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An Old-Growth Definition for Western and Mixed Mesophytic Forests

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Preface

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

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

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

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

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Introduction

Mesophytic forests can be segregated into two subgroups based on species richness and composition—western and mixed mesophytic forests. Western mesophytic forests occur primarily in the Interior Low Plateau, southern Central Lowland, Ozark Plateaus and Ouachita physiographic provinces, and the northern Coastal Plain along the Mississippi River. Typically oak (*Quercus* spp.)-dominated, this type occurs in a wide range of topographic positions, including drier sites than the more mesic, mixed mesophytic forests.

Mixed mesophytic forests occur in the Appalachian Plateau, Ridge and Valley, and Blue Ridge physiographic provinces. In the mountains, this forest type occurs on lower north- and east-facing slopes and mesic coves up to about 5,000 feet [1524 meters (m)] in elevation (McLeod 1988). In less mountainous terrain, mixed mesophytic forest may cover the entire landscape where conditions are suitable.

Mixed mesophytic forest types are among the most biologically diverse ecosystems of the United States and perhaps of temperate regions worldwide (Hinkle et al. 1993). The most common of the 25 to 30 characteristic tree species are sugar maple (*Acer saccharum* Marsh.), beech (*Fagus grandifolia* Ehrh.), hemlock [*Tsuga canadensis* (L.) Carr.], silverbell (*Halesia carolina* L.), yellow-poplar (*Liriodendron tulipifera* L.), red maple (*A. rubrum* L.), white ash (*Fraxinus americana* L.), white oak (*Q. alba* L.), northern red oak (*Q. rubra* L.) and yellow birch (*Betula alleghaniensis* Britton), yellow buckeye (*Aesculus octandra* Marsh.) and basswood (*Tilia heterophylla* Vent.) (Braun 1935, 1938, 1940, 1942, 1950; Whittaker 1956; Core 1966; Quarterman et al. 1972; Winstead and Nicely 1976; Dickison 1980) (appendix A). The latter two are indicator species for the mixed mesophytic forest type but are absent from western mesophytic forests (Braun 1938).

Species dominance patterns, or "association-segregates," may vary with geographic or physiographic region and site conditions (Braun 1950). Topographic features, including slope, aspect, elevation, and geomorphic form, and associated differences in soils, moisture, insolation, and microclimate contribute to subcommunity distributions within the mixed mesophytic forest (Caplenor 1965, Martin 1975, Dickison 1980, Muller 1982, Crownover 1988, McLeod 1988, Hinkle 1989). Many of the characteristic mixed mesophytic forest tree species are associated with high pH, and with cation exchange capacity, percent base saturation, and some nutrient contents (Muller 1982, McLeod 1988). Depth of organic soil averages 3.0 ± 0.4 inches [7.5 + 1.1 centimeters (cm)][1] in nonrocky areas.

Society of American Foresters forest cover types included within the definition of mixed mesophytic and western mesophytic forests are

25—sugar maple-beech-yellow birch (in part)
27—sugar maple
52—white oak-black oak-northern red oak
57—yellow-poplar-eastern hemlock
59—yellow-poplar-white oak-northern red oak

Human influence on eastern forests has a long history (Guffey 1977). Native Americans cleared large areas of forest and commonly set fire to woodlands to increase game populations (Eller 1982). Later, European settlers accelerated the clearing of forests for farmland. Woodlands were often heavily grazed by free-ranging hogs and livestock (Eller 1982). With the development of a logging industry capable of cutting and milling large volumes of timber, coupled with newly completed railroad access, eastern forests were extensively logged around the turn of the century (Shands 1992). Mixed mesophytic forests were clearcut or high-graded with little thought for future land condition. By the late 19th and early 20th centuries, all but the most inaccessible stands of old-growth forests were eliminated (Buttrick 1923, Westveld 1933).

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[1] McLeod, Donald E. December 3, 1996. Unpublished raw data. On file with: U.S. Department of Agriculture, Forest Service, Southern Research Station, Bent Creek Research and Demonstration Forest, 1577 Brevard Road, Asheville, NC 28806.

Introduction of exotic plants, animals, and pathogens has also dramatically affected forest dynamics. The American chestnut blight (*Cryphonectria parasitica*), introduced in the early 20th century, caused widespread death of this previously dominant tree species by 1930 and greatly changed forest species composition and regeneration patterns (Ashe 1911, Woods and Shanks 1959). Similarly, Dutch elm disease *(Ceratocystis ulmi*) dramatically affected forest dynamics and species composition where Dutch elm was dominant (Boggess and Bailey 1964). Introductions of the European wild hog (*Sus scrofa*), dogwood anthracnose (*Discula destructiva*), and gypsy moth (*Porthetria dispar*) have also significantly altered forest dynamics.

Structure and Composition of Old-Growth Forests

Government surveyors described the coves below Mount Mitchell, near Asheville, North Carolina, as "a forest of oaks, hickories, maples, (American) chestnuts [(*Castanea dentata* (Marsh.) Borkh.)], and tulip poplars, some of them large enough to be suggestive of the giant trees on the Pacific Coast."[2]

While no single attribute defines old-growth forests, a combination of several factors may serve as important indicators. Pertinent structural attributes of the living component of old-growth forests include species composition, richness and diversity of canopy, and understory and herbaceous strata; plant and animal species potentially dependent upon old growth (Martin 1992); age, diameter, density, and basal area of canopy trees; vertical stand structure; and stand age and size structure including apportionment of small and large stems (Schmelz and Lindsey 1965, Weaver and Ashby 1971, Martin 1992). Important nonliving structural features include the volume and distribution of coarse woody debris (CWD) and standing snags and their apportionment among size and decay classes; tree-fall gaps of various size and age; undisturbed soil and soil macropores; and little evidence of disturbance by humans (Martin 1992). Below, we discuss specific characteristics of structured categories that may assist in defining and identifying old-growth western and mixed mesophytic forests.

Vertical Structure

Numerous factors contribute to a complex vertical structure in old-growth, mixed mesophytic forests. Different size and age distributions of canopy tree species create a wide spread in heights. Understory trees, shrubs, and herb layers form distinct forest strata. Continual creation and closure of gaps create a temporally and spatially "shifting mosaic" of age and size-class patches.

Canopy height of eastern old-growth forests ranges from 98.4 to 131.2 feet (30 to 40 m) (Whittaker 1966, McLeod 1988). Clebsch and Busing (1989) described old-growth canopy as having overlapping and spreading crowns. Such canopy structure allows only 0.3 to 2 percent of incident light penetration to the herb stratum (Whittaker 1966, Canham 1989). The subcanopy and shrub layer tend to be sparse (5 to 30 percent cover) where they are deciduous (McLeod 1988) but can be thick where dominated by ericaceous shrubs. Likewise, a multistructural herbaceous layer may be present under a deciduous canopy but sparse to nonexistent beneath dense evergreen shrubs or in excessive shade (Caplenor 1965, McLeod 1988). McLeod (1988) reported a thick (about 100 percent cover), species-rich herbaceous cover in old-growth stands of the Black and Craggy Mountains of North Carolina.

Whittaker (1966) estimated aboveground biomass of 223 to 272 tons per acre [500 to 610 metric tons per hectare (ha)] and net productions of 3.3 to 3.9 ounces per square foot [1000 to 1200 grams per square meter (grams per m^2)] annually in mature climax mesic forests. Of total aboveground production, about 95.8 percent were trees, 0.1 percent shrubs, 3.4 percent summer herbs, and 0.7 percent vernal herbs.

Many old, living trees are hollow or severely decayed. McLeod (see footnote 1) found an average of 4.9 ± 2.4 decadent trees per acre (12 ± 6 decadent trees per ha), or 3 percent of living trees in six old-growth stands in the Southern Appalachians (table 1). Of decadent trees, 21 percent were Florida dogwood and 26 percent were beech. Most decadent trees (59 percent) were small [<7.9 inches (20 cm) in diameter at breast height (d.b.h.)] or midsize [26 percent were from 7.9 to 15.4 inches (20 to 39 cm)]. Only 15 percent were larger than 15.7 inches (40 cm) d.b.h. Hardt and Swank (in press) found 5.1 and 8.7 decadent trees $\geq$11.8 inches d.b.h. per acre (12.5 and 21.5 decadent trees $\geq$30 cm d.b.h. per ha) in two old-growth Southern Appalachian stands, respectively. They suggest that species composition has an important influence on tree decadence, since some species (such as red maple, beech, and

[2] Southern Appalachian Center, Mars Hill College. 1979. A socioeconomic overview of western Carolina for Nantahala-Pisgah Forests. 73 p. Unpublished report. On file with: Mars Hill College, College Library, Southern Appalachian Room, Mars Hill, NC 28754.

Table 1 (English units)—Standardized table of old-growth attributes for western and mixed mesophytic forests

Quantifiable attribute	Value: Range	Value: Mean	Number of stands	References
Stand density (no./acre)				
—trees ≥4 in. d.b.h.	68–184	130±34	14	Bryant 1987 Muller 1982 Palmer 1987[a] McLeod[b]
Stand basal area (ft^2/acre)				
—trees ≥4 in. d.b.h.	113–296	165±48	14	Bryant 1987 Muller 1982 Palmer 1987[a] McLeod[b]
Age of large trees (yrs) (maximum)				
Liriodendron tulipifera L.	226			in Runkle 1982
Tilia heterophylla Vent.	198			in Runkle 1982
Acer saccharum Marsh.	372			Tubbs 1977
Aesculus octandra Marsh.	431			in Runkle 1982
Fagus grandifolia Ehrh.	412			Morey 1936
Tsuga canadensis (L.) Carr.	607			Morey 1936
Number of 4-in size classes				
—trees ≥4 in. d.b.h.	1–22	17	6	McLeod[b]
Maximum d.b.h. (in)				
L. tulipifera L.	65		6	McLeod[b]
Tilia heterophylla Vent.	77			
Acer saccharum Marsh.	46			
Aesculus octandra Marsh.	41			
F. grandifolia Ehrh.	43			
Tsuga canadensis (L.) Carr.	45			
Standing snags (no./acre)				
—snags ≥4 in. d.b.h.	4–28	13±8	8	McComb and Muller 1983 Muller 1982[c] McLeod[b]
Downed logs (ft^3/acre)	943–5859	2,215±1,615	9	Muller and Liu 1991[d] McLeod[b] Hardt and Swank, in press
Decadent trees (no./acre)				
—trees ≥4 in. d.b.h.	2–8	5±2	6	McLeod[b e]
Percent of canopy in gaps	3–24	9.5	14	Runkle 1982

[a] See also Whittaker 1966, Weaver and Ashby 1971, Martin 1975, Winstead and Nicely 1976, Dickison 1980, McGee 1984, Lorimer 1985, and Clebsch and Busing 1989.
[b] McLeod, Donald E. December 3, 1996. Unpublished raw data. On file with: U.S. Department of Agriculture, Forest Service, Southern Research Station, Bent Creek Research and Demonstration Forest, 1577 Brevard Road, Asheville, NC 28806.
[c] See also Schmelz and Lindsey 1965, McGee 1984, Rosenberg et al. 1988, Poulson and Platt 1989, and Martin 1992.
[d] See also Thompson 1980; and MacMillan 1981, 1988.
[e] See also Hardt and Swank, in press.

Table 1 (metric units)—Standardized table of old-growth attributes for western and mixed mesophytic forests

Quantifiable attribute	Value		Number of stands	References
	Range	Mean		
Stand density (no./ha) —trees ≥ 10 cm d.b.h.	168–455	322±85	14	Bryant 1987 Muller 1982 Palmer 1987[a] McLeod[b]
Stand basal area (m^2/ha) —trees ≥ 10 cm d.b.h.	26–68	38±11	14	Bryant 1987 Muller 1982 Palmer 1987[a] McLeod[b]
Age of large trees (yrs) (maximum)				
Liriodendron tulipifera L.	226			in Runkle 1982
Tilia heterophylla Vent.	198			in Runkle 1982
Acer saccharum Marsh.	372			Tubbs 1977
Aesculus octandra Marsh.	431			in Runkle 1982
Fagus grandifolia Ehrh.	412			Morey 1936
Tsuga canadensis (L.) Carr.	607			Morey 1936
Number of 10-cm size classes —trees ≥ 10 cm d.b.h.	1–22	17	6	McLeod[b]
Maximum d.b.h. (cm)				
L. tulipifera L.	166		6	McLeod[b]
Tilia heterophylla Vent.	195			
Acer saccharum Marsh.	118			
Aesculus octandra Marsh.	104			
F. grandifolia Ehrh.	108			
Tsuga canadensis (L.) Carr.	115			
Standing snags (no./ha) —snags ≥ 10 cm d.b.h.	10–70	31±19	8	McComb and Muller 1983 Muller 1982[c] McLeod[b]
Downed logs (m^3/ha)	66–410	155±113	9	Muller and Liu 1991[d] McLeod[b] Hardt and Swank, in press
Decadent trees (no./ha) —trees ≥ 10 cm d.b.h.	4–20	12±6	6	McLeod[b e]
Percent of canopy in gaps	3–24	9.5	14	Runkle 1982

[a] See also Whittaker 1966, Weaver and Ashby 1971, Martin 1975, Winstead and Nicely 1976, Dickison 1980, McGee 1984, Lorimer 1985, and Clebsch and Busing 1989.
[b] McLeod, Donald E. December 3, 1996. Unpublished raw data. On file with: U.S. Department of Agriculture, Forest Service, Southern Research Station, Bent Creek Research and Demonstration Forest, 1577 Brevard Road, Asheville, NC 28806.
[c] See also Schmelz and Lindsey 1965, McGee 1984, Rosenberg et al. 1988, Poulson and Platt 1989, and Martin 1992.
[d] See also Thompson 1980; and MacMillan 1981, 1988.
[e] See also Hardt and Swank, in press.

basswood) are more susceptible to heart rot and cavity formation. Stillwell (1955) reported that 67 percent of old yellow birch were highly decayed. Williams (1936) reported that nearly all large beech trees in an Ohio climax forest were hollow, at least at the base, because of various fungal infections. Norden (1954) found that 91 percent of old sugar maples were highly decayed.

Diversity

Old-growth forests tend to have fewer tree species overall, but they have more canopy species than younger stands (<63 years) (Clebsch and Busing 1989). Gap-phase regeneration permits regeneration of both tolerant and intolerant species, which contributes to the maintenance of great canopy-species diversity in old growth. Conversely, younger stands may be dominated by yellow-poplar and other less shade-tolerant species (Clebsch and Busing 1989; Hardt and Swank, in press). Martin (1992) reported 43 tree species in 7 mixed mesophytic communities within the Lilley Cornett Woods in Kentucky. Appendix A presents tree species characteristic of old-growth, mixed mesophytic forests.

Diversity [Shannon-Weiner Index (H')] based on tree density is more variable in old-growth forests than in younger tracts. However, H' based on biomass tends to be higher in older stands than in younger stands because biomass is more evenly distributed among canopy species.

High species diversity, richness and equitability, and low dominance of canopy tree species appear to characterize old-growth, mixed mesophytic forests (Martin 1992). Martin (1992) suggests quantitative criteria for defining the canopy community composition of old-growth, mixed mesophytic forests: (1) $\geq$20 species, (2) H' >3.0, (3) evenness >0.50, and (4) Simpson's dominance values <0.30.

Shrub, tree seedling, and herbaceous species richness also tends to be high. McLeod (1988) reported an average of 51.1 vascular plant species per 0.25 acre (0.1 ha), with herbs contributing 72.2 percent of the total flora. Species richness generally increases with soil pH (McLeod 1988). Seedling density is significantly lower under ericaceous shrubs, suggesting that such shrubs may prevent seedlings from becoming established. This could be due to soil acidification, other chemical modifications, or decreased moisture or light levels beneath heath (Palmer 1987).

Although several plants are associated with old growth, no plant species is currently known to be restricted to old-growth, mixed mesophytic forests (Meier et al. 1996). Candidate species include Fraser's sedge [*Cymophyllus fraseri* (Andr.) Mackenzie] and spotted mandarin [*Disporum maculatum* (Buckley) Britt.] (Martin 1992). It is likely that if old-growth-dependent plants exist, mycorrhizal fungus species limit their distribution (Martin 1992).

Mixed mesophytic forests support rich mammalian, avifaunal, and herpetofaunal communities, several of which are rarely found in other forest types (appendix B) (Hinkle et al. 1993). No species is known to be restricted to old-growth forests, but several require the structural features (Hardt and Swank, in press) and microclimate of mature mesophytic forests (Haney and Schaadt 1996, Meier et al. 1996, Pelton 1996). Hence, moisture gradients affect the distribution of several species within the mixed mesophytic forest type (Hudson 1972, Hinkle et al. 1993).

Basal Area and Density

Basal area of old-growth, mixed mesophytic forest trees $\geq$3.9 inches (10 cm) d.b.h. ranges from 113.0 to 296.0 square feet per acre (26 to 68 m^2 per ha) (table 1). Clebsch and Busing (1989) found that basal area in second-growth forests approached that of old growth by age 63, but species composition differed. Muller (1982) reported that basal area did not significantly differ between an old-growth stand and an adjacent 35-year-old, second-growth stand in southeastern Kentucky [average 126.3 square feet per acre (29 m^2 per ha)]. However, fewer large diameter individuals comprised more basal area in old growth, while more smaller diameter individuals were present in younger growth.

Canopy trees are usually widely spaced. Reported numbers range from 68.0 to 349.0 stems per acre (168 to 863 stems per ha), but values depend on count method (table 1). Martin (1992) suggests that an average of 101.1 trees per acre (250 trees per ha) $\geq$3.9 inches (10 cm) d.b.h. may be an indicator, although not a defining attribute, of old-growth, mixed mesophytic forests.

Density of large trees may be more useful in defining old-growth mesic forests. Density of trees $\geq$29.5 inches (75 cm) ranged from 3.4 to 17.9 per acre (8.5 to 44.3 per ha) and averaged 11.3 ($\pm$ 4.9) per acre (27.8 $\pm$ 12.0 per ha) in five old-growth mixed mesophytic stands in the Southern Appalachians (see footnote 1). Martin (1992) suggests at least 2.8 trees per acre (7 trees per ha) $\geq$29.5 inches (75 cm) d.b.h. indicate old growth.

Species composition, site factors, such as soil type and moisture, and disturbance history, affect tree density (Martin 1992).

Snags

Standing dead trees, or snags, are important foraging and nesting resources for many cavity-nesting birds (Runkle 1991, Haney and Schaadt 1996). Numerous other animal species use standing snags for cover, denning, and foraging (Carmichael and Guynn 1983, Pelton 1996). Animal use may depend on the stage of decomposition (Cline and Phillips 1983). The number of snags depend on their formation rate and longevity, which vary by size, species, and cause of death (Bull 1983, McComb and Muller 1983, Raphael 1983, MacMillan 1988).

Annual snag formation rates vary from 0.7 to 9.3 per acre (1.6 to 23 per ha) (Lindsey and Schmelz 1965, Runkle 1991). Density estimates of snags ≥3.9 inches (10 cm) in old-growth, mixed mesophytic forests range from 4.0 to 28.3 per acre (10 to 70 per ha) [McComb and Muller 1983, Martin 1992, McLeod (see footnote 1)] (table 1). McComb and Muller (1983) reported that snag densities were the same or greater in a 35-year-old forest than in an old-growth, mixed mesophytic forest for all size classes. The younger forests had more than twice as many small snags than the older forests [1.0 to 3.9 inches (2.5 to 9.9 cm) d.b.h.]; both stands had 0.8 large snags 9.8 to 35.4 inches d.b.h. per acre [1.9 large snags (25 to 90 cm) d.b.h. per ha]. Martin (1992) reported ≥1.2 snags per acre (3 snags per ha) ≥23.6 inches (60 cm) d.b.h. Hardt and Swank (in press) found about 6.9 snags ≥9.8 inches d.b.h. per acre (17.0 snags ≥25 cm d.b.h. per ha) in two old-growth stands in the Southern Appalachians. They suggest that because species differ in their modes of mortality and decay rates, species composition influences snag density in old-growth stands. Muller and Liu (1991) reported that snags made up 24 percent of total CWD mass and 18 percent of total CWD volume in an old-growth forest in Kentucky.

Coarse Woody Debris

Coarse woody debris provides important microhabitat and "safe sites" for bryophytes, liverworts, fungi, and tree seedlings (Martin 1992). Many animal species use CWD for hiding, egg-laying and development, foraging for arthropods, and other functions. Thompson (1980) reported that fallen logs and pits created by tip-up mounds were important colonization sites for numerous herbaceous species. Coarse woody debris is also an important nutrient reserve, slowly releasing them as the wood decays.

Gap-phase disturbance (Barden 1980, Runkle 1981, Romme and Martin 1982) creates an uneven distribution of downed, dead logs in mixed mesophytic forests. Muller and Liu (1991) reported that 39.2 percent of CWD >7.9 inches (20 cm) d.b.h. occurred in only 12.5 percent of plots, primarily because of recent tree falls or standing snags. Estimates of the number of logs range from 7.7 to 61.1 logs ≥7.9 inches d.b.h. per acre (19.0 to 151.0 logs ≥20 cm d.b.h. per ha). Because log accumulations vary widely depending on disturbance type and history, and past and present species composition, they are poor indicators of the old-growth condition (Thompson 1980; MacMillan 1981; Martin 1992; Hardt and Swank, in press). Muller and Liu (1991) found only a weak inverse relationship between plot basal area and CWD. Species composition of CWD is largely dictated by forest species composition (Muller and Liu 1991).

Estimates of CWD volume range from 943.1 to 5,858.9 cubic feet per acre (66 to 410 m^3 per ha) [average 2,215.0 ± 1,615.0 cubic feet per acre (155.0 ± 113 m^3 per ha)] [Muller and Liu 1991; McLeod (see footnote 1); Hardt and Swank, in press] (table 1). Although McLeod (see footnote 1) recorded 98 percent of the total volume of CWD as moderately to highly decayed, Muller and Liu (1991) reported only 49 percent as moderately to highly decayed. Hardt and Swank (in press) found logs in two old-growth stands to be well distributed among decay classes, suggesting regular inputs to the forest floor.

Site conditions influence CWD volume because decomposition rates increase with increasing temperature and moisture. Hence, dry, exposed sites tend to have more CWD than moist, protected sites (Muller and Liu 1991). For similar reasons, more CWD occurs in cool deciduous forests than in warm temperate deciduous forests (Muller and Liu 1991).

Wood-decomposition rate varies among species. MacMillan (1988) reported that maple decays faster than beech, which decays faster than oak and hickory (*Carya* spp.). Fragmentation of CWD and subsequent accelerated decay varies among species. Beech, oak, and hickory fragment rapidly (MacMillan 1988). Muller and Liu (1991) reported that although American chestnut has not reached tree size [≥3.9 inches (10 cm) d.b.h.] since the mid-1940's because of the chestnut blight, it contributed 11 percent to the total CWD mass in their 1991 study. MacMillan (1988) found that the diameter of CWD affects decay rate only slightly, with large-diameter wood decaying somewhat faster than smaller-diameter debris. Such differences may affect size-class distribution of CWD.

Silsbee and Larson (1983) found 4 times more woody debris volume and 10 times more material in debris dams in streams of watersheds that were never logged than in those that were logged 45 years ago. Large, rotten wood was more than four times more common in streams of unlogged watersheds than of logged watersheds. Most of the woody debris in never-logged streams was concentrated in debris dams.

Soil

Soils of undisturbed forest stands have well developed organic horizons with no compaction (Martin 1992). Constant plant turnover maintains a thick, nutrient-rich O and A horizon that retains moisture. Old root channels and animal burrows create soil macropores in sites with undisturbed soils. These macropores may influence water availability, soil mixing, root distribution (Martin 1992), and underground use by animals.

Old-Growth Dynamics

Disturbance

Lorimer (1980) suggests that climax forests be defined as "those capable of self-perpetuation in the absence of severe disturbance." For forest types not mediated by high intensity disturbance, this definition may be suitable. Although the perpetuation of climax, mixed mesophytic forests may not depend on severe disturbance, several types of disturbance act at variable scales and frequencies to influence forest dynamics.

Wind damage, including windthrow (Lorimer 1980), tornadoes (Runkle 1982), hurricanes, and microbursts may create forest openings of various sizes (Greenberg and McNab, *in press*; Martin 1992). Ice storms, insect damage, and fungal infections, floods, and landslides (Runkle 1982, Shands 1992) are other disturbances that variously influence forest structure and composition.

The existence of association segregates dominated by shade-intolerant species, such as yellow-poplar, suggests that large-scale disturbance influences tree regeneration and species composition. Lorimer (1980) suggested that a heavy wind created the old-growth poplar cove at Joyce Kilmer Memorial Forest near Robbinsville, NC, over 300 years ago. McGee (1984) reported heavy mortality of old trees at Dick Cove, apparently from a combination of drought, heat, and defoliation by insects. Approximately 17 percent of northern red oak, 13 percent of white oak, and 19 percent of hickories died within a 3-year period.

The prevalence of mixed mesophytic forest across its geographic range, and the susceptibility of species to fire-induced damage or death suggest that large-scale, high intensity fire was infrequent (Harmon et al. 1983). Minimum fire-return interval was greater than a canopy generation (Runkle 1990). Fires within the mixed mesophytic region were probably small and/or restricted to specific topographic positions, such as xeric ridges (Harmon et al. 1983). Infrequent fire may have been the primary large-scale disturbance type, but frequency has decreased even further since fire suppression was begun by State and Federal agencies in the 1930's (Eller 1982, Runkle 1985, McLeod 1988).

Gap Dynamics

The creation of small canopy gaps by the death of a portion, entire, or group of trees accounts for the nearly constant tree turnover and species composition of old-growth, mixed mesophytic forests (Runkle and Yetter 1987, Barden 1989). Actual gap size may range from 10.8 to 16,032.4 square feet (1 to 1490 m^2) but commonly does not exceed 4,304.0 square feet (400 m^2) (Barden 1980; Lorimer 1980, 1989; Runkle 1981, 1982, 1985; Romme and Martin 1982; Runkle and Yetter 1987; Clebsch and Busing 1989). However, "expanded" or effective gaps, where more light reaches the forest floor, may exceed 21,520.0 square feet (2000 m^2).

Estimates of background tree mortality for all species range from 5 to 10 percent per decade in old-growth, mixed mesophytic forests (Christensen 1977; Lorimer 1980, 1989; Buchman 1983; Smith and Shifley 1984; Runkle 1991). Estimates of canopy turnover rates vary from <0.4 percent to 1 percent annually (Runkle 1982, 1985; Barden 1989). Gaps may close from above by lateral-branch extension of surrounding canopy trees or infill from below by sapling growth (Runkle 1982, 1990). The proportion of land area in gaps ranges from 3.2 to 24.2 percent (average 9.5 percent) (Runkle 1982) (table 1). The size and orientation of gaps may influence canopy recruitment patterns. For example, Poulson and Platt (1989) report more light in small, north-south gaps than in east-west gaps. Time required for lateral gap infilling also is greater for north-south than east-west-oriented gaps.

Tree Regeneration and Canopy Recruitment

Many characteristic, mixed mesophytic forest canopy tree species are shade tolerant; their seeds are able to germinate and persist for years as saplings beneath a tree canopy. Because light beneath a closed canopy forest can be as little as 0.3 to 2 percent, even small gaps can more than double understory radiation (Whittaker 1966, Canham 1989).

While shade-tolerant species, such as beech and sugar maple may be released by small gaps (Canham 1988), shade-intolerant species may require larger gaps that permit more light, longer daily periods of light, and greater gap longevity (the length of time for the canopy to close laterally before saplings reach canopy height). Species also vary in importance as a function of gap size and age (Runkle and Yetter 1987, Runkle 1990). Runkle (1990) reported that sugar maple was most important in small gaps of all ages; beech in all sizes of old gaps; white ash in large, young gaps; and yellow-poplar in large gaps of all ages. Barden (1981) reported that shade-tolerant species replaced most single- and multiple-tree gaps in the Great Smoky Mountains, but four species of low shade tolerance (yellow-poplar, black cherry (*Prunus serotina* Ehrhart), American ash, and northern red oak) maintained their presence in 3 percent of the canopy by infrequent captures of multiple-tree gaps.

Recruitment patterns and old-growth stand dynamics affecting future stand composition depend upon a combination of disturbance type and pattern, current species composition, and regeneration mode (Forcier 1975). For example, sugar maple produces many seeds with good dispersal ability (Fowells 1965). Hence, abundant, shade-tolerant seedlings can exploit canopy gaps as they occur (Dickison 1980). Conversely, beech seeds have poor dispersal ability (Fowells 1965). Hence, its distribution depends upon advance regeneration in gaps formed by or near parent trees or by root suckers (Williams 1936, Dickison 1980). Buckeye also has poorly dispersed seeds and low seed production (Fowells 1965). Basswood is highly clonal, so it recolonizes gaps rapidly if present (Dickison 1980, Barden 1981, Runkle 1989). Dickison (1980) reported that intolerant and two tolerant species (basswood and buckeye) regenerated periodically, while shade-tolerant species, including sugar maple, beech, and hophornbeam [*Ostrya virginiana* (Mill.) K. Koch] regenerated continuously in Walker Cove.

Interspecific differences in seed germination and seedling and sapling survival (competitive ability) also affect forest dynamics. Williams (1936) noted poorer survival of beech than sugar maple seedlings but a high mortality of sugar maple saplings. Red maple produced abundant seed, but germination was low and young trees were poor competitors with forest dominants. Variation in moisture and climate may affect germination and survival differently from year to year (Schmelz et al. 1975).

Age Structure and Diameter Distributions

Old-growth, mixed mesophytic forests are broadly uneven-aged or all aged (Lorimer 1980). The diameter distribution of uneven-aged forests is commonly negatively exponential, with many more small- than large-diameter trees (Lorimer 1980, 1985; Palmer 1987). Old-growth stands differ from younger, uneven-aged forests in having greater range of tree sizes, maximum tree age, and more large-diameter trees (table 1). Hardt and Swank (in press) reported an average of 2.4 and 2.5 trees ≥30.0 inches per acre (5.9 and 6.3 trees ≥75.0 cm d.b.h. per ha) in two old-growth stands in the Southern Appalachians. Longevity varies with species (Morey 1936, Tubbs 1977, Runkle 1982). However, few studies cite age exceeding 250 years for trees in old-growth, mixed mesophytic forests, although occasional trees much older than 250 years have been reported (table 1).

Irregular age distributions are common in old-growth stands and reflect severe natural disturbance or irregularities in seed production (Lorimer 1980). Breaks in slope or peaks in curves may indicate disturbance as it affects recruitment and mortality (Schmelz and Lindsey 1965, Schmelz et al. 1975, Lorimer 1980). Estimates of background tree mortality for all species range from 5 to 10 percent per decade in old-growth, mixed mesophytic forests. An additional 6 to 8 percent mortality caused by disturbance within a given decade is sufficient to create peaks in diameter distributions as more seedlings and saplings survive and grow into the canopy stratum (Lorimer 1980).

The diameter distributions of species within stands probably reflect their frequency of recruitment into the canopy (Palmer 1987). Palmer (1987) noted that Fraser's magnolia (*Magnolia fraseri* Walt.), a prolific basal sprouter, had a negatively exponential diameter distribution, whereas two other species that reproduce by seed did not.

Old-Growth Forests and Change

Clearly, old-growth forests are not static in species composition or structural attributes. Increases in basal area and density, and shifts in species composition have been reported for numerous old-growth stands (Weaver and Ashby 1971, Schmelz et al. 1975, MacMillan 1981, Busing 1989). Gap-model projections by Clebsch and Busing (1989) predicted a shift in species composition from yellow-poplar to sugar maple over 250 years, after which changes would stabilize, with some increase in biomass of several subdominant species. Williams (1936) noted more red oak stumps than live red oaks in a beech-maple climax in Ohio. The elimination of canopy-sized American chestnut by the chestnut blight dramatically altered canopy-species composition of old-growth stands.

Whittaker (1966) reported basal-area growth of 1.3 to 2.6 square feet per acre per year (0.3 to 0.6 m^2 per ha per year) in mature climax mesic forests of the Great Smoky Mountains. Busing (1989) reported a 52-year increase in basal area from 173.7 to 195.5 square feet per acre (39.9 to 44.9 m^2 per ha) and from 118.0 to 167.7 square feet per acre (27.1 to 38.5 m^2 per ha) in two old-growth stands in the Great Smoky Mountains National Park (Busing 1989). Increases were mainly in sugar maple and hemlock or silverbell, primarily in response to American chestnut mortality.

Conclusion

Defining old growth is enigmatic and problematic. The assignment of specific values to a host of attributes disregards the tremendous variability among and combination of features exhibited in old-growth forests. Viewed as the sum of a series of rigid criteria, a given stand may not "add up," whereas in fact, viewed as a whole it is indeed old growth. The species composition and structural attributes of old-growth western and mixed mesophytic forest stands are widely variable and depend upon the history of the specific stand. Species composition depends upon stand origin. An old-growth forest may be dominated by "pioneer" species, such as yellow-poplar, if the stand originated following a catastrophic disturbance (such as the Joyce Kilmer Memorial Forest), or of shade-tolerant species if gap dynamics has been the dominant process driving regeneration for several tree generations. Similarly, the number of snags, decadent trees, and logs depends upon tree mortality rates and mode, which in turn, depend upon disturbance history (including less dramatic disturbance such as drought), species composition and specific vulnerability to disease, heart rot, and blow down. Even-age and diameter distribution depend upon stand history and, if too rigidly defined, may exclude some stands that would otherwise be recognized as old growth. Nonetheless, assimilation of studies in which old-growth characteristics have been studied, and the drafting of general guidelines provide a starting point in defining and identifying old growth. Further work is needed to distinguish features that are unique to old growth.

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Appendix A

Tree, shrub, and select vascular herbaceous species that are characteristic of mature western mixed mesophytic forests:[a b]

Canopy and understory trees
Acer pensylvanicum L.
A. rubrum L.
A. saccharum Marsh.
Aesculus flava Solander
Amelanchier arborea (Michx. f.) Fern.
Betula lenta L.
B. alleghaniensis Britt.
Carpinus caroliniana Walt.
Carya cordiformis (Wang.) K. Koch
C. glabra (Mill.)
C. ovata (Mill.) K. Koch
C. tomentosa (Poir.) Nutt.
Cercis canadensis L.
Cladrastis kentukea (Dum.-Cours.) Rudd
Cornus florida L.
Fagus grandifolia Ehrh.
Fraxinus americana L.
Halesia carolina L.
Ilex opaca Ait.
Juglans nigra L.
J. cinerea L.
Liquidambar styraciflua L.
Liriodendron tulipifera L.
Magnolia acuminata L.
M. fraseri Walt.
M. macrophylla Michx.
M. tripetela L.
Morus rubra L.
Nyssa sylvatica Marsh.
Ostrya virginiana (Mill.) K. Koch
Oxydendrum arboreum (L.) DC.
Pinus echinata Mill.
P. rigida Mill.
P. virgiana Mill.
Prunus serotina Ehrhart
Quercus alba L.
Q. coccinea Muenchh.
Q. muhlenbergii Engelm.
Q. montana Willd.
Q. rubra L.
Q. velutina Lam.
Robinia pseudoacacia L.
Sassafras albidum (Nutt.) Nees
Tilia heterophylla Vent.
Tsuga canadensis L. (Carr.)
T. caroliniana Engelm.
Ulmus americana L.
U. alata Michx.

Shrubs
Aralia spinosa L.
Asimina triloba (L.) Dunal
Clethra acuminata Michx.
Cornus alternifolia L. f.
Euonymus americanus L.
E. atropurpureus Jacq.
Hamamelis virginiana L.
Hydrangea arborescens L.
Kalmia latifolia L.
Lindera benzoin (L.) Blume
Pyrularia pubera Michx.
Rhododendron maximum L.
Ribes cynosbati L.
Sambucus canadensis L.
Stewartia ovata (Cav.) Weatherby
Viburnum acerifolium L.

Woody vines
Aristolochia macrophylla Lam.
Bignonia capreolata L.
Celastrus scandens L.
Parthenocissus quinquefolia (L.) Planch.
Smilax tamnoides L.
Vitus spp.

Herbaceous species
Anemone lancifolia Pursh
A. quinquefolia L.
Thalictrum thalictroides (L.) Eames & Boivin
Actaea pachypoda Ell.
Aster spp.
Caulophyllum thalictroides (L.) Michx.
Claytonia caroliniana Michx.
C. virginica L.
Cypripedium calceolus L.
Delphinium tricorne Michx.
Dicentra canadensis (Goldie) Walp.
D. cucullaria (L.) Bernh.
Dioscorea villosa L.
Disporum lanuginosum (Michx.) Nicholson
Erythronium americanum Ker-Gawl.
Eupatorium rugosum Houttuyn
Hydrophyllum spp.
Phlox divaricata L.
Sanguinaria canadensis L.
Sedum ternatum Michx.
Solidago spp.
Stylophorum diphyllum (Michx.) Nutt.
Synandra hispidula (Michx.) Baill.
Tiarella cordifolia L.

Appendix A (continued)

Herbaceous species (continued)
Trillium grandiflorum (Michx.) Salisb.
T. erectum L.
Viola spp.

Ferns
Adiantum pedatum L.
Athyrium filix-femina (L.) Roth
Dryopteris carthusiana (Villars) H.P. Fuchs
D. goldiana (Hooker) A. Gray
Osmunda claytoniana L.
Thelypteris hexagonoptera (Michx.) Weath.
Polystichum acrostichoides (Michx.) Schott

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[a] Nomenclature from Wofford 1989.
[b] Compiled from Braun 1938, McLeod 1988, and Hinkle et al. 1993.

Appendix B

Common birds, mammals, and herpetofauna of mature mixed mesophytic forest:[a]

Birds

Cerulean warbler *(Dendroica cerulea)*
Black-throated green warbler (*D. virens*)
Acadian flycatcher *(Empidonax virescens)*
Black-and-white warbler *(Mniotilta varia)*
Kentucky warbler *(Oporornis formosus)*
Parula warber *(Parula americana)*
Summer tanager (*Piranga rubra*)
Ovenbird *(Seiurus aurocapillus)*
Yellow-throated vireo *(Vireo flavifrons)*

Mammals

Short-tailed shrew *(Blarina brevicauda)*
Opossum *(Didelphis virginiana)*
Big brown bat *(Eptisicus fuscus)*
Southern flying squirrel *(Glaucomys volans)*
Red bat *(Lasiurus borealis)*
Striped skunk *(Mephitis mephitis)*
Little brown bat *(Myotis lucifugus)*
Eastern woodrat *(Neotoma floridana)*
White-tailed deer *(Odocoileus virginianus)*
Hairy-tailed mole (*Parascalops breweri*)
White-footed mouse *(Peromyscus leucopus)*
Eastern pipistrelle *(Pipistrellus subflavus)*
Raccoon *(Procyon lotor)*
Gray squirrel *(Sciurus niger)*
Smoky shrew *(Sorex fumeus)*
Eastern chipmunk *(Tamias striatus)*
Gray fox *(Urocyon cinereoargenteus)*
Black bear (*Ursus americanus*)

Herpetofauna

Copperhead *(Agkistrodon contortrix)*
Green salamander *(Aneides aeneus)*
American toad *(Bufo americanus)*
Fowler's toad *(B. woodhousei)*
Black racer *(Coluber constrictor)*
Worm snake *(Corphophis amoenus)*
Mountain salamander *(Desmognathus monticola)*
Ring-necked snake*(Diadophis punctatus)*
Black rat snake *(Elaphe obsoleta)*
Coal skink *(Eumeces anthracinus)*
Five-lined skink *(Eumeces fasciatus)*
Cave salamander *(Eurycea lucifuga)*
Spring peeper *(Hyla crucifer)*
Gray treefrog *(H. versicolor)*
Red-spotted newt *(Notophthalmus viridescens)*
Slimy salamander *(Plethodon glutinosus)*
Mountain chorus frog (*Pseudacris brachyphona*)
Eastern box turtle *(Terrapene carolina)*
Garter snake *(Thamnophis sirtalis)*
Wood frog *(Rana sylvatica)*

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[a] Adapted from Hinkle et al. 1993.

Greenberg, Cathryn H.; McLeod, Donald E.; Loftis, David L. 1997. An old-growth definition for western and mixed mesophytic forests. Gen. Tech. Rep. SRS-16. Asheville, NC: U.S. Department of Agriculture, Forest Service, Southern Research Station. 14 p.

Old-growth mixed and western mesophytic forest characteristics may include high canopy species diversity; uneven-age and size distribution, including several old, decadent, large-diameter trees per hectare; low density and high basal area of canopy trees; and multiple vegetation strata. Additional indicators include the presence of snags and logs in several size and decomposition classes; undisturbed soil with no compaction, well-developed organic layer and soil macropores; and tree-fall gaps of various sizes and ages.

Keywords: Forest dynamics, forest structure, mixed mesophytic forests, old growth, western mesophytic forests.