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Riparian vegetation in the southern Appalachian mountains (USA) following chestnut blight

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Abstract

American chestnut is often listed as an important component of mesic midslopes and xeric ridges in pre-blight southern Appalachian forests, but its former importance in riparian forests has generally been considered minor. To document its importance in riparian forests, 589 American chestnut stumps were located on four sites (two previously logged, two unlogged) in the Blue Ridge physiographic province of the southern Appalachians. Diameters and basal areas of chestnut were calculated and compared among sites and to basal area (BA) of live trees. Chestnut BA ranged between 8.4 and 12.4 m^2/ha (25 and 40% of current BA). Vegetative composition on 58 random plots suggests that three community types were represented on the four study sites: (1) old-growth forest with sparse rhododendron; (2) logged forest with sparse rhododendron; and (3) forest dominated by rhododendron which controlled vegetative composition regardless of logging status. Thickets of ericaceous shrubs that developed after the blight were significantly denser in logged forest than in old-growth. Only shade-tolerant herbs such as galax and partridge-berry, as well as a rare orchid, Appalachian twayblade, were found growing in rhododendron thickets. Results of our study suggest that the gap-phase hypothesis, where species diversity is maintained in cove forests of the southern Appalachians through gap-phase disturbance, should be modified to allow for dynamics influenced by rhododendron. The reintroduction of periodic fire into southern Appalachian riparian habitat may control rhododendron dominance and improve tree regeneration. © 2002 Elsevier Science B.V. All rights reserved.

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1. Introduction

Prior to the introduction of chestnut blight (*Cryphonectria parasitica* [Murrill] Barr.) from Asia in the early 20th century which killed an estimated four billion chestnut trees (Miller, 1987), American chestnut (*Castanea dentata* [Marsh.] Borkh.) was the most common canopy tree from the southern New England states to northern Georgia, Alabama and Mississippi (Russell, 1987). In the southern Appalachians it reached its greatest size and stand density (Ayres and Ashe, 1902). Chestnut probably represented roughly 40–45% of the canopy trees in southern Appalachian forests (Reed, 1905; Keever, 1953). It was considered the predominant tree of the Blue Ridge mountains (Ashe, 1919).

Habitat requirements of the species have been listed as deep, loose, moist, but well-drained soils that are not necessarily rich in nutrients (Society of American Foresters, 1926). Due to sensitivity to frost, glaze, and ice (Parker et al., 1993), chestnut was seldom found in bottoms of ravines and valleys, and wet or cold soils (Zon, 1904). It is most often listed as a dominant species on ridges (Abrams and Ruffner, 1995), and mid-slope

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areas (Reed, 1905). Although the tree was restricted to the piedmont and mountains in the southern part of its range (Russell, 1987), it reportedly grew throughout southern New England (Metcalf, 1914). While chestnut has been recognized as a member of cove forests (Lorimer, 1980), and is known to contribute large woody debris to streams (Hedman et al., 1996), it has never been quantitatively described in riparian forests.

Our review of the literature found at least 17 studies documenting changes in forest composition and structure since the demise of American chestnut. These studies have all focused on the replacement of chestnut by other tree species with findings split between evidence for succession to an oak-hickory forest or an oak association forest. Rarely have effects of chestnut demise on the shrub and herb syunusia been studied (Keever, 1953).

Chestnut was an important species in any area in which it grew due to its prolific sprouting ability from the root crown (Schwarz, 1907), rapid growth rate (Graves, 1905), overall growth in height, longevity (Zon, 1904), great resistance to rot (Scheffer and Cowling, 1966), tolerance to shade when young (Paillet, 1982), ability to grow on poor soil, and mast production (Zon, 1904). The role of this tree as an ecological dominant and effects of the eventual loss of decaying chestnut wood in riparian ecosystems are unknown.

2. Objectives

The purpose of this study was to (1) identify whether American chestnut was an important riparian tree species in pre-blight southern Appalachian forests; (2) document the current vegetative composition of southern Appalachian riparian forests; and (3) determine the importance of changes in rhododendron stem densities on former chestnut-associated forests.

3. Methods

3.1. Study sites

Four riparian forest sites containing chestnut were identified in the Blue Ridge physiographic province of the southern Appalachians based on presence of chestnut stumps and/or coarse woody debris within 30 m of a perennial stream. Site 1 was located on Slatten branch in Sumter National Forest in northwest Oconee county, SC. Slatten branch is a first order perennial stream originating on the south flank of Ellicott mountain. The stream flows primarily west to east, with a protecting ridge ca. 40 m above the streambed. Thomas creek, a first order perennial stream on the west side of Rabun Bald in Chattahoochee National Forest in Rabun county, GA, flows through site 2. This stream flows primarily east to west and the protecting ridge on the south side of the stream is ca. 170 m above the streambed. The third site is located along the headwaters of the Tallulah river in Macon county, NC and flows off the south side of standing Indian mountain in Nantahala National Forest. This is a second order creek for most of the sampled length and flows primarily north to south. The protecting east and west ridges are approximately 470 and 400 m above the streambed, respectively. Big Scaly mountain, a peak to the south of the site is almost 1700 m high and provides protection for much of the day. Site 4 is on Little Santeetlah creek in Joyce Kilmer/Slickrock wilderness in Graham county, NC. Little Santeetlah creek flows in a southeast direction with a protecting southern ridge of ca. 1360 m elevation, about 500 m above the stream bed.

Two of the sites (Thomas creek and Tallulah river) were mature second-growth hardwood stands, but showed signs of chestnut salvage logging and general logging in the past. The other two sites (Slatten branch and Little Santeetlah creek) are considered remnant old-growth forests. Old-growth riparian forests are rare in the southern Appalachians, because these sites were preferentially cleared for agriculture by European settlers (Ayres and Ashe, 1902).

In this study, riparian forest was considered to be an area extending 30.5 m on either side of a perennial stream. As chestnut was capable of reaching heights of 36 m in southern Appalachian coves (Buttrick, 1925), trees within 30.5 m of a perennial stream could have impacted the hydric ecosystem. Sites ranged in length from 363 to 780 m and in area from 3.19 to 4.18 ha.

3.2. American chestnut sampling

Each American chestnut stump was numbered, measured for diameter at ground line (DGL) and, if possible, diameter breast height (DBH). No debris was included in the survey unless it could be identified as American chestnut by its ring-porous growth pattern and lack of visible rays (Panshin and Zeeuw, 1980). Riparian forests in the southern Appalachians often have dense ericaceous, evergreen vegetation and it is likely that not all chestnut debris was found. For this reason we consider our estimates of chestnut abundance on these sites to be conservative.

3.3. Vegetative composition of riparian forest

Composition of the current riparian forest was determined by randomly selecting ~10% (a total of 58 of 589) of the numbered chestnut stumps at each of the four sites in this study. Herbaceous vegetation was sampled by counting the stems of each species in five randomly selected 1 m^2 quadrats within a 49 m^2 sampling area around each randomly selected stump. Trees and seedlings were tallied on 0.04 ha plots and saplings on 0.025 ha plots using the Braun–Blanquet cover class method. Plots were arranged with the chestnut stump in the center of the sampling areas. Distance from the stump to each living chestnut sprout within the 0.04 ha plot was noted. Chestnut sprouts growing within 0.3 m of the decaying stump were considered to have originated from that stump.

Abundances (the number of individual stems in a plot) were tallied for all woody plants and for herbaceous vegetation (anything not a tree or shrub). Species abundance and frequency (the proportion of plots containing a species) were used to compare the composition of old-growth to logged forests. Importance values (IV) were calculated for all vegetation on a 100-point scale using the formula

$$IV = \frac{1}{2}(RD + RF)$$

where RD is the relative density and RF the relative frequency. Plots with dense (IV $>$ 50) rhododendron (*Rhododendron maximum* L.) cover were compared to those with sparse (IV $<$ 50) cover. Abundance of advance regeneration was correlated to percent rhododendron coverage. Plots were grouped into vegetative clusters using Detrended correspondence analysis (DCA) and two-way indicator species analysis (TWINSPAN) (Hill, 1979). Nomenclature for trees follows Duncan and Duncan (1988) and for herbs and shrubs follows Radford et al. (1968).

3.4. Rhododendron maximum and ericacous shrub cover

Abundance of rhododendron and mountain-laurel (*Kalmia latifolia* L.), another evergreen ericad, was tallied in each 0.04 ha plot. Because plot location was determined by the presence of a chestnut stump, open forest and dense rhododendron were often encompassed within the area of a plot. To account for this, percent of the plot covered by rhododendron was also recorded. Percent rhododendron coverage was used to determine effects of its presence on tree regeneration and herbaceous abundance. To determine the effect of logging on rhododendron density, combined mean stem densities of logged versus old-growth sites were compared.

3.5. Statistics

Of the 589 chestnut stumps identified, 207 were intact enough to obtain accurate DBH data. A regression model (PROC REG) was used in SAS (SAS Institute Inc., 1987) to estimate DBH values for the remaining chestnut stumps. DBH and basal area (BA) of chestnut stumps and of all other species of live stems were compared among sites using PROC GLM and analysis of variance (ANOVA). Orthogonal contrasts were used to determine differences based on logging activity. Vegetative composition clusters were generated by using IV for all species and analyzing them using DCA and TWINSPAN. Plant species abundances were used to further analyze differences in vegetative composition between logged and old-growth forest and between areas of dense and sparse rhododendron coverage.

4. Results

4.1. American chestnut as a component of pre-blight riparian forests

A total linear distance of 3.1 km representing 16.4 ha of southern Appalachian riparian forest was surveyed. The regression model used to estimate DBH for chestnut stumps that were unmeasurable had an R^2 of 0.95.

Chestnuts on old-growth sites tended to have larger diameters and greater BAs than did conspecifics on

Table 1
Mean DBH and BA for chestnut (based on reconstructed DBH data) and all other species of live trees on four southern Appalachian riparian forest sites

Site	Chestnut stems (reconstructed)			All other live trees		
	DBH (cm)	BA per tree (cm^2)	BA per ha (m^2)	DBH (cm)	BA per tree (cm)	BA per ha (m^2)
Old-growth						
Slatten branch	56.2 a[a]	2918.6 a	8.9 a	26.2 a	686.1 a	22.7 a
Little Santeetlah	73.7 c	4843.8 c	12.3 c	28.6 a	902.4 a	37.5 a
Logged						
Thomas creek	43.9 b	1717.7 b	8.4+ b	26.9 a	693.2 a	28.8 a
Tallulah river	53.6 a	2555.0 a	10.0 a	27.6 a	748.7 a	32.9 a

[a] Means followed by the same letter within a column are not significantly different at the 0.01 level.

logged sites (Table 1). Only at Little Santeetlah creek, an old-growth site, was chestnut DBH and BA significantly larger than chestnuts on logged sites. Orthogonal contrasts showed combined chestnut mean DBH and BA on the two old-growth sites were significantly larger than the combined mean DBH and BA of the two logged sites ($P = 0.0001$). DBH and BA of extant trees did not differ significantly among sites. Mean chestnut DBH tended to be larger than that of all extant trees on every site except Tallulah river, where it was smaller than that of white oak (*Quercus alba* L.) (Table 2). However, because of wide variation in tree diameters within species, differences among species were often not significant. On all sites chestnut DBH and BA was among the largest of all species measured.

Seedling-sized sprouts of American chestnut are still abundant in our study sites (259 were found on 17 of the 58 plots), but no sapling-sized sprouts were tallied. Chestnut sprouts were never seen growing in dense rhododendron thickets. Few of the live chestnut sprouts found in this study (<20%) grew in close proximity (within 0.3 m) of the root crowns of large, old, decaying stumps. Only 44 of 589 (~7.5%) chestnut stumps had sprouts associated with the root crown of the decaying stump.

4.2. Vegetative communities associated with logged versus unlogged sites

DCA and TWINSPAN grouped plots into four clusters, influenced by two gradients (Fig. 1). Axis 1 is a gradient from high to low rhododendron coverage with a standard deviation of 3.4. Axis 2 organized plots by logging status, i.e. old-growth or logged, with a standard deviation of 1.9. The largest group, cluster

Table 2
Mean diameter of American chestnut stems (reconstructed) and selected other co-occurring canopy tree species on four southern Appalachian riparian forest sites

Species	Mean DBH (cm)			
	Old-growth		Logged	
	Slatten branch	Little Santeetlah	Thomas creek	Tallulah river
Castanea dentata	56.2 a[a] (2.12)	73.7 a (2.42)	43.9 a (1.03)	53.6 a (1.25)
Liriodendron tulipifera	32.3 a (20.73)	62.8 ab (9.71)	28.48 bc (1.63)	26.9 b (2.35)
Quercus alba	29.6 a (4.89)	47.0 abc (7.42)	30.4 bc (3.17)	55.0 a (9.97)
Quercus prinus	27.3 a (5.35)	29.9 c (7.12)	35.0 ab (2.73)	36.0 ab (2.67)
Quercus rubra	37.8 a (7.33)	35.1 bc (7.75)	32.0 bc (3.17)	40.6 ab (5.46)
Tsuga canadensis	22.4 a (5.35)	24.8 c (5.14)	23.5 c (1.96)	25.5 b (2.49)

[a] Means followed by the same letter in a column are not significantly different at the 0.01 level. Standard errors in parentheses.

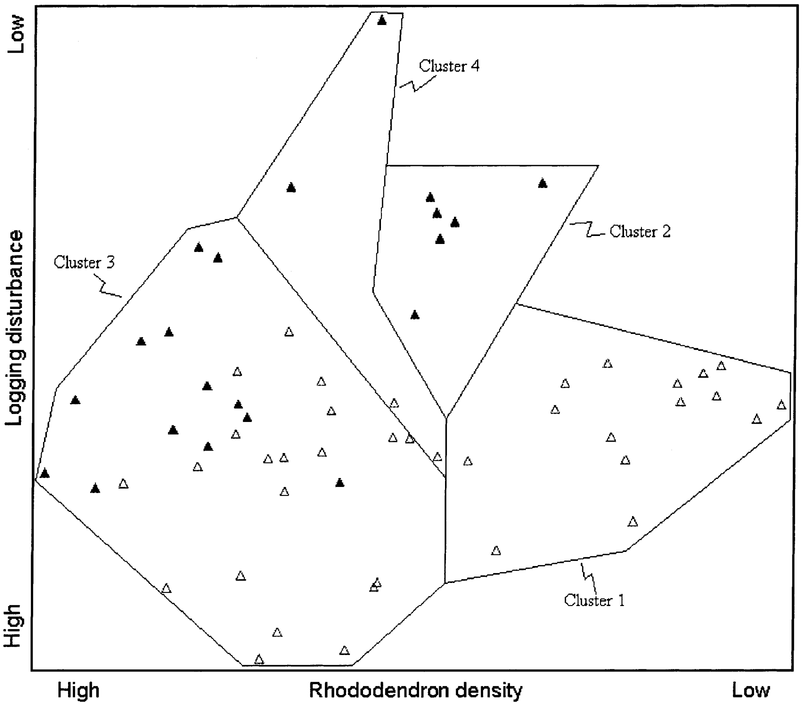

Fig. 1. DCA based on vegetative IV for 58 southern Appalachian riparian forest plots. Data points with dark triangles represent plots in old-growth forest, points without fill represent plots in logged forest. Points in clusters 1 and 2 are plots containing sparse or no rhododendron, points in clusters 3 and 4 are plots with dense rhododendron.

3, contains plots from both logged and old-growth sites whose common factor was dense rhododendron cover. Plots with sparse rhododendron cover appear in clusters 1 and 2 on the right side of the figure. Cluster 1 contains plots from logged sites Thomas creek and Tallulah river only, while cluster 2 contains plots from old-growth sites Slatten branch and Little Santeetlah creek only. The fourth cluster contains a mixture of plots with both sparse and dense rhododendron cover and from both logged and old-growth sites. This cluster is an artifact of the sampling design. It represents plots with moderate rhododendron coverage and relatively high abundance of all other species.

Only a few plant species were clearly associated with logging activity or lack thereof. Yellow birch (*Betula alleghenisis* Britton) and a species of gentian (*Gentiana decora* Pollard) were found only on old-growth sites. The life stage of a plant sometimes determined whether it would be found in old-growth or logged forest. For example, yellow-poplar (*Liriodendron tulipifera* L.) seedlings were found almost exclusively on plots of logged forest sites (41% of plots versus 0.05% in old-growth).

Current overstory composition on the old-growth sites in this study indicates forest succession following chestnut blight resulted in an oak association forest with a component of mesophytes such as eastern hemlock (*Tsuga canadensis* [L.] Carr.) and black birch (*Betula lenta* L.). On the logged sites current canopy composition is dominated by cove mesophytic species such as black birch, eastern hemlock, yellow-poplar, and red maple (*Acer rubrum* L.) (Table 3).

4.3. Rhododendron

Rhododendron was ubiquitous on the four sites analyzed in this study, occurring on 81–90% of plots at each site. From 46 to 74% of sampled plots at each site had rhododendron IV > 50. Mountain-laurel was found on only two sites, Slatten branch and Thomas

Table 3
Frequency values (percent of plots in which the species occurred) for selected tree species found in old-growth and logged forest on four southern Appalachian riparian forest sites

Species	All plots	Old-growth	Logged
Castanea dentata (sprouts)	29.3	14.3	37.8
Acer rubrum	60.3	47.6	67.6
Betula lenta	67.2	71.4	64.9
Liriodendron tulipifera	63.8	33.3	81.1
Quercus alba	50.0	66.7	40.5
Quercus prinus	58.6	57.1	59.7
Quercus rubra	51.4	52.4	48.3
Tsuga canadensis	77.6	71.4	81.1

creek, and was never as important, in terms of its density, as rhododendron. Rhododendron stem densities ranged from 726 to 1524 per ha. Tallulah river had significantly greater stem density than Little Santeetlah creek ($P = 0.0001$). Neither of these sites differed significantly from Slatten branch or Thomas creek. The two logged sites had significantly denser thickets ($P = 0.0094$) than the two old-growth sites.

Almost all herb species were more abundant where rhododendron density was sparse. Herbaceous abundance in open forest (rhododendron IV < 50) was significantly greater ($P = 0.0001$) than in plots with rhododendron IV > 50. Herb species richness was higher in logged forest than in old-growth, although this difference was not significant ($P = 0.0782$). Beggar's lice (*Desmodium nudiflorum* [L.] DC.) was the most frequent herb species, and occurred in 36.2% of all plots, but only in open forest. A few species, such as shade-tolerant galax (*Galax aphylla* L.) and partridge-berry (*Mitchella repens* L.) were found in abundance in rhododendron thickets. One rare orchid, Appalachian twayblade (*Listera smallii* Weigand), is apparently obligated to grow in rhododendron thickets (Radford et al., 1968) and was found exclusively in such habitat.

Rhododendron negatively impacted the abundance of advance regeneration. Tree regeneration decreased exponentially as ericaceous coverage increased, resulting in a regression with an R^2 of 0.68. (Fig. 2). The only tree species for which frequency seemed unaffected by dense rhododendron was eastern hemlock, which dominated advance regeneration in plots with high rhododendron cover. In plots with 100% rhododendron cover, eastern hemlock represented 43% of the advance regeneration.

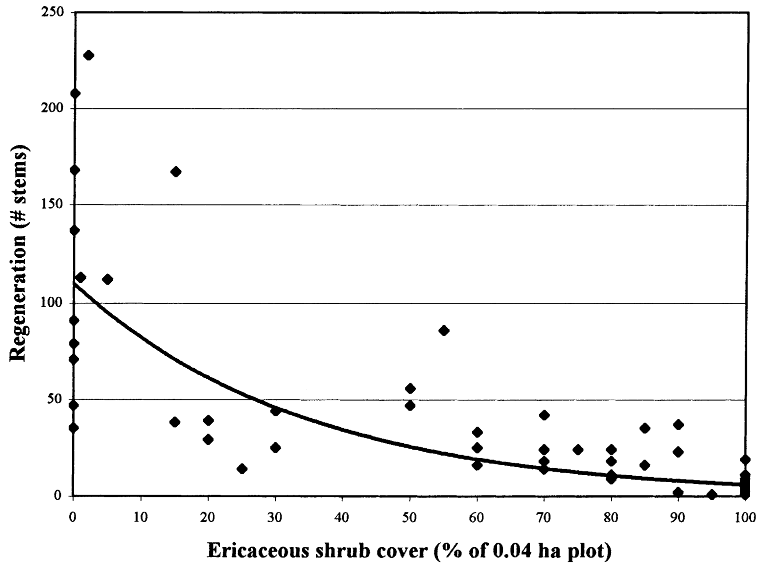

Fig. 2. Effects of ericaceous shrub cover (predominantly *R. maximum*) on abundance (number of seedlings and saplings) of advance regeneration, based on data from 58 southern Appalachian riparian forest plots.

5. Discussion

5.1. Evidence of American chestnut in riparian forests of southern Appalachia

The density, abundance, and BA of American chestnut clearly show the species was a dominant tree in southern Appalachian riparian forests. Chestnut had greater abundance, a generally larger mean DBH (with the exception of the relatively large DBH of the three white oaks on Tallulah river) and a greater contribution to BA than other tree species on every site in this study. Reconstructed chestnut BA suggests that the species represented 25–40% of BA in pre-blight stands if current conditions are similar. These findings agree with those of Gravatt and Gill (1930), who estimated that chestnut was 25% of the total southern Appalachian stand, and of Nelson (1955), who found that chestnut represented 41% of BA on Coweeta watershed 41. Results of this study suggest that chestnut was much more common in riparian forests than earlier recognized and support results of Hedman et al. (1996), who found that chestnut was an important contributor to large woody debris loadings in southern Appalachian streams.

American chestnut sprouts represented over 10% of seedling-size trees tallied. The spatial dispersion of the species across the landscape might not be as continuous as it once was. Most chestnut sprouts found in this study were located on the south side of Thomas creek. Chestnut sprouts were more common on logged sites than on old-growth sites and their abundance was greatest in open forest. Despite their apparent ability to efficiently store carbohydrates (Paillet, 1984), no chestnut sprouts were recorded in rhododendron thickets, suggesting the sprouts are at a competitive disadvantage there. Our results parallel those of Paillet (1988) who found that chestnut sprouts were not numerous in old-growth stands and that sprout distributions were clustered. Most chestnut sprouts were found >0.3 m from old chestnut stumps, supporting suggestions of Keever (1953) and Paillet (1988) that most current chestnut sprouts arise not from root crowns of former large canopy trees, but from root crowns of chestnuts that were suppressed trees at the time of the blight.

5.2. Composition of the post-chestnut blight riparian forest

Current composition of canopy trees on the four riparian sites indicates succession following chestnut blight on the two old-growth sites proceeded to an oak association forest type dominated by white, chestnut (*Quercus prinus* L.) and northern red (*Quercus rubra* L.) oaks with a strong component of black birch and eastern hemlock. This pathway was recognized by Woods and Shanks (1959), who noted the replacement of chestnut on mesic sites by eastern hemlock and suggested the blight may have promoted a greater abundance of mesophytes than in pre-blight forests. In contrast, logging appears to have reduced the importance of oak in post-blight riparian forests, at least temporarily. The successional pathway on these sites has proceeded towards a cove forest type dominated by the mesophytes yellow-poplar, eastern hemlock, red maple, and black birch.

The successional pathway taken by a forest after chestnut blight may be determined by the level of disturbance and the propensity of rhododendron to recolonize or spread into disturbed areas. Multivariate analysis using DCA and TWINSPAN suggested rhododendron cover impacted the vegetative communities on the four sites more than did logging disturbance. Rhododendron overwhelmed the effect of logging disturbance as evidenced by the combining of old-growth and logged forest plots into the same diagnostic cluster when its cover was high. Open forest old-growth sites differed from logged sites primarily in their reduced herbaceous abundance and the different composition of canopy trees. Where rhododendron was dense, old-growth and logged forest differed only in their canopy composition.

Composition of the old-growth forests in this study with sparse rhododendron cover suggests they are controlled by gap-phase dynamics. Small gaps, those that affect 0.5–2.0% of the landscape annually, are thought by some to be the primary disturbance in southern Appalachian cove forests (Runkle, 1982). Presence of trees such as yellow-poplar in old-growth forests in this study is often attributed to their regeneration in single-tree gaps (Clebsch and Busing, 1989) such as occurred with the decline of chestnut.

5.3. Effect of rhododendron on southern Appalachian riparian forests

Demise of overstory chestnut trees has been implicated in the spread of rhododendron thickets in the southern Appalachians (Clinton et al., 1994). Results of this study implicate logging disturbance as another important factor, concurring with the suggestion of McGee and Smith (1967). Rhododendron is ubiquitous in southern Appalachian riparian forests and, as a long-lived, dense shrub, exhibits a controlling influence over co-occurring vegetation. Rhododendron stem densities can be as high as 17,000 per ha, but even at low densities this shrub adversely affects tree regeneration (Baker and Van Lear, 1998).

Composition of post chestnut-blight forests has been attributed to three processes: (1) expansion of dominant and codominant trees; (2) growth of advance regeneration; and (3) seedling growth (Woods and Shanks, 1959). Results of this study indicate that rhododendron may have significantly affected the latter two processes. Regardless of whether a forest was subjected to small canopy gaps from the death of chestnut or was more severely impacted by salvage logging, the presence of rhododendron controlled tree regeneration. Rhododendron adversely affects vegetative richness and abundance in the southern Appalachians by limiting gap-phase regeneration.

Current canopy composition of rhododendron-affected plots in this study is fairly diverse, but advance regeneration is not. On plots with rhododendron IV > 50, eastern hemlock was by far the most important regenerating species (Table 4). As Baker and Van Lear (1998) noted, much of the regenerative element in rhododendron thickets is unlikely to attain overstory status. On sites in this study, only eastern hemlock demonstrated that ability. If current conditions persist, forests growing in dense rhododendron may converge to a cove mesophytic type dominated by eastern hemlock.

Most herbaceous species in this study were found in open deciduous forest, and are apparently unable to persist in low-light environments such as in rhododendron thickets. Baker and Van Lear (1998) noted a marked decline in herbaceous species richness as the density of rhododendron thickets increased. Herb species abundance on the 58 plots in this study also declined with increasing rhododendron coverage. Some of the herbs found in rhododendron thickets, e.g. galax and Appalachian twayblade, demonstrated a high degree of fidelity to rhododendron, possibly because they are more competitive in a low light, acidic environment. Baker and Van Lear (1998) found Appalachian twayblade frequently in rhododendron thickets.

Logging disturbance had a long-lasting effect on rhododendron stem densities and apparently contributed to thicket advancement. The high stem densities of rhododendron thickets and their control over the herbaceous layer and tree regeneration suggest rhododendron may have replaced American chestnut as the ecological dominant on sites in this study. Day and Monk (1974) found that rhododendron and mountain-laurel represented over 58% of all stems > 2.5 cm DBH on their sites at Coweeta Hydrologic Laboratory. During the present study, we noted that several canopy

Table 4
Frequency values (percent of plots in which the species occurred) for selected tree species by life stage (trees, saplings, and seedlings) based on *R. maximum* IV

Species	*R. maximum* IV > 50			*R. maximum* IV < 50		
	Tree	Sapling	Seedling	Tree	Sapling	Seedling
Castanea dentata (sprouts)	0.0	0.0	12.5	0.0	0.0	66.7
Acer rubrum	70.0	32.5	10.0	38.9	27.8	44.4
Betula lenta	70.0	35.0	2.5	61.1	22.2	38.9
Liriodendron tulipifera	60.0	20.0	10.0	72.2	38.9	55.6
Quercus alba	47.5	10.0	2.5	55.6	16.7	33.3
Quercus prinus	75.0	10.0	7.5	22.2	5.5	33.3
Quercus rubra	37.5	17.5	22.5	72.2	5.5	72.2
Tsuga canadensis	75.0	62.5	67.5	83.3	33.3	50.0

gaps apparently caused by the death of chestnut had not yet been filled by canopy tree species, apparently because rhododendron dominance has prevented development of competitive seedlings and sprouts. We suggest that the prevailing hypothesis (Barden, 1981; Runkle, 1982) that species richness is maintained in cove forests of the southern Appalachians through gap-phase disturbance should be modified to account for the influence of rhododendron.

Succession in rhododendron thickets appears to fit into the inhibition pathway model proposed by Connell and Slatyer (1977). In this model, plants modify their environment so that recruitment of other species is inhibited as long as current vegetation remains intact. Rhododendron apparently will continue to dominate plant succession until a disturbance event, e.g., fire, suppresses it, at least temporarily, as a controlling influence. An intermediate disturbance regime (Loucks, 1970), e.g., the introduction of fire, may enhance species diversity in riparian forests (Naiman et al., 1993). In other southern Appalachian habitats, fire is being used to temporarily control ericaceous shrub cover and promote tree regeneration (Elliott et al., 1999). Many of the chestnuts in this survey showed signs of past fires (charcoal and fire-caused cat-faces). Native American use of fire has been implicated in the increased abundance and maintenance of chestnut in the southern Appalachians (Delcourt and Delcourt, 1998).

6. Conclusions

American chestnut was an important component of southern Appalachian riparian forests. Chestnut sprouts continue to be one of the most abundant seedling-sized tree species, but occur in riparian forests only in areas unaffected by ericaceous shrubs. Chestnut sprouts are more abundant in logged areas where the canopy has been removed in the recent past.

Following chestnut blight, forest succession on old-growth riparian sites proceeded to an oak association forest type, while on logged sites current forest composition is dominated by cove mesophytic species. Composition of advance regeneration in rhododendron-affected areas indicates the composition of the current forest may not be duplicated as extant canopy trees die. Without an intermediate disturbance regime, such as periodic fire, or the restoration of an ecologically dominant species, such as American chestnut, to limit rhododendron dominance, regeneration in rhododendron thickets may proceed to a climax vegetative type dominated by an ericaceous shrub or an extremely shade-tolerant tree species, i.e. eastern hemlock.

Logging apparently accelerated growth of rhododendron thickets. Rhododendron abundance prior to logging, presence of bare mineral soil for rhododendron germination, and presence of nurse logs for layering may all influence the propensity of rhododendron to regenerate and expand after logging. Potential for rhododendron response to logging disturbance and its subsequent effect on vegetative community composition should be taken into account when forming management plans for southern Appalachian riparian forests.

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