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Three Decades of Overstory and Species Change in a Mixed Mesophytic Forest in Eastern Kentucky

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ABSTRACT

The objectives of this study were to document changes, between 1971 and 1999, in overstory vegetation structure and composition at Lilley Cornett Woods (LCW), an old-growth mixed mesophytic forest in eastern Kentucky. Similar to other old-growth forests, overstory density (284 to 347 trees/ha) and basal area (26.4 to 29.9 m^2/ha) have significantly increased during this time. The increase in density was primarily due to recruitment into the smallest overstory diameter-class (12.5–30.0 cm). Six species have comprised over 60% of total overstory importance since 1971; *Fagus grandifolia* has remained the most important species. The overstory composition in 1999 was not similar to 1971 (C = 63.4%) as several changes have occurred during the 28-year period, including increases in the importance of maples and eastern hemlock and decreases in oaks. These trends are consistent with other reports in the eastern United States.

INTRODUCTION

As the human population continues to increase, so does the scope and scale of our disturbance on forests (Vitousek et al. 1996, Likens et al. 1996, Sauer 1998). Long-term observations in undisturbed, old-growth forests are essential, as they can provide a baseline of information against which anthropogenic and non-anthropogenic effects over time can be evaluated (Martin 1992, Bakker et al. 1996, Likens et al. 1996).

More than 80 years ago, the structure and composition of the eastern deciduous forest began to be altered by the fungal-induced death of the American chestnut [*Castanea dentata* (Marsh.) Borkh.] (Braun 1950, Woods and Shanks 1959). As one of the dominant trees in the Mixed Mesophytic forest, chestnut reached its greatest size and density in the southern Appalachian Mountains before the Asian pathogenic ascomycete, [*Cryphonectria parasitica* (Murrill) Barr.], entered the United States in the early 1900s and prompted the tree's demise (Braun 1950, Keever 1953). The elimination of chestnut in the overstory provided openings for other sapling species to attain light and energy; many predicted that oaks and hickories would be the replacements (e.g., Korstian and Stickel 1927, Braun 1950, Nelson 1955). However, in stands where they were previously dominant, oak populations have continued to "decline" through overstory mortality and an absence of understory regeneration (e.g., Shotola et al. 1992, Lorimer et al. 1994, Zaczek et al. 2002).

Beginning in the early 1900s, droughts were observed as factors contributing to declining oak populations (Balch 1927, Hursh and Haasis 1931). Compounding the effects of drought, fire-suppression forest management and the gypsy moth [*Lymantria dispar* L.] have continued to be oak stressors in the eastern United States (Steinman 1999). The caterpillars of the gypsy moth are destructive defoliators that feed primarily on oak trees (Hoffard et al. 1995) causing growth loss, crown dieback, and tree mortality (Fosbroke and Gottschalk 1999). Further, an increase in

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fire suppression during the last half of the twentieth century appears to have decreased the ability of shade-intolerant oaks to regenerate and attain canopy status with increasing understory density and canopy closure (Harrod et al. 1998). Without an understory-clearing disturbance, such as fire, oaks cannot successfully compete with shade-tolerant species, particularly sugar maple (*Acer saccharum* Marsh.) and red maple (*A. rubrum* L.) (Abrams 1992, Lorimer et al. 1994, McDonald et al. 2002, Zaczek et al. 2002).

Forest compositional shifts from less mesic to more mesic species have been reported widely in the eastern United States (e.g., Parker et al. 1985, Shotola et al. 1992, Dodds and Smallidge 1999, Rhoades 2002, McDonald et al. 2002, Zaczek et al. 2002). In addition to the changes in composition, several studies have documented changes in structure, but with conflicting results, as some report increases in total forest density and basal area (e.g., Miceli et al. 1977, Parker et al. 1985, Shotola et al. 1992), while others have observed decreases (e.g., Rhoades 2002, Zaczek et al. 2002).

Ideal for comparison to these and other similar studies conducted in forests with long-term databases, Lilley Cornett Woods (LCW) has been studied for three decades through the use of permanent plots among the 104-ha of old-growth forest. LCW is located in southeastern Kentucky at the geographic center of the Mixed Mesophytic Forest Region recognized by Dr. E. Lucy Braun (1950). Although a long-term study at this single old-growth site restricts the conclusions that can be made about the changes and trends in forest composition on a regional basis, it is the only site that has been studied through time in the immediate area of Braun's classic field research on the Cumberland Plateau and in the Cumberland Mountains (Braun 1935, 1940, 1942).

Using the vegetation parameters of density, basal area, and composition, the following questions were asked to document change at LCW: (1) Have there been changes in vegetation structure (e.g., density and basal area) in the forest overstory during 28 years at LCW?, (2) If changes in density have occurred, which diameter-classes have experienced change?, (3) Have the most important forest species remained so?, (4) Have there been changes in relative values of density and basal area of dominant overstory species?, and (5) How do these results compare with similar studies in other eastern United States forests?

MATERIALS AND METHODS

Study Site

Lilley Cornett Woods (LCW) is located between latitudes 37°4′ and 37°6′ north and longitudes 82°59′ and 83°1′ west in Letcher County, Kentucky. This forest lies in the rugged eastern area of the Cumberland Plateau, which is immediately west of the Cumberland Mountains in southeastern Kentucky; there are approximately 222 ha of forest at LCW, of which 104 ha are old-growth upland forests. The forest has been protected as a natural area since 1969 and is currently under the management of the Division of Natural Areas, Eastern Kentucky University. LCW has not undergone grazing, logging, fire, or any other deliberate human disturbances since protection began. Although there is no evidence that the forest has ever been logged, grazing by domestic livestock occurred in the Woods and the region until the 1950s; evidence of fire in the 20th century is confined to the oldest trees of the exposed ridge crests.

The elevation at LCW ranges from 315 to 588 m, where topography is greatly dissected and steep. The surface rocks are of middle and lower Pennsylvanian age consisting of interbedded sandstones, siltstones, shales, and coal of the Breathitt formation (Martin 1975). Soils of the old-growth are predominantly silt loam to clay loam developed in colluvium and residuum of these rocks and their detailed characteristics were discussed in more detail by Martin (1975). Climate at LCW is usually mild and humid and greatly modified by the dissected topography. Weather records from a nearby station at 440 m for a 22-yr period showed the mean annual precipitation is 133 cm, mean temperature is 13°C, and the mean growing season is about 170 days.

Described as a stable, old-growth forest, at least nine overstory communities were recognized and mapped at LCW (Martin 1975): Beech, Beech-buckeye, Beech-sugar maple, Beech-white oak, Chestnut oak, Mixed oak, White oak, Hemlock, and Sugar maple-basswood-tulip poplar. The Woods possesses the multiple characteristics typical of an old-growth mixed mesophytic forest, including a forest overstory of trees at least 200 years old and a density approximately 250 trees/ha, a basal area near 25 m^2/ha, a high diversity of species and communities, a presence of logs and snags of various sizes and stages of decomposition, the lack of human disturbance, non-compacted soils with macropores, and an uneven-aged canopy with species in several size-classes (Parker 1989, Martin 1992).

Sampling Methods

From May through August 1999, forest vegetation was sampled on 135 permanent, circular, 0.08 ha plots established in 1971 in the old-growth forest. Representing approximately 10 percent of the upland area, plots had been placed at each slope position with corresponding slope shape (i.e., convex "leads" or concave "draws"), and aspect recorded by degrees from north in 1971 (Martin 1975). Each plot was categorized with a slope position (i.e., lower, middle, upper, ridge), a slope aspect (i.e., one of eight cardinal points), and a community type. All community types were based on Martin's (1975) vegetation descriptions and map, except for the 1999 designation of a scarlet oak community that was added because of the current oak decline, which has particularly affected red oaks in eastern forests.

Within the 0.08 ha plots, radii were adjusted for slope steepness and woody plants greater than or equal to 12.5 cm dbh were designated as overstory or canopy trees. As in all other sample years, overstory trees were identified and measured to the nearest 0.1 cm dbh by species. Data on understory trees (<12.5 cm) were also collected but will not be discussed directly in this paper. Species nomenclature followed Gleason and Cronquist (1991). All plots were inventoried in 1971, and re-inventoried in 1981, 1991, and 1999.

Analytical and Statistical Methods

Density, basal area, and IV. Calculations for each plot in each sample year of 1971, 1981, 1991, and 1999, included: (1) total density (trees/ha), (2) species density and (3) species relative density, (4) total basal area (m^2/ha), (5) species basal area, and (6) species relative basal area. An importance value (IV) for each species was then calculated by summing the relative values of density and basal area; an IV for a species can range from 0 (absent) to 200 (complete dominance). By using the importance values of 1971 and 1999, the Bray-Curtis similarity coefficient ($C = 2w/a+b$) (Bray and Curtis 1957) was calculated to evaluate how similar the forest composition was between these two years.

Tests for significant change over time were done for (1) the entire forest and (2) sixteen selected species: red maple, sugar maple, yellow buckeye (*Aesculus octandra* Marsh.), pignut hickory [*Carya glabra* (Mill.) Sweet], mockernut hickory [*C. tomentosa* (Poir. ex Lam.) Nutt.], flowering dogwood (*Cornus florida* L.), American beech (*Fagus grandifolia* Ehrh.), tulip poplar (*Liriodendron tulipfera* L.), sourwood [*Oxydendrum arboreum* (L.) DC], white oak (*Quercus alba* L.), scarlet oak (*Q. coccinea* Muenchh.), chestnut oak (*Q. prinus* Willd.), northern red oak (*Q. rubra* L.), black oak (*Q. velutina* Lam.), white basswood (*Tilia heterophylla* L.), and hemlock [*Tsuga canadensis* (L.) Carr]. Species were chosen based on forest and community importance as dominants, co-dominants, or major associates (Martin 1975); frequency among the plots; and the extent of focus within recent literature on forest health and mortality (Jenkins et al. 1999, Steinman 1999, McEwan et al. 2000).

A variation of the repeated measures (RM) analysis of variance (ANOVA) was used to evaluate if there were differences in the forest overstory in 1971, 1981, 1991, and 1999. RM is typically applied when observations are taken on the same subject at different points in time. However, in this study, the individual trees were never tagged. Thus, data for a given sample year could be from trees that were not present or measured in previous years, which would consequently make a standard RM analysis invalid.

However, since the data recorded year after year were from the same plots, a correlation between observations does exist. To account for this correlation, simple linear regressions were calculated for each year, where z = observed values (e.g., mean density, relative basal area, species IV), α = intercept, β = slope, and e = residual: $z_1 = (\alpha + \beta \times 1971 + e)$, $z_2 = (\alpha + \beta \times 1981 + e)$, $z_3 = (\alpha + \beta \times 1991 + e)$, and $z_4 = (\alpha + \beta \times 1999 + e)$. From these four regressions, the observations [z-values (e.g., species IV)] over the sample years were combined into one expression: $\beta\_hat = [z_1 \times (-14.5) + z_2 \times (-4.5) + z_3 \times (5.5) + z_4 \times (13.5)]/[(-14.5)^2 + (-4.5)^2 + (5.5)^2 + (13.5)^2]$. By summing the four data values into one correlated value (β_hat), the ANOVA assumption of independence is not violated. Then, β_hat was tested using PROC MIXED and adjusted for plot [SAS Institute]. And, by using one value (β_hat), a multiple comparisons (e.g., Tukey) analysis was not applicable. Most trends are apparent nevertheless.

Diameter Classes. Four diameter classes were used to assess overstory change between 1971 and 1999: 12.5–30.0 cm, 30.1–50.0 cm, 50.1–75.0 cm, >75.0 cm. Again, analyses were done for (1) the entire forest and (2) the sixteen selected species. Chi-square goodness of fit was used (at a significance level of *critical* $\chi^2 < 0.05$) (Zar 1996) to test the difference in the number of stems (using diameter class as the class variable) over the two sample years of 1971 & 1999; any diameter class with zero values for both years was not included in the test. Diameter class data were used to evaluate growth, since they could help show if a change in density was primarily due to, (1) recruitment from the understory (i.e., saplings < 12.5 cm) into the overstory, or (2) increases within higher diameter overstory classes. Available tree diameter data were used to describe growth rather than other methods (e.g., coring).

RESULTS

Density, Basal Area, and IV

Total forest. Significant changes in density and basal area have occurred during the 28-year period (Figure 1). Between 1971 and 1999, mean overstory density increased 22.2% from 284 to 347 trees/ha (PROC MIXED, $P < 0.0001$), while mean basal area oscillated from 26.4 to 29.9 m^2/ha ($P = 0.02$). The greatest change between consecutive samples for density (+16.6%) and basal area (+13.0%) was from 1991 to 1999. Through time, density and basal area have both fluctuated with higher values in 1981 and 1999. Compositionally, the Bray-Curtis similarity coefficient showed that the 1999 overstory was not similar (C = 63.4%) to 1971. This percentage is considerably below the value designated for forests defined as "similar" (i.e., C = 80%) (Bray and Curtis 1957). Across the forest, the total number of species has remained relatively stable: 43 species were recorded in 1971 and 1981, 41 species in 1991, and 39 species in 1999.

Selected Species. Relative to the other species, beech had the greatest density, basal area, and IV in each of the four samples over 28 years; none of these beech values changed during this time (Figure 2, Table 1). However, changes occurred for other species. In 1971, the two groups of species with the greatest density were beech (52.0 trees/ha) and the white oaks (white oak, chestnut oak) (44.8 trees/ha), while hemlock (21.0 trees/ha) was the least dense. But by 1999, the maples (red maple, sugar maple) (78.2 trees/ha) had significantly increased ($P < 0.0001$) and were more dense than beech (63.8 trees/ha), while hemlock (53.9 trees/ha) had also increased ($P < 0.0001$) becoming the third most dense species. The densities of all three red oaks (red oak, scarlet oak, black oak), white oak ($P < 0.0001$), and chestnut oak ($P = 0.001$) densities significantly declined (Table 1).

In 1971 and 1999, beech and the white oaks had the highest basal areas (Table 1). White oak significantly decreased from 4.2 to 3.9 m^2/ha ($P < 0.01$) during this time, but chestnut oak basal area did not change. By 1999, red maple (2.3 m^2/ha) ($P = 0.001$) and hemlock (3.4 m^2/ha) ($P < 0.0001$) had increased, while scarlet oak declined ($P = 0.001$).

The top six important species in 1971 remained so in 1999: beech, hemlock, red maple, white oak, sugar maple, and chestnut oak (Table 1). These species comprised at least 60% of the total forest IV in all four sample years. However, the order of importance has changed, as four species either highly differed (red maple, hemlock) or differed (white oak, sugar maple) across the

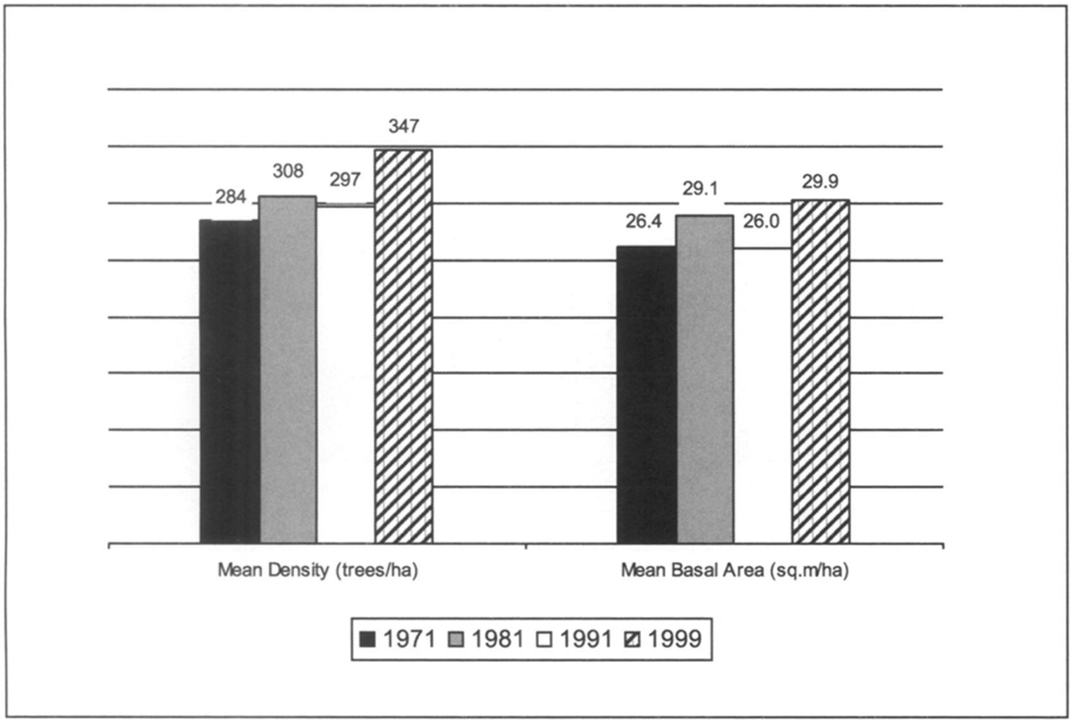


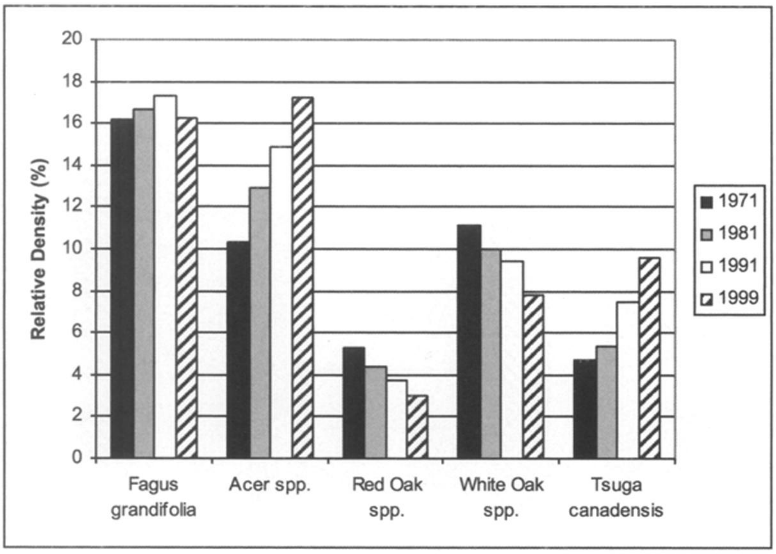
Figure 1. Mean values of density and basal area for the overstory old-growth forest at Lilley Cornett Woods, Letcher County, Kentucky: 1971–99. Both values significantly differed over time (PROC MIXED): mean density ($P < 0.0001$) and mean basal area ($P = 0.02$). Standard errors for mean values are <40%.

28 years (Table 1). While hemlock was the fifth important in 1971, the doubling of the IV by 1999 made it second only to beech. These significant changes among the top species appear to have contributed to the dissimilarity between years observed through the Bray-Curtis coefficient.

Diameter Classes

Between 1971 and 1999, increases in abundance in all four diameter-classes were observed (Figure 3). The overall change in the number of stems, per size class, was highly significant between 1971 and 1999 (Chi-square, $P < 0.001$). The largest increase, from 2050 to 2570 stems (+25.4%), was in the smallest size-class (12.5–30.0 cm); smaller percentage increases were in the higher diameter classes.

Of the sixteen species analyzed for changes in stems per diameter-class between 1971 and 1999, nine highly differed ($P < 0.001$): red maple, sugar maple, mockernut hickory, flowering dogwood, American beech, tulip poplar, white oak, chestnut oak, and hemlock (Table 2). Only three species did not significantly change between these two sample years (yellow buckeye, black oak, white basswood). Also shown by the forest analysis (Figure 3), most of the species changes occurred within the smallest diameter-class, including: flowering dogwood (−75.6% stems), white oak (−34.4%), red maple (+106.7%), sugar maple (+101.6%), and hemlock (+142.9%). In the 30.1–50.0 cm class, the maples, mockernut hickory, and chestnut oak (+29.1%) increased, while the number of northern red oak (−50.0%) and scarlet oak (−48.9%) trees decreased. The most noticeable characteristic of the two largest classes (50.1–75.0 cm, >75.0 cm) was stability. The changes of these established trees, relative to the smaller classes, are minimal. The oaks have been especially stable and dominant in the larger class sizes. However, of all the sixteen species analyzed, hemlock was the only one to increase in tree count



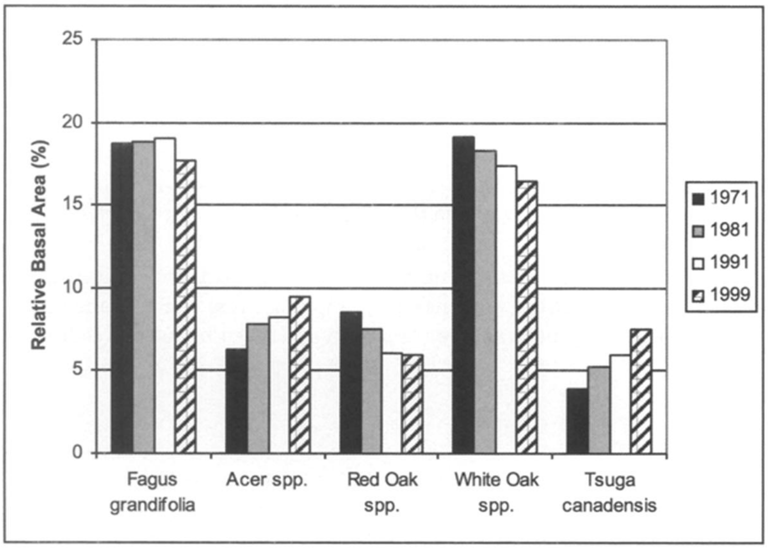


Figure 2. Relative values of density and basal area for selected overstory species[1] in the old-growth forest at Lilley Cornett Woods, Letcher County, Kentucky: 1971–99. See Table 1 for levels of significance per species.[1] *Acer* spp. = *Acer rubrum*, *A. saccharum*; Red Oak spp. = *Quercus rubra*, *Q. coccinea*, *Q. velutina*; White Oak spp. = *Q. alba*, *Q. prinus*.

in each of the four diameter classes: +142.9% (12.5–30.0 cm), +62.5% (30.1–50.0 cm), +25.0% (50.1–75.0 cm), +100.0% (>75.0 cm).

DISCUSSION

Through her 1950 book, *Deciduous Forests of Eastern North America*, the authoritative description of eastern United States forests has continued to belong to Dr. E. Lucy Braun. Within this volume, Dr. Braun identified the region on the Cumberland Plateau and in the Cumberland Mountains of southeastern Kentucky as the geographic center of the "Mixed Mesophytic Forest." Braun and others (Martin 1975, 1992; Romme and Martin 1982; Runkle

Table 1. Old-growth overstory[1] forest composition through time, Lilley Cornett Woods, Letcher County, Kentucky: 1971–99[2]

	Mean Values											
	Relative Density (×100)				Relative Basal Area (×100)				IV[3]			
Species	**1971**	**1981**	**1991**	**1999**	**1971**	**1981**	**1991**	**1999**	**1971**	**1981**	**1991**	**1999**
Fegus grandifolia	16.2	16.7	17.3	16.3	18.7	18.8	19.0	17.7	34.8	35.5	36.3	34.0
Tsuga canadensis	4.7	5.4	7.5	9.6***	3.9	5.2	6.0	7.5***	8.6	10.5	13.5	17.1***
Acer rubrum	6.2	8.5	9.7	10.0***	3.4	4.4	5.3	5.5**	9.6	12.9	15.1	15.5***
Quercus alba	6.8	6.3	6.1	4.7***	12.0	11.5	10.7	9.4**	18.8	17.8	16.8	14.1**
Acer saccharum	4.1	4.4	5.2	7.2***	2.9	3.4	2.9	4.0	7.0	7.8	8.1	11.2**
Quercus prinus	4.2	3.6	3.3	3.1**	7.0	6.7	6.7	7.1	11.2	10.3	10.0	10.2
Oxydendium arboreum	5.3	5.6	5.1	4.7	2.0	2.4	2.1	1.9	7.2	8.0	7.2	6.5
Liriodendron tulipfera	1.8	2.1	2.0	2.7*	2.4	2.9	2.7	3.6**	4.2	5.0	4.7	6.3**
Carya glabra	4.0	3.2	2.8	2.7*	2.3	2.4	2.2	2.3	6.3	5.6	5.0	5.0
Tilia heterophylla[4]	1.5	1.9	1.8	1.8	1.7	2.4	2.3	2.1	3.2	4.3	4.1	3.9
Aesculus octandra[4]	2.6	2.3	2.5	2.0	1.4	1.3	1.4	1.4	3.9	3.6	3.9	3.4
Quercus velutina	1.9	1.7	1.8	1.3**	2.6	2.4	2.3	2.1	4.6	4.1	4.1	3.3**
Quercus coccinea	2.2	1.7	1.1	1.0**	3.6	3.1	2.1	2.2**	5.8	4.8	3.2	3.2**
Carya tomentosa	1.6	1.9	1.5	1.5	0.9	1.2	1.2	1.3	2.5	3.0	2.6	2.8
Quercus rubra	1.0	0.9	0.7	0.7*	1.9	1.9	1.6	1.6	3.0	2.9	2.3	2.3
Sum[2]									201	201	202	201

[1] Overstory trees ≥ 12.5 cm dbh.
[2] 31 additional species with IVs < 2.0 (in 1999) are not listed.
[3] IV = (Rel. Density × 100) + (Rel. Basal Area × 100).
[4] Indicator species of mixed-mesophytic forest (Braun 1950), all species present in 1999 were listed by Braun in 1950 (Table 1), except *O. arboruem* and *Q. coccinea*.
*P < 0.05, **P < 0.01, ***P < 0.0001.

2000) have described the mesic deciduous forests of the Southern Appalachians among the most stable of North American ecosystem types; that is, dynamic, but relatively unchanging in vegetation structure and composition over time (Bormann and Likens 1979, Busing 1998). However, between 1971 and 1999, there have been significant changes in these LCW characteristics.

At LCW, six species have comprised at least 60% of the total importance values for the forest over 28 years: beech*, hemlock, red maple, white oak*, sugar maple*, and chestnut oak [*Braun (1950) identified as co-dominants in this forest type]. The continuing dominance of the same species is typically indicative of stability of the vegetation composition. This may be true, but the forest overstory at LCW in 1999 was not similar to 1971 (C = 63.4%). While some studies have described a lack of change in the old-growth forests in the Mixed Mesophytic Forest region (e.g., Busing 1993, 1998; Runkle 2000), the compositional changes of LCW are similar to other eastern US studies (e.g., Barton and Schmelz 1987, Fralish et al. 1991, Shotola et al. 1992).

In old-growth forests, density typically ranges from 161 to 427 trees/ha in the Central Hardwoods region (Parker 1989), to greater than 250 trees/ha in the mixed mesophytic forest (Martin 1992). Forests with stable basal areas can range from 50 to 64 m^2/ha in the Great Smoky Mountains (Whittaker 1966), from 25 to 32 m^2/ha (Held and Winstead 1975), and greater than 25 m^2/ha (Martin 1992) in eastern old-growth forests. The number of species in a stable, old-growth overstory of mixed mesophytic forest should be at least 25 (Martin 1992); there were 39 species at LCW in 1999. This is in agreement with Braun (1950), as she noted that an "all-deciduous mixed mesophytic forest" would be composed of "some 30 or more canopy species of which a dozen or more or less constantly present."

In synthesizing three decades of LCW data, mean density significantly increased 22% from 284 to 347 trees/ha, while mean basal area significantly rose 13% (26.4 to 29.9 m^2/ha). These values follow given ranges for old-growth (Held and Winstead 1975, Parker 1989, Martin

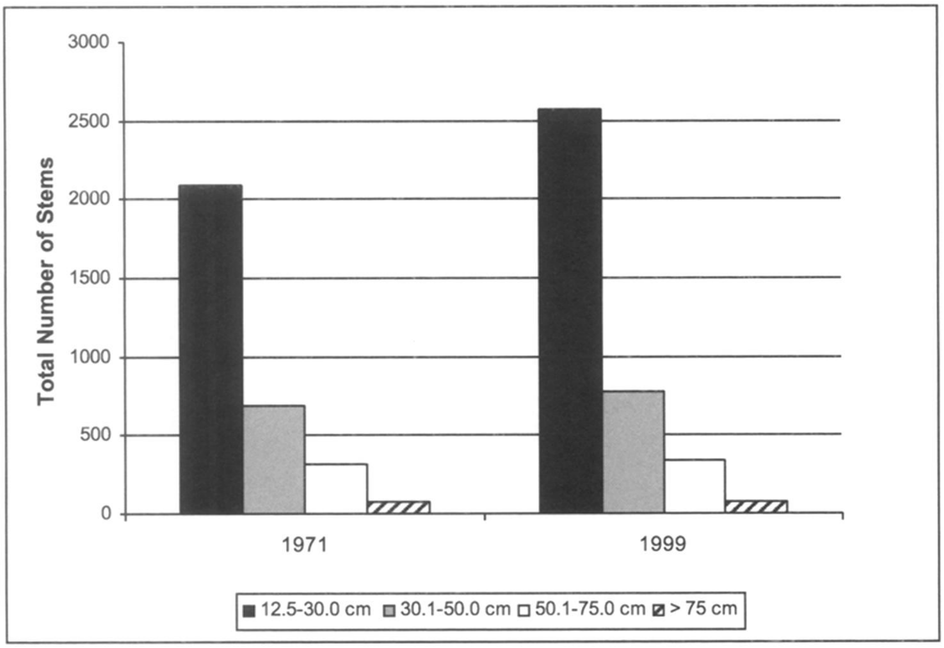


Figure 3. Total number of stems per diameter class for the overstory old-growth forest at Lilley Cornett Woods, Letcher County, Kentucky: 1971 and 1999. There was a highly significant (Chi-square, $P < 0.001$) difference between the number of stems in these two sample years.

1992) and can be compared to a few temporal studies which used similar overstory size-classes (i.e., "trees" $\geq$ 10 cm dbh) (Table 3). Of these studies, density and basal area at LCW most closely resemble the Indiana forest at Davis-Purdue, which is also a mature research forest with little human disturbance since 1900 (Parker et al. 1985). While the actual density and basal area values may not be equivalent, the general increasing trend is apparent in other forests with multi-year databases (e.g., Miceli et al. 1977, Shotola et al. 1992, Hemond et al. 1983).

The increases in both overstory density and basal area, between 1971 and 1999, are somewhat contrary to conventional wisdom. That is, as trees age and grow into larger size-classes, consequently occupying canopy space and using light resources, competition for recruitment becomes severe among members of the lower diameter classes (Franklin et al. 1987, Peet and Christenson 1987). Therefore, once the trees of the forest reach relatively large heights with increased basal area, the density should decrease. At LCW, however, both density and basal area have significantly increased with fluctuations among the four sample years; 1971 and 1991 had the lower values, while 1981 and 1999 were higher. The overall change in density was primarily due to the smallest dbh size-class of 12.5–30.0 cm, which had an increase of 25% over the three decades. This may be expected, since canopy tree-fall gaps are frequent disturbances in these forests and promote sapling growth into the overstory (Romme and Martin 1982, Martin 1992, Runkle 2000).

Increases in all diameter classes (i.e., 12.5–30.0, 30.1–50.0, 50.1–75.0, >75.0 cm) emphasized the significant density increase for the entire forest. Abundance in the smallest class increased more than 100% for three species: red maple, sugar maple, and hemlock. In each of the four size-classes, these three species had more trees in 1999 than in 1971. All three are shade-tolerant and capable of living suppressed in the understory for many years; hemlock is a slow-grower and can live up to 100 years as a tree of 2.5 cm dbh (Godman and Lancaster 1990). As overall density has increased throughout the forest, more shade has become present and the relative densities and basal areas of species such as sugar maple, red maple, and hemlock have risen. Over the 28 years, the relative density of hemlock increased over 100%. Other eastern

Table 2. Diameter-class distribution of abundance for sixteen selected species, Lilley Cornett Woods, Letcher County, Kentucky: 1971 and 1999

			Diameter-Class (Total Number of Stems)							
			12.5–30.0 cm		30.1–50.0 cm		50.1–75.0 cm		>75 cm	
			Year							
		df[3]	1971	1999	1971	1999	1971	1999	1971	1999
Acer rubrum	P < 0.001[1]	3	223	461	37	70	11	10	1	0
Acer saccharum	P < 0.001	3	124	250	18	38	12	12	2	2
Aesculus octandra	ns[2]	2	59	53	10	12	2	4	0	0
Carya glabra	P < 0.025	2	136	106	31	37	4	5	0	0
Carya tomentosa	P < 0.001	2	56	41	9	28	2	2	0	0
Cornus florida	P < 0.001	1	45	11	1	1	0	0	0	0
Fagus grandifolia	P < 0.001	3	292	433	161	151	97	87	21	17
Liriodendron tulipfera	P < 0.001	3	26	48	30	19	9	19	4	10
Oxydendrum arboreum	P < 0.005	1	244	284	7	3	0	0	0	0
Quercus alba	P < 0.001	3	163	107	93	91	57	57	19	15
Quercus coccinea	P < 0.01	3	21	19	47	24	16	18	2	1
Quercus prinus	P < 0.001	3	72	51	48	62	42	49	13	21
Quercus rubra	P < 0.025	3	20	10	18	9	7	10	4	5
Quercus velutina	ns	3	37	31	35	25	13	17	1	1
Tilis heterophylla	ns	3	24	32	21	23	11	13	0	1
Tsuga canadensis	P < 0.001	3	191	464	64	104	20	25	3	6
Species represent % of total stems			85	93	91	90	94	96	97	98

[1] Chi-square analysis tested the difference in the number of stems (using diameter-class as the class variable) over the two sample years of 1971 & 1999; diameter-classes with zero values for both years were not included in the test (e.g., *C. glabra* test used df = 2); critical χ^2 values were used at the P < 0.05 level; amount of significant changer per species is shown as a P-value.

[2] ns = number of stems is not significantly different between 1971 & 1999.

[3] df = degrees of freedom.

United States studies have reported similar trends of increasing abundances of mesic species in areas such as, Indiana (Parker et al. 1985, Barton and Schmelz 1987, Shotola et al. 1992), the Great Smoky Mountains (Busing 1998, SAMAB 1996), Michigan (Woods 2000), and Illinois (Miceli et al. 1977, Fralish et al. 1991).

The elimination of American chestnut during the first half of the twentieth century (Braun 1950) prompted studies, many of which suggested oaks (e.g., Nelson 1955, Woods and Shanks 1959, Thor and Summers 1971, Martin 1975) and possibly red maple (Nelson 1955) would enter the vacated chestnut niche of eastern United States forests. Because of its near 100% increase in density, ubiquitous nature, and persistence on ridge-tops (former locations of LCW chestnuts [Martin 1975]), it appears that red maple may be chestnut's replacement at LCW. This species has also been suggested as replacing chestnut in other eastern forests (Busing 1993, Dodds and Smallidge 1999, Vandermast and Van Lear 2002).

While several shade-tolerant species at LCW have been thriving in the lowest size-class during the last three decades, dogwood and oaks have declined or have had relatively low increases. Devastated primarily by the fungal anthracnose *Discula destructiva* (McEwan et al. 2000), the abundance of dogwood has declined over 75% between 1971 and 1999. Fire suppression, which has contributed to increased shade in the LCW understory during most of the 20th century, has helped limit understory regeneration of shade-intolerant oaks throughout these woods and other eastern United States forests (e.g., Lorimer et al. 1994, Harrod et al. 1998). This was evident at LCW, as the relative values of density and basal area for both the red oak and white oak groups declined between 1971 and 1999. In the 12.5–30.0 cm size-class, the five selected oak species, as a group, decreased in relative abundance from 15.3 (out of 100.0) to 8.5 across the entire forest. This trend of decreasing oak importance and regeneration is similar

Table 3. Characteristics of temporal and non-temporal studies in eastern United States forests

Woods	dbh Used ≥ (cm)	Author(s)	Forest Type[1]	Time Period	Time Span (yr)	Density[2] (first–last yr)	Basal Area[3] (first–last yr)
Lilley Cornett Woods, KY	12.5	this study	MM o-g	1971–1999	28	284–347	26.4–29.9
Lilley Cornett Woods, KY	10.0	Muller (1982)	MM o-g	1979	0	428	27.8
Price Mountain, VA	10.0	Rhoades (2002)	OC	1971–1999	28	630–540	40.0–41.5
Kaskaskia Woods, IL	4.0	Zaczek et al. (2002)	CH o-g	1935–1997	62	892–588	22.7–34.3
Davis-Purdue, IN	10.2	Parker et al. (1985)	CH o-g	1926–1976	50	165–320	23.7–31.0
Connecticut Arboretum, CT	14.0	Hemond et al. (1983)	CH o-g	1952–1972	20	236–530	20.3–33.2
Brownfield Woods, IL	6.4	Miceli et al. (1977)	CH o-g	1925–1975	50	284–483	23.7–31.1
Weavers Woods, IL	6.6	Shotola et al. (1992)	o-g	1956–1983	27	93–121	19.5–26.1
GSMNP[4], eastern TN	10.0	Harrod et al. (1998)	MM o-g	1970s–1995	~20	618–625	25.9–25.9
Dinsmore's Woods, northern KY[5]	10.0	Held et al. (1998)	o-g	1973–1994	21	334–261	25.0–22.0
Hamilton County (Cincinnati), OH[6]	10.0	Bryant (1987)	o-g	1980s	0	199–396	26.1–39.2
Greenwood Forest, KY	10.2	Chester et al. (1995)	o-g	1993	0	373	37.8
Adirondack Park, NY	10.0	McGee et al. (1999)	NH o-g	1990s	0	392	33.7
Spitler Woods, IL	10.0	Roovers and Shifley (1997)	CH o-g	1992	0	406	28.7
Drew Woods, OH	10.0	Boerner and Kooser (1991)	o-g	1989	0	456	44.1
Holden Arboretum, OH	10.0	Forrester and Runkle (2000)	BM o-g	1990s	0	236	37.3
Huestons Woods, OH	10.0	Swanson and Vankat (2000)	MM o-g	1986–1987	0	401	42.6

[1] Primarily based on Braun's (1950) description of eastern forests; MM = Mixed Mesophytic, CH = Central Hardwoods, NH = Northern Hardwoods, BM = Beech-Maple, OC = Oak-Chestnut, o-g = old-growth.
[2] Density (trees/ha) is based on the dbh used to classify "overstory."
[3] Basal Area (m^2/ha).
[4] GSMNP = Great Smoky Mountains National Park.
[5] Tornado disturbance occurred in 1975.
[6] Six old-growth forests were sampled in Hamilton County, OH; density and basal area values are are ranges for these six forest.

to other forests that also have longer fire cycles due to fire suppression (Fralish et al. 1991, Shotola et al. 1992, Lorimer et al. 1994). However, it is interesting to note that while the oaks have relatively fewer stems in the smaller size classes (12.5–30.0, 30.1–50.0 cm), they have continued to be the most dominant species in the two largest classes (50.1–75.0, >75.0 cm).

SUMMARY

Direct, long-term observations in permanent plots are essential in testing and creating hypotheses about characteristics of late-successional, and sometimes stable, communities (Bormann and Likens 1979, Bakker et al. 1996). Further, undisturbed, old-growth forests such as LCW provide a baseline of information against which long-term effects of threats to forests, anthropogenic and non-anthropogenic, can be evaluated (Likens et al. 1996). In the eastern United States most "long-term" studies have spanned 10 to 20 years (e.g., Bell 1997, Elliott et al. 1999, Runkle 2000), while others have encompassed at least 50 years (Della-Bianca 1983, Parker et al. 1985, Volk and Fahey 1994, Busing 1998). This study evaluated change over 28 years.

The values of LCW mean density, mean basal area, and number of species, are within the ranges given for old-growth mixed mesophytic overstory forests and are similar to several other eastern and southeastern studies. There have been significant increases in mean density and mean basal area between 1971 and 1999, with the smallest overstory diameter-class (12.5–30.0 cm) comprising most of this density change. There have been substantial changes in the dominant species, as the forest composition in 1999 differed from 1971. And, while the six most important species (American beech, Eastern hemlock, red maple, white oak, sugar maple, chestnut oak) in 1971 were the same in 1999, the rankings of species have shifted considerably. Overall, most shade-tolerant species have increased in importance, through density and basal area, while several oaks have decreased at LCW. Hemlock and red maple have had the highest overall increase (density, basal area, importance) during the last 28 years, while beech remains the most stable dominant species. However, though not known to exist at LCW, the presence of the gypsy moth and hemlock wooly adelgid could quickly change the composition of the forest as it is described today.

This study has reported the increasing importance of shade-tolerant species and a concurrent decline of shade-intolerant oaks, a trend that has been stated by several other recent eastern United States studies. The descriptions of oak decline in eastern forests have been reported since the 1960s, and it appears this decline will continue as a result of management practices (e.g., fire suppression) and various site-specific biological conditions (e.g., gap dynamics, chestnut replacement). This gradual, yet steady, and apparent shift in the composition of many forests based on the descriptions given by Braun and her early 20th century colleagues reflects the dynamic nature of forest ecosystems.

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