A COMPARATIVE ANALYSIS OF THE DIVERSITY OF WOODY VEGETATION IN OLD-GROWTH AND SECONDARY SOUTHERN APPALACHIAN COVE FORESTS

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ABSTRACT.—Characteristics of woody vegetation were compared across six different southern Appalachian cove forests. Trees greater than 6.35 cm dbh were point sampled and regeneration was tallied on 25 m^2 subplots at all study sites. Overstory composition and structure differed between secondary and old-growth sites, which were dominated by yellow-poplar and eastern hemlock, respectively. Mean species richness and density-based diversity indices were higher in the secondary sites for both the overstory and regeneration strata. Shade tolerant species were favored in the regeneration strata at all sites, and yellow-poplar regeneration was rare throughout the study.

Southern Appalachian mixed mesophytic or cove forests occupy valleys and lower slopes at low elevations, spreading outward on sheltered and northerly slopes at higher elevations to around 1,400 meters (Whittaker 1956). Old-growth remnants of this forest type are commonly recognized as some of the most diverse of any in the eastern United States (Martin 1992), in which many characteristic tree species have been noted to grow to record sizes (Stupka 1960). The vegetational diversity of the more commonly found second-growth cove forests in this region is not as widely documented.

The intermediate disturbance hypothesis (Connell 1978) states that the highest levels of diversity in forest communities often occur in intermediate seral stages after a large-scale disturbance event where the presence of both pioneer and climax-associated species overlaps. If many of the second-growth cove forests in the southern Appalachians are indeed in an intermediate stage of succession (Busing 1998), the diversity of these second-growth stands may, in fact, be higher than their old-growth counterparts. It was therefore the objective of the present study to clarify this issue by surveying the woody vegetation (both overstory and regeneration) in several representative stands each of old-growth and second-growth southern Appalachian cove forests and comparatively analyzing them in terms of diversity and other stand-level attributes.

Great Smoky Mountains National Park contains perhaps one of the largest contiguous tracts of old-growth forest in the eastern United States (NPS 1981, Kemp 1993, White and others 1996), and estimates of actual old-growth within the park vary from 16 to 40 percent (Pyle 1985). How-ever, a large portion of these estimates includes high elevation spruce-fir forests, and old-growth mixed mesophytic communities are fairly limited in extent even in protected areas within this region such as the National Park (Martin 1992). According to Whittaker (1956) anthropogenic disturbances in this mountainous region (e.g., logging, farming, and other settlement-related activities) were heavily concentrated in lower elevations due primarily to accessibility, and undisturbed areas in lower valleys are relatively rare. The establishment of the national park in the 1930s resulted in the cessation of such activities, and heavily disturbed areas within park boundaries were subsequently left to recover through natural processes. Protected natural areas such as this have since afforded excellent opportunities to study and monitor the process of natural succession in mixed mesophytic forests of this region. The existence of old-growth remnants of the same forest type in such close proximity provides an integral source of baseline data against which attributes of younger, second-growth stands can be evaluated (Martin 1992).

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Southern Appalachian mixed mesophytic communities can contain about 25-30 tree species with up to eight occurring as dominants or codominants, including eastern hemlock (*Tsuga canadensis* (L.) Carr.), yellow buckeye (*Aesculus octandra* Marsh.), white basswood (*Tilia heterophylla* Vent.), Carolina silverbell (*Halesia tetraptera* Ellis), sugar maple (*Acer saccharum* Marsh.), yellow birch (*Betula alleghaniensis* Britton), yellow-poplar (*Liriodendron tulipifera* L.), and American beech (*Fagus grandifolia* Ehrh.). Composition as well as dominance may vary between different stands, and not all of these eight species necessarily occur at any one given site (Braun 1950). More detailed descriptions of the forest type can be found in Braun (1950), Whittaker (1956), and Martin (1992).

Natural disturbances in cove forests consist primarily of relatively small-scale single or multiple-tree canopy gaps created by windthrow or senescence of large individuals comprising the forest canopy (Lorimer 1980, Runkle 1982, Busing 1994). The importance of canopy gap dynamics in old-growth cove forests is well documented in the literature (Runkle 1981, Runkle and Yetter 1987, Busing and White 1997). These and other studies (Buckner and McCracken 1978, Barden 1989, Busing 1989, Runkle 1998) indicate that these forests are more or less at equilibrium compositionally, and that canopy gap dynamics are, and have been, sufficient in the perpetuation of this compositional stability over time.

Second-growth cove forests in the southern Appalachians are often heavily dominated by yellow-poplar, which is a pioneer species and rapidly colonizes abandoned agricultural or cut over lands (Buckner and McCracken 1978). Yellow-poplar is relatively long lived and may persist as the dominant canopy species in successional forests for up to about 150 years, and an additional 150-250 years may be required for the species to decline in abundance to levels found in old-growth forests in this region (Busing 1995).

Although the diversity of second-growth cove forests has not been documented as extensively in the literature as old-growth cove forests, the issue has been addressed. Clebsch and Busing (1989) found that mid-successional cove forests had greater stem densities and tree species richness than old-growth forests, and linked this to the co-occurrence of shade intolerant species in the overstory and shade tolerant species in the understory. Clebsch and Busing (1989) also reported that while Shannon-Wiener (H′) diversity indices were higher for old-growth forests than second-growth forests when those indices were based on biomass, no clear trends were apparent when they were based on densities, although the highest value reported was for a second-growth forest.

Busing (1998) suggests that second-growth cove forests in the southern Appalachians may persist in the transition phase anywhere from 100-300 years before reaching the final steady state phase in Bormann and Likens (1979) four-phase model of forest succession, and furthermore that little is known about the dynamics of the transition phase in cove forests. The results of the present study therefore address not only the issue of diversity as it relates to successional and old-growth cove forests, but also provide a timely source of benchmark data pertaining to second-growth cove forests as they approach the long transition phase of their development. Improved understanding of the natural dynamics of successional yellow-poplar stands may also prove beneficial in the management of this economically important timber species.

METHODS

Three old-growth and three second-growth southern Appalachian cove forests were chosen for the study and sampled in the fall of 1996 and the summer of 1997 (table 1). All of the study sites are located within Great Smoky Mountains National Park (GSMNP) except Little Santeetlah Creek, which is located in Joyce Kilmer Memorial Forest (JKMF), North Carolina. The three old-growth sites are well noted in the literature for their old-growth attributes. More detailed descriptions of the Little Santeetlah Creek watershed and Joyce Kilmer Memorial Forest can be found in Oosting and Bourdeau (1955), Lorimer (1980), USFS (1988), and Hedman and Van Lear (1995). Detailed descriptions of the Albright Grove site can be found in Busing (1993) and Houk (1993). Descriptions of the Ramsay Cascades site can be found in Houk (1993) and Kemp (1993).

Two of the second-growth sites, Maddron Bald Trail and Middle Prong, are characterized by a diffuse settlement-related disturbance history (e.g., selective harvesting, grazing, and farming) and are located between areas of concentrated settlement at lower elevations on the fringe of the park and undisturbed areas at higher elevations (Pyle 1985). Remnants of stone fences and stone piles are present at both sites (Martin

1992). Although the aspect at the Middle Prong site is primarily to the southwest, the relatively flat topography is typical of a broad, lower elevation cove. The Curry Mountain site is located in an area classified as disturbed by greatly mechanized, highly intensive, and nonselective pre-park corporate logging operations (Pyle 1985).

The sampling procedure at each site consisted of first establishing line transects with randomly determined starting points. Compass headings were also randomly chosen whenever possible, but due to topographical constraints some transects simply paralleled the lower-lying streambeds often associated with cove forest vegetation. Sample plots were then located at evenly spaced intervals along the line transects. The number of sample plots at each site varied considerably due primarily to spatial constraints (table 1).

The overstories of the old-growth and second-growth sites were sampled using 20 factor and 10 factor prisms, respectively. Information collected for the overstory data consisted of species identification and stem diameters at breast height (dbh) for all tallied live trees greater than 6.35 cm dbh, as well as the heights of 2 dominant or codominant trees per plot. Recorded data were used to determine site species richness and compositional parameters such as density, basal area, and frequency. Importance values were calculated as the summation of relative density, relative basal area, and relative frequency. Average canopy height at each site was determined from recorded tree heights. Diversity at each site was quantified using Shannon-Wiener (H′) diversity indices and corresponding equitability (E) indices, as well as Simpson's (D) index of diversity (Krebs 1994). All Shannon-Wiener functions were calculated using base 2 logarithms. Sorensen's similarity indices were used to quantify compositional similarity between sites (Mueller-Dombois and Ellenberg 1974).

Regeneration data were obtained from 25 m^2 subplots located in previously determined quadrants off of the line transect points. All live tree and shrub species greater than 30.5 cm in height and less than 6.35 cm in diameter were tallied in the subplots. Due to its multi-stemmed growth form, rosebay rhododendron (*Rhododendron maximum* L.) was recorded as percent coverage of the subplot when present. Regeneration importance values were calculated as the summation of relative density and relative frequency. Shannon-Wiener and Simpson's diversity indices as well as equitability indices were also computed for the regeneration component at each site. Sorensen's similarity indices were again used to compare each of the sites, as well as to measure the compositional similarity of tree species in the overstory and regeneration within sites. All regeneration diversity and similarity indices were calculated using only data for tree species.

RESULTS AND DISCUSSION

Overstory

Overstory site attributes are presented in table 2. Mean species richness was higher in the secondary sites (mean=19.0) than in the old-growth sites (mean=11.7). Site densities (stems ha^{-1}) were also higher in the secondary sites (mean=1014.7) than in the old-growth sites (mean=360.5). The unusually high stem density at Curry Mountain can be attributed to high numbers of several maple species and flowering dogwood (*Cornus florida* L.) in the smaller diameter classes. Basal areas (m^2 ha^{-1}) and average canopy heights were similar across all sites, with means slightly higher in the old-growth stands.

Table 1.–*Study site characteristics*

Site	Description	Elevation	Aspect	Plots	Location
		- m -			
Albright Grove	Old-growth	1,020	N	12	GSMNP
Ramsay Cascades	Old-growth	1,000	N	8	GSMNP
Little Santeetlah Creek	Old-growth	750	N	31	JKMF
Maddron Bald Trail	Second-growth	750	N	31	GSMNP
Middle Prong	Second-growth	550	SW	15	GSMNP
Curry Mountain	Second-growth	700	NE	15/13[1]	GSMNP

[1]At Curry Mountain there were 15 overstory plots and 13 regeneration subplots.

Table 2.–*Overstory attributes of old-growth and second-growth sites*

	OLD-GROWTH			SECOND-GROWTH		
Site	Albright Grove	Ramsay Cascades	Little Santeetlah Creek	Maddron Bald Trail	Middle Prong	Curry Mountain
Density ha^{-1}	456.1	258.2	367.3	546.0	590.4	1,907.6
Basal area (m^2 ha^{-1})	45.9	40.2	36.4	36.7	32.6	46.5
H′ (density)	1.62	2.48	2.90	2.01	3.46	3.21
H′ (basal area)	2.26	2.90	2.58	0.96	2.82	3.49
E (density)	0.49	0.77	0.72	0.54	0.76	0.73
E (basal area)	0.68	0.91	0.65	0.26	0.62	0.79
D (density)	0.54	0.77	0.81	0.66	0.88	0.85
D (basal area)	0.70	0.85	0.71	0.30	0.74	0.88
Species richness	10	9	16	13	23	21
Mean height of canopy trees (m)	42	47	42	39	41	38

Mean Shannon-Wiener diversity indices based upon stem densities were higher in the secondary sites (mean=2.9) than in the old-growth sites (mean=2.3), and corresponding equitability (E) indices had similar means and ranges in the old-growth and secondary sites (table 2). Simpson's index of diversity yielded the same results as the Shannon-Wiener index. When based upon basal areas, however, Shannon-Wiener diversity indices spanned a much greater range and had a slightly lower mean in the secondary sites (mean=2.4) than in the old-growth sites (mean=2.6). Corresponding equitability indices also had a greater range and lower mean in the secondary sites (mean=0.56) than in the old-growth sites (mean=0.75). Simpson's diversity indices again yielded the same results as the Shannon-Wiener indices when based on basal area.

Eastern hemlock was clearly the dominant species throughout the old-growth sites and had the highest relative density, relative basal area, and importance value at all three of them (table 3). Other species with relatively high importance values at the old-growth sites varied considerably by site, but included Carolina silverbell, red maple (*Acer rubrum* L.), white basswood, sweet birch (*Betula lenta* L.), yellow-poplar, yellow buckeye, and American beech. Other typical southern Appalachian cove forest overstory species such as sugar maple, yellow birch, and cucumbertree (*Magnolia acuminata* L.) (Braun 1950, Whittaker 1956) were relatively minor species over the three sites. American holly (*Ilex opaca* Ait.) and mountain holly (*I. montana* Torr. & Gray) were the only understory tree species tallied in any of the old-growth sites, and were only present at Little Santeetlah Creek.

Yellow-poplar was dominant in two of the three secondary sites, and a relatively important species in the third (table 4). Red maple, sugar maple, or both were consistently important species throughout the secondary sites. Sweetgum (*Liquidambar styraciflua* L.) was an important overstory species at the Middle Prong site, and northern red oak (*Quercus rubra* L.) and chestnut oak (*Q. montana* Willd.) were important overstory species at Curry Mountain. Oak and hickory species were much more prevalent in the secondary sites than in the old-growth sites. Understory tree species also occurred more commonly in the secondary sites, including flowering dogwood, striped maple (*Acer pensylvanicum* L.), musclewood (*Carpinus caroliniana* Walt.), sassafras (*Sassafras albidum* (Nutt.) Nees), and American holly. Black locust (*Robinia pseudoacacia* L.) was present in the overstory at all three secondary sites.

Overall diameter distributions of the old-growth and secondary sites are presented in figure 1. Although some irregularities are apparent, most of the site diameter distributions exhibit or approach the negative log-linear shape characteristic of uneven-aged stands (Daniel and others 1979). At the Maddron Bald Trail site there was a noticeable increase in stem density in the intermediate diameter classes.

Diameter distributions of the six most important species at each site are presented in figure 2. In the old-growth sites, the largest diameter classes were consistently occupied by yellow-poplar, although typically at low densities. Eastern hemlock consistently dominated the smaller diameter classes with a variable assemblage of other shade tolerant species, but was also

Table 3.–*Overstory composition of old-growth sites*

Species	ALBRIGHT GROVE				RAMSAY CASCADES				L. SANTEETLAH CREEK			
	RD[1]	RBA[2]	%F[3]	IV[4]	RD	RBA	%F	IV	RD	RBA	%F	IV
Tsuga canadensis	64.7	44.2	100.0	44.8	39.0	22.9	75.0	26.5	32.1	49.6	100.0	36.0
Halesia tetraptera	16.5	30.0	100.0	24.0	11.5	14.3	62.5	13.5	5.0	2.4	19.4	4.2
Fagus grandifolia	12.6	5.8	41.7	9.7	1.9	2.9	12.5	2.6	2.9	4.5	25.8	4.7
Liriodendron tulipifera	0.7	5.8	41.7	5.7	4.0	12.9	37.5	8.5	1.9	13.4	61.3	10.5
Acer rubrum	0.9	5.0	25.0	4.1	20.3	14.3	62.5	16.4	0.7	2.0	16.1	2.3
Acer saccharum	2.3	2.5	25.0	3.7	--	--	--	--	10.2	2.0	9.7	4.9
Betula alleghaniensis	1.1	2.5	25.0	3.3	2.8	5.7	37.5	5.8	3.2	0.4	3.2	1.5
Tilia heterophylla	0.5	1.7	16.7	2.1	13.6	14.3	75.0	15.2	4.0	8.5	45.2	8.1
Magnolia fraseri	0.5	1.7	8.3	1.4	--	--	--	--	1.7	1.2	6.5	1.5
Prunus serotina	0.2	0.8	8.3	1.1	--	--	--	--	--	--	--	--
Aesculus octandra	--	--	--	--	6.3	11.4	50.0	9.8	--	--	--	--
Betula lenta	--	--	--	--	0.7	1.4	12.5	1.7	13.1	9.8	51.6	12.1
Ilex montana	--	--	--	--	--	--	--	--	22.5	1.2	6.5	8.5
Magnolia acuminata	--	--	--	--	--	--	--	--	0.7	2.0	12.9	2.0
Fraxinus americana	--	--	--	--	--	--	--	--	0.2	1.2	9.7	1.3
Quercus rubra	--	--	--	--	--	--	--	--	0.1	0.8	6.5	0.9
Ilex opaca	--	--	--	--	--	--	--	--	1.2	0.4	3.2	0.8
Carya cordiformis	--	--	--	--	--	--	--	--	0.7	0.4	3.2	0.6

[1] Relative density.
[2] Relative basal area.
[3] Percent frequency.
[4] Importance value.

present at low densities in large diameter classes. In the second-growth sites, a pronounced spike in yellow-poplar density occurred in the 40 cm dbh class at Maddron Bald Trail and in the 60 cm dbh class at Middle Prong. At Curry Mountain, yellow-poplar, northern red oak, and chestnut oak dominated the intermediate and upper diameter classes. The smallest diameter class at this site was clearly dominated by sugar maple and red maple, which were also present at low densities in some of the larger diameter classes.

The Shannon-Wiener diversity index combines the two components of species richness and the proportional allocation of these species within a stand. A greater number of species and a proportional distribution of these species within a stand equates to a higher diversity index value. For example, Ramsay Cascades and Middle Prong both have relatively high density-based equitability indices, which indicates a proportional allocation of density among species in these stands (table 2). Middle Prong has over twice as many species as Ramsay Cascades, however, and therefore has greater diversity according to the Shannon-Wiener index. A similar argument holds for the Curry Mountain site, which also has high equitability and diversity indices. When the indices are based on basal area, however, the situation changes.

Basal area was not as evenly distributed among species at Middle Prong as density, and the Shannon-Wiener index value was accordingly lower. Ramsay Cascades had an even higher equitability index based on basal area than based on density, and the diversity index was accordingly greater. The relatively low diversity indices at Albright Grove and Maddron Bald Trail reflect the dominance of eastern hemlock and yellow-poplar at those sites, respectively. Basal area was more equitably distributed among species than density at Albright Grove, but the opposite was true at Maddron Bald Trail, where yellow-poplar accounted for over 80 percent of the relative basal area (table 4).

Clebsch and Busing (1989) also reported higher Shannon-Wiener diversity indices in some secondary cove stands than in old-growth stands when these indices were based on density. When the indices were based on biomass, however, the old-growth stands had higher diversity indices. This indicates that biomass is more equitably distributed among species in old-growth cove forests than in secondary forests dominated by yellow-poplar. Clear dominance

Table 4.–*Overstory composition of second-growth sites*

Species	MADDRON BALD TRAIL				MIDDLE PRONG				CURRY MOUNTAIN			
	RD[1]	RBA[2]	%F[3]	IV[4]	RD	RBA	%F	IV	RD	RBA	%F	IV
Liriodendron tulipifera	42.3	82.9	100.0	55.3	12.2	46.5	100.0	26.1	2.4	15.1	80.0	9.6
Acer rubrum	40.1	12.1	80.6	28.4	9.5	14.1	40.0	10.5	18.3	16.4	86.7	15.7
Halesia tetraptera	4.4	1.6	16.1	4.2	0.6	0.9	6.7	0.9	1.6	2.3	20.0	2.2
Betula lenta	1.8	0.8	9.7	2.2	1.3	0.9	13.3	1.6	1.3	2.3	26.7	2.5
Cornus florida	2.4	0.4	6.5	1.8	10.2	2.3	26.7	5.9	20.0	5.3	40.0	10.3
Robinia pseudoacacia	0.3	0.6	9.7	1.6	1.5	3.8	53.3	5.3	0.4	3.0	40.0	3.0
Acer pensylvanicum	3.0	0.2	3.2	1.5	--	--	--	--	9.7	2.3	20.0	4.9
Tsuga canadensis	2.7	0.4	3.2	1.5	5.7	0.5	6.7	2.5	7.1	3.0	33.3	4.9
Acer saccharum	1.1	0.2	3.2	0.9	22.2	8.0	53.3	13.6	25.2	19.4	93.3	19.3
Quercus rubra	1.1	0.2	3.2	0.9	0.04	0.5	6.7	0.6	1.3	6.6	80.0	6.4
Carpinus caroliniana	0.7	0.2	3.2	0.8	5.7	0.5	6.7	2.5	1.8	0.3	6.7	1.0
Fraxinus americana	0.1	0.2	3.2	0.5	--	--	--	--	--	--	--	--
Nyssa sylvatica	0.1	0.2	3.2	0.5	1.5	1.4	20.0	2.3	1.0	1.0	13.3	1.3
Liquidambar styraciflua	--	--	--	--	17.0	11.3	73.3	14.3	--	--	--	--
Quercus alba	--	--	--	--	3.7	1.9	6.7	2.3	--	--	--	--
Ilex opaca	--	--	--	--	3.2	0.5	6.7	1.7	--	--	--	--
Prunus serotina	--	--	--	--	1.5	0.9	13.3	1.7	--	--	--	--
Carya glabra	--	--	--	--	0.8	0.9	13.3	1.5	1.4	3.3	26.7	2.8
Juglans nigra	--	--	--	--	0.7	0.9	13.3	1.4	--	--	--	--
Carya cordiformis	--	--	--	--	0.5	0.9	13.3	1.4	0.3	1.3	26.7	1.8
Sassafras albidum	--	--	--	--	0.9	0.9	6.7	1.1	1.6	1.6	6.7	1.4
Carya tomentosa	--	--	--	--	0.3	0.9	6.7	0.8	--	--	--	--
Betula alleghaniensis	--	--	--	--	0.4	0.5	6.7	0.7	2.0	0.7	13.3	1.5
Aesculus octandra	--	--	--	--	0.4	0.5	6.7	0.7	--	--	--	--
Quercus montana	--	--	--	--	0.1	0.5	6.7	0.6	2.5	14.1	60.0	8.4
Carya ovata	--	--	--	--	--	--	--	--	0.2	0.7	13.3	0.9
Magnolia fraseri	--	--	--	--	--	--	--	--	1.1	0.7	6.7	0.9
Tilia heterophylla	--	--	--	--	--	--	--	--	1.0	0.3	6.7	0.8
Magnolia acuminata	--	--	--	--	--	--	--	--	0.2	0.3	6.7	0.5

[1] Relative density.
[2] Relative basal area.
[3] Percent frequency.
[4] Importance value.

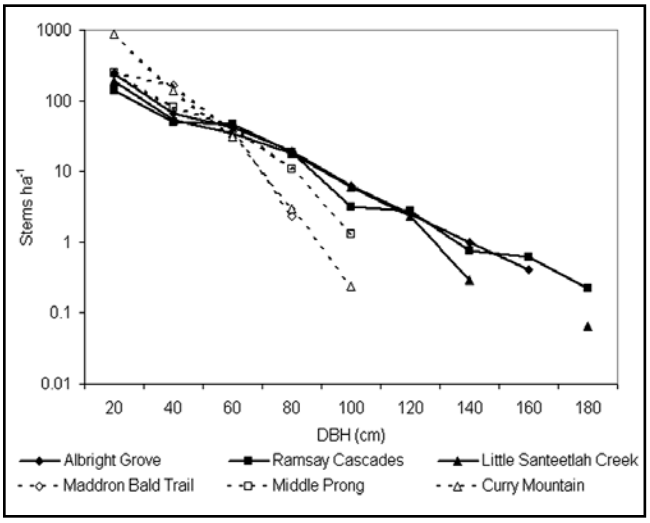

Figure 1.–*Site diameter distributions.*

by any one species did not occur at Curry Mountain, which is reflected by this site's relatively high diversity and evenness indices (table 2).

Regeneration

Regeneration site attributes are presented in table 5. Mean tree species richness of the regeneration component was higher in the secondary sites (mean = 16.3) than in the old-growth sites (mean = 9.7). Mean shrub species richness was higher in the old-growth sites, although numbers and types of shrub species present varied considerably across sites. Mean tree species regeneration density was higher in the secondary sites (mean = 3,979.1 ha-1) than in the old-growth sites (mean = 2,573.7 ha-1). Mean shrub species density was also higher in the secondary sites

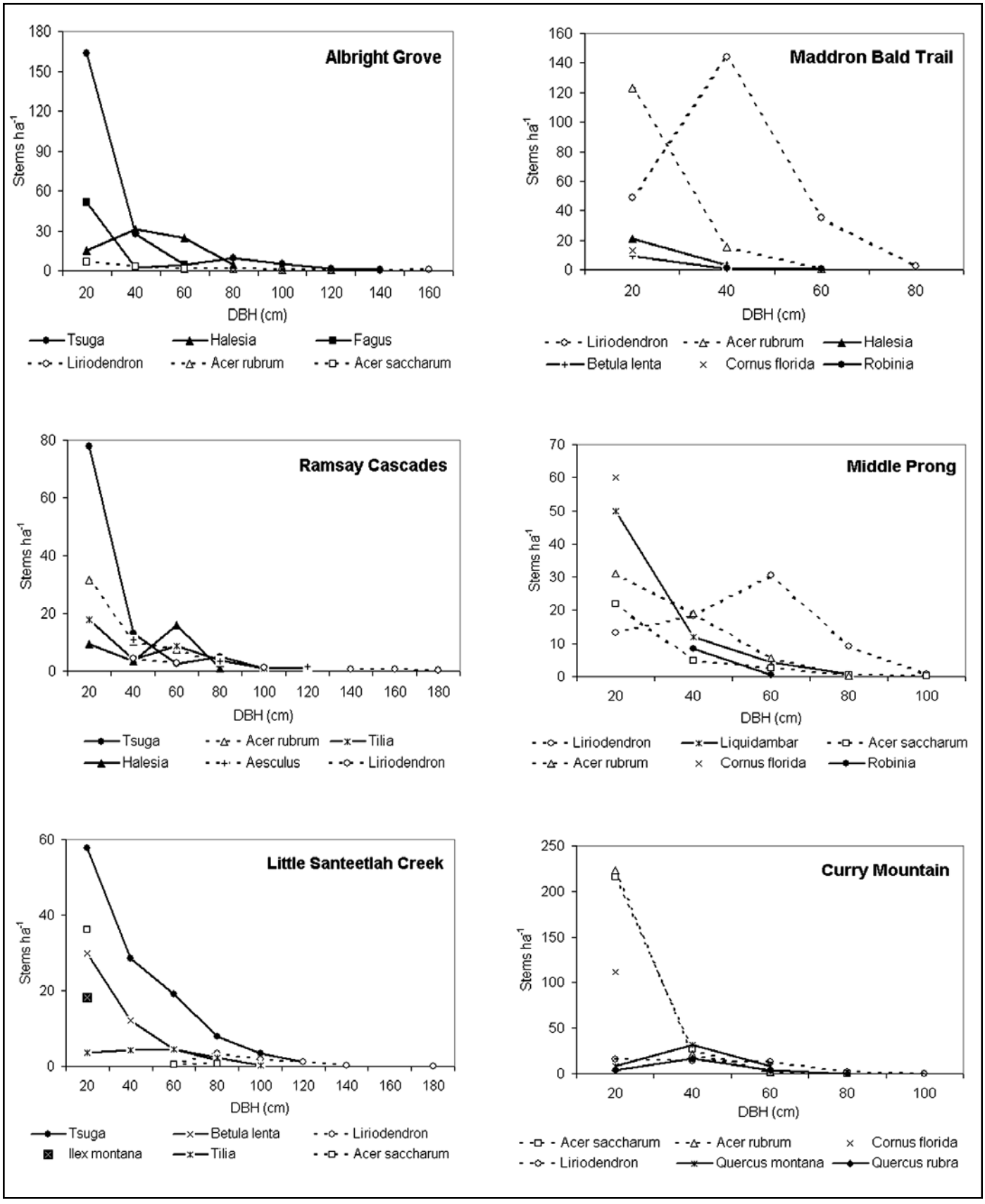

Figure 2.–*Species diameter distributions by site.*

Table 5.–*Regeneration attributes of old-growth and second-growth sites*

	OLD-GROWTH			SECOND-GROWTH		
Site	Albright Grove	Ramsay Cascades	Little Santeetlah Creek	Maddron Bald Trail	Middle Prong	Curry Mountain
Tree density ha-1	2,933.0	2,750.0	2,038.2	4,785.9	5,920.7	1,230.8
Shrub density ha-1	—-	1,850.0	1,651.2	490.2	2,000.3	4,830.9
H' (density)	2.40	1.60	3.38	3.36	2.90	2.96
E (density)	0.76	0.62	0.89	0.79	0.70	0.83
D (density)	0.76	0.52	0.86	0.87	0.81	0.82
Tree richness	9	6	14	19	18	12
Shrub richness	1	3	8	4	4	1

(mean = 2,440.5 ha-1) than in the old-growth sites (mean = 1,167.1 ha-1). Mean Shannon-Wiener diversity indices were higher in the secondary sites (mean = 3.1) than in the old-growth sites (mean = 2.5). Equitability indices spanned a greater range in the old-growth sites, but means were similar between the old-growth and secondary sites. Simpson's diversity indices again yielded results identical to the Shannon-Wiener indices.

The composition of the regeneration strata within both old-growth and secondary sites was dominated by a combination of shade tolerant canopy species, understory tree species, and a site-specific assemblage of shrub species. For example, at Albright Grove, the three most important regeneration species were sugar maple, American beech, and eastern hemlock (table 6). Red maple, yellow buckeye, and the shrub species *Viburnum* spp. were the most important species at Ramsay Cascades, the old-growth site with the lowest regeneration diversity. Little Santeetlah Creek was the most diverse old-growth site, and dominance of the regeneration component was relatively evenly distributed between a variety of canopy species, understory tree species, and a species-rich shrub layer dominated by serviceberry (*Amelanchier* spp.).

Red maple, striped maple, and Carolina silverbell had the highest importance values at Maddron Bald Trail, the secondary site with the highest regeneration diversity (table 7). Sweetgum had the second highest importance value in both the overstory and regeneration at Middle Prong. Regeneration at the Curry Mountain site was heavily dominated by the shrub species *Gaylusacia* spp.

Yellow-poplar was a relatively rare regeneration species in the cove forests sampled in this study, with minor importance values at the two sites where it was present, Little Santeetlah Creek and Curry Mountain. Oaks and hickories were common in the regeneration component of the secondary sites. Black locust was present in the regeneration component of two of the secondary sites, and American chestnut sprouts (*Castanea dentata* (Marsh.) Borkh.) were encountered at the Maddron Bald Trail site. Rosebay rhododendron was present in all three old-growth sites and one secondary site. Due to the tendency of rhododendron to exist in discrete patches or thickets commonly associated with riparian zones in this region, its presence in a sub-plot was merely noted and it was not treated similarly to other regeneration-level species in the analyses in this study. The dynamics of rhododendron in the southern Appalachians have been addressed by McGee and Smith (1967), Phillips and Murdy (1985), and Hedman and Van Lear (1995), among others.

Sorensen's similarity indices indicated a greater compositional similarity among old-growth site overstories and second-growth site overstories than between old-growth and second-growth site overstories (table 8). No clear trends were apparent from such comparisons of regeneration at the six study sites. The regeneration component was highly variable between different stands, and this was reflected in the relatively lower regeneration similarity indices. Overall, Sorensen's indices indicated a high degree of similarity between overstory and regeneration composition within individual sites. The lower similarity index for Ramsay Cascades is likely an artifact of the low regeneration species richness at that site.

CONCLUSION

Differences in community attributes were apparent between old-growth and secondary

Table 6.–*Regeneration composition of old-growth sites*

	ALBRIGHT GROVE			RAMSAY CASCADES			L. SANTEETLAH CREEK		
Tree species	**RD[1]**	**% F[2]**	**IV[3]**	**RD**	**% F**	**IV**	**RD**	**% F**	**IV**
Acer saccharum	38.6	50.0	33.6	--	--	--	6.6	22.6	7.6
Fagus grandifolia	25.0	16.7	17.3	--	--	--	2.4	12.9	3.7
Tsuga canadensis	12.5	33.3	15.8	4.3	25.0	8.1	4.5	19.4	5.9
Acer pensylvanicum	9.1	25.0	11.7	3.3	12.5	4.6	10.8	22.6	9.7
Halesia tetraptera	3.4	16.7	6.5	--	--	--	5.6	16.1	5.8
Betula alleghaniensis	8.0	8.3	6.4	1.1	12.5	3.5	--	--	--
Magnolia fraseri	1.1	8.3	3.0	--	--	--	--	--	--
Prunus serotina	1.1	8.3	3.0	--	--	--	--	--	--
Fraxinus americana	1.1	8.3	3.0	--	--	--	1.4	9.7	2.5
Acer rubrum	--	--	--	40.2	50.0	31.9	--	--	--
Aesculus octandra	--	--	--	3.3	37.5	10.5	1.4	6.5	1.9
Nyssa silvatica	--	--	--	7.6	12.5	6.8	--	--	--
Betula lenta	--	--	--	--	--	--	7.0	22.6	7.7
Ilex montana	--	--	--	--	--	--	8.0	9.7	5.9
Ilex opaca	--	--	--	--	--	--	2.1	9.7	2.9
Liriodendron tulipifera	--	--	--	--	--	--	2.4	6.5	2.5
Asimina triloba	--	--	--	--	--	--	1.4	6.5	1.9
Tilia heterophylla	--	--	--	--	--	--	0.7	6.5	1.6
Quercus rubra	--	--	--	--	--	--	0.7	6.5	1.6
Shrub species									
Viburnum spp.	--	--	--	39.1	50.0	31.4	--	--	--
Cornus alternifolia	--	--	--	1.1	12.5	3.5	2.1	12.9	3.5
Amelanchier spp.	--	--	--	--	--	--	22.0	12.9	13.4
Calycanthus floridus	--	--	--	--	--	--	11.9	16.1	9.0
Hamamelis virginiana	--	--	--	--	--	--	3.8	29.0	7.4
Euonymus americanus	--	--	--	--	--	--	1.7	9.7	2.7
Lindera benzoin	--	--	--	--	--	--	2.8	6.5	2.6
Leucothoe fontanesiana	--	--	--	--	--	--	0.3	3.2	0.8
Rhododendron maximum	X[4]	X	X	X	X	X	X	X	X

[1]Relative density.
[2]Percent frequency.
[3]Importance value.
[4]X indicates presence of rhododendron at a site.

sites in this study. Whether or not the compositional differences among secondary site overstories is an artifact of their respective disturbance regimes or other factors is unclear. Yellow-poplar has been noted to grow in almost pure stands on clearcuts and abandoned fields in this region (Buckner and McCracken 1978, Beck 1990). If the Maddron Bald Trail site was not affected by corporate logging (Pyle 1985), evidence suggests that it was an abandoned agricultural site. The diameter distribution at this site also suggests that it originated as an even-aged stand.

The high incidence of dead-standing black locust and sassafras trees witnessed at the Curry Mountain site suggests that the even-aged origin of this stand has been masked by the mortality of a number of pioneer species that comprised the initial overstory. The relatively greater oak-hickory component and steeper slopes at Curry Mountain also indicate that this site may be more accurately characterized as a cove transition forest. This forest type is spatially located between mesic cove forests and more xeric oak-hickory forests as described by Whittaker (1956). The high species richness at Curry Mountain may therefore be related to the co-existence of species common to these two different community types.

Middle Prong is the lowest elevation cove forest in this study, and this is likely related to the importance of sweetgum at this site (Kemp 1993). The diameter distribution at Middle Prong and lack of evidence of self-thinning

Table 7.–*Regeneration composition of second-growth sites*

	MADDRON BALD TRAIL			MIDDLE PRONG			CURRY MOUNTAIN		
Tree species	**RD[1]**	**% F[2]**	**IV[3]**	**RD**	**% F**	**IV**	**RD**	**% F**	**IV**
Acer pensylvanicum	22.0	80.6	20.0	3.0	20.0	3.7	4.1	30.8	9.2
Acer rubrum	15.4	61.3	14.5	4.4	13.3	3.7	1.5	7.7	2.6
Halesia tetraptera	10.0	41.9	9.7	21.5	80.0	19.5	1.0	15.4	4.1
Acer saccharum	8.3	32.3	7.8	8.4	13.3	5.7	--	--	--
Quercus rubra	5.1	38.7	6.9	--	--	--	--	--	--
Betula alleghaniensis	6.6	29.0	6.5	0.3	6.7	0.9	--	--	--
Betula lenta	6.4	25.8	6.1	--	--	--	--	--	--
Tsuga canadensis	5.6	19.4	5.0	0.3	6.7	0.9	0.5	7.7	2.1
Fraxinus americana	2.4	22.6	3.7	0.3	6.7	0.9	--	--	--
Magnolia fraseri	1.2	16.1	2.4	--	--	--	0.5	7.7	2.1
Carpinus caroliniana	3.2	6.5	2.3	6.1	53.3	8.9	1.0	7.7	2.3
Cornus florida	1.2	12.9	2.1	2.7	33.3	5.0	6.6	38.5	12.3
Nyssa silvatica	1.0	6.5	1.2	0.7	13.3	1.8	1.0	15.4	4.1
Sassafras albidum	0.5	6.5	1.0	2.0	20.0	3.2	--	--	--
Magnolia acuminata	0.5	6.5	1.0	--	--	--	--	--	--
Castanea dentata	0.5	3.2	0.6	--	--	--	--	--	--
Magnolia tripetala	0.2	3.2	0.5	--	--	--	--	--	--
Carya glabra	0.2	3.2	0.5	--	--	--	--	--	--
Carya cordiformis	0.2	3.2	0.5	--	--	--	--	--	--
Liquidambar styraciflua	--	--	--	21.5	66.7	18.0	--	--	--
Ilex opaca	--	--	--	0.7	13.3	1.8	--	--	--
Aesculus octandra	--	--	--	1.0	6.7	1.3	--	--	--
Robinia pseudoacacia	--	--	--	0.7	6.7	1.1	0.5	7.7	2.1
Prunus serotina	--	--	--	0.3	6.7	0.9	--	--	--
Quercus alba	--	--	--	0.3	6.7	0.9	--	--	--
Juglans nigra	--	--	--	0.3	6.7	0.9	--	--	--
Pinus strobus	--	--	--	--	--	--	2.5	15.4	4.9
Liriodendron tulipifera	--	--	--	--	--	--	0.5	7.7	2.1
Morus rubra	--	--	--	--	--	--	0.5	7.7	2.1
Shrub species									
Lindera benzoin	6.1	9.7	4.2	11.4	40.0	10.1	--	--	--
Amelanchier spp.	1.7	19.4	3.0	3.7	20.0	4.1	--	--	--
Viburnum spp.	1.5	3.2	1.1	--	--	--	--	--	--
Calycanthus floridus	--	--	--	2.7	6.7	2.1	--	--	--
Gaylusacia spp.	--	--	--	7.4	13.3	5.2	79.7	46.2	50.6
Rhododendron maximum	X[4]	X	X	--	--	--	--	--	--

[1]Relative density.
[2]Percent frequency.
[3]Importance value.
[4]X indicates presence of rhododendron at a site.

suggest a more complex disturbance history consistent with the diffuse disturbance classification of Pyle (1985).

The high species richness and diversity of the secondary sites is related to the presence of less tolerant species such as black locust that presumably became established following the major disturbance affecting those sites. Successional theory suggests that these species will eventually be replaced by more tolerant species, which could lower site species richness over time (Busing 1998). High old-growth diversity and equitability indices based on biomass (Busing 1998, Clebsch and Busing 1989) and basal area reflect that overstory dominance in old-growth mixed mesophytic stands is typically shared by multiple species (Braun 1950, Whittaker 1956).

Table 8.–*Sorensen's similarity indices*

Site	OLD-GROWTH			SECOND-GROWTH		
	Albright Grove	Ramsay Cascades	Little Santeetlah Creek	Maddron Bald Trail	Middle Prong	Curry Mountain
Albright Grove	**0.737**[1]	0.737[2]	0.692	0.435	0.424	0.516
Ramsay Cascades	*0.400*[3]	**0.533**	0.640	0.455	0.438	0.467
Little Santeetlah Creek	*0.522*	*0.300*	**0.733**	0.552	0.513	0.649
Maddron Bald Trail	*0.500*	*0.400*	*0.424*	**0.688**	0.611	0.706
Middle Prong	*0.519*	*0.500*	*0.438*	*0.595*	**0.780**	0.727
Curry Mountain	*0.381*	*0.444*	*0.308*	*0.516*	*0.533*	**0.606**

[1]Bold text: within site comparisons
[2]Plain text: overstory comparisons
[3]Italics: regeneration comparisons

The old-growth and second-growth cove forests sampled in this study suggest a continuity of species composition over successional time. Characteristic cove forest canopy species were typically present in the regeneration layers of these forests with the notable exception of yellow-poplar, which currently showed very little evidence of successful regeneration in any of the study sites. Although the overstory at Maddron Bald Trail was the least diverse of the second-growth sites, possibly reflecting the relative severity of an agricultural-related disturbance history, the regeneration component at this site was the most species rich of all the study sites. As the yellow-poplar overstory begins to thin, other more shade-tolerant cove forest canopy species should be present to replace it, bringing the overstory composition of this site closer to that found in old-growth mixed mesophytic forests.

Continued monitoring of second-growth southern Appalachian cove forests is essential to understanding the ecological processes involved in the succession of these forests towards the composition and structure seen in old-growth cove forests. Continued monitoring of old-growth cove forests is also essential to the establishment of solid baseline data related to these forests. This baseline data is not only useful for comparison with successional sites, but would also be highly useful in the advent of unforeseen future shifts in composition within old-growth cove forests. For example, if the hemlock woolly adelgid (*Adelges tsugae* Annand) eventually reaches the southern Appalachian region with the same impacts seen in some New England states (Jenkins and others 1999), the composition and structure of old-growth cove forests could be dramatically altered. With a solid foundation of baseline data, however, sensitive areas could be identified and impacts could be addressed and possibly mediated.

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