

TWENTY-TWO YEAR CHANGES IN REGENERATION POTENTIAL IN AN OLD-GROWTH *QUERCUS* FOREST ON THE MID-CUMBERLAND PLATEAU, TENNESSEE

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Abstract—A study was initiated in 1983 and then reexamined in 2005 to determine regeneration potential and species composition changes in an old-growth forest on the mid-Cumberland Plateau. Response to a 1980s mortality event was evident in the increased density of the largest size class, with *Acer saccharum* (Marsh.) showing the greatest increase (>100 percent). Large (2.5-5.4 inches d.b.h.) *Carya* and *Quercus* regeneration and all *Cornus florida* (L.) regeneration are no longer present, except for *Q. prinus* (L.) (4 percent). Regeneration models predicted similar regeneration outcomes in response to stand-replacing disturbance events: *Acer saccharum* (53 percent), *Fraxinus americana* (L.) (7-13 percent), and *Liriodendron tulipifera* (L.) (7-9 percent). We hypothesize that the potential of this forest to maintain overstory oak species will diminish if current disturbance trends continue.

INTRODUCTION

Many mature forests in eastern North America are losing their *Quercus* component due to changes in the historic disturbance regime (Abrams 1992, Abrams and Downs 1990, Lorimer 1980). The removal of Native Americans and land use changes associated with European settlement have resulted in less frequent disturbances of higher intensity (Ruffner and Abrams 2002). Silvicultural techniques have been developed to improve *Quercus* regeneration potential on high-quality upland sites (Brose and Van Lear 1998, Loftis 1990); however, forest manipulations may not be feasible in older stands where the seed source may be limited or management options may be restricted. In addition to *Quercus*, *Cornus* appears to be decreasing in many undisturbed forest stands due to an introduced anthracnose (*Discula destructiva*) disease (Hiers and Evans 1997). The implications of species composition changes in the absence of management are relatively unknown, but are likely important to ecosystem processes and values (e.g., wildlife habitat, aesthetics, soil chemistry) and will be economically important at a local level.

Studies of old-growth forests on the Cumberland Plateau have concentrated primarily on characterizing community types (Haney and Lydic 1999, Hinkle 1978, Schmalzer and others 1978). Natural forest development in undisturbed forests, particularly those dominated by *Quercus* spp., is not well understood. Of special interest to forest and wildlife ecologists and managers in the region are conditions that benefit oak recruitment into the canopy. As a result, models have been developed that predict species response to stand-replacing disturbances based on current densities, size classes, and sprouting probabilities (Loftis 1989, Loftis 1990, Loftis 1993, Schweitzer and others 2004).

We examined successional development of the understory over the last 22 years in an old-growth forest on the mid-Cumberland Plateau. A previous study in 1983 examined and predicted species composition changes in this forest after a mortality episode that resulted in 20 percent of *Quercus* and *Carya* trees dying in a period of 2 to 3 years (McGee 1984, McGee 1986). The mortality resulted in an approximately 18-percent reduction in basal area in the dominant and codominant trees [>17 inches diameter breast height (d.b.h.)]. In 1983, the *Quercus* and *Carya* trees were underrepresented in the understory and were

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predicted to be replaced by shade-tolerant competitors, primarily *Acer saccharum* (Marsh.). We test these earlier predictions through modeling and current stand inventories and examine if the 1980s mortality event affected oak regeneration potential. We also examine if regeneration potential following simulated disturbance events has changed over the last two decades. Data collected will help refine regeneration models for the Cumberland Plateau region.

SITES

The study area lies on the mid-Cumberland Plateau in Franklin County, Tennessee, near the community of Sewanee, on The University of the South's Forest Domain. This portion of the plateau has been described as a weakly dissected plateau surface with strongly dissected sides (Smalley 1982). The stand is located within Dick Cove and has been designated as a Natural Area by The University of the South's Office of Domain Management. The vegetation of Dick Cove is similar to the mixed-mesophytic forests in the Cliff Section of the Cumberland Plateau escarpment as described by Braun (1950). Dick Cove has been designated as landtype association 16, which corresponds to the north aspect of the Plateau escarpment and upper sandstone benches (Smalley 1982). We examined vegetation within an 80-acre portion of the stand that lies below the escarpment and extends in elevation from 1,780 to 1,600 feet. The University's forest records show no logging or other human-caused disturbances in Dick Cove since 1858 until a road was built through a portion of the cove in 1965.

McGee (1986) documented *Carya* and *Quercus* trees with ages in excess of 400 years in the stand. Current forest inventories (Clark, S. 2005. Unpublished data. On file with: USDA Forest Service, Southern Research Station, Alabama A&M University, P.O. Box 1387, Normal, AL 35762.) show that approximately 25 tree species are present in Dick Cove. Primary overstory species are *Acer saccharum* (40 percent), *Quercus* spp. (16 percent), *Carya* spp. (11 percent), *Liriodendron tulipifera* (L.) (8 percent), and *Tilia americana* (L.) (6 percent).

PROCEDURES

In September 1983, woody plant species were tallied on nested circular plots placed systematically throughout the forest using a 208 foot by 208 foot grid pattern (n=100) (McGee 1984, 1986). Seedlings were enumerated by species in two size classes (0-0.9 feet and 1.0-4.4 feet) in 0.001-acre plots. Saplings were enumerated by species and size class based on height (≥ 4.5 feet but < 2.5 inches d.b.h. and 2.5-5.4 inches d.b.h.) in 0.01-acre plots.

In June 2005, we relocated 18 of the 1983 vegetation plots using written descriptions of plot locations and by finding the original wooden stakes used to mark plot centers. We established a 0.01-acre circular regeneration plot at the center of each original vegetation plot and tallied woody plants by species and size class based on height (0-0.9 feet, 1.0-1.9 feet, 2-2.9 feet, 3-3.9 feet, > 4 feet but ≤ 1.5 inches d.b.h., and > 1.5 inches d.b.h.). We measured d.b.h. for trees in the largest size class. If there were more than 25 stems within a species and size class, we did not tally any additional stems, but tallied the stem count as 25 within the individual plot.

In analyses of the 1983 data, we only used data from the 18 plots we were able to relocate in 2005. For the analyses to compare data among years, we grouped the 2005 data into the same size classes as the 1983 data. The only discrepancy was that the maximum height tallied was 4.5 feet in 1983 and 4.0 feet in 2005. We assume that this discrepancy is minimal and would not affect comparison among datasets. Additionally, we did not include trees larger than 5.5 inches d.b.h. for the 2005 dataset. The seedling data from 1983, taken on a 0.001-acre plot, were blown up by a factor of 10 to allow comparisons with the 2005 seedling data, which were taken on a 0.01-acre plot. For both datasets, relative stem density for each species was calculated as a percentage of the total density. Frequency was calculated as the percentage of plots in which the species occurred.

Prediction of species response following a simulated disturbance was conducted using the REGEN for EXCEL computer program based on population models for *Quercus* species (Loftis 1990, 1993; Schweitzer and others 2004). The model uses 0.01-acre plot data to predict composition of a new stand 10 years after a disturbance of high intensity (e.g., a clearcut or other major disturbance that removes all or most of the overstory). The model uses height as a basis to predict seedling performance after disturbance, with larger seedlings ranked as more successful competitors than smaller seedlings. Additionally, each species that can produce sprouts receives a ranking for each size class (Schweitzer and others 2004) and an associated sprouting probability for stump sprouts (defined as sprouts from trees >1.5 inches d.b.h.). In some cases, data have been collected to develop logistic estimates of sprouting probabilities as a function of stem d.b.h.. In some cases, no significant relationship between sprouting probability and stem d.b.h. existed, and the simple proportion of stems sprouting is used as the probability of sprouting. The species ranking and probability data are partially based on field data collected from tests in the southern Appalachians (Loftis 1990, Loftis 1993). If no data were available for a species, the ranking was based on field experience and knowledge of the species regeneration mechanisms and growth rates; sprouting probabilities were set to 0.5. Because *Liriodendron tulipifera* was present in the overstory, we used an option in the model to add additional *L. tulipifera* seedlings to the stand at time of disturbance to account for new seedlings that would germinate from dormant seed in the ground. The model chooses six “winners” per plot, based on their competitive ranking, to predict the dominant and codominant trees at crown closure on each individual plot. Algorithms are used in the case of ties between individuals with the same ranking. Combined plot data are summarized to produce stand-level results, which provide predicted species composition and density of dominant and codominant trees at crown closure (estimated to be 10 years after disturbance). The model used 100 simulations to provide the mean and range of probable regeneration outcomes for the stand.

The model uses the following height classes: 0-1.9 feet, 2-3.9 feet, ≥ 4 feet height but <1.5 inches d.b.h., and ≥ 1.5 inches d.b.h.. The 2005 data could be divided into these size classes for use in the model, but the 1983 tally did not afford this ability. We therefore assigned all trees 0-0.9 feet in height from the 1983 dataset to the smallest height category for the model (0-1.9 feet). We similarly assigned the remaining categories: 1-4.4 feet to the 2-3.9 feet model category, ≥ 4.5 feet height but <2.5 inches d.b.h. to the ≥ 4 feet height but <1.5 inches d.b.h. model category, and 2.5-5.4 inches d.b.h. to the ≥ 1.5 inches d.b.h. model category. We then assigned a d.b.h. of 4.0 inches (midpoint between 2.5 and 5.4 inches) to all trees in the largest size class.

RESULTS

Twenty-five species were tallied in 1983 and 24 in 2005. Total regeneration density decreased by 44 percent from 1983 to 2005 with the majority of this loss in trees 1-4.4 feet in height (table 1). The only size class to show an increase in density was the largest size class, which increased by 67 percent.

The decrease in stem density from 1983 to 2005 was greatest for *Cornus florida* (L.), which once occurred in 72 percent of the plots and had accounted for 8 percent of the total stem density (table 2). This species

Table 1—Total number of stems per acre (standard deviation) by size class in Dick Cove, Sewanee, TN (n = 18) in 1983 and 2005

Size class	1983	2005
Total	9,266.7 (4,894.5)	5,150.0 (2,181.0)
0–0.9 feet height	4,750.0 (2,896.5)	3,944.4 (1,767.8)
1–4.4 feet height	3,666.7 (2,689.9)	433.3 (524.7)
> 4.5 feet, < 2.5 inches d.b.h.	783.3 (296.5)	694.4 (469.6)
2.5–5.4 inches d.b.h.	66.7 (76.7)	111.1 (102.3)

Table 2—Species relative density and frequency by size class in Dick Cove, Sewanee, TN (n = 18) in 1983 and 2005

Species	Total		0–0.9 feet height				1–4.4 feet height				> 4.5 feet height, < 2.5 inches d.b.h.				2.5–5.4 inches d.b.h.						
	Density		Frequency		Density		Frequency		Density		Frequency		Density		Frequency		Density		Frequency		
	1983	2005	1983	2005	1983	2005	1983	2005	1983	2005	1983	2005	1983	2005	1983	2005	1983	2005	1983	2005	
<i>Acer rubrum</i> (L.)	2.4	0.3	16.7	11.1	3.4	0.3	16.7	5.6	1.8	0	5.6	0	0	0	0	0	0	0	0	0	0
<i>Acer saccharum</i> (Marsh.)	32.3	47.2	94.4	100.0	36.5	48.3	72.2	94.4	26.3	11.9	50.0	22.2	33.8	69.1	94.4	94.4	27.8	59.6	16.7	50.0	
<i>Aesculus glabra</i> (Willd.)	0.5	2.3	11.1	55.6	0	1.4	0	38.9	0	15.2	0	22.2	1.9	1.9	11.1	5.6	0	7.7	0	5.6	
<i>Asimina triloba</i> (L.) Dunal	0	0.5	0	11.1	0	0.5	0	11.1	0	0	0	0	0	0.3	0	5.6	0	0	0	0	
<i>Carya</i> spp.	4.5	3.2	38.9	66.7	10.4	4.1	27.8	66.7	0.7	0	5.6	0	1.8	0	11.1	0	22.2	0	11.1	0	
<i>Cercis canadensis</i> (L.)	3.4	0.2	38.9	11.1	1.3	0	5.6	0	6.3	0	5.6	0	5.1	2.8	33.3	5.6	0	7.7	0	5.6	
<i>Cladastis kentuckea</i> (Dum.-Cours.) Rudd	1.2	2.0	11.1	5.6	1.3	0.8	5.6	5.6	1.8	5.4	5.6	5.6	0.4	3.3	5.6	5.6	0	3.8	0	5.6	
<i>Cornus florida</i> (L.)	7.6	0	72.2	0	4.1	0	11.1	0	9.3	0	16.7	0	21.0	0	72.2	0	38.9	0	22.2	0	
<i>Euonymus atropurpureus</i> (Jacq.)	0	0.7	0	11.1	0	1.1	0	11.1	0	0	0	0	0	2.2	0	5.6	0	3.8	0	5.6	
<i>Fraxinus americana</i> (L.)	11.0	10.0	44.4	72.2	9.7	11.2	27.8	66.7	15.1	11.5	38.9	22.2	4.8	1.9	27.8	16.7	0	0	0	0	
<i>Hydrangea</i> spp.	8.1	0	22.2	0	4.5	0	11.1	0	9.4	0	11.1	0	2.4	0	11.1	0	0	0	0	0	
<i>Lindera benzoin</i> (L.) Blume	5.6	6.7	38.9	55.6	3.9	4.0	11.1	44.4	5.9	27.8	11.1	33.3	6.8	5.3	33.3	11.1	0	0	0	0	
<i>Liriodendron tulipifera</i> (L.)	2.0	5.4	16.7	22.2	4.0	5.6	11.1	22.2	0	2.7	0	5.6	0.4	0	5.6	0	0	3.8	0	5.6	
<i>Magnolia acuminata</i> (L.)	1.5	0	16.7	0	1.4	0	11.1	0	1.5	0	5.6	0	1.7	0	11.1	0	0	0	0	0	
<i>Nyssa sylvatica</i> (Marsh.)	0.5	6.8	5.6	44.4	0.7	7.1	5.6	33.3	0	12.3	0	22.2	0	3.3	0	5.6	0	0	0	0	
<i>Oxydendrum arboreum</i> (L.) DC.	0.1	0	5.6	0	0	0	0	0	0	0	0	0	1.0	0	5.6	0	0	0	0	0	
<i>Pinus serotina</i> Ehrh.	1.6	0.5	16.7	16.7	0	0.6	0	16.7	7.8	0	11.1	0	0.6	0	5.6	0	0	0	0	0	
<i>Quercus alba</i> (L.)	0.1	0.5	11.1	16.7	0	0.6	0	16.7	0	0	0	0	2.4	0	11.1	0	0	0	0	0	
<i>Quercus muehlenbergii</i> Engelm.	0.6	0.1	22.2	5.6	0	0.1	0	5.6	0.7	0	5.6	0	1.2	0	11.1	0	11.1	0	11.1	0	
<i>Quercus prinus</i> (L.)	0.1	0.6	5.6	11.1	0	0.4	0	11.1	0	0.9	0	5.6	0.8	1.1	5.6	5.6	0	3.8	0	5.6	
<i>Quercus rubra</i> (L.)	0.9	3.4	5.6	55.6	1.8	4.2	5.6	55.6	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Quercus velutina</i> Lam.	0.8	0	5.6	0	1.1	0	5.6	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Rhododendron</i> spp.	0.1	0	5.6	0	0	0	0	0	0	0	0	0	1.0	0	5.6	0	0	0	0	0	
<i>Robinia pseudoacacia</i> (L.)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Sassafras albidum</i> (Nutt.) Nees	1.6	2.9	11.1	11.1	0	3.5	0	11.1	4.5	1.8	5.6	5.6	0.9	1.1	5.6	5.6	0	0	0	0	
<i>Staphylea trifolia</i> (L.)	0	1.7	0	5.6	0	0.3	0	5.6	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Tilia americana</i> (L.)	3.6	1.1	33.3	16.7	1.6	0.1	5.6	5.6	5.9	1.2	22.2	5.6	3.0	3.1	16.7	16.7	0	5.8	0	5.6	
<i>Ulmus alata</i> Michx.	0	0.1	0	5.6	0	0	0	0	0	0	0	0	0	0.9	0	5.6	0	0	0	0	
<i>Ulmus rubra</i> Muhl.	8.0	2.0	50.0	33.3	10.9	2.1	27.8	22.2	3.2	0.4	11.1	5.6	9.1	3.6	44.4	16.7	0	3.8	0	5.6	
<i>Vaccinium</i> spp.	0	0.5	0	5.6	0	0.5	0	5.6	0	1.8	0	5.6	0	0	0	0	0	0	0	0	
<i>Viburnum</i> spp.	2.1	1.2	11.1	11.1	3.5	1.1	11.1	11.1	0	7.1	0	5.6	0	0	0	0	0	0	0	0	

was particularly important as a small sapling (2.5-5.4 inches d.b.h. size class) in 1983, averaging 26 stems per acre. *Acer saccharum* had the largest total increase in relative density and was the only species to occur in all plots in 2005. In 1983, *Quercus* spp. and *Carya* spp. were present in all size classes, but by 2005 we did not tally any oaks > 0.9 feet in height. One exception was *Quercus prinus* (L.), which had a slight increase in abundance in all size classes. *Quercus rubra* (L.) was the most frequent and abundant oak species in 2005, averaging 161 stems per acre, but was never larger than 0.9 feet tall.

The REGEN model predicted similar species composition and density outcomes for both time periods following a simulated disturbance that removed the majority of the overstory (table 3). The model predicted that the stand would be dominated by sugar maple [>50 percent trees per acre (TPA)] after disturbances in 1983 and 2005. Oak regeneration potential was similar and comprised < 3 percent of the dominant and codominant trees following a disturbance. The density of hickory increased slightly from 2 to 5 TPA, but was not well represented in either model prediction. The potential for *Prunus serotina* (Ehrh.) regeneration decreased from 32.4 TPA in 1983 to 11.1 TPA in 2005. *Fraxinus americana*, *Liriodendron tulipifera*, and *Aesculus octandra* (Marsh.) were the next most common competitors after *Acer saccharum* in model predictions for both years.

DISCUSSION

Regeneration potential of *Carya* or *Quercus* was low in 1983 and 2005, and did not increase during the mortality episode of the 1980s. Management recommendations to enhance oak regeneration on high-quality sites prescribe reductions in the midstory rather than in the main canopy (Loftis 1983, Loftis 1993). We speculate that the increased light from the 1980s mortality benefited the *Acer saccharum* and *Tilia americana* understory trees that were already established. *Quercus* and *Carya* species could not compete after the mortality episode without a simultaneous reduction of these competing species in the midstory. *Acer saccharum* is a strong competitor under a variety of light conditions, particularly shade (Clark and Schlarbaum 2003, Logan 1965), and this species limited *Quercus* regeneration in this stand, similar to results of another study on the mid-Cumberland Plateau (Schweitzer and others 2004). In addition, high levels of deer browsing are probably having a negative effect on *Quercus* regeneration.

A stand-replacing disturbance would not have increased the contribution of *Quercus* and *Carya* species due to the low density of large advanced regeneration (>4.5 feet height) that existed in 1983 and in 2005. We would expect to have fewer *Prunus serotina* stems and more *Liriodendron tulipifera* stems than predicted by the REGEN model; the former is not a strong competitor in Cumberland Plateau forests (Schweitzer and others 2004), while the latter is a strong competitor, particularly in productive environments like cove forests (Loftis 1993, Kolb and others 1990). Schweitzer and others (2004) also found a higher than expected density of *Prunus serotina* and a lower than expected density of *Liriodendron tulipifera* on high-quality sites in the Cumberland Plateau using the REGEN model. The competitive ability of these species may be different in the Cumberland Plateau than in the Blue Ridge Mountains, where developmental model data were collected, and species rankings and sprouting probabilities need to be refined.

This forest, once dominated by *Quercus* and *Carya*, will likely lose diversity in the midstory and overstory and succeed to an *Acer saccharum* dominated forest if the currently observed trends continue. The complete loss of *Cornus florida* was not surprising given its relatively low abundance and loss on nearby sites on the Plateau top and escarpment (Kuers and Kuthe 1998, Schweitzer and others 2004). Dogwood anthracnose was likely playing a role in this loss, but lack of fire or sunlight is probably also a limiting factor (Holzmueller and others 2006).

The forest has a decreased potential to recruit soft-mast *Cornus florida* and hard mast *Quercus* and *Carya* species at the present disturbance levels. These species are particularly important to wildlife (McShea and Healy 2002) and their loss may have important community-level consequences (Hiers and Evans 1997).

Table 3—Predicted density (trees per acre) of dominant and codominant competitors following simulated stand-replacing disturbance using the REGEN for EXCEL model for Dick Cove, Sewanee, TN

Species	1983	2005
<i>Acer rubrum</i> (L.)	15.0	4.3
<i>Acer saccharum</i> (Marsh.)	170.0	166.1
<i>Aesculus glabra</i> (Willd.)	2.7	4.1
<i>Asimina triloba</i> (L.) Dunal	0	0
<i>Carya</i> spp.	1.9	5.0
<i>Cercis canadensis</i> (L.)	1.1	< 0.1
<i>Cladrastis kentukea</i> (Dum.-Cours.) Rudd	0	0.2
<i>Cornus florida</i> (L.)	0.2	0
<i>Euonymus atropurpureus</i> (Jacq.)	0	0
<i>Fraxinus americana</i> (L.)	21.8	38.8
<i>Hydrangea</i> spp.	0	0
<i>Lindera benzoin</i> (L.) Blume	< 0.1	< 0.1
<i>Liriodendron tulipifera</i> (L.)	24.7	28.8
<i>Magnolia acuminata</i> (L.)	11.8	3.9
<i>Nyssa sylvatica</i> (Marsh.)	0.1	6.8
<i>Oxydendrum arboreum</i> (L.) DC.	0.1	0
<i>Prunus serotina</i> Ehrh.	32.4	11.1
<i>Quercus alba</i> (L.)	0	0
<i>Quercus muehlenbergii</i> Engelm.	3.1	< 0.1
<i>Quercus prinus</i> (L.)	0.1	0
<i>Quercus rubra</i> (L.)	0	9.0
<i>Quercus velutina</i> Lam.	0	0
<i>Rhododendron</i> spp.	0	0
<i>Robinia pseudoacacia</i> (L.)	0	0
<i>Sassafras albidum</i> (Nutt.) Nees	< 0.1	1.8
<i>Staphylea trifolia</i> (L.)	0	< 0.1
<i>Tilia americana</i> (L.)	26.5	28.2
<i>Ulmus alata</i> Michx.	0	< 0.1
<i>Ulmus rubra</i> Muhl.	0	< 0.1
<i>Vaccinium</i> spp.	0	0
<i>Viburnum</i> spp.	0	0
Total	318.3	308.5

Lack of disturbance has been cited as an important factor in the loss of the *Quercus* component in many forest ecosystems (Abrams and Downs 1990, Lorimer 1984, Orwig and others 2001). Our results support the theory that *Quercus* will not become more competitive on high-quality upland sites with single minor disturbances (Gilbert and others 2003, Glitzenstein and others 1990, Johnson and others 2002). Fire has maintained oak forest communities, particularly on xeric sites over time (Abrams 1992, Clark and Hallgren 2003, Cutter and Guyette 1994, Ruffer and Abrams 1998). The historical role of fire in mesic ecosystems is less certain, but *Quercus* generally succeeds to more shade tolerant competitors in the absence of disturbance (Abrams and others 1997, Ruffner and Abrams 2002). Fire and harvesting benefit oak regeneration on highly productive sites (Brose and Van Lear 1998), but management may not be an option in old-growth areas because of conflict with public opinion (Proctor 1998).

The origin of existing *Quercus* and *Carya* overstory trees in Dick Cove is unknown, but is likely a result of repeated or sustained disturbances such as those caused by fire or drought or both. A future study will examine stand history using dendrochronology and reconstruct *Quercus* and *Carya* establishment over time in relation to drought and fire events.

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