X	48
Carya spp.		X							X															9
Cercis canadensis		X	X								X													13
Cornus florida	X	X	X	X	X						X			X	X		X						X	43
Fagus grandifolia	X		X	X	X									X										22
Fraxinus americana	X	X	X	X	X						X		X						X	X				39
Fraxinus pennsylvanica																							X	4
Ilex opaca																							X	4
Ilex vomitoria																							X	4
Liquidambar styraciflua																							X	4
Liriodendron tulipifera		X		X	X																			13
Magnolia fraseri									X															4
Nyssa sylvatica	X	X	X	X	X				X		X	X	X	X	X		X	X			X	X	X	70
Ostrya virginiana			X		X										X						X	X		22
Oxydendrum arboretum		X	X	X	X	X		X	X															30
Persea borbonia																							X	4
Pinus echinata		X		X										X				X			X	X	X	30
Pinus strobus						X	X																	9
Pinus taeda		X																			X	X	X	17
Sassafras albidum																							X	4
Symplocos tinctoria																							X	4
Quercus alba	X	X	X	X	X		X	X		X	X	X	X	X	X	X	X	X	X	X	X	X	X	91
Quercus coccinea	X	X	X	X			X	X	X			X						X						39

	Piedmont		Appalachian Mts.								Interior Low Plateaus			Interior Highlands							Coastal Plain			Percent of Sites where This Species Occurred
			Allegheny/ Cumberland Pl.			Ridge & Valley		Blue Ridge			S. IN	S. ILL		Ouachita Mts.		Bost. Mts.	Springfield Pl.	Salem Pl.	Missouri River Hills		Western Gulf			
SPECIES	HMF [a]	DF	HW	LCW	SG	Upper Slope	Mid-Slope	SO	CO	OH	MW	S. Slope	Upper N. Slope	HSPNP	RBRNA	WM	RRSP	BS	EW	WW	BC	OSLS	BT	
Quercus falcata														X								X	X	13
Quercus nigra																							X	4
Quercus phellos																							X	4
Quercus marilandica		X										X		X	X	X								22
Quercus prinus			X	X	X	X	X	X	X	X														35
Quercus rubra	X	X	X	X	X	X	X		X	X	X	X	X	X	X	X	X	X	X	X				83
Quercus stellata		X										X			X	X	X	X	X		X	X	X	43
Quercus velutina	X	X	X	X	X	X	X		X	X	X	X	X	X	X		X	X						70
Robinia pseudoacacia				X	X										X									13
Tsuga canadensis									X	X														9

[a] HMF = Hutcheson Memorial Forest [48]. Not listed in the table above and only found on this site: *Prunus avium*, *Acer Platanoides*, *Ulmus americana*, *Quercus palustris* and *Quercus Bicolor*. DF = Duke Forest [13]. HW = Hawk Woods, white oak, oak-hickory and oak-heath types [16]. LCW = Lilley Cornett Woods, chestnut oak-red maple species group [19]. Lilley Cornett Woods, white oak, mixed oak, chestnut oak communities [17]. SG = Savage Gulf, mockernut hickory-northern red oak and chestnut oak community types [21]. Ridge and Valley = unpublished plot data from upper and mid-slopes, central Pennsylvania, G. Nowacki. SO = Scarlet Oak [27]. CO = Chestnut oak forest, Great Smoky Mountains National Park [26]. OH = Oak-hickory forest, Great Smoky Mountains National Park [26]. MW = Mauntel's Woods [28]. S. IL = Southern Illinois [29]. HSNP = Hot Springs National Park, upland hardwoods and oak-hickory-pine types [30]. RBRNA = Roaring Branch Research Natural Area, mid and upper north slopes [31]. WM = Boston Mts. = Wedington Mountain [32]. RRSP = Roaring River State Park (unpublished data provided by S. Shifley, USDA-Forest Service, North Central Experiment Station, Columbia, MO, USA). BS = Big Spring (unpublished data provided by S. Shifley, USDA-Forest Service, North Central Experiment Station, Columbia, MO, USA). EW = Englemanns's Woods, (unpublished data provided by S. Shifley, USDA-Forest Service, North Central Experiment Station, Columbia, MO). WW = Wegener Woods [35]. BC = Bob's Creek stand, Kisatchie National Forest [36]. OSLS = Old Shortleaf Slope stand, Kisatchie National Forest [36]. BT = Big Thicket, midslope oak-pine forest [37]. An X in the Table Represents the Presence of a Species within the Respective Site.

Appendix B. Shrub and Vine Species Characteristic of Old-Growth Dry Mesic Oak Forests

	Piedmont		Appalachian Mts.				Interior Low Plateaus	Interior Highlands					Coastal Plain	
			Alleghany/ Cumberland Pl.	Blue Ridge			S.IN	Ouachita Mts.		Salem Pl.	Missouri R. Hills		Western Gulf	
SPECIES	HMF [a]	DF	SG	SO	CO	OH	MW	HSNP	RBRNA	BS	EW	WW	BC	OSLS
Calycanthus floridus					X									
Chionanthus virginicus		X												
Crataegus spp.		X								X				
Gaylussacia baccata				X	X								X	
Hamamelis virginiana									X					
Kalmia latifolia			X	X	X	X								
Lindera benzoin	X													

	Piedmont		Appalachian Mts.				Interior Low Plateaus	Interior Highlands					Coastal Plain	
			Alleghany/ Cumberland Pl.	Blue Ridge			S.IN	Ouachita Mts.		Salem Pl.	Missouri R. Hills		Western Gulf	
SPECIES	**HMF** [a]	**DF**	**SG**	**SO**	**CO**	**OH**	**MW**	**HSNP**	**RBRNA**	**BS**	**EW**	**WW**	**BC**	**OSLS**
Lonicera japonica	X													
Parthenocissus quinquefolia	X	X						X	X			X	X	X
Polycodium spp.		X												
Rhododendron calendulaceum						X								
Rhododendron maximum					X									
Rubus spp.	X					X								
Rosa multiflora	X													
Rosa virginiana		X												
Smilax glauca					X				X					
Smilax herbacea						X								
Smilax rotundifolia					X	X								
Smilax spp.			X										X	X
Toxicodendron radicans	X	X					X	X	X			X		
Vaccinium arboreum								X	X	X				X
Vaccinium pallidum						X		X						
Vaccinium stamineum				X		X		X						
Vaccinium vacillans				X					X	X				
Vaccinium spp.			X		X									
Viburnum acerifolium	X					X								
Viburnum lantanoides			X											
Viburnum affine var. hypomalacum		X												
Viburnum prunifolium	X	X												
Viburnum rufidulum								X						
Vitis aestivalis	X	X												
Vitis rotundifolia		X						X					X	X
Vitis spp.			X									X		

[a] HMF = Hutcheson Memorial Forest [12]. Not listed in the table above and only found at this site: *Viburnum dentatum*, *Lonicera maackii*, *Sambucus canadensis*, *Berberis thunbergii* and *Ligustrum vulgaris*. DF = Duke Forest [13]. SG = Savage Gulf, mockernut hickory-northern red oak and chestnut oak community types [21]. SO = Scarlet Oak [27]. CO = Chestnut oak forest, Great Smoky Mountains National Park (NPS unpublished data). OH = Oak-hickory forest, Great Smoky Mountains National Park (NPS unpublished data). MW = Mauntel's Woods [28]. HSNP = Hot Springs National Park, upland hardwoods and oak-hickory-pine types [30]. RBRNA = Roaring Branch Research Natural Area, mid and upper north slopes [31]. BS = Big Spring (unpublished data provided by S. Shifley, USDA-Forest Service, North Central Experiment Station, Columbia, MO. WW = Wegener Woods [35]. BC = Bob's Creek stand, Kisatchie National Forest [36]. OSLS = Old Shortleaf Slope stand, Kisatchie National Forest [36]. Note: No Shrub Data available for HW, LCW, Ridge and Valley, S. ILL, Boston Mountains, RRSP, or EW. An X in the Table Represents the Presence of a Species within the Respective Site.

Appendix C. Herbaceous Species Table

Herb Species	Piedmont		Cumberland Plateau	Appalachian Mts.		Interior Low Plateau	Interior Highlands			Coastal Plain	
			Central Eastern TN	Great Smoky Mountains NP		Southern IN	Ouachita Mts.		MO River Hills	Western Gulf	
	HMF [a]	DF	FCSP *	CO	OH	MW	HSNP	RBRNA	WW	BC	OSLS
Ageratina altissium					X						
Agrostis perennans					X	X					
Amphicarpaea bracteata	X				X						
Anemonella thalictroides	X										
Antennaria plantaginifolia			X					X			
Arisaema dracontium									X		
Arisaema spp.			X								
Arisaema triphyllum	X				X				X		
Aureolaria laevigata					X						
Aster spp.			X								
Botrychium virginianum	X				X	X					
Brachyelytrum erectum						X					
Carex leptonervia				X							
Carex spp.		X								X	X
Chasmanthium spp.										X	X
Chimaphila maculata		X		X							
Circaca quadrisculcata	X										
Claytonia virginica	X								X		
Clintonia umbellulata					X						
Conopholis americana				X	X						
Desmodium glutinosum								X			
Desmodium laevigatum		X					X	X			
Desmodium marilandicum								X			
Desmodium nudiflorum		X	X		X			X			
Desmodium rotundifolium						X					
Desmodium spp.			X								
Dicentra cucullaria									X		
Dichanthelium dichotomum							X				
Dioscorea villosa					X						
Disporum lanuginosum					X						
Dryopteris marginalis			X								

Herb Species	Piedmont		Cumberland Plateau	Appalachian Mts.		Interior Low Plateau	Interior Highlands			Coastal Plain	
			Central Eastern TN	Great Smoky Mountains NP		Southern IN	Ouachita Mts.		MO River Hills	Western Gulf	
	HMF [a]	DF	FCSP *	CO	OH	MW	HSNP	RBRNA	WW	BC	OSLS
Epigaea repens					X						
Eupatorium dubium			X								
Eupatorium steelei					X						
Galium lanceolatum					X						
Gillenia stipulata						X					
Goodyera pubescens				X	X						
Heuchera americana						X					
Heuchera pubescens					X						
Hepatica americana			X								
Hieracium gronovii		X									
Hieracium venosum		X									
Hieracium scabrum						X					
Houstonia purpurea					X						
Houstonia longifolia								X			
Iris cristata						X					
Lilium superbum					X						
Liparis liliifolia						X					
Luzula echinata					X						
Maianthemum racemosa					X						
Medeola virginiana					X						
Melampyrum lineare					X						
Mitchella repens										X	X
Monarda clinopodia					X						
Monotropa uniflora				X							
Oenothera fruticosa					X						
Panicum sphaerocarpoa							X				
Panicum spp.		X			X			X		X	X
Phegopteris hexagonoptera						X					
Poa alsodes					X						
Polygonatum biflorum	X										
Polystichum acrostichoides			X		X	X	X				
Porteranthus trifoliatus					X						
Potentilla canadensis			X								
Prenanthes spp.					X						
Pteridium aquilinum							X				
Pycnanthemum spp.								X			
Ranunculus spp.					X						

Herb Species	Piedmont		Cumberland Plateau	Appalachian Mts.		Interior Low Plateau	Interior Highlands			Coastal Plain	
			Central Eastern TN	Great Smoky Mountains NP		Southern IN	Ouachita Mts.		MO River Hills	Western Gulf	
	HMF [a]	DF	FCSP *	CO	OH	MW	HSNP	RBRNA	WW	BC	OSLS
Solidago curtisii					X						
Solidago spp.			X		X						
Symphyotrichum anomalus								X			
Symphyotrichum cordifolium					X						
Symphyotrichum undulatum					X						
Thalictrum thalictroides					X						
Tradescantia subaspera					X						
Uvularia puberula					X						
Viola hastata					X						
Viola spp.			X		X						

[a] HMF = Hutcheson Memorial Forest [12]. Not listed in the above table and only found at this site: *Lonicera japonica* V, *Parthenocissus quinquefolia* V., *Smilacina racemosa*, *Pilea pumila*, *Impatiens biflora*, *Toxicodendron radicans* V, *Phytolacca americana*, *Vitis aestivalis* V and 25 others listed as "other species" in [12]. DF = Duke Forest ([13] Oosting 1942). FCSP = Falls Creek State Park, Tennessee [92]. CO = Chestnut oak forest, Great Smoky Mountains National Park (NPS unpublished data). OH = Oak-hickory forest, Great Smoky Mountains National Park (NPS unpublished data). Note that this site had a total of 51 species, however we only list 38 of those in this table. MW = Mauntel's Woods [28]. HSNP = Hot Springs National Park, upland hardwoods and oak-hickory-pine types [30]. RBRNA = Roaring Branch Research Natural Area, mid and upper north slopes [31]. WW = Wegener Woods [35]. BC = Bob's Creek stand, Kisatchie National Forest [36]. OSLS = Old Shortleaf Slope stand, Kisatchie National Forest [36]. * Major species listed for Falls Creek State Park. For an extensive list see [93]. An X in the Table Represents the Presence of a Species within the Respective Site.

Appendix D. Common Birds, Mammals, and Herpetofauna of Oak-Hickory Forests

Birds (Compiled from [94,95])
Acadian flycatcher (*Empidonax virescens*)
Tufted Titmouse (*Parus bicolor*)
Wood Thrush (*Hylocichla mustelina*)
Red-eyed Vireo (*Vireo olivaceus*)
Ovenbird (*Seiurus aurocapillus*)
Scarlet tanager (*Piranga olivacea*)
Hooded Warbler (*Wilsonia citrina*)
Cardinal (*Richmondi cardinalis*)
Mammals (Compiled from [96,97])
Short-tailed shrew (*Blarina brevicauda*)
White-footed mouse (*Peromyscus leucopus*)
Eastern chipmunk (*Tamias striatus*)
Fox squirrel (*Sciurus niger*)
Gray squirrel (*Sciurus carolinensis*)
Flying squirrel (*Glaucomys volans*)
Gray fox (*Urocyon cinereoargeneteus*)
Raccoon (*Procyon lotor*)
Opossum (*Didelphis virginiana*)
Striped skunk (*Mepjotos mephitis*)
White-tailed deer (*Odocoileus virginianus*)
Herpetofauna (Compiled from [96])
Hognose snake (*Heterdon platyrhinos*)
Five-lined snake (*Eumeces fasciatus*)
Black rat snake (*Elaphe obsoleta*)

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