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# Age and distribution of an evergreen clonal shrub in the Coweeta Basin: *Rhododendron maximum* L.[1]

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# Age and distribution of an evergreen clonal shrub in the Coweeta Basin: *Rhododendron maximum* L.[1]

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Elliott, K. J. and J. M. Vose (Coweeta Hydrologic Laboratory, Center for Forest Watershed Science, SRS-4353, Southern Research Station, USDA Forest Service, Otto, NC 28763). Age and distribution of an evergreen clonal shrub in the Coweeta Basin: *Rhododendron maximum* L. J. Torrey Bot. Soc. 139: 149–166. 2012.—*Rhododendron maximum* L. is an evergreen, clonal shrub that forms a dominant sub-canopy layer and is a key species in southern Appalachian forests. We investigated the age and distribution of *R. maximum* across the Coweeta Basin, a 1626 ha watershed in western North Carolina. We selected 16 perennial, second-order streams and used a Global Positioning System to establish site boundaries and map the coverage of *R. maximum* across the hillslopes from stream to ridge. In each site, three transects from stream edge to the ridge were used to measure diameters of overstory trees ($\geq$ 2.5 cm dbh), tree saplings ($<$ 2.5 cm dbh) and shrubs including *R. maximum* stems. Along each transect, we cut cross-sections of *R. maximum* ramets and extracted increment cores from nearest neighbor trees to determine ages. The 16 sites ranged in size from 0.3 to 1.9 ha depending on the distance from stream to ridge. *Rhododendron maximum* cover ranged from 25 to 100% and ages ranged from 6 to 120 years. *Rhododendron maximum* establishment year showed a skewed unimodal distribution with the peak establishment occurring between 1928 and 1940. Although the *R. maximum* age and distance-from-stream relationship was statistically significant, the relationship was not meaningful as distance-from-stream only explained 2.6% of the variation in *R. maximum* age ($r^2 = 0.026$, $P = 0.0003$, $n = 487$). Distance from stream only explained 4.2% of the variation in overstory tree age ($r^2 = 0.042$, $P = 0.0015$, $n=237$). It appears that *R. maximum* has not expanded upslope over the last 100 years; rather the ranges in sizes and ages suggest that ramets are recruiting under established *R. maximum* canopies particularly in the wetter, near stream locations.

Key words: Dendrochronology, riparian areas, Southern Appalachians, streams.

In many areas of the southern Appalachians, two evergreen shrubs, *Rhododendron maximum* L. and *Kalmia latifolia* L. form a dominant and extensive sub-canopy. *Rhododendron maximum* in particular is a key species in southern Appalachian forests for several reasons: (1) it is thought to contribute to landslide initiation (Wooten et al. 2007, Hales et al. 2009, Latham et al. 2009, Band et al. 2011); (2) it inhibits regeneration of herbaceous and woody species, particularly tree species (Neary et al. 1984, Phillips and Murdy 1985, Clinton and Vose 1996, Walker et al. 1999, Rivers et al. 1999, Beckage et al. 2000, Nilsen et al. 2001, Beier et al. 2005, Lei et al. 2006); and (3) it can alter ecosystem processes, such as net ecosystem productivity, water and carbon balance, and biogeochemistry (McGinty 1972, Monk et al. 1985, Chastain et al. 2006, Wurzburger and Hendrick 2007).

Although much is known about the ecophysiology of *Rhododendron maximum* (Muller 1991, Dighton and Coleman 1992, Lipp and Nilsen 1997, Russell et al. 2009, Brantley and Young 2010) and how its presence affects tree seedling establishment and growth; fewer studies have examined its population dynamics (McGee and Smith 1967, Plocher and Carvell 1987, Cooper and McGraw 1988, McGraw 1989) related to establishment, growth, and lateral spread. Several life history characteristics of *R. maximum* may affect its distribution: (1) it reproduces both vegetatively (asexual) and from seed germination (sexual); (2) it is a clonal plant that produces many ramets through branch layering and stem sprouting; (3) an individual plant (genet) could be very old, whereas ramets (new stems that form from layering or root sprouting) are much younger; (4) an individual genet is very

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difficult to define, and almost impossible without DNA testing and extensive and exhaustive sampling (Widén et al. 1994, Pornoni and Escaravage 1999); and (5) it may spread by "phalanx" and "guerrilla" modes of growth, which allows it to reproduce beneath its own canopy, spread laterally, and create disjunct patches of the same genet (Royo and Carson 2006).

A few studies have examined *Rhododendron maximum* establishment and discussed its extent of spread in southern Appalachian forests (McGee and Smith 1967, Plocher and Carvel 1987, Baker and Van Lear 1998, Dobbs and Parker 2004). Much of the literature focusing on *R. maximum*'s ecological role in Appalachian forests has been conducted under the assumption that *R. maximum* has increased in coverage over the last several decades (e.g., Rivers et al. 1999, Walker et al. 1999, Nilsen et al. 2001, Van Lear et al. 2002, Yeakley et al. 2003, Beier et al. 2005, Wurzburger and Hendrick 2007, Hales et al. 2009). The empirical evidence to validate this statement is scant and conflicting, with a few studies supporting the idea of *R. maximum* expansion over the last several decades due to lack of disturbances (Dobbs 1998, Baker and Van Lear 1998, Dobbs and Parker 2004), while others suggest that *R. maximum* expanded earlier in the 20th century due to disturbance events that opened the canopy (McGee and Smith 1967, McGinty 1972, Plocher and Carvell 1987, Chastain and Townsend 2008). Thus, the extent of establishment and spread of *R. maximum* in Appalachian forests during the past century remains an unsettled question.

*Rhododendron maximum* is considered a mesic forest species that occurs primarily along streams and within acidic coves (Schafale and Weakley 1990, Newell and Peet 1995, 1996, Newell et al. 1997, Clinton 2002). Earlier studies reported that *R. maximum* was historically confined to riparian areas and other mesic sites (Harshberger 1903, Oostings and Billings 1939, Clinton 2002), where it prefers deep well-drained acid soils high in organic matter (Clinton 2002). Acidic cove forests with *R. maximum* canopy cover have a limited number of forest herbs (low richness) with extremely low abundance (density or cover) compared to forests without *R. maximum* (Newell and Peet 1995, 1996). According to aerial photos from the Smoky Mountains National Park taken in 1936 and 1953, acidic cove forest stands were generally located along upland streams and overstory canopies were dominated by widely-spaced relatively mature crowns of roughly equal size; currently (1997–2002) these acidic coves are dominated by *Tsuga canadensis* L. Carr. and *Liriodendron tulipifera* L. with a *R. maximum* subcanopy (Webster et al. 2005).

Fire exclusion is one hypothesis that has been endorsed to explain *Rhododendron maximum* expansion (Baker and Van Lear 1998, Van Lear et al. 2002); whereby, fire occurred periodically, probably during drought cycles, and these fires would have top-killed *R. maximum* stems; and subsequent repeated burning during longer drought periods would have constrained *R. maximum* to wetter, riparian habitats. As a result, it has been suggested that the exclusion of fire in the 20th century altered this historic pattern (Brose et al. 2001) and contributed to the upslope expansion of *R. maximum* (Baker and Van Lear 1998), yet little or no direct evidence is available to support this suggestion. Our objective was to determine if *R. maximum* has spread by expanding from near stream, riparian areas to upland forests over the last 100+ years. We used dendrochronological techniques to test the following hypotheses: (1) ramets closer to the stream are older than ramets further away, which suggests that *R. maximum* is spreading laterally from stream edge to upslope positions, and (2) trees within patches are older than *R. maximum* ramets suggesting that *R. maximum* became established under a closed canopy forest. We also analyzed permanent plot data and compared archival data (1934 survey) with more recent surveys (2009–2010) to determine if *R. maximum* has increased in abundance overtime in the Coweeta Basin.

**Methods.** STUDY SITE. Coweeta Hydrologic Laboratory is a research site of the USDA Forest Service, Southern Research Station. It is located in the Nantahala Mountain Range of western North Carolina, USA, within the Blue Ridge Physiographic Province, near the southern end of the Appalachian Mountain chain (latitude 35° 03′ N, longitude 83° 25′ W). The 2185 ha laboratory consists of two adjacent, east-facing, bowl-shaped basins; Coweeta Basin and Dryman Fork Basin. The Coweeta Basin encompasses 1626 ha and is drained by Ball Creek and Shope Fork, two

Table 1. Sixteen stream locations within Coweeta Basin, western North Carolina.

| Stream | Code | Latitude, Longitude | Elevation (m) | Aspect (slope-facing) | Size (ha) | Rhododendron cover (%) |
|---|---|---|---|---|---|---|
| Ball Creek | BC | 35°02″14′, 83°27″33′ | 1249 | W | 0.833 | 74 |
| Creasman Branch | CB | 35°03″32′, 83°25″39′ | 701 | E | 0.340 | 94 |
| Cunningham Creek | CC | 35°03″11′, 83°27″05′ | 914 | S | 0.885 | 55 |
| Hurricane Branch | HC | 35°04″02′, 83°26″35′ | 792 | W | 0.552 | 56 |
| Hensen Creek | HL | 35°03″12′, 83°26″20′ | 716 | S | 1.569 | 15 |
| Hensen Creek | HM | 35°02″50′, 83°27″17′ | 945 | N | 0.952 | 45 |
| Hensen Creek | HU | 35°02″11′, 83°28″01′ | 1189 | N | 0.429 | 91 |
| Hugh White Branch | HW | 35°03″15′, 83°25″40′ | 732 | E | 0.730 | 88 |
| Jenny Branch | JB | 35°03″32′, 83°26″35′ | 762 | E | 0.496 | 100 |
| No-name Branch | NN | 35°03″44′, 83°25″42′ | 685 | W | 0.809 | 20 |
| Pinnacle Branch | PB | 35°03″27′, 83°28″18′ | 1158 | S | 0.879 | 52 |
| Reynolds Branch | RB | 35°02″26′, 83°27″05′ | 914 | W | 0.273 | 92 |
| Snake Den Branch | SD | 35°02″40′, 83°26″22′ | 853 | E | 0.345 | 93 |
| Upper Shope Fork | SF | 35°03″10′, 83°27″54′ | 1067 | W | 1.885 | 37 |
| Wolf Rock Branch | WR | 35°03″45′, 83°27″33′ | 945 | E | 0.835 | 25 |
| Wykle Branch | WB | 35°03″10′, 83°28″00′ | 1036 | E | 0.645 | 83 |

fourth-order streams. These streams join to form Coweeta Creek, which flows 7 km east to the Little Tennessee River. Elevations range from 675 to 1592 m. Slopes are steep ranging from 30 to over 100 percent. Soils are deep sandy loams and are underlain by folded schist and gneiss. Two soil orders are found within Coweeta, immature Inceptisols and older developed Ultisols (Thomas 1996). The relief has a major influence on hydrologic, climatic, and vegetation characteristics (Elliott et al. 1999). Streams flow throughout the year, fed by approximately 1800 mm of precipitation per year, most of which is rain. Mean annual temperature is 12.6 °C and ranges from an average of 3.3 °C in January to 21.6 °C in July. Frequent rain, more than 130 storms distributed throughout the year, sustains high evapotranspiration rates and a humid climate (Swift et al. 1988). Vegetation is southern mixed deciduous forest. The principal overstory species are of the genera *Quercus*, *Acer*, *Carya*, and *Liriodendron*. Evergreen shrubs (*R. maximum* and *Kalmia latifolia*) combine with *Cornus*, *Robinia*, *Acer*, and *Betula* to form a dense understory cover (Day et al. 1988).

Numerous disturbances, such as logging, drought, hurricanes, and invasive insects and pathogens, have influenced forest structure, composition and the distribution of species in the Coweeta Basin (Elliott and Vose 2011). The Forest Service purchased the Basin in 1918, but rights to timber over 38 cm (15 inches) at the stump were reserved for the J.A. Porter Logging Company. Logging began in 1919, and selective but heavy cutting continued until 1923. By 1923, when the Forest Service took over administration of the Coweeta Basin, 8 million board feet of timber had been removed (Douglas and Hoover 1988). While rainfall is usually abundant in this region, dry years, such as the recorded droughts between 1985–1988 and 1998–2002, are increasingly common (Coweeta Hydrologic Laboratory, http://www.coweeta.uga.edu, Laseter et al. 2012). There have been no recorded fires within the Basin since the Forest Service acquisition in 1918, except for slash pile burning in experimental Watershed 6, which was not included in our study sites.

STREAM LOCATIONS AND SITE ESTABLISHMENT. We selected 16 stream locations across low to high elevation sites from a topographic map of the Coweeta Basin. All streams are perennial, second order streams (Table 1) that drain into Ball Creek on the south-side or Shope Fork Creek on the north-side of the basin. Two sites were selected from treated watersheds: Hurricane Branch (HC) is within WS7, a watershed that was clearcut in 1977, including *Rhododendron maximum* stems ≥ 2.5 cm diameter (Boring and Swank 1986); and Snake Den Branch (SD) is within WS19, a watershed where all evergreen shrubs, *R. maximum* and *Kalmia latifolia*, were cut in 1948 (Johnson and Kovner 1952).

For each stream map point, we randomly selected one side of the stream to delineate the site boundary, and then, located the map point in the field to establish the site boundary. From the stream point, a 100 m stream stretch was marked, 50 m upstream and 50 m downstream from this point. To delineate the site boundary, a compass bearing was taken at the upstream marker roughly perpendicular to stream towards the ridge, and the same compass bearing was taken at the downstream marker to transpose the 100 m stream length to a parallel line on the ridge. With this procedure, the sites were different sizes depending on the distance from stream to ridge (Table 1). For each site, a Global Positioning System (GPS) receiver (Trimble GeoExplorer XH, Sunnyvale, CA) was used to establish points around the site boundary and around *Rhododendron maximum* patches to calculate site area and map the distribution and area of *R. maximum* (Table 1). GPS points were differential corrected (DGPS). ArcGIS 10.0 (ESRI, Redlands, CA) was used for data collection. Position Dilution of Precision (PDOP) value of 10 and Signal to Noise Ratio (SNR) setting of 2.5 were used to ensure accurate location collection. GPS Pathfinder Office 2.90 was used for DGPS. Base station files from Conover and Franklin, North Carolina were used for DGPS. Preliminary tests over known locations verified positional errors of less than two meters after differential correction.

SAMPLING DESIGN. Within each stream site, we established three transects extending from the stream edge to the ridge. Transects were arrayed perpendicular to the stream with two transects along the site boundaries and one at the midpoint of each site. Overstory trees ($\geq$ 2.5 cm diameter at breast height (dbh, 1.37 m above ground) were measured in 10 meter width belts extending the entire length of each transect. The understory layer was measured in 1.0 meter width belts and included all shrubs and tree saplings ($<$ 2.5 cm dbh and $\geq$ 0.5 m height). Diameter of overstory trees was measured to the nearest 0.1 cm at dbh and recorded by species. Diameter of understory woody stems was measured to the nearest 0.1 cm at diameter base of stem (dbs, 10 cm above ground) and recorded by species.

A cross-section of rhododendron was cut at 0, 5, 10, 15, 20 m, and then every 10 m along each transect, from stream edge to ridge, within each site to determine the age of individual ramets. We selected the ramet closest to the transect line regardless of size. A total of 487 rhododendron cross-sections were collected ranging in size from 0.9 to 26.3 cm dbs. An increment core was extracted from the nearest neighbor tree ($\geq$ 10 cm dbh) to determine its age and radial growth. A total of 237 trees were sampled ranging in size from 13.5 to 79.0 cm dbh.

DENDROCHRONOLOGY. Cross-sections of *Rhododendron maximum* ($n$ = 487) and mounted increment cores from nearest neighbor trees ($n$ = 237) were air dried and sanded with progressively finer grit sandpaper using standard dendrochronological methods (Fritts 1976, Phillips 1985, Stokes and Smiley 1996). All tree cores were visually cross-dated using common signature years (Yamaguchi 1991). We used skeleton plotting to date cores with missing rings, cracks, or damage during sampling and to insure that all trees were dated accurately (Stokes and Smiley 1996). After dating, annual ring widths were measured to the nearest 0.00l mm using a Velmex Unislide (Velmex Inc., Bloomfield, NY) and an Olympus SZ40 Stereozoom microscope (Olympus America Inc., Center Valley, PA) interfaced with Measure J2X software. A tree-ring record was corrected for false or locally absent rings using signature years, narrow ring widths that are prominent and synchronous across samples (Stokes and Smiley 1996), and cross-dating verification with COFECHA (Holmes 1983). However, drought induced missing rings and monsoon induced false rings are rare outside of the Southwestern U.S. (Yamaguchi 1991). A pith locator was used to add rings to cores that missed the pith by ca. $\leq$15mm (Applequist 1958, Villalba and Veblen 1997).

We were unable to cross-date *Rhododendron maximum* because signature years were not apparent; however, we were able to count annual rings using the SZ40 Stereozoom microscope to determine ramet age. The annual growth rings were discernable in *R. maximum* because leaves are not photosynthetically active during the winter (Nilsen 1992). In addition, we had the entire cross-section, rather than an increment core, to validate the age determination. *Rhododendron maximum* stems tended to show non-symmetric growth from the center in response to stem bending during shrub growth, as it is typically impacted by tree- and limb-falls during its development (Wilson 1997).

To compare *Rhododendron maximum* to aboveground biomass and leaf area index (LAI) of deciduous trees, we used published, species-specific allometric equations from Martin et al. (1998) to calculate aboveground biomass (foliage, branches, and stem) of deciduous trees; equations from Santee and Monk (1981) for hemlock; and equations from Baker and Van Lear (1998) for *R. maximum* and *Kalmia latifolia* stems $\geq$ 1.5 cm diameter base of stem (dbs, $\approx$ 10 cm above ground level). For understory woody stems and *R. maximum* and *K. latifolia* stems $<$ 1.5 cm dbs, we used species-specific allometric equations from Boring and Swank (1986). Leaf area index (LAI, $m^2\ m^{-2}$) was estimated by multiplying the specific leaf area (SLA, $cm^2\ g^{-1}$) of individual species by their foliage mass ($g\ m^{-2}$) (Martin et al. 1998).

Statistical Analyses. We used simple linear models (Littell et al. 2002) in PROC GLM (SAS 2002–2003) to explore relationships among *Rhododendron maximum*, overstory trees, and distance-from-stream. We evaluated *R. maximum* biomass or LAI as the dependent variable and overstory tree biomass or LAI as the independent variable. Diameter-age relationships for *R. maximum* and overstory trees were evaluated, where age was the dependent variable and diameter was the independent variable. Finally, we evaluated the distance-from-stream and *R. maximum* age and overstory tree age relationships; where *R. maximum* age or overstory tree age was the dependent variable and distance-from-stream was the independent variable. Data complied with assumptions of normality and equal variance and were not transformed. Significance for all statistical tests was based on $\alpha \leq 0.05$ (SAS 2002–2003).

Archival Data. From 1934 to 1935, 979 permanent 0.08 ha (20 × 40 m) plots were established along 13 parallel, approximately North–South transects (330°) spanning the Coweeta Basin at 200 m intervals. The presence and percent cover of evergreen clonal shrubs, *Rhododendron maximum* and *Kalmia latifolia,* were recorded for the original 979 permanent plots surveyed between 1934 and 1935. Data were recorded on USDA Forest Service Form 289, for a total of 13 record books, one book for each survey line that transects the Coweeta Basin. We only sampled cross-sections and aged one of the evergreen species, which was the focus of our study; therefore, we present only the archival data for *Rhododendron maximum*. Chestnut stakes were used to establish plot corners in 1934 and most of these stakes were still standing when these plots were again inventoried in the 1970s and the 1990s. Trees 1.37 m height and $\geq$ 2.5 cm dbh were tallied by species in 2.5 cm diameter classes in each plot and these data were recorded on survey sheets separate from the Form 289 record books. The 1934 tree survey included diameter classes for live but chestnut blight (*Cryphonectria parasitica* (Murr.) Barr) infected *Castanea dentata* (Marshall) Borkh (Elliott and Swank 2008). Results from early surveys have been published (Elliott et al. 1999, Elliott and Swank 2008) and the most recent survey of these permanent plots has been conducted 2009–2011 (Elliott, unpublished data).

**Results.** Based on the 1934–35 survey, *Rhododendron maximum* occurred in 31% of the 979 plots and its average cover across the Basin was 9.1%; where it was present, its average cover was 29.5%. It co-occurred with *Kalmia latifolia* in 14% of the plots, and where *R. maximum* and *Kalmia* were mixed their combined evergreen cover was 55% (Table 2). For plots that were recorded as mixed *Rhododendron* and *Kalmia* with a total combined cover, we assumed a 50% contribution from each species (e.g., 40% cover of mixed = 20% *Rhododendron* + 20% *Kalmia*). Based on this assumption, the percent cover of either species individually could have been an over or under estimate.

Across our stream-to-ridge transects, *Rhododendron maximum* was the dominant understory species; it accounted for 82.6%, 82.2%, and 79.7% of the understory biomass, leaf mass, and leaf area, respectively (Table 3). In addition, *R. maximum* was more abundant than many of the overstory tree species, since it accounted for 6.3%, 41.6%, and 16.1% of the total aboveground biomass (overstory + understory), leaf biomass, and leaf area, respectively (Table 3). In contrast, deciduous species (including oaks) in the understory contributed $<$ 1% to the understory biomass and only 2.7% to the leaf area index (Table 3).

We found no significant relationships between *Rhododendron maximum* and overstory tree total biomass ($r^2 = 0.0174$, $P = 0.1033$, $n = 154$) or LAI ($r^2 = 0.0114$, $P = 0.1868$, $n = 154$) and distance from stream (Table 4). *Rhododendron maximum* density was much higher near the stream, with many more stems

Table 2. Frequency and average cover of *Rhododendron maximum* and frequency of plots with mixed *Rhododendron/Kalmia latifolia* recorded in 1934–1935*.

| Species recorded | Presence no. of plots | Frequency (%) | Average cover (%) | Cover (%, where present) |
|---|---|---|---|---|
| *Rhododendron* | 301 [167 single]** | 30.7 | 9.1 (SE = 0.57, $n$ = 979) | 29.5 (SE = 1.18, $n$ = 301) |
| Mixed****Rhododendron /Kalmia* | 134 | 13.7 | | 55.8 (SE = 2.00, $n$ = 134) |

* Data were collected from 979 permanent plots and recorded on USDA Forest Service Form 289, 1934–1935, a total of 13 record books are kept in a vault at Coweeta Hydrologic Laboratory.

** Value in brackets is the number of plots with a single evergreen species.

*** For plots that were recorded as mixed Rhododendron and Kalmia with a total combined cover, we assumed a 50% contribution from each species (e.g., 40% cover of mixed = 20% Rhododendron + 20% Kalmia).

Standard errors and number of plots are in parentheses.

< 2.5 cm dbs within 10 m of the stream (Fig. 1). Density of size classes > 2.5 cm dbs were comparable up to 40 m distance from the stream, then density declined exponentially beyond 40 m distance (Fig. 1).

The youngest *Rhododendron maximum* specimen was 6 years and the oldest specimen was 120 years based on the 487 cross-sections. *Rhododendron maximum* establishment year showed a slightly skewed modal distribution with the peak establishment occurring between 1928 and 1940 (Fig. 2); where 41% of the stems were < 60 years old, 49% were between 61–90 years old, and 10% were > 90 years old. *Rhododendron maximum* average age for the 10 m distance intervals from stream-to-ridge ranged from 60 to 74 years (Table 5). Nearest neighbor trees, ranged in age from 22 to 341 years, and average age for the 10 m distance intervals ranged from 91 to 151 years (Table 5). Overstory trees were older than *R. maximum* across the hillslopes from stream-to-ridge (Table 5). We found no significant relationship between the difference in *R. maximum* age and nearest neighbor tree age and distance from stream ($r^2$ = 0.0143, $P$ = 0.0621, $n$ = 237).

Overstory tree density of those that co-occurred with a *Rhododendron maximum* subcanopy was much lower (148 stems $ha^{-1}$) than tree density without a *R. maximum* subcanopy (737 stems $ha^{-1}$); i.e., interspaces between *R. maximum* patches (Figure 3). The diameter size class distribution showed an inverse-J shape with many more small trees than large trees (Figure 3). However, small trees were not necessarily young trees. The diameter-age relationship for all tree species combined was statistically significant, but not strongly predictive ($r^2$ = 0.198, $P < 0.001$, $n$ = 237). Species-specific relationships were more predictive for some of the species (Fig. 4). *Acer rubrum* L., *Quercus rubra* L., and *Quercus montana* Willd. had significant diameter-age relationships (Fig. 4), but diameter was only a moderate predictor of age.

Although the distance-from-stream and *Rhododendron maximum* age relationship was statistically significant, we found no interpretable relationship as distance-from-stream only explained 2.6% of the variation in *R. maximum* age (Fig. 5a). This relationship was not improved by removing the two sites in treated watersheds, HC and SD ($r^2$ = 0.018, $P$ = 0.0053, $n$ = 436). *Rhododendron maximum*

Table 3. Mean density, basal area, aboveground biomass, and leaf area index of *Rhododendron maximum*, *Kalmia latifolia*, other deciduous understory, and overstory trees.

| | Density (stems ha$^{-1}$) | Basal area (m$^2$ ha$^{-1}$) | Total mass* (Mg ha$^{-1}$) | Leaf mass* (kg ha$^{-1}$) | Leaf area index (m$^2$ m$^{-2}$) |
|---|---|---|---|---|---|
| All understory ($<$ 5.0 cm dbh) | 22,779 (2365) | 18.97 (2.10) | 21.21 (2.63) | 4,023 (493) | 1.47 (0.15) |
| *Rhododendron* | 15,593 (2414) | 15.69 (1.88) | 17.52 (2.52) | 3,306 (476) | 1.06 (0.15) |
| *Kalmia* | 5,035 (527) | 3.12 (0.76) | 3.61 (0.84) | 682 (159) | 0.34 (0.08) |
| Other deciduous understory | 5,842 (1532) | 0.26 (0.06) | 0.17 (0.04) | 55 (14) | 0.07 (0.02) |
| Overstory trees ($\geq$ 5.0 cm dbh) | 887 (120) | 31.2 (1.57) | 255.90 (20.94) | 3,930 (220) | 5.27 (0.29) |

* To estimate total aboveground biomass and leaf biomass we used allometric equations from Boring and Swank (1986) for *Rhododendron* and *Kalmia* stems $\leq$ 1.5 cm diameter base of stem (dbs, $\approx$ 10 cm above ground level) and all deciduous species; and equations from Baker and Van Lear (1998) for *Rhododendron* and *Kalmia* stems $>$ 1.5 cm dbs. Standard errors are in parentheses.

diameter explained 60% of the variation in *R. maximum* age (Fig. 5b). Diameter was a moderate predictor of *R. maximum* age; 10 cm stems ranged in age from 30 to 120 years old (Fig. 5b). We found no interpretable relationship between distance-from-stream and tree age; distance-from-stream only explained 4.2% of the variation in overstory tree age ($r^2$ = 0.042, $P$ = 0.0015, $n$ = 237).

**Discussion.** Others have found that the presence of an evergreen understory layer can have a profound influence on the structural characteristics of forest stands in the Appalachians (Phillips and Murdy 1985, Chastain and Townsend 2006, 2008, Nilsen et al. 2009). In the Coweeta Basin of the southern Appalachians, evergreen shrubs are currently abundant and likely to have influenced, and will continue to influence, stand development over the coming decades. Across our stream-to-ridge sites, *Rhododendron maximum* coverage ranged from 15 to 100%, and its contribution to the total leaf biomass and leaf area index was considerable across the hillslopes. Has *R. maximum* been expanding its coverage across the Basin and if so, should we expect this expansion to continue? To answer these questions, we used three approaches: (1) comparing archival data of *R. maximum* with more recent surveys, (2) examining the age distribution of *R. maximum* ramets and associated overstory species, and (3) relating *R. maximum* age to distance from stream.

COMPARISON OF ARCHIVAL DATA. We found that *Rhododendron maximum* frequency increased from 1934 to the 1970s, and then remained nearly constant. Based on archival data ($n$ = 979 plots), *R. maximum* frequency was 31% in 1934 and increased by 50% over

Table 4. Mean aboveground biomass and leaf area index for *Rhododendron maximum* and overstory trees at 10 m distance intervals from stream-to-ridge.

| | | Total biomass (Mg ha$^{-1}$) | | Leaf area index (m$^2$ m$^{-2}$) | |
|---|---|---|---|---|---|
| *N** | Distance | *Rhododendron* | Trees | *Rhododendron* | Trees |
| 16 | 0–10 | 22.13 (2.68) | 290.01 (49.35) | 1.413 (0.155) | 5.168 (0.757) |
| 16 | 11–20 | 18.54 (3.77) | 281.44 (48.58) | 1.181 (0.216) | 4.758 (0.608) |
| 16 | 21–30 | 18.04 (3.46) | 220.69 (29.83) | 1.153 (0.191) | 4.712 (0.548) |
| 16 | 31–40 | 22.94 (4.92) | 208.43 (23.85) | 1.435 (0.290) | 4.596 (0.411) |
| 15 | 41–50 | 19.75 (2.93) | 245.90 (28.26) | 1.215 (0.174) | 5.376 (0.498) |
| 14 | 51–60 | 16.86 (3.48) | 191.43 (27.26) | 1.044 (0.204) | 4.351 (0.422) |
| 13 | 61–70 | 18.01 (3.71) | 231.32 (41.58) | 1.237 (0.207) | 5.247 (0.702) |
| 13 | 71–80 | 12.12 (2.76) | 220.34 (55.61) | 0.798 (0.158) | 4.772 (0.820) |
| 9 | 81–90 | 11.92 (3.70) | 344.55 (61.69) | 0.845 (0.219) | 7.085 (0.818) |
| 8 | 91–100 | 13.72 (4.27) | 170.71 (41.90) | 0.954 (0.256) | 4.488 (0.776) |
| 7 | 101–110 | 15.19 (9.96) | 433.56 (108.40) | 1.072 (0.585) | 7.656 (1.666) |
| 6 | 111–120 | 4.12 (3.29) | 266.63 (83.44) | 0.420 (0.210) | 5.393 (1.488) |
| 4 | 121–130 | 9.91 (5.63) | 223.38 (58.36) | 0.768 (0.303) | 5.254 (1.488) |

* *N* = number of sites that extended to the corresponding distance from the stream. Standard errors are in parentheses.

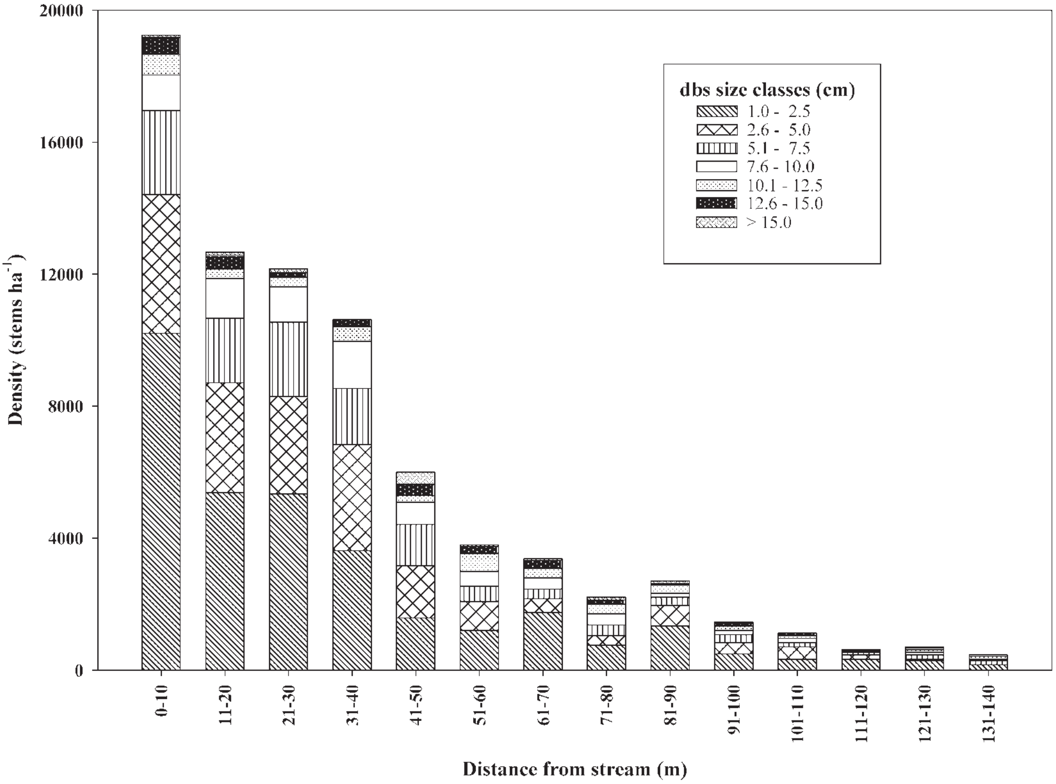

FIG. 1. Diameter (dbs, diameter at 10 cm above groundline) size class distributions of *Rhododendron maximum* with distance from stream. Stem counts were summed for each 10 m distance interval for the entire transect from stream edge to ridge and then averaged across sites. Only two of the 16 sites had a distance greater than 140 m from the stream to the ridge.

the approximate 35 yr period between 1934 and the 1970s. Elliott et al. (1999) used a subset ($n$ = 283) of the original permanent plots and found that *R. maximum* was well distributed across the Coweeta Basin. *Rhododendron maximum* frequency was 81% in the 1970s, 83% in the 1990s (Elliott et al. 1999), and 87% in the 2010s (Elliott, unpublished data). Because the frequency estimates from Elliott et al. (1999) were obtained from a smaller data set than the original 1934 survey, we recalculated frequency for 1934 based on the smaller sample size with the information in the 1934–35 archival records. *Rhododendron maximum* was present in 27% of the 283 plots, only slightly less than its estimated frequency of 31% from the full data set (Table 2), which verifies that the reduced data set was not preferentially biased towards *R. maximum* occupancy and gave a reasonable frequency estimate of later survey periods.

While *Rhododendron maximum* frequency increased substantially sometime between 1934 and the 1970s surveys, its frequency has remained nearly the same over the 40-year period between the 1970s and the 2010s. In addition, *R. maximum* average density had changed little between surveys, 1366 in the 1970s (Elliott et al. 1999) compared to 1285 stems ha$^{-1}$ in the 2010s (Elliott, unpublished data). In the nearby Great Smoky Mountains National Park, *R. maximum* importance value has also remained relatively constant since the late 1970s (Jenkins and White 2002, Webster et al. 2005). These findings conflict with Dobbs and Parker (2004) who concluded that *R. maximum* expanded in the Coweeta Basin. Dobbs (1998) and Dobbs and Parker (2004) used aerial photographs from 1976 and 1993, to estimate expansion of evergreen understories in undisturbed areas within the Coweeta Basin, western North Carolina and concluded that evergreen vegetation had expanded by 13% over the 17-year period. Uncertainties in the estimations of *R. maximum* distribution and expansion were outlined by Dobbs (1998)

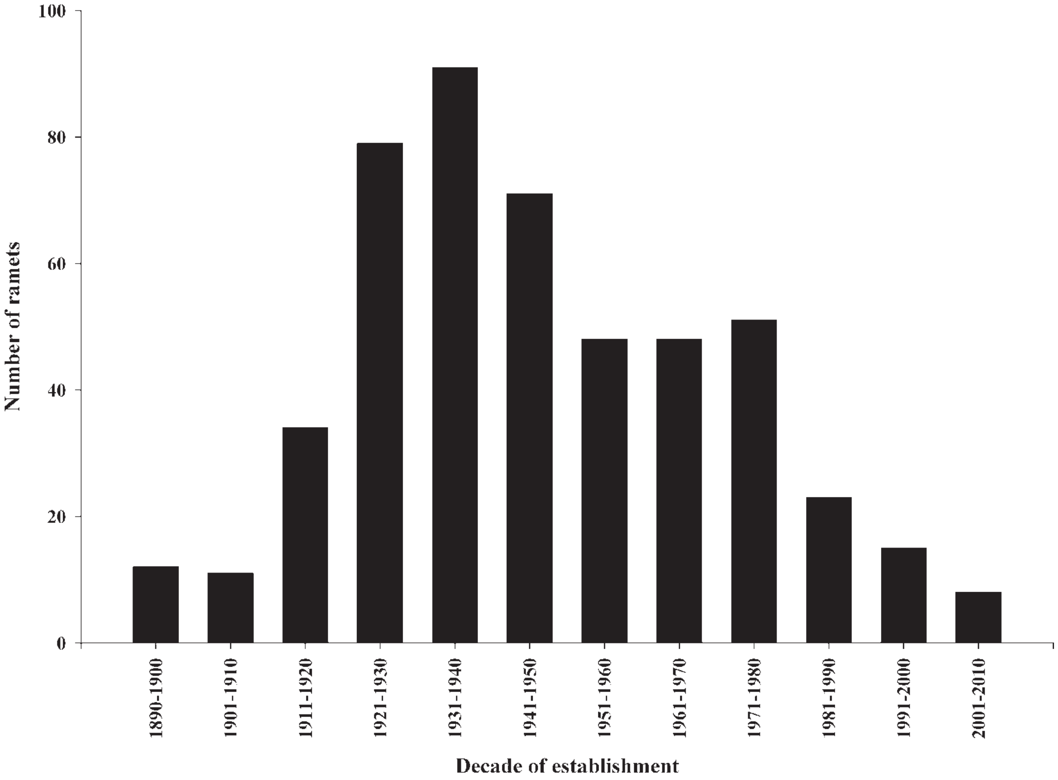

FIG. 2. Establishment year for *Rhododendron maximum* ramets ($n$ = 487 cross-sections) for the 16 stream-to-ridge sites.

and included: (1) reference data was derived from interpretation of aerial photographs whose accuracy was assessed at ~78%; (2) initial classification of vegetation was subjective “predominately *R. maximum*’ vs. “mixed *R. maximum /K. latifolia*”; and (3) vegetation boundaries were fuzzy, but were necessarily delineated nonetheless in making of maps.

Table 5. Mean age of *Rhododendron maximum* and nearest neighbor trees at 10 distance intervals from stream-to-ridge.

| Distance (m) | $n$* | Rhododendron age | $n$* | Tree age | Difference (Tree - Rhododendron) |
|---|---|---|---|---|---|
| 0–10 | 137 | 60 (2) [6–117] | 61 | 94 (6) [24–341] | 34 |
| 11–20 | 86 | 60 (3) [8–120] | 37 | 113 (11) [22–292] | 53 |
| 21–30 | 83 | 63 (4) [11–118] | 21 | 98 (12) [25–229] | 35 |
| 31–40 | 50 | 64 (3) [10–120] | 29 | 98 (8) [34–216] | 34 |
| 41–50 | 36 | 63 (4) [9–109] | 26 | 109 (11) [25–276] | 46 |
| 51–60 | 28 | 63 (3) [17–105] | 14 | 110 (14) [32–252] | 47 |
| 61–70 | 17 | 65 (4) [14–95] | 10 | 91 (9) [50–152] | 26 |
| 71–80 | 21 | 67 (3) [25–92] | 9 | 93 (7) [68–129] | 26 |
| 81–90 | 15 | 76 (5) [37–113] | 7 | 144 (24) [74–217] | 68 |
| 91–100 | 9 | 73 (5) [51–94] | 6 | 102 (15) [70–171] | 29 |
| 101–110 | 6 | 58 (7) [39–86] | 3 | 124 (27) [83–176] | 66 |
| 111–120 | 3 | 71 (2) [68–75] | 1 | 119 (–) | 48 |
| 121–130 | 2 | 70 (1) [69–71] | 4 | 119 (22) [61–171] | 49 |
| 131–140 | 4 | 74 (1) [72–76] | 2 | 128 (48) [80–176] | 54 |
| > 140 | 20 | 74 (4) [34–104] | 7 | 158 (11) [116–210] | 84 |

* $n$ = number of *Rhododendron maximum* cross sections or number of tree increment cores for each 10-m distance interval from stream. Standard errors are in parentheses and ranges are in brackets.

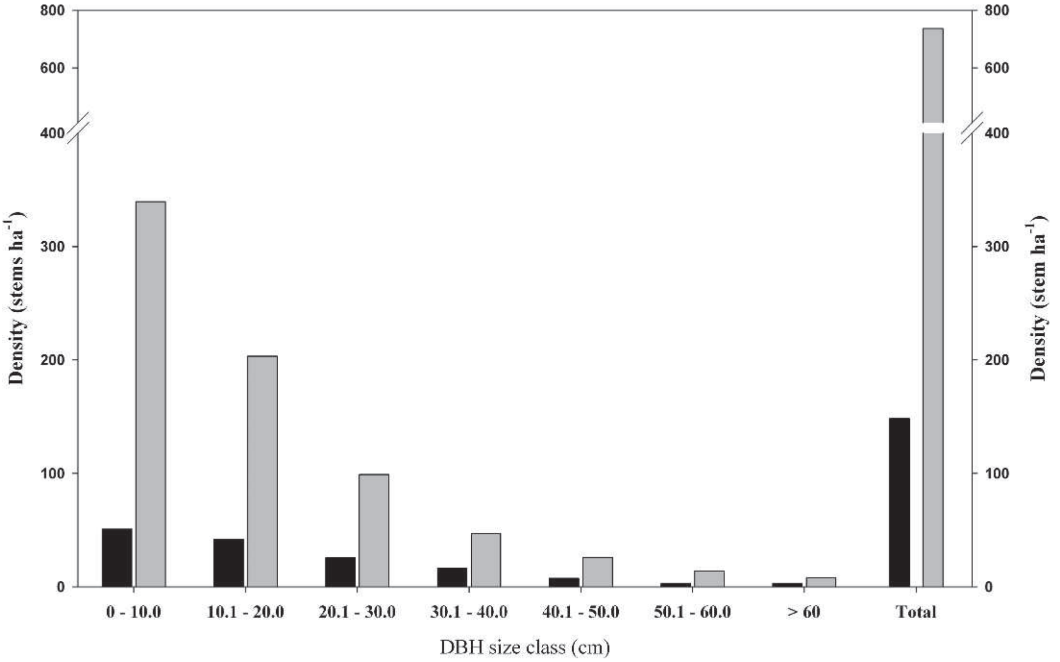

Fig. 3. Diameter (dbh, diameter at 1.37 m above groundline) size class distribution of overstory trees $\geq$ 2.5 cm dbh with (black bars) and without (gray bars) a *Rhododendron maximum* subcanopy.

Forests within the Coweeta Basin were relatively closed canopy 75 years ago, at the time of the first survey in 1934 (Elliott and Swank 2008). *Castanea dentata* had not yet succumbed to the chestnut blight; i.e., most trees were standing live or dying stems and its basal area was 36% of the Basin's total basal area (Elliott and Swank 2008). By the 1970s survey, all *C. dentata* had died and fallen, its basal area was reduced substantially from 10.1 to only 0.38 m$^2$ ha$^{-1}$; whereas, the total basal area for the Basin was nearly the same after 35 years of forest growth, 28.0 m$^2$ ha$^{-1}$ in 1934 versus 27.0 m$^2$ ha$^{-1}$ in the 1970s as *C. dentata* was gradually replaced by other hardwoods (Elliott and Swank 2008). Between the 1934 and the 1970s surveys, *Rhododendron maximum* frequency had increased from 30 to 81%. Most likely *R. maximum* recruited into plots as a single cohort soon after the 1934 survey based on its peak modal age.

Age Class Distribution of Rhododendron and Associated Overstory Trees. In our study, the peak modal establishment of *Rhododendron maximum*, between 1928 and 1940, coincides with the period of *Castanea dentata* mortality (mid-to-late 1930s) due to the chestnut blight in the Coweeta Basin (Elliott and Swank 2008). This finding is consistent with McGinty (1972) who determined the age of 30 *R. maximum* specimens in a small watershed within the Coweeta Basin and speculated that the establishment of *R. maximum* thickets coincided with the opening of the canopy caused by the death of *C. dentata* trees.

Overstory trees were older than *Rhododendron maximum* across the hillslopes from stream to ridge. Average tree age was 113 years with many trees > 150 years old. However, overstory density (887 stems ha$^{-1}$) was much lower across our stream-to-ridge sites compared to the average overstory density for the Coweeta Basin (1372 stems ha$^{-1}$, Elliott and Swank 2008). Indeed, where trees occurred within a *R. maximum* thicket, overstory density was very low (148 stems ha$^{-1}$) compared to density in interspaces between thickets (737 stems ha$^{-1}$). At the time of peak *R. maximum* establishment, overstory canopies were sparse and would have allowed enough light penetration for *R. maximum* seed germination. Once *R. maximum* was established, further recruitment of tree species was less likely under the dense understory layer (Beckage et al. 2000, Nilsen et al. 2001, Beier

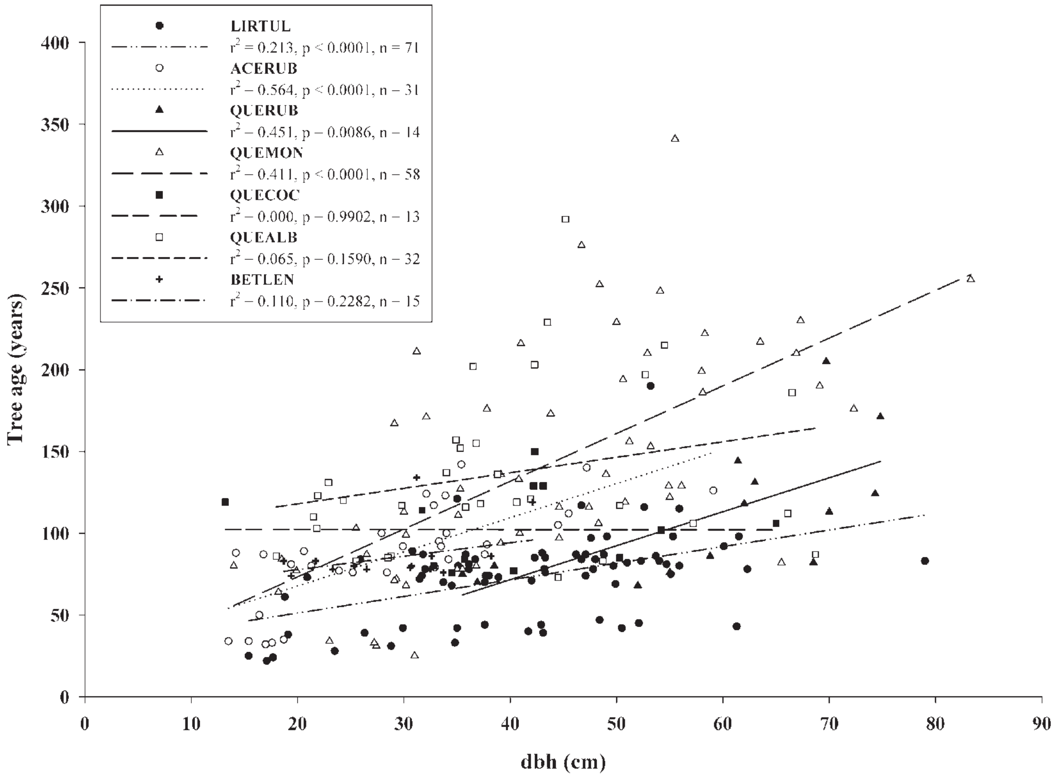

FIG. 4. Species-specific diameter-age relationships for overstory trees ≥ 10 cm dbh. Codes are LIRTUL, *Liriodendron tulipifera* L.; ACERUB, *Acer rubrum* L.; QUERUB, *Quercus rubra* L.; QUEMON, *Quercus montana* Willd.; QUECOC, *Quercus coccinea* Münch.; QUEALB, *Quercus alba* L.; and BETLEN, *Betula lenta* L.

et al. 2005, Lei et al. 2006). We found higher numbers of small trees than large trees across the hillslopes, but the low predictive power of the diameter-age relationships confirmed that the small trees were not necessarily young trees. For example, trees > 100 years-old ranged in size from 13.6 to 77.8 cm dbh.

Earlier studies have also concluded that *Rhododendron maximum* expanded soon after large scale disturbance (McGee and Smith 1967, McGinty 1972, Plocher and Carvell 1987). McGee and Smith (1967) measured eight *R. maximum* thickets near Asheville, NC and reported that thickets were even-aged and most of the *R. maximum* became established between 1897 and 1917, a period that parallels the cessation of fire and grazing, but more importantly coincides with the period of heavy logging (1880s to 1920s) across the region. In addition, they maintained that no outward spreading had occurred in the eight thickets they sampled (McGee and Smith 1967). In West Virginia, Plocher and Carvell (1987) found that *R. maximum* thickets were also relatively even-aged and dated from the most recent logging; thicket ages ranged from 57 to 122 years-old. They used excavation to identify root suckers versus seedlings and concluded that thickets with drier conditions and open canopies produced seedlings nearby and exhibited no layering; whereas, thickets with wetter conditions and denser canopies produced very few seedlings and exhibited profuse layering. Plocher and Carvell (1987) may have identified root suckers versus seedlings, but they likely could not have distinguished branch layering from seedlings. Vegetative reproduction via root sprouts or stump sprouts may be distinguished by excavation since roots maintain a connection, however, vegetative reproduction via branch layering would be difficult to distinguish from sexual reproduction using excavation alone. With branch layering, branches are weighed down by heavy snow or fallen debris, where the branch makes contact with the ground rooting

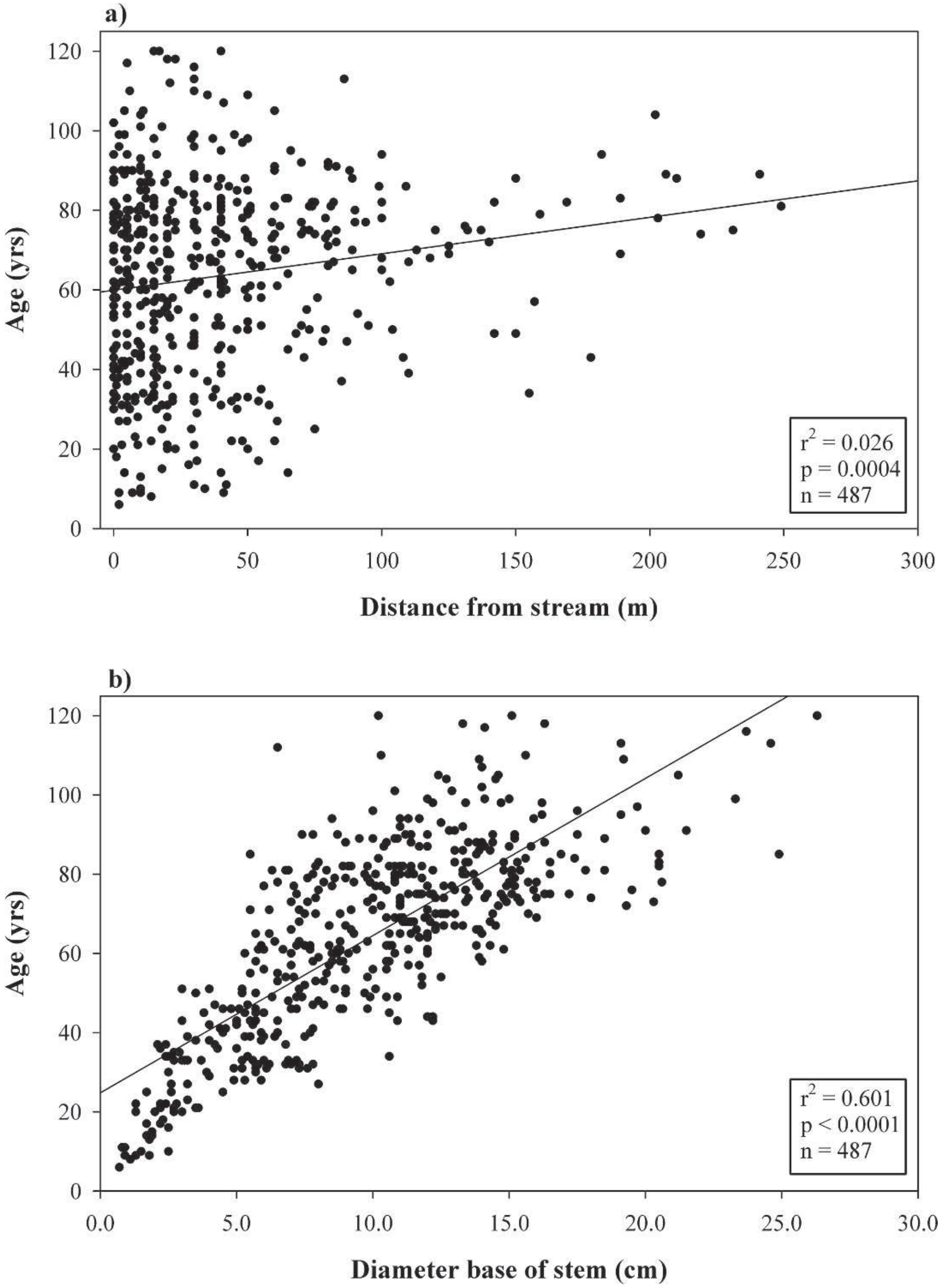

FIG. 5. Relationships between age of *Rhododendron maximum* and a) distance from stream; and b) *Rhododendron* stem diameter for the stream-to-ridge sites.

may occur, subsequently as the branch decomposes there is a separation of the branch from the parental plant, and finally independent ramets are formed without a shared root system and there is no obvious connection with the parent plant (Erfmeier and Bruelheide 2004). For existing populations, it remains unknown how much *R. maximum* recruitment established from layering versus how much established from seed germination. For clonal plants, such as *R. maximum*, either DNA analysis of existing stems or detailed demographic information over an extended period are required to determine the relative contributions of sexual and asexual reproduction (Pornoni and Escaravage 1999, Doescher et al. 2003, Arnaud-Haond et al. 2007, deWitte and Stocklin 2010).

We found a greater number of small diameter *Rhododendron maximum* stems near the stream with a decreasing trend further away from the stream suggesting that recruitment, possibly through layering, was more prolific in wetter conditions. Thickets were uneven-aged, as we found a range in stem sizes and ages. Uneven-aged stand structure is common for a shade-tolerant woody species (Eşen *et al.* 2004) and stem diameter is commonly used instead of age for assessing stand vegetation structure. This may result in erroneous conclusions about the population growth because diameter-age relationships are generally weak for shade-tolerant tree species (Smith *et al.* 1997). In our study, *R. maximum* had a moderate correlation between diameter and age, similar to that seen in other rhododendron species (Eşen et al. 2004). The inverse J-shaped diameter distribution also confirmed the uneven-aged structure across the hillslopes (Eşen et al. 2004, Eşen et al. 2006). This finding is in contrast with others who described even-aged *R. maximum* thickets (McGee and Smith 1967, Plocher and Carvell 1987, Baker and Van Lear 1998).

Baker and Van Lear (1998) measured *Rhododendron maximum* thickets in the southern Appalachians and found that cohort age was younger in sparse thickets compared to dense thickets, and *R. maximum* cover declined as distance from the stream increased (Baker and Van Lear 1998). However, they did not age *R. maximum* stems beyond 20 m from the stream bank and they do not provide an age vs. stream distance relationship (Baker and Van Lear 1998). In their study, *R. maximum* was younger (averaged 19–28 years-old, depending on thicket density) than the overstory trees (averaged 42–44 years-old); and they concluded that *R. maximum* regenerated under the tree canopy (Baker and Van Lear 1998); however, *R. maximum* ages ranged from 1–47 years. Thus, the initial recruitment, the older stems that exceeded the age of the overstory, occurred soon after the last harvest in the 1940s, and then numbers increased. Baker and Van Lear (1998) did not distinguish between seed germination and vegetative reproduction, nonetheless, their conclusions conflict with other studies, including ours, that suggest establishment of *R. maximum* requires canopy openings (McGee and Smith 1967, Plocher and Carvell 1987, Chastain and Townsend 2008).

RHODODENDRON AGE VS. DISTANCE FROM STREAM. Our results correspond more closely with studies that found *Rhododendron maximum* thickets established soon after a disturbance that opened the canopy (McGee and Smith 1987, Plocher and Carvell 1987) and concluded that *R. maximum* thickets do not expand laterally without partial canopy removal. We found no meaningful relationships between age of *R. maximum* stems and distance from stream suggesting that it expanded significantly following the chestnut blight pandemic in the mid-to-late 1930s and has remained in its current position across the hillslope for at least 40 years. In our study and others (McGee and Smith 1987, Plocher and Carvell 1987, Chastain and Townsend 2008), maximum age of *R. maximum* stems (ramets) was 120 years; as older ramets died they were replaced by younger ramets through vegetative reproduction, thus an individual genet survives for much longer than the maximum ramet age.

*Rhododendron maximum* density was highest near the stream and declined as distance from stream increased; yet average age remained relatively constant across the hillslopes from stream to ridge. All ages were represented within the first 10 m of the stream bank where density was highest, but there were few young stems (< 20 yrs) beyond 70 m from the stream edge (Table 5). In the upslope positions, layering may be limited due to dry soils and seedling establishment may be limited due to low light availability under a closed canopy. Thus, without further disturbances that create canopy openings, *R. maximum* may recede towards the riparian areas where wetter soil conditions would allow for adventitious rooting of branches (Rein et al. 1991), i.e., branch layering.

Studies have shown than *Rhododendron maximum* requires more light than is available in a typical forest understory for seed germination (Romancier 1970, Blazich et al. 1991) and stem growth (Russell et al. 2009, Ford et al. 2011). For example, Blazich et al. (1991) studied *R. maximum* seed germinations in a growth chamber which provided photosynthetic photon flux (PPFD, 400–700 nm) of 40 μmol $m^{-2}$ $s^{-1}$. At 30 days and 25 °C, germination of *R. maximum* was $\leq$ 17% for photoperiods $\leq$ 4 hr, increased to 70% with 8 hr photoperiod, and a further increase to 24 hr photoperiod did not appreciably influence germination (82% at day 30). However, light under forest canopies are most often lower than that required for seed germination (Clinton 2003). Beier et al. (2005) found that mean midday PPFD under *R. maximum* was below 10 μmol $m^{-2}$ $s^{-1}$ on both clear and overcast days and the cumulative sunfleck of greater than 10 μmol $m^{-2}s^{-1}$ was only 0–20 min per day. In contrast, forest without *R. maximum* received a mean PPFD of 18–25 μmol $m^{-2}$ $s^{-1}$ on clear days and cumulative sunfleck duration of 100–220 min per day in all sky conditions (Beier et al. 2005). Thus, even under closed canopy hardwood forests the light level would be too low for *R. maximum* seeds to germinate.

A more recent canopy disturbance that may create canopy openings sufficient for *Rhododendron maximum* recruitment is the loss of *Tsuga canadensis* L. Southern riparian *T. canadensis* forests tend to occur as mixed *Tsuga*-hardwoods often with a *R. maximum* understory (Elliott and Swank 2008, Kincaid and Parker 2008, Roberts et al. 2009). Hemlock woolly adelgid (*Adelges tsugae* Annand) was first noted in 2003 in the Coweeta Basin (Elliott and Vose 2011); and in the most recent 2011 survey, a complete loss of *T. canadensis* trees was found (Elliott, unpublished data). Incident light in riparian corridors with heavy *T. canadensis* mortality is often higher than that of adjacent hardwood forests (Ford et al. 2011) due to gap creation. With the disturbance to riparian forest canopy caused by *T. canadensis* mortality, it is possible that *R. maximum* could expand along formerly *T. canadensis* dominated riparian corridors and prevent the recruitment of hardwood canopy-tree seedlings. Thus, dense *R. maximum* thickets without overstory tree species may become more prevalent in the riparian forest of the southern Appalachians (Roberts et al. 2009, Ford et al. 2011).

Perhaps, a combination of factors must coincide before *Rhododendron maximum* can expand beyond near stream habitats. Upslope expansion appears to depend on seed dispersal into safe sites where seed germination can be successful. Canopy disturbance is necessary to provide adequate light for seed germination and seedling growth and development. Following seedling establishment, the lack of understory disturbance, such as livestock grazing, deer browsing and surface fires, may also be necessary to provide enough time for seedlings to grow into mature shrubs. There have been no fires or grazing in the Coweeta Basin for 100 years or more, whereas, peak *R. maximum* recruitment followed canopy disturbance in the mid 1930s. However, the lack of fire (or other possible understory disturbances) cannot explain the relatively constant frequency of the *R. maximum* in the understory since the 1970s. If *R. maximum* had expanded due to fire suppression, it would have expanded under a closed canopy, yet this is contrary to the biology of *R. maximum* and the evidence outlined above.

**Conclusions.** *Rhododendron maximum* has likely been present in the Appalachians for centuries (Harshberger 1903, Oostings and Billings 1939). Oostings and Billings (1939) described an old growth, high elevation (1340 m) forest near Highlands, NC. "Along the streams and in the depressions, rhododendron was the principal understory shrub, almost, to the exclusion of other species. In places, the rhododendron layer was as dense and tangled as to be practically impenetrable…" (Oostings and Billings 1939). What is uncertain is whether *R. maximum* has expanded over the last several decades due to lack of disturbance (Dobbs 1998, Baker and Van Lear 1998, Dobbs and Parker 2004) or expanded earlier in the 20th century due to disturbance events that opened the canopy (McGinty 1972, Plocher and Carvell 1987, Chastain and Townsend 2008).

Our data suggest that, at least within the Coweeta basin, *Rhododendron maximum* expanded in the early 1900s due to a combination of widespread logging and the chestnut blight that resulted in major canopy disturbances. Archival data showed that *R. maximum* occupied 30% of the survey plots in 1934, more than doubled by the 1970s, and has remained relatively constant for the last 40 years. *Rhododendron maximum* establishment year showed a unimodal distribution with a pulse of recruitment between 1928 and 1940. Although overstory trees were older than *R. maximum* across the hillslopes, tree density was low, particularly within *R. maximum* thickets, indicating a sparse canopy at the time of the *R. maximum* recruitment pulse. We found no meaningful relationships between *R. maximum* age and distance from stream indicating that *R. maximum* has not moved upslope overtime.

Little is known about the demography of *Rhododendron maximum*, despite earlier attempts to describe its mode of reproduction, expansion, and rate of spread, due to small sample size, constrained spatial extent, unsuitable methodologies, or a combination of these problems. Our study has only begun to answer questions concerning *R. maximum* expansion by using dendrochronology and stream-to-ridge measurements to describe *R. maximum* age structure across hillslopes. While our study showed a maximum age of 120 years for ramets, we have no knowledge of (1) the life span of the genet, (2) if *R. maximum* establishes primarily via seed dispersal and seedling survival or primarily via branch layering, or (3) the lateral expansion rate and what environmental factors constrain the expansion rate. For a better understanding of the population dynamics of clonal plants, genetic methods have been used to fingerprint individuals in order to differentiate between genets and ramets. This methodology would allow researchers to answer these more difficult demographic questions.

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