VEGETATIVE STRUCTURE AND COMPOSITION OF SOUTHERN APPALACHIAN RIPARIAN FORESTS

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Vegetative structure and composition of Southern Appalachian riparian forests[1]

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HEDMAN, CRAIG W. (Southlands Experiment Forest, International Paper, Bainbridge, GA 31717) AND DAVID H. VAN LEAR (Department of Forest Resources, Clemson University, Clemson, SC 29634-1003). Vegetative structure and composition of Southern Appalachian riparian forests. Bull. Torrey Bot. Club 122: 134–144. 1995.—Vegetative characteristics of twelve Southern Appalachian riparian forests were sampled as part of a larger study which examined functional attributes of riparian zones. Riparian forests were representative of the mixed mesophytic forest, eastern hemlock forest, and transitions between these types. Early- and mid-successional stages were generally dominated by an overstory of pioneering shade-intolerant species and had an even-aged structure. The diameter distribution of these relatively young stands of mixed species was typically inverse J-shaped. Late-successional and old-growth stages were dominated by shade-tolerant or moderately tolerant overstory species and were uneven-aged. Diameter distribution in these older stands approximated a rotated sigmoid curve. Rhododendron (*Rhododendron maximum* L.) was the dominant understory species and controlled understory and midstory composition. Characterization of riparian forests in different stages of succession will help understanding of vegetative processes and forms the basis of subsequent ecological studies of riparian functional dynamics.

Key words: mixed mesophytic forest, stand dynamics, diameter distribution, *Tsuga canadensis, Rhododendron maximum.*

Riparian zones, i.e., areas of direct interactions between terrestrial and aquatic environments (Swanson et al. 1982; Waring and Schlesinger 1985), have many important functions. Ecologically, riparian zones furnish and affect the quality, quantity, and chemistry of food used by stream organisms in low-order streams; influence the composition of aquatic communities and functional group dominance; regulate solar energy inputs to streams; buffer nutrient and sediment inputs from upslope and upstream sources; stabilize streambanks and floodplains by binding alluvial sediments of bed and bank together; regulate streamflow; and supply large woody debris to streams (Zimmerman et al. 1967; Swantson 1970; Brown and Krygier 1970; Swift and Messer 1971; Burton and Likens 1973; Smith 1976; Graf 1978; Beschta 1979; Cummins 1980; Likens and Bilby 1982; Swanson et al. 1982; Miller 1987). Functionally defined, the riparian zone forms a zone of interaction extending upward and outward from the stream through the overhanging canopy and root system (Swanson et al. 1982).

Vegetative descriptions of Southern Appalachian riparian zones are lacking. Characterization of the composition and structure of riparian zone vegetation is integral to any discussion/analysis of riparian zone functions and provides the foundation for subsequent ecological and management studies. Therefore, the objective of this study was to describe the structure and composition of riparian forests in the Southern Appalachians along a sere from recently disturbed through old-growth conditions.

Methods. STUDY AREAS. The study was conducted in the Blue Ridge Mountain physiographic province of the southeastern United States with the USDA Forest Service Coweeta Hydrologic Laboratory near Franklin, North Carolina serving as the central location. Additional sites were located throughout the Wayah and Cheoah Ranger Districts of the Nantahala National Forest in North Carolina, the Andrew Pickens Ranger District of the Sumter National Forest in South Carolina, the Tallulah Ranger District of the Chattahoochee National Forest in Georgia, the City of Greenville Municipal Watershed in

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Table 1. Characteristics of study streams and their watersheds.

Stream	State	Stream order	Watershed area (ha)	Sample area elevation (m)	Watershed aspect
Albert	NC	2	44	1082	ENE
Thompson River Tributary	NC	1	98	899	SE
Dicks	NC	2	393	1036	SE
Dryman-4	NC	4	468	853	NE
Jones	NC	2	547	883	NNE
Henson	NC	3	217	884	NE
Dryman-3	NC	3	159	899	NNE
Galloway	SC	2	185	472	S
Reed	GA	2	1068	640	SW
Harden	GA	1	97	701	SE
Indian Camp	SC	3	352	768	SSE
Little Santeetlah	NC	3	1106	774	ESE

northwestern South Carolina, and private industrial forestland near the Nantahala National Forest in North Carolina.

Study streams ranged from first to fourth order and drained watersheds as small as 44 ha to as large as 1106 ha (Table 1). Elevation of study reaches ranged from 472 m to 1082 m. Aspects of most streams had an easterly component, except for Galloway and Reed Creeks, which faced southerly and southwesterly, respectively.

SITE SELECTION. The goal of site selection was for stage of succession or time since stand-replacing disturbances (or at least disturbances which replaced major portions of a stand) to be the primary variant. Twelve riparian zones and associated stream systems representing four seral stages, i.e., early-successional, mid-successional, late-successional, and old-growth, were selected after field reconnaissance of nearly 60 riparian/stream systems. Each seral stage had at least two replicates.

AGING OF RIPARIAN ZONES. Riparian zone ages were determined by coring trees at breast height. The number of trees cored ranged from 14 for an even-aged stand to 38 for an old-growth uneven-aged riparian area. Age-class structure of riparian stands necessitated the usage of different aging procedures. Even-aged stands, i.e., stands with a single age class in which the range of tree ages is usually less than 20 percent of rotation (Smith 1986; Society of American Foresters 1993), were typically aged by coring tulip poplar (*Liriodendron tulipifera* L.) and black birch (*Betula lenta* L.). If the associated coefficient of variation (CV) of the entire sample set was < 10%, then this mean age was used. Additional methods of characterizing age of even-aged stands were used when it was apparent that outliers, e.g., remnant, scattered, large, hemlocks (*Tsuga canadensis* (L.) Carr.), were included and disproportionately skewed the mean. Therefore, when a mean age with a CV > 10% resulted, the mode and median were calculated as was an "adjusted mean" based on 10-yr spreads about median age. Overall stand age was based on the method(s) which resulted in the lowest CV and whose age "matched" ages obtained by at least two other methods (Hedman 1992).

In uneven-aged stands, i.e., stands with at least three age classes (Smith 1986; Society of American Foresters 1993), an attempt was made to determine the age of the oldest major cohort—a difficult task. Since anthropogenic and/or natural disturbances of varying magnitude lead to the establishment of Southern Appalachian riparian forests or major portions thereof (Lorimer 1980), the oldest individuals of pioneering species such as tulip poplar and black birch were used as indicators of stand age, i.e., time since stand- or cohort-establishing disturbances. These species occurred in all stands in varying densities and were used exclusively for aging when their presence substantially contributed to the overall composition of the stand (based on relative frequency, relative basal area, and importance value).

As in the even-aged stands, pioneering species were utilized in assessing stand age of late-successional and old-growth forests when available. The basic premise behind using early colonizers was that if large long-lived pioneers such as tulip poplar and black birch are present today, then they probably regenerated soon after a major disturbance and therefore mark the inception of all or much of the current stand. Additionally, moderately shade tolerant white pine (*Pinus strobus* L.) and oaks (*Quercus* spp.) to tolerant hemlock provided supporting evidence in determining riparian zone age when true pioneers were either underrepresented or displayed unclear patterns.

Since large, old trees were important components of these stands, their ages gave a good indication of time since stand- or cohort-establishing disturbances. However, even within species, variations in age exist for similar sized individuals. Therefore, across-species cohorts of the oldest tulip poplar, black birch, hemlock, white pine, and oaks were used in computing mean cohort age. The oldest cohort-member ages were identified and these ages were averaged to obtain a representative stand age. Hence, the establishment age for uneven-aged stands was based on mean age of the oldest across-species cohort with a CV $<$ 10% (Hedman 1992).

Classification of riparian stands into four seral stages was verified via age analysis and a test of least significant differences (LSD), modelling of diameter frequency distributions where the log of diameter frequency was plotted against diameter classes, and discriminant function analysis (DFA) of diameter frequencies. DFA was performed by plotting the log of diameter frequencies for 5.1-cm diameter classes over the diameter class interval 10.2 cm through 50.8 cm. This range was selected because it represented the highest variability in diameter frequencies among sites.

VEGETATION. Six riparian zone sample plots (20 × 20 m) were randomly established along 500-m reaches of each stream, i.e., three plots on either side. Sample plots of this size and configuration were chosen to incorporate all above- and below-ground functions of the riparian zone without overcompensating for any particular function (Van Sickle and Gregory 1990; McDade et al. 1990; Robison and Beschta 1990).

Overstory, midstory, understory, and herbaceous vegetation was measured and recorded in nested plots. Measurements and resultant summary statistics were similar to a system utilized for classifying Coastal Plain vegetation communities (Jones et al. 1984), except plots were square rather than circular. Species and diameter at breast height (DBH) of all trees larger than 10.2 cm, which included overstory and midstory species, were recorded in 400-m^2 plots; saplings and tall shrubs in the understory between 10.2 and 0.25-cm diameter were recorded in 100-m^2 nested plots; and herbaceous species were recorded in three 1-m^2 nested plots. Woody seedling regeneration $<$ 0.25-cm diameter were also tallied in herbaceous plots. Herbaceous plots were located systematically within 400-m^2 parent plots and resulted in 18 understory plots per riparian forest. Total height of dominant overstory trees and those cored for age determinations were measured in each parent plot.

Vegetation data were summarized by canopy stratum for each plot. Relative density, basal area, and importance value (relative density + relative basal area/2⋆100) were calculated for trees, tall shrubs, and saplings. Herbaceous vegetation and woody regeneration presence were summarized by species counts (Jones et al. 1984).

The majority of individuals occurring in sample plots were identified to the species level. When this degree of specificity could not be achieved (due to seasonal changes in plant expression and physiological development), identification was made to the genus level.

Results and Discussion. SERAL STAGE CLASSIFICATION. Riparian stands selected for study represented conditions and ages ranging from 28 yr through 334 yr post stand-level disturbances (Table 2). While stages of succession were replicated, it was not possible to equally replicate each stage. We sought stands that had regenerated following a stand-replacing disturbance such as heavy cutting, fire, or windthrow. Given other study objectives related to large woody debris, it was important to sample stands without streamside buffer strips. Recently cutover riparian zones (early-seral stage) were particularly hard to locate given the size of stream under study (1st–4th order) and the fact that the U.S. Forest Service has consistently left streamside buffer strips adjacent to streams of this size for the past two to three decades (Wayne Swank, pers. comm.). Additionally, old-growth stands are scarce in the eastern United States and finding riparian/stream systems which met our geomorphological criteria and covered 500 m of stream was difficult. As a result, early-successional and old-growth candidate sites accounted for 50% and 10% of all sites inspected, respectively. Hence, we utilized only 20 percent of the sites inspected and our desired goal of three replicates per seral stage could not be achieved.

Classifying riparian stands into seral stages was accomplished using several methods. Stand age

Table 2. Age class data for riparian forests[a] of varying successional stages.

		Mean age (yr) per DBH class (cm) and sample set summary statistics[b]								Age of oldest cohort (yr)		
Stream	Seral stage	*N*	10.2–25.4 cm (1 SE)	25.5–50.8 cm (1 SE)	50.9–76.2 cm (1 SE)	76.3+ cm (1 SE)	Mean (% CV)	Median (yr)	Mode (yr)	*n*	Range	Mean age (% CV)
AL[c]	Early	—					28			—		28
TT	Early	14	35.1 (10.0)	40.2 (4.9)	—	63.0 (0.0)	39.0 (29)	38	38	6	38–45	40 (7)
DK	Mid	19	55.9 (4.7)	60.0 (7.4)	—	—	57.4 (10)	56	57	14	45–69	57 (10)
D4	Mid	20	57.8 (12.0)	64.4 (13.6)	99.8 (25.6)	—	70.2 (31)	65	64	11	55–75	65 (9)
JN	Mid	19	—	72.4 (18.5)	93.0 (0.0)	—	69.9 (35)	69	66	13	57–80	67 (10)
HN	Mid	20	65 (0.0)	79.0 (18.1)	96.0 (1.4)	—	80.0 (22)	70	65	11	64–82	69 (8)
D3	Mid	20	—	76.3 (18.6)	157.5 (16.6)	255.0 (0.0)	93.4 (52)	70	68	15	55–82	70 (5)
GL	Late	20	—	123.5 (33.7)	134.3 (35.9)	217.8 (53.5)	—	—	—	7	158–213	180 (10)
RD	Late	22	75.8 (22.6)	137.4 (66.6)	106.6 (59.9)	107.0 (8.9)	—	—	—	3	191–210	203 (5)
HR	Late	29	79.6 (24.0)	106.1 (37.5)	134.9 (42.3)	186.4 (50.4)	—	—	—	6	203–245	221 (9)
IC	Old-Growth	38	76.1 (25.3)	119.0 (59.9)	188.9 (94.2)	213.3 (89.4)	—	—	—	9	262–340	287 (9)
LS	Old-Growth	25	—	166.6 (70.5)	219.3 (75.2)	311.7 (38.6)	—	—	—	7	317–342	334 (3)

[a] Streams: AL = Albert, TT = Thompson River Tributary, D4 = Dryman-4, JN = Jones, HN = Henson, D3 = Dryman-3, GL = Galloway, RD = Reed, HR = Harden, IC = Indian Camp, LS = Little Santeetlah.
[b] DBH class sampling intensity for aging was influenced by species composition and relative basal area per DBH class.
[c] Albert Branch's entire 44 ha watershed was clearcut in 1963 for watershed study at Coweeta Hydrologic Laboratory.

Table 3. Regression coefficients (slope estimates) per degree of regression for the diameter distribution of riparian zone trees in 12 study stands.

Stream	β	$\bar{x}^2$	$\bar{x}^3$	$\bar{x}^4$	R^2	Curve
Albert	−0.270	0.0070	−7e−05[a]	—	0.94	Inverse J
Thompson River Tributary	−0.310	0.0100	−0.0001	—	0.93	Inverse J
Dicks	−0.140	0.0020	—	—	0.90	Inverse J
Dryman-4	−0.070	0.0008	—	—	0.86	Inverse J
Jones	−0.110	0.0020	—	—	0.96	Inverse J
Henson	−0.100	0.0010	—	—	0.94	Inverse J
Dryman-3	−0.104	0.0010	—	—	0.94	Inverse J
Galloway	−0.072	0.0008	—	—	0.94	Inverse J
Reed	−0.179	0.0050	−5e−06	—	0.94	Rotated Sigmoid
Harden	−0.390	0.0220	−0.0006	5e−07	0.81	Rotated Sigmoid
Indian Camp	−0.169	0.0050	−4e−06	—	0.90	Rotated Sigmoid
Little Santeetlah	−0.359	0.0250	−0.0007	7e−07	0.76	Rotated Sigmoid

[a] $-7e-05 = -7 \times 10^{-5}$.

was used to initially identify riparian zone groupings. A LSD test placed the seven youngest stands in the same early- and mid-successional groups as diameter-distribution modelling techniques (see below). Of the five oldest stands, only Reed and Harden Creeks were placed in the same group. Galloway, Indian Camp, and Little Santeetlah Creeks were solitary.

Grouping of older, uneven-aged stands into seral stages was accomplished through analysis of diameter frequency distributions (Goff and West 1975). Mature/late-successional stands marked a transition from inverse-J curves to rotated sigmoid curves to describe diameter distribution (Table 3). The diameter distribution of Galloway Creek was a quadratic, Reed Creek was

Table 4. Summary statistics for overstory and midstory vegetation for twelve riparian stands in the Southern Appalachians.

			Overstory and midstory					Understory		
						Canopy Height				
Stream	Age (yr)	Seral stage	Mean ± 1 SE DBH (cm)	Stems/ha	Basal area (m^2/ha)	N	Mean ± 1 SE (m)	Mean ± 1 SE diameter (cm)	Stems/ha	Basal area (m^2/ha)
Albert	28	Early	19.5 (6.6)	892	29.7	6	19.7 (2.7)	2.8 (1.9)	5542	4.9
Thompson River Tributary	40	Early	17.5 (9.3)	729	22.6	10	17.6 (2.5)	3.3 (2.3)	11,636	14.8
Dicks	57	Mid	19.5 (7.8)	825	28.5	18	22.8 (4.2)	3.7 (2.1)	6009	8.5
Dryman-4	65	Mid	28.4 (14.8)	378	30.4	11	26.8 (4.5)	2.0 (2.0)	6645	4.2
Jones	67	Mid	23.8 (12.8)	741	42.5	13	26.2 (5.9)	1.9 (1.8)	8782	4.8
Henson	69	Mid	25.9 (13.3)	534	35.5	7	32.0 (3.2)	1.8 (1.8)	8214	4.2
Dryman-3	70	Mid	24.5 (11.7)	492	28.4	11	29.0 (4.9)	2.5 (2.3)	6178	5.4
Galloway	180	Late	27.7 (18.1)	474	40.7	12	33.4 (3.1)	2.3 (2.2)	9232	7.3
Reed	203	Late	21.5 (14.6)	620	32.8	7	35.1 (4.8)	2.7 (2.9)	6511	8.2
Harden	221	Late	24.4 (20.3)	516	40.8	10	35.9 (5.8)	1.5 (1.9)	13,057	5.9
Indian Camp	287	Old-Growth	22.5 (16.6)	546	33.1	17	33.5 (5.7)	2.0 (2.1)	9600	6.4
Little Santeetlah	334	Old-Growth	33.3 (25.1)	339	45.9	14	38.2 (4.2)	2.5 (1.9)	7863	6.1

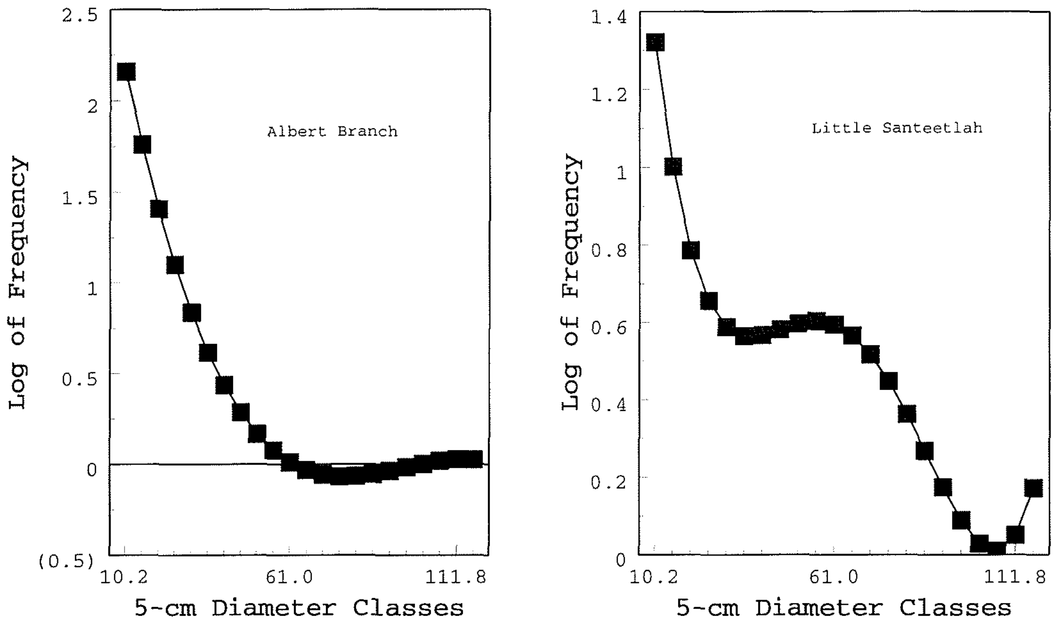

Fig. 1. Typical inverse J-shaped diameter distribution of an even-aged early-successional mixed species stand (Albert Branch) and the rotated sigmoid pattern of an uneven-aged old-growth stand (Little Santeetlah Creek).

a weak cubic or rotated sigmoid, and Harden Creek was a quartic or rotated sigmoid. Old-growth stands on Indian Camp Creek and Little Santeetlah Creek were best described by cubic rotated sigmoid and quartic rotated sigmoid functions, respectively.

Classification of riparian stands into seral stages was also verified via DFA. DFA placed the twelve stands in the same seral stages (100% classification into class) identified by the regression analysis of diameter-distributions. DFA also confirmed the early- and mid-successional groupings identified by the LSD test.

STAND STRUCTURE. In this paper, structure is defined as the variation in species and age classes, the arrangement of species into different canopy layers, and the distribution of individuals among diameter classes (Smith 1986). No attempt was made to quantify snags and large woody debris in the riparian zone, although a major objective of another part of the study was to quantify and describe in-stream large woody debris loading (Hedman 1992).

Broken, heterogeneous overstories created various sized canopy gaps in late-successional and old-growth stands which were typically occupied by various sized and aged trees interspersed among superdominants and dominants. Even though superdominants and dominants have attained impressive dimensions within these old stands, the high frequency of smaller sized trees colonizing gaps effectively diluted mean basal area and DBH across seral stages (Table 4). A transition from even-aged to uneven-aged structure was found along the time-line of stands under study. Field observations, stand histories (Douglass and Hoover 1988), and corings of early-successional stands (28–40 yr) and mid-successional stands (57–70 yr) indicated that they were even-aged. Diameter distributions of 28–70 yr stands were inverse J-shaped (Table 3, Fig. 1). Even-aged mixed-species stands commonly display varying degrees of J-shaped diameter distributions that would otherwise indicate a true balanced, uneven-aged structure if comprised of a single species (Smith 1986). None of the stands under study, including those in the 28–70 age-group, were single-species and therefore the inverse J-shaped curves were not anomalous.

Stands 180–334 yr were uneven-aged as evidenced by stand structural and compositional features, as well as tree corings. In addition, the rotated sigmoid pattern of diameter distributions for the 180–334 yr riparian forests (Table 3, Fig. 1) is indicative of uneven-aged stands (Goff and

Table 5. Importance value for overstory and midstory trees in riparian zones of study streams (AL = Albert, TT = Thompson River Tributary, DK = Dicks, D4 = Dryman-4, JN = Jones, HN = Henson, D3 = Dryman-3, GL = Galloway, RD = Reed, HR = Harden, IC = Indian Camp, and LS = Little Santeetlah).

	Increasing age of riparian stands →											
Species	AL	TT	DK	D4	JN	HN	D3	GL	RD	HR	IC	LS
Liriodendron tulipifera	36	21	17	18	21	46	30			13	6	5
Tsuga canadensis		2	4	1	22	2	11	36	7	40	24	54
Betula lenta	6	13	45	20	23	3	16	3		2	8	4
Pinus strobus		8						14	29		17	
Tilia heterophylla	9			22	5	10	12			1		
Quercus alba		8						7	18	14	9	
Rhododendron maximum									17	13	11	
Betula alleghaniensis	2		13	10	3	4						7
Acer rubrum		16			3			8	4	7		
Magnolia fraseri	2	15	6			6	1	2				3
Prunus serotina	31											
Acer saccharum			3		5		13		4	1	2	
Carya spp.					4			7	4	7	3	
Oxydendrum arboreum			1					4	9		6	
Quercus rubra		5	4			7		3				
Aesculus octandra				8	1	8	2					
Robinia pseudoacacia	11											
Quercus prinus					4			7				
Acer saccharinum				2							7	
Kalmia latifolia												8
Fagus grandifolia				2	2							2
Nyssa sylvatica								3	2			
Halesia carolina		2								1		
Cladrastis lutea	1											2
Fraxinus americana				2								
Total	98	90	93	85	93	86	85	94	94	99	93	86

West 1975; Jones et al. 1981). The rotated sigmoid distribution curve for diameters is related to the pattern of vertical structure and to the dynamics of regeneration and stand development in old-growth ecosystems. Within the initial steep slope position of the Little Santeetlah curve, diameters are relatively small (up to 30 cm) and density levels high, which indicates an understory of transgressive species with a high mortality rate. Once individual stems reach the overstory, they are likely to live a long time and their mortality rate is low. This period accounts for the plateau portion of the curve (30–70 cm). As trees mature to maximum age, mortality rates increase and the 70–100 cm part of the curve takes on a steep declining slope. The final upsurge is attributed to the extreme longevity of the relatively few superdominant tulip poplar and hemlock individuals.

OVERSTORY AND MIDSTORY VEGETATION. Riparian stands were representative of the mixed mesophytic deciduous forest or cove hardwood type, eastern hemlock forest, and transitions between these types (Whittaker 1956). Tulip poplar, black birch, white basswood (*Tilia heterophylla* Vent.), and black cherry (*Prunus serotina* Ehrh.) were important overstory species for early- (28–40 yr) and mid- (57–70 yr) seral stages, indicating that these riparian stands belonged to the mixed mesophytic/cove hardwood type (Table 5). Except for white basswood, which is shade tolerant, canopy dominants were intolerant pioneering species.

An abundance of shade-intolerant species in these early- to mid-successional stands is not surprising given the relatively short time elapsed since stand establishment, the narrow distribution of ages, gap dynamics in the Southern Appalachians (Barden 1981), and probable methods of stand regeneration. These stands occupied steep slopes (average bankslopes ranged from 19–58%) and previously contained American chestnut (*Castanea dentata* (Marshall) Borkh.), as evidenced by numerous stumps. Woods and Shanks (1959) found dense stands of tulip poplar and black birch on steep Appalachian slopes where large canopy gaps resulted from blight-induced chestnut mortality. Heavy cutting in the 1920s and 1930s would also have created medium to

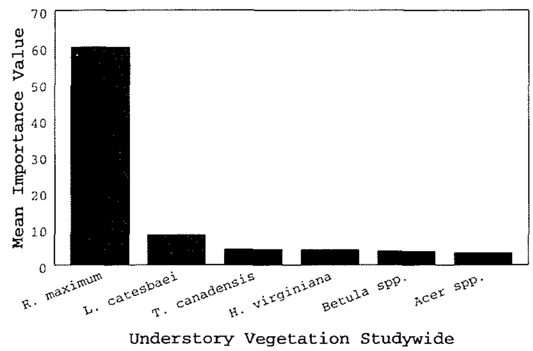

Fig. 2. Mean importance value for various understory species in riparian zones of study streams.

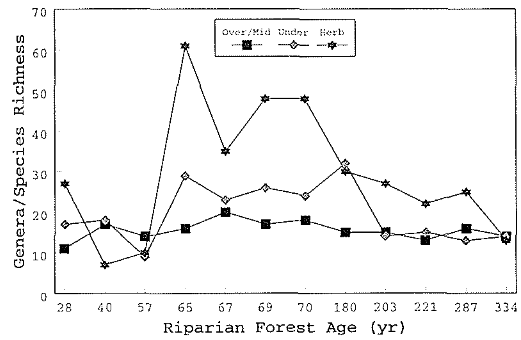

Fig. 3. Genera/species richness per canopy layer (overstory/midstory, understory, herbaceous layer) for 12 riparian study areas.

large sized gaps and encouraged the regeneration of dense stands dominated by shade-intolerant species.

Late-successional through old-growth riparian zones, i.e., stands where the oldest cohort ranged in age from 180 through 334 yr, had a greater presence of moderately tolerant (white pine and oaks) and tolerant species (hemlock) than did younger riparian stands. Galloway Creek, a 180-yr cove hardwood transition type, was dominated by hemlock (Importance Value = 36) and white pine (IV = 14), but also included oaks (IV = 17), hickories (*Carya* spp.: IV = 7), and red maple (*Acer rubrum* L.: IV = 8). Reed Creek (203 yr) was dominated by white pine (IV = 29) and white oak (*Quercus alba* L.: IV = 18), with major associates including hemlock and rhododendron (*Rhododendron maximum* L.). Rhododendron, normally an understory or midstory species, occasionally exceeded the diameter required for inclusion in the tree component (>10.2 cm) and reached heights of 8 m. The species composition of Reed Creek and its southwest aspect suggest it was the most xeric study site—it was considered a cove hardwood transition type. Harden Creek (221 yr) was a cove hardwood type dominated by hemlock (IV = 40), white oak (IV = 14), and tulip poplar (IV = 13).

The oldest stands, Indian Camp Creek and Little Santeetlah Creek, were 287 and 334 yr, respectively. Indian Camp Creek was comprised of hemlock (IV = 24), white pine (IV = 17), white oak (IV = 9), black birch (IV = 8), and silver maple (*Acer saccharinum* L.: IV = 7), among others, and was considered a cove hardwood type. Little Santeetlah Creek, located in the Joyce Kilmer Memorial Forest, was dominated by hemlock (IV = 54); yellow birch (*Betula alleghaniensis* Britton: IV = 7) and tulip poplar (IV = 5) were of minor importance. Oosting and Boudreau (1955) classified vegetation along the lower slopes and flats at Joyce Kilmer as hemlock forest with a midstory dominated by rhododendron. Lorimer (1980) sampled the same area of Little Santeetlah Creek reported in this study and classified riparian stands as either hemlock/rhododendron or hemlock/herb forest. Species composition of overstory trees in these two referenced studies was comparable to that found in the current study, indicating the hemlock forest type.

The high occurrence/presence of oak in some stands was curious but not surprising when considering stand dynamics of chestnut replacement. Chestnut was once a major member of the rich cove forests of the Southern Appalachians and the former oak-chestnut association (Braun 1950). Across the Southern Appalachians, oak accounted for 41% of chestnut replacements and subsequent stand compositions resembled cove hardwood transitional types (Woods and Shanks 1959). In strictly mesic cove sites, Woods and Shanks detected a developmental shift towards more mesophytic species that included hemlock, tulip poplar, Fraser magnolia (*Magnolia fraseri* Walter), Carolina silverbell (*Halesia carolina* L.), white basswood, and sugar maple (*Acer saccharum* Marsh.). Depending upon site conditions, oaks or other mesic tree species have benefitted by the demise of chestnut.

UNDERSTORY VEGETATION. Rhododendron usually formed a dense, shading canopy, generally 4–6 m high, which dominated other understory species (Fig. 2). It was a dominant or codominant understory species across all sites (Table 6). Understory importance value for rhododendron ranged from 29 to 90 with an average

Table 6. Importance value for most important species comprising understories in riparian zones of study streams (Al = Albert, TT = Thompson River Tributary, DK = Dicks, D4 = Dryman-4, JN = Jones, HN = Henson, D3 = Dryman-3, GL = Galloway, RD = Reed, HR = Harden, IC = Indian Camp, and LS = Little Santeetlah).

	Increasing age of riparian stands →											
Species	AL	TT	DK	D4	JN	HN	D3	GL	RD	HR	IC	LS
Rhododendron maximum	42	48	89	29	71	68	58	58	63	38	66	90
Leucothoe catesbaei		14						3	14	44	25	
Tsuga canadensis	2			6	7	1	7	16	5	5	2	1
Hamamelis virginiana	15	2		10	2	2	7	1		4	4	3
Acer saccharum	13			4	1		5				1	
Betula alleghaniensis	2		3	9	2	1	5					1
Betula lenta	11	4	3				3					1
Kalmia latifolia		10							9			
Halesia carolina	1	7				7		2		1		
Acer pennsylvanicum				6	2	6	1					
Aesculus octandra	1			4	1	6	2	1				
Tilia heterophylla	4			2	3	5				1		
Carpinus caroliniana				11								
Cornus florida					1		5	1		1		
Fagus grandifolia				6	1							
Magnolia fraseri	2	1	2						1			1
Liriodendron tulipifera	2								2			
Total	95	86	97	87	91	96	93	82	94	94	98	97

value of 60. At Harden Creek (221 yr), rhododendron was a close second (IV = 38) to dog-hobble (*Leucothoe catesbaei* (Walter) Gray: IV = 44) in importance. At Reed, Harden, and Indian Camp Creeks, rhododendron and dog-hobble had a combined importance value of 77, 82, and 91, respectively.

In Dryman Fork-4, rhododendron had an importance value of 29, the lowest of all study sites. Here the distribution of rhododendron was patchy, which allowed development of a diverse understory, including witch-hazel (*Hamamelis virginiana* L.: IV = 10), American beech (*Fagus grandifolia* Ehrh.: IV = 6), bluebeech (*Carpinus caroliniana* Walt.: IV = 11), wild hydrangea (*Hydrangea arborescens* L.: IV = 10), yellow birch (IV = 9), hemlock (IV = 6), and yellow buckeye (*Aesculus octandra* Marsh.: IV = 4).

Galloway Creek had the highest understory genera richness (31) of all sites. Rhododendron (IV = 58) and hemlock (IV = 16) were the most important species—virtually all other genera/species had importance values less than 2. The Galloway Creek watershed faced due south and its exposure/aspect contributed to a patchy distribution of rhododendron (a mesic species), which in turn favored a larger variety of species.

HERBACEOUS VEGETATION. The most important genera/species in this stratum were foamflower (*Tiarella cordifolia* L.), partridgeberry (*Mitchella repens* L.), windflower (*Thalictrum thalictroides* (L.) Boivin), violet (*Viola* spp.), wood anemone (*Anemone quinquefolia* L.), and galax (*Galax aphylla* L.). Genera/species richness (Fig. 3) and abundance (Table 7) were relatively low in many stands, especially where rhododendron dominated the understory (Table 6).

A general impression throughout reconnaissance and sampling, and later supported via regression analysis (Fig. 4), was that herbaceous and woody regeneration richness was closely linked with understory richness. Since rhododendron dominated most understories and even extended into the tree stratum in some stands (Reed, Harden, and Indian Camp Creeks), its presence appeared to influence richness of the herbaceous layer. This condition was exemplified at Little Santeetlah Creek where herbaceous richness was low (13 species), understory richness was low (12), and rhododendron midstory abundance (relative abundance = 92%), basal area (relative basal area = 89%), and importance value (IV = 90) were all high (Fig. 3). Whittaker (1956) reported that dense shading and the production of acidic leaf litter by rhododendron contribute to the inhibition of other midstory and understory species. Baker (1994) has recently verified the inverse relationship between rhododendron density and species richness in the Wine Spring Creek drainage in western North Carolina.

Table 7. Dominant herbaceous species based on percent frequency in riparian zones of study streams (AL = Albert, TT = Thompson River Tributary, DK = Dicks, D4 = Dryman-4, JN = Jones, HN = Henson, D3 = Dryman-3, GL = Galloway, RD = Reed, HR = Harden, IC = Indian Camp, and LS = Little Santeetlah).

	Increasing age of riparian stands →											
Species	AL	TT	DK	D4	JN	HN	D3	GL	RD	HR	IC	LS
Galax aphylla		69							22	12		
Mitchella repens								59				37
Thelypteris noveboracensis									23	9	35	
Tiarella cordifolia	29			14	10		14					
Vaccinium spp.		8							11	9	12	23
Anemone quinquefolia				30	8		24					
Smilax glauca		14	21									
Trillium spp.					8	10				14		
Thalictrum thalictroides					10	14						
Viola spp.	10										10	
Athyrium filix-femina			18									
Urtica gracilis	13											
Leucothoe catesbaei										13		
Viola emarginata					10							
Viola hastata					10							
Viola latiuscula						9						
Total	52	91	39	44	56	33	38	59	56	57	57	60

The increasing dominance of rhododendron may have far-reaching implications for the structure and composition of future riparian forests and their long-term functionality. Field observations indicated that recent canopy gaps resulting from tree falls were colonized by adjacent rhododendron at the exclusion of overstory regeneration. This trend was particularly prevalent at the three oldest sites (221–334 yr) where overstory regeneration was conspicuously absent. Many late-successional through old-growth riparian forests in the Southern Appalachians will experience significant structural and compositional changes over the next century if the dominance of rhododendron becomes fully expressed. This study identified some preliminary trends regarding the influence of rhododendron based upon field observations and analyses of limited data sets. Additional research specifically designed to more carefully explore the relationship of rhododendron to understory development is warranted.

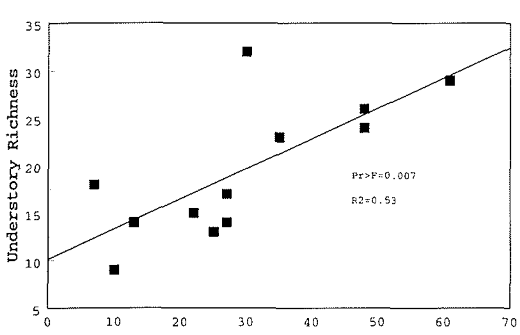

Fig. 4. Relationship of understory richness to herbaceous and woody regeneration layer richness.

Conclusions. Vegetative characterizations of Southern Appalachian riparian forests are essential to understanding ecotone dynamics. The composition of riparian forests in the Southern Appalachians concurred with the mixed mesophytic/cove hardwood type and its variants. The structure of riparian zone stands changed from even-aged to uneven-aged in progressing along the 300+ year timeline of the study. Stands in the early- and mid-seral stages were characteristically even-aged, while old-growth stands were uneven-aged. Diameter distributions of the former were typically inverse J-shaped (common for stands of mixed species), while those of the latter tended to be of a rotated sigmoid pattern.

Riparian forests underwent compositional changes over time related to shade tolerance and adaptability of species to disturbance. Early- and mid-successional riparian stands were primarily dominated by tulip poplar, birch, white basswood, and black cherry. Late-successional and old-growth stands were dominated by more shade-tolerant species including hemlock, white pine, and oak. Late-successional and old-growth riparian forests were characterized by the presence of a relatively small number of large diameter trees, a high frequency of small diameter gap-replacement species, and multi-aged canopy layers.

Rhododendron dominated understory canopy layers in most riparian stands and appears to adversely affect development and richness of herbaceous and understory strata. In some older stands, rhododendron limited advanced regeneration of overstory tree species and may ultimately influence future overstory structure and composition.

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