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# Relations between density of rhododendron thickets and diversity of riparian forests

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**Abstract**

Rosebay rhododendron (*Rhododendron maximum* L.) is increasing its range and abundance in understories of southern Appalachian forests, reducing species richness, and altering patterns of succession. This study characterized the density and biomass attributes of *R. maximum* thickets and examined their effects on plant species richness, percent cover, and regeneration patterns within a southern Appalachian riparian ecosystem. *R. maximum* reached densities exceeding 17,000 stems $ha^{-1}$ with biomass reaching 34 Mg $ha^{-1}$. Species richness and percent cover in the regeneration layer were inversely related to *R. maximum* thicket density in both Spring and Fall samplings. On average, 6 plant species were found on plots with high *R. maximum* stem density as compared to 26 species found on plots with lower stem density. The regeneration layer was dominated by *R. maximum* with only low numbers of tree species present. Both woody and herbaceous species regenerated poorly under the dense canopy of these thickets. Based on the age of cut stems, *R. maximum* became increasingly dominant in the understory of Wine Spring Creek over the last three decades. Its proliferation is altering the richness of riparian forests and changing historical patterns of community succession. © 1998 Elsevier Science B.V.

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## 1. Introduction

Rosebay rhododendron (*Rhododendron maximum* L.) has long been an understory component of southern Appalachian riparian zones. However, the frequency of this species along stream banks and in adjacent uplands has steadily increased throughout this century due to changes in forest composition and structure (Monk et al., 1985; Phillips and Murdy, 1985; McGinty, 1972). A dominant component of the overstory canopy of southern Appalachian forests was lost through the death of American chestnut (*Castanea dentata* L.) trees (Smith, 1995). Several authors suggest that canopy openings resulting from this disturbance permitted *R. maximum* thicket establishment (Clinton et al., 1994; Woods and Shanks, 1959) and one study concluded that no overstory tree recruitment occurred since that time (McGee and Smith, 1967). It has also been suggested that abandonment of agricultural land, high-grading, and exclusion of fire from southern Appalachian forests all contributed to the increasing abundance of *R. maximum* (Horsley, 1988;

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Phillips and Murdy, 1985; McGee and Smith, 1967). The ecological consequences of this increasing abundance are unclear.

The literature documents similar dominance by other understory species in other regions. Salmonberry (*Rubus spectabilis* Pursh), salal (*Gaultheria shallon* Pursh), and Kalmia (*Kalmia* sp.) have all been implicated in preventing successful establishment and regeneration of a variety of tree species (Ducey et al., 1996; Moser et al., 1996; Huffman et al., 1993; Mallik, 1995; Tappeiner et al., 1991) in a number of environments. In fact, one study cautioned that logging in some temperate forests with an ericaceous understory could spell the demise of these systems if effective silvicultural systems techniques were not developed to control the shrubs and ensure forest regeneration (Mallik, 1995).

Crucial to understanding the ecological effects of *R. maximum* are the structural characteristics of its thickets and the physiological characteristics of the species itself. An evergreen species, it commonly forms extremely dense thickets which allow minimal light penetration (Clinton et al., 1994) and produces recalcitrant litter that is slow to decompose, often resulting in thick litter and humus layers (Boettcher and Kalisz, 1990). In addition, *R. maximum* may possess allelopathic properties which inhibit growth of other species (Rice, 1979). As a result of these characteristics, other plant species may be excluded under *R. maximum* canopies and the pattern of succession altered in ecosystems with an abundance of the species.

While a number of studies have addressed *R. maximum* in upland communities, comparatively little information is available that characterizes the structure of *R. maximum* thickets and its effects on plant diversity and succession in riparian forests. Given the current interest in maintenance of riparian forest structure and function with regard to in-stream processes and aquatic health in general, the role of *R. maximum* in these systems needs to be addressed. We hypothesized that increasing densities of *R. maximum* reduces species richness and negatively affects regeneration potential in riparian forests. Objectives of this study were to: (1) characterize the density and biomass of *R. maximum* thickets in the riparian forest of the Wine Spring Creek drainage, and (2) relate density of *R. maximum* thickets to species richness and percent cover in the regeneration layer over two years. We will use this information to speculate about the effects that increasing abundance and density of *R. maximum* thickets have on successional patterns in riparian forests and the implications for riparian and aquatic health.

## 2. Methods

### 2.1. Study area

This study was conducted as part of the Wine Spring Creek Ecosystem Management Project on the Wayah Ranger District, Nantahala National Forest in the Blue Ridge Physiographic Province of western North Carolina. The study area is located between Nantahala Lake (909 m elev.) and Wine Spring Bald (1645 m elev.), and encompasses approximately 1800 ha. Soils within the watershed are classified as coarse loamy, mixed mesic Typic Dystrochrepts (frigid Typic Haplumbrepts in the higher elevations), commonly 50–152 cm deep, and are derived from metasedimentary and metamorphic parent material (McNab and Browning, 1992). The Wine Spring Creek watershed experiences a temperate humid climate with approximately 180 growing season days annually and a mean annual precipitation of 152 cm, most of which occurs during the growing season.

### 2.2. Historic land use

Cherokee Indians occupied much of the area in and around Wine Spring Creek for thousands of years. Around 1750, Europeans settled the Wine Spring Creek area and changes in land use occurred. At the time of their removal in 1839, approximately 1500 Cherokees lived in the Wine Spring Creek area, with greater numbers in surrounding areas (Alger, 1993). Throughout their occupation of the Wine Spring Creek area, and southern Appalachians in general, Native Americans felled trees for building and fuelwood and cleared land by burning for grazing and agriculture.

The first recorded timber harvest occurred around 1880, coinciding with the construction of additional railroad lines to remove timber and a brief agricultural depression (Alger, 1993). Prior to acquisition by the U. S. Forest Service, the last timber harvest within the

Wine Spring Creek area occurred during the mid to late 1940s. Following this harvest, much of the riparian forest regenerated to the current stand dominated by intolerant pioneer species, e.g., birch (*Betula* sp.) with intermittently occurring eastern hemlock (*Tsuga canadensis* L.), black cherry (*Prunus serotina* Ehrh.), tulip poplar (*Liriodendron tulipifera* L.), and a few others. That *Betula* sp., an intolerant tree, could regenerate so well suggests that dense thickets of *R. maximum* were not nearly as abundant in the riparian ecosystem at this time.

### 2.3. Plot layout

Fifty-five 10×20 m sample plots were randomly located along Wine Spring Creek. Two plots had to be narrowed and lengthened to accommodate topographic considerations (e.g., rock outcrops, ledges) resulting in 5×40 m plots. Wine Spring Creek is approximately 6.5 km long and plots were located along all but approximately 0.7 km of the uppermost portion of the creek. This reach of Wine Spring Creek contained virtually no *R. maximum* and was therefore excluded from the study. In an effort to restrict our sampling to the riparian system, plots were oriented parallel to the stream and were installed within 20 m of the stream bank.

### 2.4. Vegetation survey

All stems>1 cm basal diameter at 10 cm above the forest floor were recorded by species in each plot. Stems<1 cm basal diameter were considered to be part of the regeneration layer and therefore excluded from this survey. These stems were considered during subsequent regeneration layer inventories discussed below. All stems <10 cm diameter-breast-height (dbh−1.37 m above ground level) were considered to be in the understory strata and all stems>10 cm dbh were considered to be in the overstory strata. Average dbh, density (stems $ha^{-1}$), basal area ($m^2\ ha^{-1}$), and importance value (IV200) ([relative density+relative basal area/2]×100) (Barbour et al., 1987) were calculated for each species by strata. For brevity, only the most important species (IV200) are presented – less important species are included as 'others'. The significance of individual species, including *R. maximum*, in this study will be addressed in terms of their importance values, hereafter referred to as IV200.

### 2.5. Density, biomass, and extent of *R. maximum* thickets

Diameter of each *R. maximum* stem that appeared as a separate individual was measured and placed into 1 cm diameter classes (e.g., 1.5, 2.5, etc.). *R. maximum* foliar and stem dry biomass was estimated from basal diameter using allometric equations developed with data collected from 41 randomly chosen *R. maximum* stems ranging from 1 to 4 cm basal diameter. This diameter range represented the majority of *R. maximum* stem diameters (>90%) found on the Wine Spring Creek project area. Leaves and stems were separated and each component was dried to a constant weight at 80°C. Resulting equations were applied to basal diameter values from the inventory of *R. maximum* stems to estimate biomass (see Table 3 for equations).

Discriminant analysis, using basal area and number of stems $ha^{-1}$, were used to quantitatively classify the 55 sample plots into four discrete thicket-density categories (High, Medium, Low, and Scarce) based on the range of densities encountered in this study. In some instances, values overlap between two adjacent thicket-density categories, implying that the categories were not entirely discrete but existed on a continuum. Plots were distributed as follows: 15, 13, 14, and 13 plots in the High, Medium, Low, and Scarce thicket-density categories, respectively.

The extent to which *R. maximum* occurred upslope from the stream was determined from transects systematically placed perpendicular to the direction of streamflow every 300 m on all streams in the drainage. Ocular estimates of *R. maximum* cover were made for 15 m segments along each 90 m transect.

### 2.6. Sampling of the regeneration layer

Species richness in the regeneration layer (woody and herbaceous stems<1 cm basal diameter) was inventoried in Fall, 1993 and Spring, 1994 on five line-transects (10 m each), systematically placed 2 m apart, across the width of each plot. Transects were further divided into 1 m lengths in which the frequency and percent cover of each species that intersected the transect within each meter were recorded (Conde et al., 1983; Brown, 1954). These measurements yielded frequency and percent cover estimates for each species from which calculations of importance value 200 (IV200={[relative frequency+relative coverage}/2]×100) were estimated for each species by thicket-density category. Species distance curves were generated and suggested that regeneration layer sampling intensity was sufficient to capture most species during the fall and spring samples (Monk, 1971; Cain, 1938).

### 2.7. Vegetation age

Twelve of the 55 plots (22% of total sample) were randomly chosen on which to approximate age of *R. maximum* thickets along Wine Spring Creek. Within each of the 12 plots, ages of the dominant *R. maximum* cohort were estimated by counting rings on cross sectional slices of at least three randomly chosen stems/plot at 10 cm above ground level. In addition, maximum age was determined by coring the occasional largest-diameter stem. Also, five randomly chosen stems from the most frequently occurring overstory species were cored at breast height (1.37 m) using a standard increment borer. Average ages of dominant overstory and *R. maximum* cohorts were compared among thicket-density categories. The average age of dominant *R. maximum* cohorts was also compared among thicket-density categories to determine if there were significant differences in the age of *R. maximum* among thicket-density categories.

### 2.8. Statistical analysis

Sample plots were classified into discrete *R. maximum* thicket-density categories (e.g., High, Medium, Low and Scarce) using the PROC DISCRIM procedure (SAS Institute, Inc. 1987). *R. maximum* foliar and stem biomass prediction equations were developed using the PROC REG procedure. Statistically significant differences in regeneration layer species richness and percent cover among thicket-density categories were determined using the PROC GLM procedure. Statistically significant differences between ages of the dominant *R. maximum* and overstory cohorts within thicket-density categories and among *R. maximum* cohorts in each thicket-density category were also determined using the PROC GLM procedure.

## 3. Results

### 3.1. Composition of the riparian forest

In the overstory, *Betula alleghaniensis* Britton was the most important species across all thicket-density categories (Table 1). *B. lenta* L. was the second most

Table 1
Understory and overstory species, listed by importance, encountered in four *R. maximum* thicket-density categories along Wine Spring Creek, Macon County, NC

| Species | IV200 | Species | IV200 |
|---|---|---|---|
| **Overstory** | | | |
| High plots | | Medium plots | |
| *Betula alleghaniensis* | 31.46 | *Betula alleghaniensis* | 32.08 |
| *Betula lenta* | 20.20 | *Betula lenta* | 15.30 |
| *Prunus serotina* | 10.61 | *Tsuga canadensis* | 12.74 |
| *Liriodendron tulipifera* | 8.91 | *Acer rubrum* | 7.75 |
| *R. maximum* | 4.56 | *Liriodendron tulipifera* | 4.50 |
| Other sp. | 24.27 | Other sp. | 27.64 |
| Low plots | | Scarce plots | |
| *Betula alleghaniensis* | 30.44 | *Betula alleghaniensis* | 30.26 |
| *Tsuga canadensis* | 25.37 | *Liriodendron tulipifera* | 12.86 |
| *Betula lenta* | 10.28 | *Betula lenta* | 10.27 |
| *Liriodendron tulipifera* | 8.99 | *Tilia americana* | 9.59 |
| *Acer rubrum* | 6.58 | *Tsuga canadensis* | 8.56 |
| Other sp. | 18.34 | Other sp. | 28.47 |
| **Understory** | | | |
| High plots | | Medium plots | |
| *R. maximum* | 88.57 | *R. maximum* | 77.41 |
| *Betula alleghaniensis* | 4.38 | *Kalmia latifolia* | 5.02 |
| *Betula lenta* | 1.81 | *Betula alleghaniensis* | 4.02 |
| *Tsuga canadensis* | 1.12 | *Tsuga canadensis* | 3.82 |
| *Kalmia latifolia* | 0.89 | *Betula lenta* | 2.15 |
| Other sp. | 3.25 | Other sp. | 7.58 |
| Low plots | | Scarce plots | |
| *R. maximum* | 63.13 | *R. maximum* | 31.20 |
| *Betula alleghaniensis* | 15.26 | *Betula alleghaniensis* | 11.87 |
| *Tsuga canadensis* | 7.23 | *Fagus grandifolia* | 8.11 |
| *Fagus grandifolia* | 2.17 | *Tsuga canadensis* | 7.92 |
| *Kalmia latifolia* | 2.15 | *Ilex ambigua* var. *montana* | 7.40 |
| Other sp. | 10.05 | Other sp. | 33.49 |

important species in the High and Medium thicket-density categories, while *Tsuga canadensis* L. and *Liriodendron tulipifera* L. were second in the Low and Scarce thicket-density categories, respectively. Other important overstory species included *Prunus serotina* Ehrhart, *Acer rubrum* L., and *Tilia americana* L.

*R. maximum* was the most important understory species in the riparian forest with IV200s of 89, 77, and 63 in the High, Medium, and Low thicket-density categories, respectively (Table 1). Even in the Scarce category, *R. maximum* occupied 39% (IV=31) of understory basal area. No other understory species had an IV200 more than five in the High and Medium thicket-density categories, indicating the complete dominance of *R. maximum*.

### 3.2. Density, biomass, and extent of *R. maximum* thickets

*R. maximum* thickets reached maximum densities of over 17,000 stems $ha^{-1}$ (Table 2). The density of the species in plots where *R. maximum* was scarce ranged from 0 to 2,600 stems $ha^{-1}$. In plots where thicket-density was high, basal area of *R. maximum* ranged from 11 to 22 $m^2$ $ha^{-1}$.

Aboveground biomass of *R. maximum* thickets differed markedly among thicket-density categories (Table 3). Biomass totaled 34 Mg $ha^{-1}$ on one plot where thicket-density was high. Stems and leaves accounted for 81% and 19%, respectively, of total aboveground biomass of *R. maximum* (Table 3). Biomass allocation between stems and leaves did not change markedly among the thicket-density categories.

*R. maximum* was not confined solely to the riparian forest. Transects indicated that thickets extended upslope at least 90 m, although cover tended to decline with increasing distance from the stream (Fig. 1).

Table 2
Basal area and density of *R. maximum* for each thicket-density category along Wine Spring Creek, Macon County, NC

| Thicket density category | Basal area ($m^2$ $ha^{-1}$) | Number of stems (×1000 $ha^{-1}$) |
|---|---|---|
| High | 11–22 | 7.95–17.4 |
| Medium | 5.5–11.3 | 5.05–10.5 |
| Low | 2.05–4.75 | 2.8–6.5 |
| Scarce | 0–1.8 | 0–2.6 |

Table 3
Range of *R. maximum* biomass (Mg $ha^{-1}$)[a], by leaf and stem component, within each thicket density category along Wine Spring Creek, Macon County, NC

| Thicket density category | Leaf | Stem | Total aboveground |
|---|---|---|---|
| High | 3.40–6.41 | 14.66–27.59 | 18.06–34.00 |
| Medium | 1.64–3.44 | 7.08–14.82 | 8.71–18.26 |
| Low | 0.53–1.57 | 2.33–6.79 | 2.86–8.36 |
| Scarce | 0–0.57 | 0–2.46 | 0–3.03 |

[a] Biomass prediction equations where $y$=biomass (g) and $x$= basal diameter (cm): leaf($y$)=175.96$x$−257.73 ($r^2$=0.82), stem($y$)= 755.15$x$−1099.07 ($r^2$=0.77), total($y$)=931.11$x$−1356.8 ($r^2$=0.82).

### 3.3. Density of *R. maximum* thickets: effects on regeneration layer

Species richness and percent cover in the regeneration layer decreased as the density of *R. maximum* thickets increased (Table 4). Species richness was about four times greater in plots where thicket-density was scarce than in plots where thicket-density was high. Percent cover for the same comparison was approximately 9 and 12 times greater for the fall and spring sampling, respectively. Regeneration layer species richness and percent cover were significantly different among all thicket-density categories in both the spring and fall samples, except between High and Medium plots.

Table 4
Differences in regeneration layer species richness (# species) and percent cover (%) among *R. maximum* thicket-density categories along Wine Spring Creek, Macon County, NC

| | Fall sampling | | Spring sampling | |
|---|---|---|---|---|
| Thicket density category | Species richness | Percent cover | Species richness | Percent cover |
| High | 6 a | 5 a | 7 a | 5 a |
| Medium | 9 ab | 9 ab | 12 a | 11 ab |
| Low | 18 c | 24 c | 22 c | 27 c |
| Scarce | 26 d | 43 d | 29 d | 62 d |

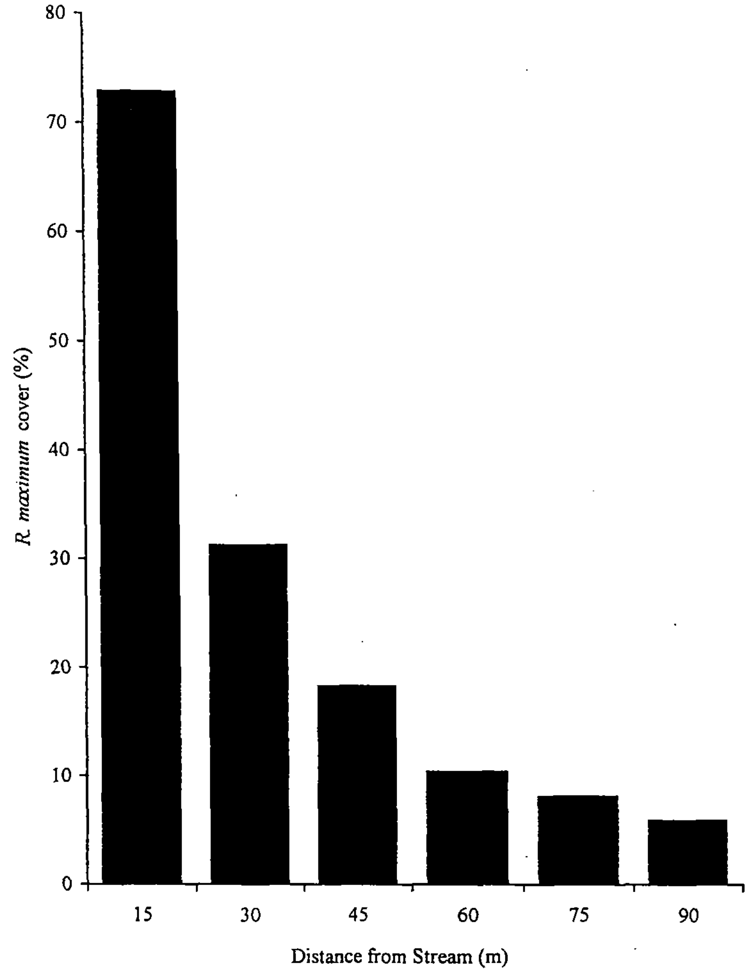


Fig. 1. Percent cover of *R. maximum* along 90 m transects placed perpendicular to the stream for all streams in the Wine Spring Creek watershed, Macon County, NC.

The relationship between *R. maximum* thicket-density and total species richness in the regeneration layer was best described by a negative exponential function (Fig. 2). Percent cover in the regeneration layer exhibited similar trends (data not shown).

Species encountered during sampling of the regeneration layer were categorized according to their 'strata potential' – that is, the strata they would be expected to achieve in mature or late-successional stands. *T. canadensis*, *Acer rubrum*, *Fagus grandifolia*, *B. alleghaniensis*, and *Quercus rubra* were the major potential overstory species in the regeneration layer (Table 5), but occurred only in small numbers. *R. maximum* was by far the most important potential understory species in the regeneration layer within all thicket-density categories (Table 5).

### 3.4. Age of R. maximum thickets and overstory trees

Average age of overstory trees regenerating after the last logging was significantly greater ($P$>0.0001) than that of the dominant cohort of *R. maximum* across all plots sampled for age (Table 6). The dominant cohort of *R. maximum* averaged 26 years while the average age of overstory trees was about 43 years, indicating that the dominant *R. maximum* cohort

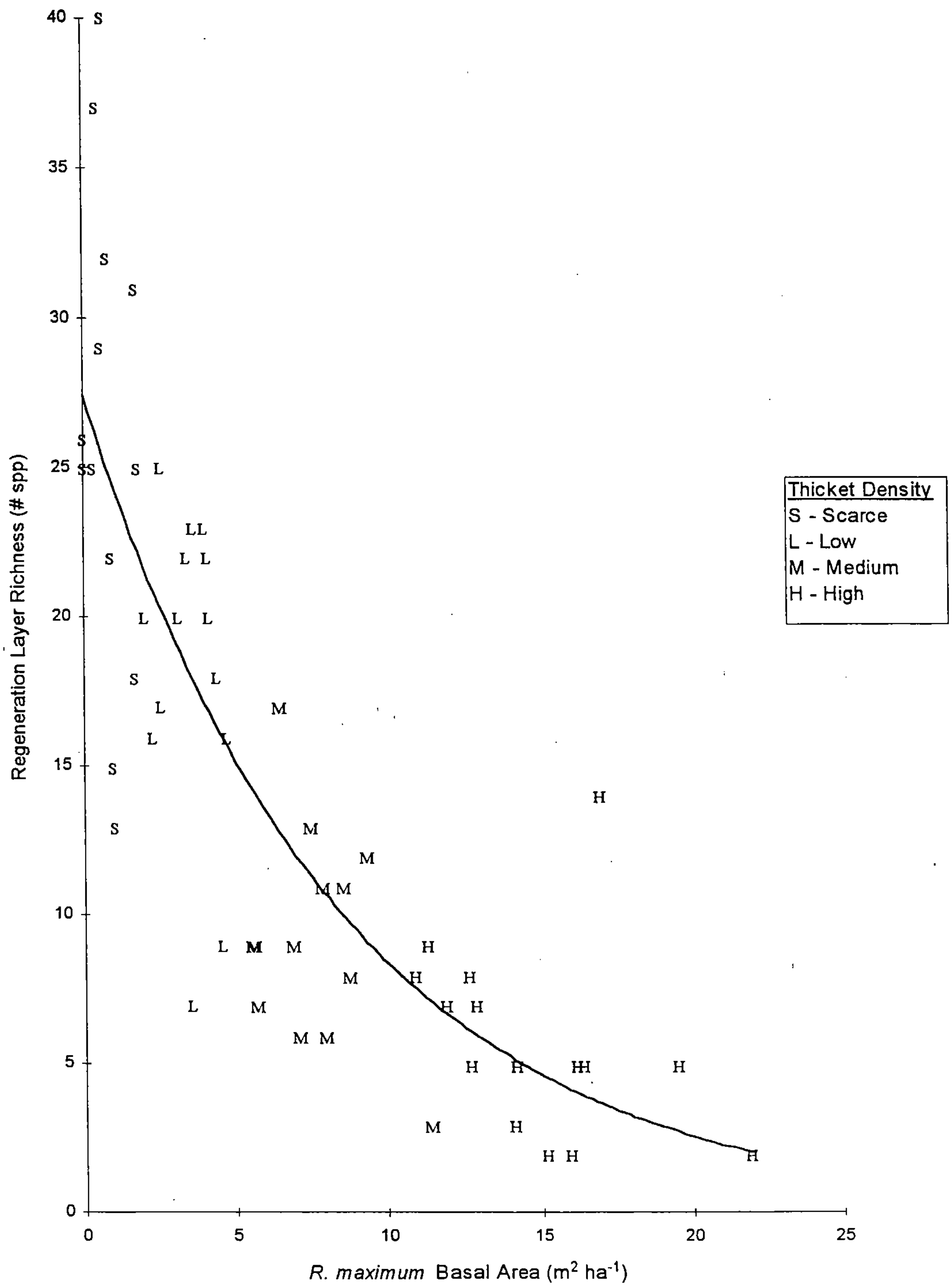


Fig. 2. Exponential decay model ($y=28.39\times e^{-0.1131x}$, estimated $r^2$=0.92) that characterizes the relation of regeneration layer species richness (Fall, 1993) to *R. maximum* basal area ($m^2$ $ha^{-1}$) along Wine Spring Creek, Macon County, NC.

Table 5
Five most important regeneration layer (<1 cm basal diameter) species (Fall, 1993), categorized by their probable strata potential, for each thicket-density category along Wine Spring Creek, Macon County, NC

| Species | IV200 | Species | IV200 |
|---|---|---|---|
| **Potential overstory species** | | | |
| High plots | | Medium plots | |
| *Tsuga canadensis* | 2.34 | *Tsuga canadensis* | 4.45 |
| *Acer rubrum* | 1.61 | *Betula alleghaniensis* | 1.56 |
| *Fagus grandifolia* | 0.75 | *Acer rubrum* | 1.34 |
| *Betula alleghaniensis* | 0.73 | *Quercus rubra* | 0.61 |
| *Quercus rubra* | 0.20 | *Fagus grandifolia* | 0.58 |
| Other sp. | n/a | Other sp. | 0.30 |
| Total | 5.62[a] | Total | 8.83 |
| Low plots | | Scarce plots | |
| *Tsuga canadensis* | 2.51 | *Acer rubrum* | 1.90 |
| *Acer rubrum* | 2.05 | *Tsuga canadensis* | 1.66 |
| *Fagus grandifolia* | 1.05 | *Fagus grandifolia* | 1.19 |
| *Prunus serotina* | 0.90 | *Quercus rubra* | 0.46 |
| *Betula alleghaniensis* | 0.75 | *Betula alleghaniensis* | 0.42 |
| Other sp. | 0.37 | Other sp. | 0.63 |
| Total | 7.62 | Total | 6.26 |
| **Potential understory/midstory species** | | | |
| High plots | | Medium plots | |
| *R. maximum* | 60.32 | *R. maximum* | 43.12 |
| *Clethra acuminata* | 2.44 | *Ilex ambigua var. montana* | 1.84 |
| *Ilex ambigua var. montana* | 2.04 | *Clethra acuminata* | 1.60 |
| *kalmia latifolia* | 1.33 | *Acer spicatum* | 1.24 |
| *Amelanchier arborea* | 0.98 | *Hamamelis virginiana* | 1.18 |
| Other sp. | 0.81 | Other sp. | 2.27 |
| Total | 67.92 | Total | 51.26 |
| Low plots | | Scarce plots | |
| *R. maximum* | 17.38 | *R. maximum* | 4.59 |
| *Clethra acuminata* | 1.65 | *Hamamelis virginiana* | 1.31 |
| *Viburnum alnifolium* | 1.09 | *Acer pennsylvanicum* | 1.28 |
| *Acer pennsylvanicum* | 0.98 | *Acer spicatum* | 1.22 |
| *Acer spicatum* | 0.98 | *Amelanchier arborea* | 0.83 |
| Other sp. | 3.16 | Other sp. | 2.39 |
| Total | 25.24 | Total | 11.62 |
| **Potential herbaceous species** | | | |
| High plots | | Medium plots | |
| *Athyrium asplenioides* | 10.39 | *Athyrium asplenioides* | 10.79 |
| *Smilax sp.* | 3.27 | *Oxalis acetosella* | 3.36 |
| *Lycopodium alopercuroides* | 2.73 | *Smilax sp.* | 3.30 |
| *Aster sp.* | 2.24 | *Epifagus virginiana* | 2.49 |
| *Ligusticum canadense* | 1.65 | *Arisaema triphyllum* | 1.35 |
| Other sp. | 6.17 | Other sp. | 10.62 |
| Total | 26.46 | Total | 39.91 |
| Low plots | | Scarce plots | |
| *Athyrium asplenioides* | 14.75 | *Athyrium asplenioides* | 13.30 |
| *Oxalis acetosella* | 9.31 | *Ligusticum canadense* | 7.34 |
| *Aster sp.* | 7.73 | *Oxalis acetosella* | 6.30 |
| *Poaceae sp.* | 6.36 | *Aster sp.* | 6.06 |
| *Ligusticum canadense* | 5.95 | *Tiarella cordifolia* | 5.27 |
| Other sp. | 23.49 | Other sp. | 44.02 |
| Total | 67.59 | Total | 82.29 |

[a] Total represents the sum of individual species' Importance Values in each strata potential within each thicket-density category (e.g., total importance values for potential overstory, understory/midstory, and herbaceous species in regeneration layer of High thicket-density plots were 5.62, 67.92, and 26.46, respectively – suggesting the dominance of potential understory/midstory species in the regeneration layer of dense *R. maximum* thickets).

became established later. The mean ages of *R. maximum* in the High, Medium, and Low thicket-density categories were significantly greater ($P>0.0307$, $P>0.0002$, and $P>0.0002$, respectively) than that of the Scarce category.

## 4. Discussion

### 4.1. Composition of the riparian forest

*Betula alleghaniensis* and *B. lenta*, both pioneer species, dominated the overstory of the riparian forest (Table 1) and probably became established following harvesting in the watershed approximately 50 years earlier (Alger, 1993). At this time, *R. maximum*, based on the paucity of large (>10 cm) stems, was apparently much less abundant in the watershed. Although *B. alleghaniensis* was the most important tree species in the understory of the current stand, its seedlings grow slowly in dense shade and are normally overtopped by more shade-tolerant species within five years unless released by overstory disturbance (Erdmann, 1990). Neither of the *Betula* species are successfully regenerating in the dense *R. maximum* understories.

*R. maximum* occasionally appeared as overstory individuals in some High density thickets, suggesting

Table 6
Ages of dominant cohorts of *R. maximum* and overstory trees by thicket-density category along Wine Spring Creek, Macon County, NC

| Thicket density category | Age of dominant *R. maximum* cohort (Std err) | Range of *R. maximum* ages | Age of dominant overstory cohort (Std err) |
|---|---|---|---|
| High | 28 (3.07) a[a] A[b] | 1–46 | 44 (3.96) b |
| Medium | 28 (1.59) a A | 1–47 | 43 (2.05) b |
| Low | 26 (1.79) a A | 1–32 | 42 (2.26) b |
| Scarce | 19 (0.84) a B | 1–21 | 44 (1.03) b |

[a] Least squared means compared between dominant *R. maximum* and overstory cohort – those with the same lower case letter within each thicket-density category are not significantly different ($a$=0.05).
[b] Least squared means of *R. maximum* ages compared among thicket-density categories – those with the same upper case letter are not significantly different ($a$=0.05).

that larger, perhaps older, individuals provided the foundation from which other stems spread vegetatively in the decades following logging (Phillips and Murdy, 1985). This is further supported by age analyses which indicated that the occasional larger-diameter, older *R. maximum* individual was surrounded by numerous smaller, younger individuals (Table 6).

### 4.2. Density, biomass, and extent of *R. maximum* thickets

*R. maximum* generally occurred rather continuously in dense or moderately dense thickets throughout the riparian forest, making it difficult to locate and establish plots of low to scarce density. No thickets were found adjacent to the stream above an elevation of 1372 m. In his 1947 inventory of the Great Smoky Mountains, Whittaker (1956) noted that the upper limit of the species' distribution was 1364 m, which concurs with our findings.

The greater abundance and cover of *R. maximum* close to the stream as compared to upslope positions indicates the suitability of the riparian environment to the species (Fig. 1). If, however, management practices such as exclusion of fire from forest ecosystems is permitting the gradual spread of *R. maximum* to upslope positions, this could jeopardize the regeneration potential of tree species even in upslope environments. Depending upon the extent of this spread upslope, inadequate tree regeneration may adversely affect the future of allochthonous inputs such as coarse woody debris (CWD) and leaf litter to the stream and riparian systems (Hedman and Van Lear, 1994).

### 4.3. Density of *R. maximum* thickets: effects on regeneration layer

Even low densities of *R. maximum* substantially reduced species richness and cover in the regeneration layer (Table 4). The decrease in richness occurred rapidly as thicket basal area increased from low levels, then gradually leveled off as higher basal areas were encountered (Fig. 2).

Composition of the regeneration layer often reflects the future composition of the stand, especially in the absence of catastrophic disturbances which may favor pioneer species. Categorizing the regeneration layer species, woody and herbaceous stems<1 cm basal diameter, into their growth form or 'strata potential' (i.e., herbaceous, understory/midstory, or tree species – the vegetation layer that a species would likely occupy in mature or late-successional stands) permitted evaluation of *R. maximum*'s probable effect on future stand composition and structure. Phillips and Murdy (1985) reported that *T. canadensis* and *A. rubrum*, both extremely shade-tolerant species, are capable of becoming established and competing under a *R. maximum* canopy. However, the vigor and density of this relatively young *R. maximum* understory and the apparent low vigor and sparseness of these potential shade-tolerant overstory species suggest that succession will be difficult at best in the Wine Spring Creek watershed.

*R. maximum* was the most important potential understory species in the regeneration layer among all thicket-density categories, strongly suggesting that the species was not only capable of replacing itself but was gradually advancing into openings where it had been relatively scarce (Table 5). The dominance of *R. maximum* in the regeneration layer is indicated by the fact that its IV200 is 23 to 24 times higher than the next most important species in the High to Medium thicket-density categories.

The presence of scattered potential overstory and understory/midstory tree and shrub species in the regeneration layer does not mean that these stems will be able to grow through the dense *R. maximum* canopy. Most of these regenerating species were in very early growth stages and will likely succumb to unfavorable growing conditions in the thickets. Low light intensity (Clinton, 1995), extreme competition for moisture and nutrients, acidic litter (Boettcher and Kalisz, 1990), and possibly allelopathic effects (Rice, 1979) within *R. maximum* thickets all discourage establishment and growth of other species in the regeneration layer (Clinton and Vose, 1996; Clinton et al., 1994; Tobe et al., 1992). The low numbers of potential overstory, understory/midstory, and herbaceous species in these dense thickets indicate that, in the absence of major disturbance, the future diversity of riparian ecosystems will be reduced as *R. maximum* thicket density and coverage continue to expand. Vertical structure in the forest has become two-tiered, with an overstory dominated by *Betula* species and understory effectively dominated by *R. maximum* (Fig. 3).

Although it was not the purpose of this study to determine processes that historically would have suppressed *R. maximum* and allowed other species to regenerate, we believe that fire occurred periodically, probably during drought cycles, in these mesic riparian forests. Based on observations of fire effects in other mesic forests as well as fire scars on large relic trees on this study site, these fires would probably have top-killed *R. maximum* stems and allowed other woody species the opportunity to grow ahead of the resprouting thickets. Repeated burning during longer drought periods could have completely killed individual stems. Fire suppression for the past 70 years has altered this historic pattern.

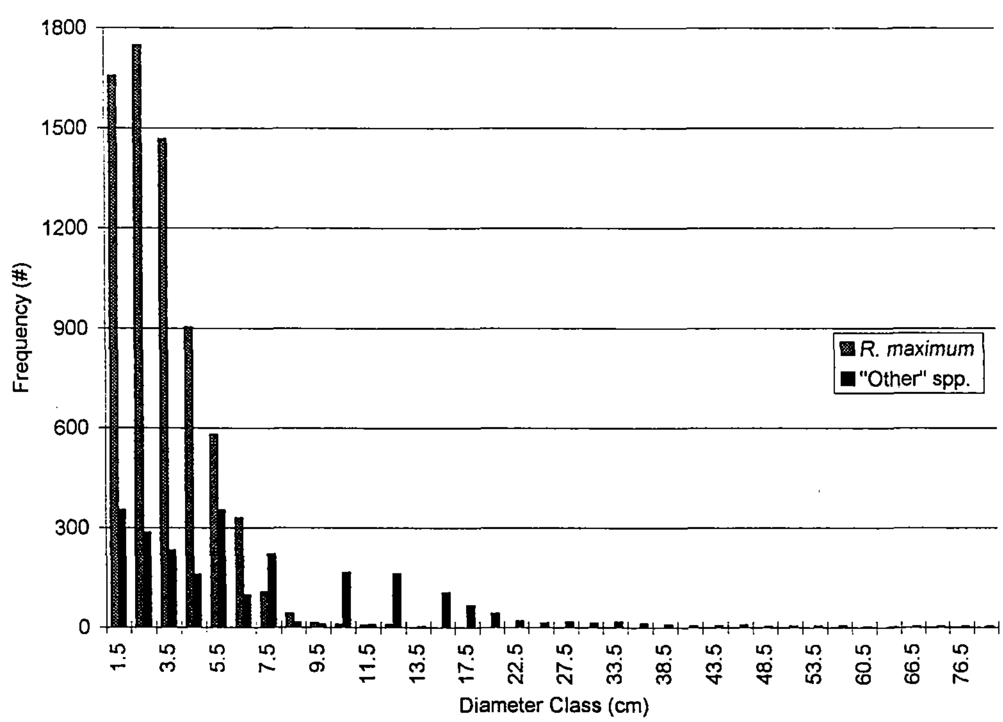


Fig. 3. Frequency distribution for *R. maximum* and other species (>1 cm basal diameter) in each diameter class along Wine Spring Creek, Macon County, NC. The largest diameter class measured was 81.5 (not apparent in graph).

### 4.4. Age of R. maximum thickets and overstory trees

In the High and Medium thicket-density categories, the average age of the occasional large (>10 cm) *R. maximum* individuals slightly exceeded that of the overstory, indicating that a few stems of the species were present prior to overstory establishment. Since *R. maximum* is thought to propagate primarily through root suckering (McGee and Smith, 1967), layering (Phillips and Murdy, 1985), and rhizomes (Radford et al., 1968) it is probable that the most frequently occurring diameter class originated from these older individuals. However, the disparity in ages of the dominant overstory and *R. maximum* cohorts suggests that the species is not initially competitive at low densities with vigorous potential overstory trees following major disturbances. However, once it has become established *R. maximum* is completely capable of preventing other species from regenerating and competing under its dense canopy.

Because of the extensive development of *R. maximum* thickets, it appears unlikely that shade-intolerant species such as *Betula* sp. or *Liriodendron tulipifera* could successfully regenerate even with future overstory disturbance, unless followed by an intense fire. The paucity of even shade-tolerant midstory and overstory species in the regeneration layer under these thickets indicates that they too will have difficulty regenerating. The current composition of the riparian forest in Wine Spring Creek and the trends indicated by the potential strata analysis of the regeneration layer suggest that future succession may lead to a forest of widely scattered overstory species with lower strata dominated by dense thickets of *R. maximum*. Some very old (>200 years) riparian forests in the southern Appalachians resemble this general description (Hedman and Van Lear, 1994). That *R. maximum* was significantly younger (Table 6) in the Scarce plots further indicates that the species is advancing into areas with more open understories.

## 5. Conclusions

*R. maximum* thickets reach extreme densities in southern Appalachian riparian forests. Because of the characteristic features of the species, these thickets exclude other species from various canopy strata, reducing species richness. *R. maximum* dominates the understory and often extends into the midstory severely limiting light penetration to the forest floor. Increasingly dense thickets of *R. maximum* prevent potential midstory and overstory species from becoming established.

*R. maximum* has been a component of understories of riparian forests in the southern Appalachians for millennia. However, the increasing abundance and dominance of *R. maximum* in riparian forests could alter historical patterns of succession and may result in significant changes in the structural, compositional, and functional diversity of these systems.

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