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Tree Species Composition and Structure in an Old Bottomland Hardwood Forest in South-Central Arkansas

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ABSTRACT Tree species composition and structure was determined for an old bottomland hardwood forest located in the Moro Creek Bottoms Natural Area in south-central Arkansas. Diversity for this forest was high with species richness ranging from 33 for the overstory and sapling strata to 26 for the seedling stratum and Shannon-Weiner values of 2.54 to 1.02 for the overstory and seedling strata. Sweetgum (*Liquidambar styraciflua* L.) and oaks (*Quercus* spp.) dominated the overstory stratum with 66 percent of the importance values. American hornbeam (*Carpinus caroliniana* Walter) dominated the midstory and sapling strata with 32 and 42 percent of the importance values. Despite the large tree sizes and ages of several trees, comparison of the forest with models of bottomland hardwood succession and eastern United States old-growth definitions indicate the forest can best be described as old pioneer in transition to changing old growth.

INTRODUCTION Interest in locating and understanding the floral and faunal composition of eastern United States old-growth forests has increased considerably over the past two decades (Davis 1993, 1996; Nowacki and Trianosky 1993; Tyrrell et al. 1998 Mitchell et al. 2009). With the aid of new technology, such as geographical information systems and landscape simulation models (Scheller and Mladenoff 2007), previously unknown eastern old-growth forests are identified with each passing year (Stahle and Chaney 1994, Therrell and Stahle 1998, Foti 2001). Concurrent with the need for locating these forests is the necessity to understand their composition and structure (Sheppard and Cook 1988, Martin 1992). This need is particularly acute with the possible rediscovery of the ivory-billed woodpecker (*Campephilus principalis*) in eastern Arkansas (Fitzpatrick et al. 2005), whose habitat requirements include large, decadent trees in bottomland hardwood forests for foraging (Tanner 1942). Such trees are an integral part of old-growth forests (Davis 1996, Oliver and Larson 1996).

Old-growth composition and structure information can also be used to develop strategies for conserving current old-growth forests (White and Lloyd 1995, Mitchell et al. 2009) and for creating structural characteristics that can promote the development of ''new'' old-growth forests (Guldin 1991, Runkle 1991, National Council on Science and Sustainable Forestry 2008, Bauhus et al. 2009). This information is critical for southern United States bottomland hardwood forests where flooding and subsequent sediment deposition patterns result in a variety of topographic features or microtopography (Gosselink et al. 1990, Hodges 1997). These features increase ground surface and soil variability, leading to more complicated compositions and structures relative to upland forests (Wharton et al. 1982, Richardson 1994).

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Unfortunately, old-growth location and study in bottomland hardwood forests is difficult due to the scarcity of such areas (Hamilton et al. 2005, Mitchell et al. 2009). Though estimates vary, conversion of bottomland hardwood forests to other land uses has resulted in the disappearance of about 2.8 million ha (78 percent) of bottomland hardwood forests in Arkansas, and similar trends have occurred in other states with appreciable bottomland hardwood acreage (Dahl 1990). Fragmentation and management of much of the remaining bottomland hardwood forests has changed the composition and structure of these forests to non old-growth characteristics. Further, alterations in the hydrologic regime through channel straightening, elevated highway roadbeds, dams, and levees have also changed flooding patterns and disturbance regimes, and the subsequent development of bottomland hardwood forests (Maki et al. 1980, Johnson 1992, Collier et al. 1996, Shankman 1996). Therefore, it is imperative to gather information on the composition and structure of the few remaining bottomland hardwood old-growth forests. The objectives of this study were to determine the tree species composition and structure of a protected old bottomland hardwood forest located in south-central Arkansas and discuss the successional status of this forest. Our question is "Can the bottomland hardwood forest at the Moro Creek Bottoms Natural Area be called old growth?"

METHODS The Moro Creek Bottoms Natural Area is a 70-ha forest located within the floodplain of Moro Creek in Cleveland and Calhoun Counties, Arkansas (33°46′N, 92°21′W). The area is owned jointly by the Arkansas Natural Heritage Commission and The Nature Conservancy after a 1986 acquisition from Georgia-Pacific Corporation. This forest was considered old based on the large diameters of the overstory trees and ages of selected trees. Two red oak (*Quercus* spp.) and three white oak (*Q. alba* L.) trees were cored. The red oaks were about 150 yr old while the white oaks were about 250 yr old, which is near the age of senescence for bottomland red oaks and white oak, respectively (Stringer 2007). An ongoing age chronology project at the site has the oldest known sweetgum at 354 yr and willow oak (*Q. phellos* L.) at 154 yr (Dr. Margaret Devall, Research Ecologist, United States Forest Service, Center for Bottomland Hardwoods Research, Stoneville, Mississippi, pers. comm.).

The Moro Creek floodplain is considered a minor floodplain within the West Gulf Coastal Plain (Hodges and Switzer 1979). The soil is Wehadkee fine sandy loam (fine-loamy, mixed, active, nonacid, thermic Fluvaquentic Endoaquepts; United States Department of Agriculture 1968). This soil is considered deep, poorly-drained, and moderately acidic. Mean annual temperature is 16.6°C with a high of 27.1°C in July and a low of 4.7°C in January (WorldClimate 2009). Mean annual precipitation is 1,336 mm with a high of 134 mm in December and a low of 77 mm in August (WorldClimate 2009).

Moro Creek is a braided stream system, with several channels and numerous cutoffs, small bayous, and overflow areas that render access to the area difficult, even in dry years. This difficult access undoubtably contributed to its protection from recent logging activities. There was evidence of light selective logging in the 1950s that used mules to salvage windthrow trees (Mr. Roy Johnson, retired, Georgia-Pacific Corporation, Fordyce, Arkansas, pers. comm.).

All woody plants were tallied by species and measured for diameter at breast height (d.b.h. at 1.37 m in height) in 1989 using a systematic design. On the eastern side of Moro Creek over an area of about 40 ha, a 60 m by 60 m grid was installed. The intersection of each grid line was used as plot center for a series of nested plots (123 0.08-ha plots total). The overstory tree stratum ($\geq$25 cm d.b.h.) was measured in a 0.08-ha circular plot. The midstory tree stratum (10 to 25 cm d.b.h.) was measured in a 0.04-ha circular plot while the sapling stratum (1.0 to 9.9 cm d.b.h.) was measured in two 0.004-ha circular plots. The latter plots were located 6.1 m north and south of the plot center used for each of the larger plots. The seedling stratum ($<$1.0 cm d.b.h. but $\geq$0.34 m in height) was measured on two 0.0004-ha circular plots using the same plot centers as the 0.004-ha plots.

Density (stems/ha) and basal area (m^2/ha) were calculated for the overstory, midstory, and sapling strata at the plot level and

Table 1. Descriptive statistics at the stand level by strata on the Moro Creek Bottoms Natural Area in east-central Arkansas. Values in parenthesis represent ± one standard error

	Overstory	Midstory	Saplings	Seedlings
Richness	33	27	33	26
Evenness	0.73	0.67	0.65	0.31
Shannon-Weiner Diversity Index	2.54	2.21	2.28	1.02
Stems per hectare	102 (4)	211 (13)	1,077 (52)	16,035 (2,979)
Basal area per hectare	23.2 (0.8)	3.7 (0.2)	1.4 (0.1)	—[1]

[1] The seedling stratum included stems <1.4 m in height, therefore, d.b.h. could not be measured for basal area calculations.

averaged across all plots. Density only was calculated for the seedling stratum. Importance values were calculated for individual species by strata by pooling the plot-level data then summing relative density, relative basal area, and relative frequency (the percentage of plots containing at least one individual of the specified species) (Curtis and McIntosh 1950, Skeen 1973). A modified importance value (sum of relative density and relative frequency) was calculated for the seedling stratum since these plants were too short to have a d.b.h. Species richness, evenness (H'/H_{max}), and the Shannon-Weiner Index of Species Diversity were calculated for each stratum (Gurevitch et al. 2002). Diameter distributions were developed for the major tree species by stratum to determine if recruitment of new trees was occurring to replace individuals in the larger size classes.

As a side note, the Moro Creek Bottoms Natural Area received a major, linear wind event in August 1989. This storm resulted in severe blowdown of trees in the forest (Guldin et al. 1995). While the stand no longer exists in the condition described in the results, we felt that it was important to report the stand composition and structure prior to blowdown for future reference given the increasing interest in eastern old-growth forests and possible rediscovery of the ivory-billed woodpecker. Studies are underway to characterize the gap-phase regeneration dynamics following this disturbance (see Devall et al. 2001, Skojac et al. 2003, Castleberry et al. 2005).

RESULTS Forty-eight species of trees, shrubs, and woody vines were recorded in the Moro Creek Bottoms Natural Area. Species richness by stratum ranged from 33 for overstory and saplings to 26 for seedlings (Table 1). Evenness was similar among the overstory, midstory, and sapling strata, ranging from 0.73 to 0.65, while the seedling stratum was considerably less even at only 0.31 (Table 1). Further, the former three strata showed high diversity with Shannon-Weiner values ranging from 2.54 in the overstory stratum to 2.21 in the midstory stratum (Table 1). The seedling stratum was less diverse at only 1.02.

Tree density for the overstory and midstory strata (d.b.h. ≥10 cm) was 313 stems per ha, 33 percent which were part of the overstory stratum (Table 1). The sapling stratum had over 1,000 stems per ha, while the seedling stratum had over 16,000 stems per ha, though sampling in these strata was highly variable (Table 1). Basal area for the overstory, midstory, and sapling strata was 28 m^2/ha with 82 percent distributed among overstory trees (Table 1).

The overstory strata was dominated by sweetgum and oaks (Table 2, Figure 1). Sweetgum accounted for 28 percent of importance, 30 percent of stems, and 34 percent of basal area. Willow oak, overcup oak (*Q. lyrata* Walter), cherrybark oak (*Q. pagoda* Raf.), blackgum (*Nyssa sylvatica* Marshall), and baldcypress (*Taxodium distichum* (L.) Rich.) were next in importance, respectively, but their values were three to four times less than sweetgum. The oaks as a whole accounted for 38 percent of importance, and 34 and 39 percent, of stems and basal area, respectively. Six hickory (*Carya.*) species were identified in the overstory strata with a combined importance of 37. These hickories were a significant component of the 30 to 50 cm d.b.h. classes, while sweetgum and oaks were a majority of the stems throughout the 20 to 140 cm d.b.h. classes (Figure 1).

The largest tree measured in this study was a 144 cm sweetgum. Other notable large trees

Table 2. Density, basal area, and importance values for species in the overstory and midstory strata on the Moro Creek Bottoms Natural Area in east-central Arkansas

	Overstory Stratum			Midstory Stratum		
Species	Density[1]	Basal Area[1]	Importance Value	Density[1]	Basal Area[1]	Importance Value
Acer rubrum L.	—[2]	—	—	0.2	0.03	3.4
Carpinus caroliniana Walter	<0.1	0.04	1.4	13.1	1.20	96.1
Carya cordiformis Asch. & Graebn.	0.1	0.07	1.7	—	—	—
Carya glabra (Mill.) Sweet	0.7	0.61	12.1	0.1	0.01	1.5
Carya ovata (Mill.) K. Koch	0.7	0.70	13.7	0.1	0.01	1.1
Carya tomentosa (Lam.) Nutt.	0.5	0.58	9.2	—	—	—
Fraxinus caroliniana Mill.	—	—	—	2.0	0.17	11.9
Fraxinus pennsylvanica Marshall	0.2	0.19	4.1	4.8	0.47	35.1
Ilex opaca Ait.	0.3	0.12	4.4	0.9	0.12	10.9
Liquidambar styraciflua L.	5.0	7.88	84.5	3.1	0.46	31.6
Nyssa sylvatica Marshall	1.1	0.95	18.8	2.9	0.33	28.8
Pinus taeda L.	0.7	0.98	11.4	0.1	0.01	1.5
Planera aquatica J. F. Gmel.	—	—	—	0.3	0.04	3.4
Quercus alba L.	0.2	0.72	6.2	—	—	—
Quercus lyrata Walter	1.2	1.53	23.2	1.0	0.14	12.0
Quercus michauxii Nutt.	0.6	1.60	15.4	0.3	0.04	4.1
Quercus nigra L.	0.8	1.16	17.0	0.9	0.12	10.6
Quercus pagoda Raf.	1.0	1.36	19.0	0.3	0.03	3.8
Quercus phellos L.	1.7	2.50	28.8	1.5	0.17	15.1
Quercus velutina Lam.	0.1	0.15	2.4	—	—	—
Taxodium distichum (L.) Rich.	1.0	1.54	18.1	0.9	0.10	8.7
Ulmus alata Michx.	—	—	—	1.1	0.12	12.8
Ulmus americana L.	0.1	0.05	1.9	—	—	—
Ulmus crassifolia Nutt.	—	—	—	0.2	0.02	2.3
Other species[3]	0.4	0.29	6.8	0.5	0.05	5.5

[1] Density and basal area values were calculated after pooling plot-level data.

[2] Values not shown due to either no specimens measured in this stratum or the importance value was <1.0.

[3] Other species included *Betula nigra* L., *Carya aquatica* (Michx. f.) Nutt., *Carya texana* Buckl. *Cornus florida* L., *Crataegus* spp., *Diospyros virginiana* L., *Fagus grandifolia* Ehrh. *Ilex decidua* Walt., *Morus rubra* L., *Ostrya virginiana* (Mill.) K. Koch, *Quercus falcata* Michx., *Salix nigra* Marsh., *Sassafras albidum* (Nutt.) Nees, and *Ulmus rubra* Muhl.

included a 119 cm baldcypress and 112 cm swamp chestnut oak (*Q. michauxii* Nutt.). An acquisition inventory of the forest by a consulting forester in 1986 identified a 150 cm cherrybark oak, 121 cm white oak (*Q. alba* L.), and a 115 cm overcup oak (report on file with the United States Forest Service, Center for Bottomland Hardwoods Research, Stoneville, Mississippi).

The midstory stratum was dominated by American hornbeam (*Carpinus caroliniana* Walter), with about one-third of the importance and basal area, and 38 percent of the stems (Table 2). Two additional species with importance values >30 included green ash (*Fraxinus pennsylvanica* Marshall) and sweetgum. Other species in the midstory stratum with importance values ≥10 included blackgum, willow oak, overcup oak, winged elm (*Ulmus alata* Michx.), Carolina ash (*F. caroliniana* Mill.), American holly (*Ilex opaca.*Ait.), and water oak (*Q. nigra* L.) (Table 2). American hornbeam and the ash species comprised a majority of the 10 to 16 cm d.b.h. classes (Figure 2). Other species, including the oaks, sweetgum, elms, hickories, and blackgum, maintained two to seven trees per ha from the 10 to the 22 cm d.b.h. classes (Figure 2).

American hornbeam also dominated the sapling stratum, with 42 percent importance, 47 percent stems and 45 percent basal area (Figure 3, Table 3). In contrast, sweetgum had ≤2 percent importance, stems, and basal area. Oak species had only 7 percent of importance. Overcup oak dominated the seedling stratum (Table 3), with 32 percent importance and 50 percent of the stems. Sweetgum contained only two percent of importance among seedlings, while oak species in total had 62 percent importance and 77 percent of the stems, primarily among overcup and willow oaks. Other species in the

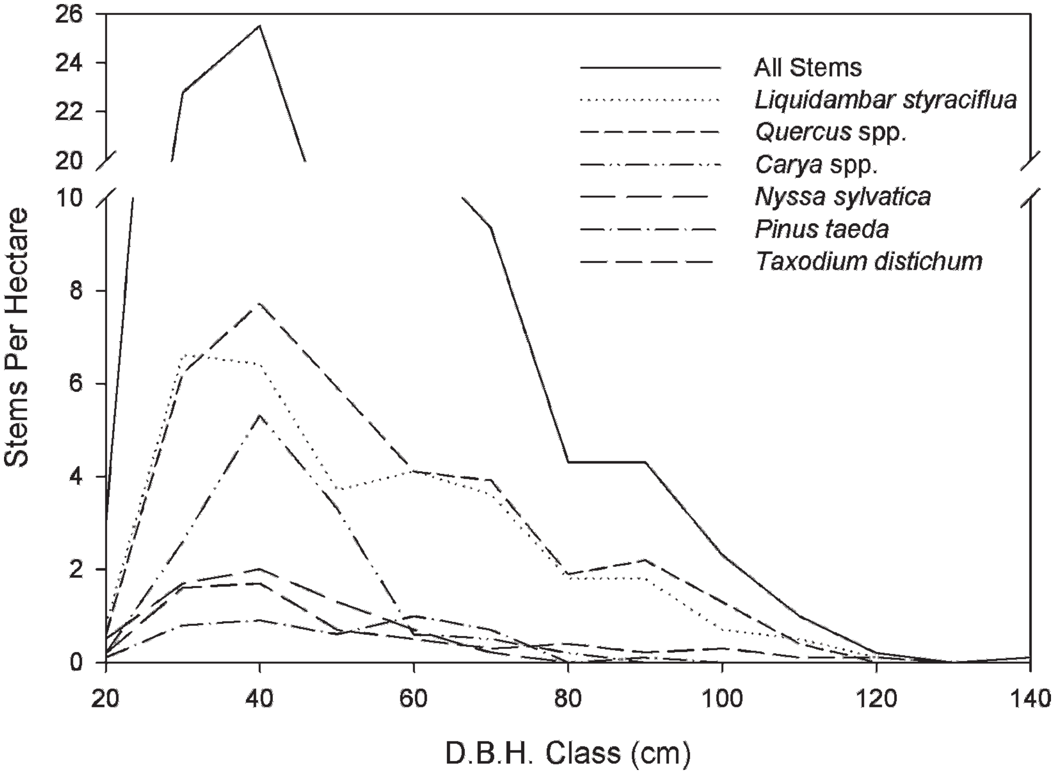

Figure 1. Diameter distributions by 10-cm d.b.h. classes for all trees and selected species in the overstory stratum on the Moro Creek Bottoms Natural Area in south-central Arkansas.

reproduction size classes (sum of importance values for both the sapling and seedling strata) with importance values ≥10 included green ash, blackgum, swamp-privet (*Forestiera acuminata* Michx.), Carolina ash, deciduous holly (*I. decidua* Walter), American holly, and *Vaccinium* species (Table 3).

DISCUSSION

Diversity

Bottomland hardwood forests in the southeastern United States are characterized as highly productive ecosystems rich in flora and fauna (Sharitz and Mitsch 1993). Nutrient-rich sediments deposited during annual or periodic floods along with abundant water through much of the growing season provide ample resources for growth during relatively long growing seasons (Tockner et al. 2000). Further, disturbances, such as periodicity and length of hydroperiods and channel migrations (White 1979) – disturbances unique to floodplain forests (Sharitz and Mitsch 1993) – along with major wind events, lead to high spatial (microtopography) and temporal environmental heterogeneity (Battaglia et al. 1995) which can contribute to high levels of diversity (Battaglia et al. 1999, Schnitzler 1994).

Hoagland et al. (1996) reported tree species richness of 27 to 30, evenness of 0.76 to 0.82, and Shannon-Weiner diversity of 2.60 to 2.72 in floodplain forests along the Little River in southeastern Oklahoma. Zhao et al. (2006) measured pre-Hurricane Hugo richness of 12 to 22 in the Congaree National Park, South Carolina, which contains the largest contiguous area of old-growth bottomland hardwoods remaining in the United States. Further, Schnitzler (1994) reported high levels of Shannon-Weiner diversity (2.6 to 3.6) in floodplain forests along the Rhine River in France. The forest at Moro Creek Bottoms Natural Area had greater tree species richness than those reported above. Evenness and Shannon-Weiner diversity was slightly lower than Hoagland et al. (1996) due to the dominance of sweetgum and several oak

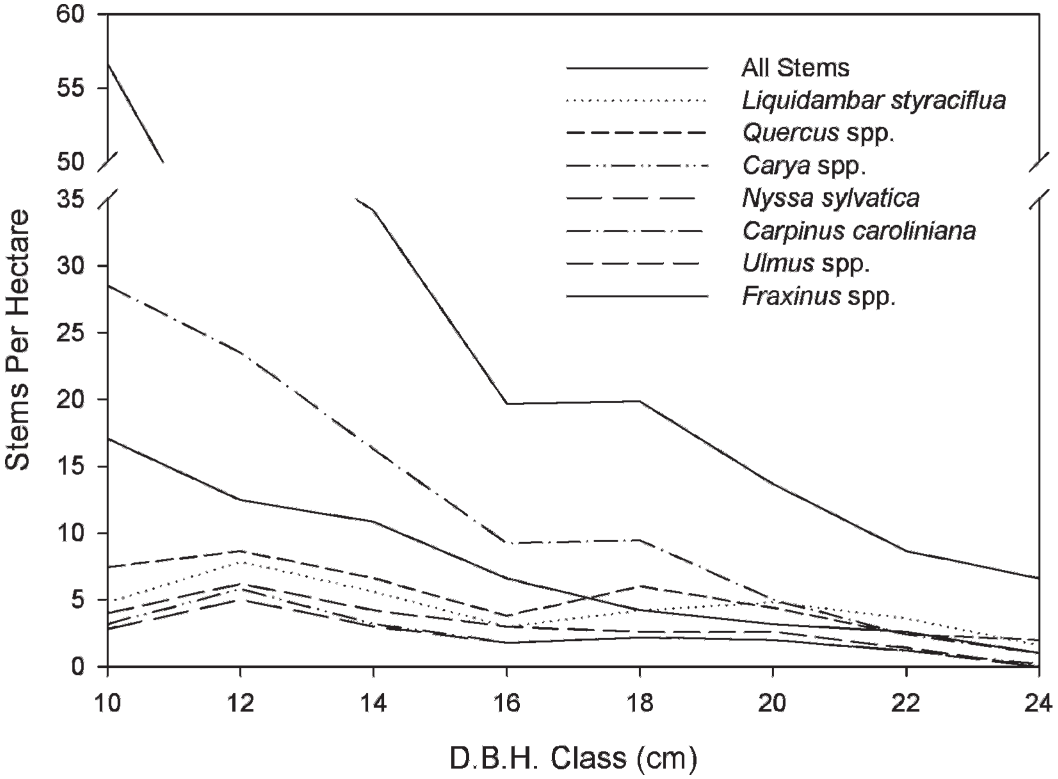

Figure 2. Diameter distributions by 2-cm d.b.h. classes for all trees and selected species in the midstory stratum on the Moro Creek Bottoms Natural Area in south-central Arkansas.

species. On the other hand, Grell et al. (2005) found considerably lower values for richness, evenness, and Shannon-Weiner diversity for the "Lost Forty," an old-growth bottomland hardwood forest in Wolf Creek, a tributary of Moro Creek. Richness was 6 to 8 species, evenness was 0.9 to 1.0, and diversity was 1.6 to 2.0 depending on elevation classes. These values though are not directly comparable to our study since they were calculated at the plot level and segregated by microtopography (elevation class).

The number of trees per ha in Moro Creek Bottoms Natural Area (≥10 cm) was three to five time higher than those reported in other old bottomland hardwood forests (Lindsey 1963, Phillippe and Ebinger 1973, Jackson and Barnes 1975, Nyboer and Ebinger 1976). Nixon et al. (1991) reported 1,675 stems per ha for trees ≥0.5 cm d.b.h. in an old-growth forest in the Neches River floodplain in east Texas which is greater than the 1,390 stems per ha found in our study. Basal area in the Moro Creek Bottoms Natural Area was lower than those reported in the studies cited above but similar to the Sweetgum Natural Area in Sharkey County, Mississippi (Wiseman 1982).

Stand Development

Without the benefit of age sampling, we believe the forest in the Moro Creek Bottoms Natural Area was an old, possible single cohort, sweetgum-oak forest that was undergoing autogenic successional changes, along with changes induced by a meandering stream system, prior to the 1989 major disturbance. We draw this conclusion based on four lines of thought.

First, the large sweetgum and oaks showed visible signs of decline, including broken tops, bark scuffing, and bark discoloration due to the presence of wood borers, especially among the oaks. Concurrently, the trees were relatively tall and straight, with long branch-free boles. These are visible indicators of a mature forest that possibly developed as a single-cohort stand that is or soon will be in transition to a multi-age forest among the

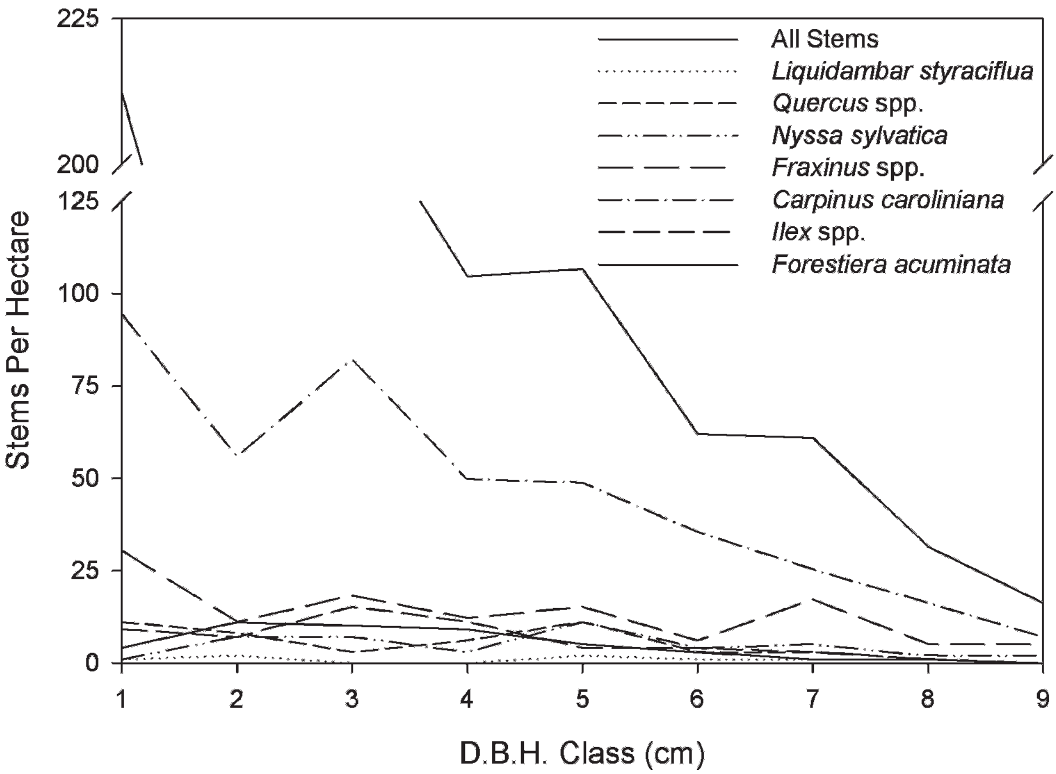

Figure 3. Diameter distributions by 1-cm d.b.h. classes for all trees and selected species in the sapling stratum on the Moro Creek Bottoms Natural Area in south-central Arkansas.

overstory trees (Oliver and Larson 1996). This transition is commonly called the understory reinitiation stage of stand development (Oliver 1981) or transition stage in forest ecosystem development (Bormann and Likens 1979).

Second, the development of a mixture of sweetgum and oak follows "normal" stand development patterns in minor creek floodplains in the Coastal Plain Region. Clatterbuck and Hodges (1988) showed even-aged mixtures of oak and sweetgum are common following abandonment of pastures and agriculture fields. Sweetgum would initially dominate the stand for the first 20 to 25 yr, then oaks would stratify above the sweetgum. A similar pattern was found by Johnson and Krinard (1976, 1983, 1988) following complete overstory removal and subsequent natural regeneration and stand development. The proportion of oak to sweetgum that developed into overstory trees following the disturbance was correlated to the pre-harvest proportion of oak to sweetgum. Bowling and Kellison (1983) also found a similar pattern of oak-sweetgum development 22 yr after harvesting. They further mentioned the high density of American hornbeam that developed in the understory, a conclusion also reached by Crouch and Golden (1997) in a mature bottomland hardwood forests in Alabama.

Third, the dominance of the overstory by sweetgum, and to a lesser extent oak, is indicative of a past major disturbance(s). Regeneration mechanisms for sweetgum include wind dissemination of seed and good sprouting ability (Kormanik 1990). These characteristics allow sweetgum to rapidly regenerate an area following a major disturbance. The larger trees (80–145 cm d.b.h.) formed, along with oaks, a single canopy layer over much of the area. This canopy dominance may indicate the existence of a single cohort that established following a major disturbance such as a wind event or harvest, or following the abandonment of a former Native American agriculture field.

Table 3. Density, basal area, and importance values for species in the sapling and seedling strata on the Moro Creek Bottoms Natural Area in east-central Arkansas

	Sapling Stratum			Seedling Stratum	
Species	Density[1]	Basal Area[1]	Importance Value	Density[1]	Importance Value
Acer rubrum L.	1.2	0.01	3.2	4.9	1.1
Asimina triloba (L.) Dunal	0.8	<0.01	2.3	—[2]	—
Berchemia scandens (Hill) Trelease	1.0	<0.01	1.4	—	—
Carpinus caroliniana Walter	67.3	0.55	126.3	55.9	16.6
Carya glabra (Mill.) Sweet	—	—	—	3.3	1.5
Carya myristiciformis (Michx. f.) Nutt.	0.8	<0.01	2.1	4.9	2.2
Carya tomentosa (Lam.) Nutt.	0.3	<0.01	1.2	—	—
Cephalanthus occidentalis L.	—	—	—	11.5	1.5
Cornus florida L.	1.2	0.02	3.3	—	—
Crataegus spp.	1.3	0.01	3.5	—	—
Diospyros virginiana L.	1.5	<0.01	2.9	—	—
Forestiera acuminata (Michx.) Poir.	7.2	0.05	13.4	—	—
Fraxinus americana L.	—	—	—	13.2	4.7
Fraxinus caroliniana Mill.	6.4	0.09	14.0	42.8	10.1
Fraxinus pennsylvanica Marshall	13.2	0.10	25.7	28.0	7.7
Hamamelis virginiana L.	1.2	0.01	2.0	—	—
Ilex decidua Walter	4.3	0.03	8.4	9.9	2.6
Ilex opaca Ait.	4.6	0.04	10.4	6.6	3.0
Liquidambar styraciflua L.	1.3	0.02	4.9	8.2	3.1
Nyssa sylvatica Marshall	6.9	0.10	21.9	—	—
Ostrya virginiana (Mill.) K. Koch	4.4	0.03	8.0	9.9	1.4
Planera aquatica J. F. Gmel.	0.7	<0.01	2.0	—	—
Quercus alba L.	—	—	—	16.5	4.4
Quercus lyrata Walter	0.8	0.01	2.8	615.3	63.5
Quercus michauxii Nutt.	2.0	0.01	4.9	46.4	14.0
Quercus nigra L.	1.0	0.02	3.2	34.6	7.0
Quercus pagoda Raf.	0.3	<0.01	1.2	24.7	5.0
Quercus phellos L.	3.3	0.02	8.3	199.1	30.1
Robinia pseudoacacia L.	—	—	—	8.2	1.3
Styrax grandifolius Ait.	1.0	<0.01	1.8	40.0	6.2
Taxodium distichum (L.) Rich.	0.3	<0.01	1.4	—	—
Ulmus alata Michx.	1.5	0.02	5.2	—	—
Vaccinium spp.	7.6	0.01	10.7	26.3	7.6
Other species[3]	1.3	0.04	3.8	13.2	4.7

[1] Density and basal area values were calculated after pooling plot-level data.

[2] Values not shown due to either no specimens measured in this stratum or the importance value was <1.0.

[3] Other species included, *Carya cordiformis* (Wang) K. Koch., *Pinus taeda* L., *Poncirus trifoliata* (L.) Raf., *Quercus falcata* Michx., *Quercus velutina* Lam., *Sassafras albidum* (Nutt.) Nees.

Further, while acting as a pioneer species in its regenerative mechanisms, sweetgum, unlike a typical pioneer species, is a long-lived species with reported ages over 250 yr (Devall and Ramp 1992).

Finally, the tree d.b.h. distribution on the Moro Creek Bottoms Natural Area shows the "reverse-J" shaped curve typical of even-aged, mature, mixed-species bottomland hardwood stands (Figures 1, 2, and 3). Past interpretations of similar d.b.h. distributions indicated an uneven-aged stand in which the smaller trees, being of assumed younger age, would replace the larger (and supposedly older) trees upon overstory mortality (Oliver and Larson 1996). A closer look at individual species d.b.h. distributions indicates that the smaller diameter classes (1 to 16 cm d.b.h.) are dominated by shade-tolerant species such as American hornbeam. Larger diameter classes, beginning at 20 to 30 cm d.b.h., are composed primarily of sweetgum and oak species. This stratification of species into different canopy strata follows Ashton and Peters (1999) concept of "static" stratification in which different long-lived species occupy different strata in a mature forest. Trees in such stands, despite the large differences in d.b.h., may actually be similar in age.

Bottomland Hardwood Succession

Pathways of bottomland hardwood succession involve different seres that are dependent on the relative elevation of the site. Different elevations are the result of flooding and sediment deposition patterns as part of the flood-pulse concept in floodplain ecosystem development (Junk et al. 1989). These elevations and associated seres are commonly referred to as bottomland hardwood species-site relationships (Hodges 1997). Examples of species-site relationships in minor floodplains, such as the one found adjacent Moro Creek, include river birch (*Betula nigra* L.) on point bars; sweetgum, American sycamore (*Platanus occidentalis* L.), green ash, and elms as the site increases in elevation, then oak-hickory when deposition is greatly reduced (Hodges 1997). A different pathway occurs if the initial conditions are poorly drained, such as the deposition of former channels (sloughs) with fine-textured soil particles following migration of the main channel. Several seres of more flood-tolerant species, such as baldcypress, water tupelo, overcup oak, and water hickory (*C. aquatica* (Michx. f.) Nutt.) develop on these sites. Continued deposition eventually leads to similar conditions as with better drained conditions leading to the oak-hickory sere (Hodges 1997). Therefore, succession on floodplains is driven by tree species composition and soil maturation (autogenic processes) and by allogenic (disturbance) processes, such as flooding and sediment deposition patterns, in addition to wind events (White 1979, Battaglia et al. 1995).

Conversely, Nixon et al. (1977) stated that a remnant bottomland hardwood forest in eastern Texas was a ''topographic climax'' based on the species composition located on ridges (American hornbeam, water oak, deciduous holly and Carolina ash) and flats (Carolina ash, American snowbell (*Styrax americanus* Ait.), red maple (*Acer rubrum* L.), and baldcypress. The topographic climax concept differs from Hodges' (1997) models in that it appears to assume a static state in floodplain deposition patterns and morphology, including the river channel bed and soil development, leading to a cessation of successional development to oak-hickory. Our observations are that floodplain development is dynamic and not static in minor or major floodplains; therefore, sedimentation will continue on this site. Tree succession will also continue to proceed towards the oak-hickory sere until a major disturbance reverts tree species composition to earlier seres.

Shear et al. (1996), in comparing restored and mature bottomland hardwood forests, also indicated that the oak-hickory climax may not occur on reforested floodplain sites due to the lack of heavy-seeded species occurring at the time of old-field regeneration and changes in surface and subsurface water flow resulting from erosion in adjacent uplands. Given the soils were classified as Entisols (young soils with little or no profile development) and the early seral species composition of sweetgum, red maple, and American sycamore, all light-seeded species which can rapidly invade old fields, then hard-mast species will appear over time as the current tree species and the site mature.

Using Hodges' (1997) models, the forest in the Moro Creek Bottoms Natural Area contains various sere depending on microtopography. Deposition on the higher elevation sites, such as terraces and ridges, has essentially ceased allowing the soil profile to mature. Final species composition, upon these relatively stable site conditions, will eventually be dominated by oak and hickory species until the next major disturbance. Hickory species already constitute 12 percent of the overstory importance in the natural area. American beech (*Fagus grandifolia* Ehrh.) may also become a more prominent component of the forest due to its shade tolerance and ability to grow into the overstory (Tubbs and Houston 1990). At present, it is only a minor component. Lower elevation sites, such as flats and sloughs, still receive annual sediment deposition. The species compositions on these sites, such as willow oak and overcup oak on the flats and baldcypress in the sloughs, reflect these wet conditions. These sites may take hundreds of years to build elevation to the point that sediment deposition ceases and succession proceeds to the oak-hickory sere. But, during this time, the Moro Creek channel will have meandered elsewhere in the floodplain, cutting ridges at some points that contain the oak-hickory sere and "creating" new land at other points. Therefore, an old-growth bottomland hardwood forest in minor floodplain ecosystems will be a forest composed of different seres, ranging from early-successional species such as river birch to later-successional species such as oaks, hickories, and American beech depending on the microtopography. In general, bottomland hardwood old-growth can be considered as a sedimentation-driven, shifting mosaic of seres influenced by both autogenic and allogenic forces acting in concert.

Is the Moro Creek Bottoms Natural Area Old Growth?

Characterizations of old growth have recently been developed for specific bottomland hardwood forest cover types (Meadows and Nowacki 1996, Kennedy and Nowacki 1997, Shear et al. 1997, Devall 1998), but a broad definition is lacking. Oliver and Larson (1996), in their general model of forest stand development, depict two types of old growth: "transition" and "true" old growth. Transition old growth consists of stands containing relics from the cohort of trees following the last major disturbance. When none of these trees remain, then true old growth is attained.

Runkle (1996) distinguishes three types of old growth for central mesophytic forests in the east-central United States, based on various attributes, as either equilibrium old growth, changing old growth, or old pioneer. Equilibrium old growth consists of forests in which canopy species are replacing themselves. Such forests meet listed functional, structural, and historical attributes commonly associated with old growth. Changing old growth consists of continuously-forested areas but the species composition is changing in response to a new disturbance regime. Old pioneer consists of situations during succession in which the forest is relatively young but the trees (pioneer species) are relatively old. Such conditions can be found in old eastern cottonwood (*Populus deltoides* Bart. ex. Marsh.) and black willow (*Salix nigra* Marsh.) stands on relatively new land formed along major river channels (Meadows and Nowacki 1996).

Finally, Lynch (1996) provides a qualitative description for bottomland old-growth located on the Atlantic Coastal Plain as being (1) composed of a canopy of native species with a mean age of canopy dominants near the maximum age reported for that species, (2) understory and ground layers dominated by native plant species commonly associated with that forest, (3) soil horizons showing no signs of anthropomorphic disturbance, and (4) absence of human-related disturbances that would affect the natural regeneration of native plant species.

Using the above criteria for determining old growth in bottomland hardwood forests, the Moro Creek Bottoms Natural Area appears to be old pioneer. As previously noted, the Moro Creek Bottoms Natural Area is dominated by sweetgum and oaks, indicative of a past major disturbance or old-field succession. The development of these trees is consistent with a mature bottomland hardwood forest. Following the 1989 wind event, numerous canopy gaps, 0.1 to 0.5 ha in size, were created along with abundant standing and dead course woody debris (unpublished final project report on file in the United States Forest Service, Southern Research Station, Center for Bottomland Hardwoods Research, Stoneville, Mississippi). Today, 20 yr since the major wind event, the Moro Bottoms Research Natural Area could be classified as in transition to Runkle's (1996) changing old growth since six percent of the trees in the overstory stratum were lost in the 1989 wind event, primarily among sweetgum and oaks (Guldin et al. 1995). Many of the remaining trees were senescent, and several have died since 1989. Further, we observed sweetgum not replacing itself (Figure 3). Another example of a sweetgum-dominated bottomland hardwood forest in transition exists in the Redgum Research Natural Area on the Delta National Forest in west-central Mississippi. Reports and personal observations indicate the sweetgum trees are also senescent and not replacing themselves (Wiseman 1982, Devall and Ramp 1992).

Given the changes made in river surface and subsurface water flow through human-made structures, especially in past 100 yr, it may be reasonable to assume that all bottomland hardwood old growth is changing old growth. Changes in the hydrologic condition, especially timing and duration of flooding and surface/subsurface water flow, along with subsequent changes in deposition patterns have resulted in new deposition patterns. These changes are probably more prominent on major river systems, through channelization, elevated highway roadbeds, and building of locks and dams, than on minor stream systems such as Moro Creek. Therefore, current tree species compositions in bottomland hardwood ecosystems (old growth and non old-growth) are reflecting adjustments to different patterns of anthropogenic-induced, hydrologic-oriented disturbances (Carter 1978 in Devall and Ramp 1992).

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