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Origin, development, and impact of mountain laurel thickets on the mixed-oak forests of the central Appalachian Mountains, USA

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ABSTRACT

Throughout forests of the northern hemisphere, some species of ericaceous shrubs can form persistent understories that interfere with forest regeneration processes. In the Appalachian Mountains of eastern North America, mountain laurel (*Kalmia latifolia*) may interfere in the regeneration of mixed-oak (*Quercus* spp.) forests. To verify this possibility, I conducted a dendroecology study from 2001 to 2005 in three mixed-oak stands with mountain laurel thickets to elucidate how and when the thickets originated, developed, and were impacting hardwood seedlings. At all three sites, the oldest mountain laurel dated to the 1930s when the stands emerged from a period of recurring disturbance. However, most of the mountain laurel has originated since the 1950s when the stands were generally undisturbed. More recently, insect defoliations have accelerated the development of the thickets by increasing available sunlight. A strong negative relationship exists between the percent cover of mountain laurel and the density of hardwood seedlings with 20–30% cover being sufficient to inhibit seedling establishment and survival. Perpetuating mixed-oak forests that contain mountain laurel thickets will require reducing shrub cover to less than 20–30% at the beginning of the regeneration process to help ensure adequate densities of hardwood seedlings.

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1. Introduction

Of all the forest types found in eastern North America, natural resource professionals, landowners, and the general public especially value the upland mixed-oak (*Quercus* spp.) forest because of its biological diversity, ecological services, and economic worth (Smith, 2006). Depending on local conditions, this widespread forest type often contains several species of oak, an assortment of other hardwood species, and a diverse understory plant community. Despite its extensive range, the upland mixed-oak forest has chronic regeneration difficulties because of competing and interfering vegetation, excessive browsing by whitetail deer (*Odocoileus virginianus*), disease/insect problems, lack of periodic fire, and unsustainable harvesting practices (Abrams and Downs, 1990; Aldrich et al., 2005; Schuler and Gillespie, 2000). Consequently, perpetuation of upland mixed-oak forests is in doubt (Healy et al., 1997; McWilliams et al., 2004; Woodall et al., 2008). Of these factors, the competing/interfering vegetation problem is probably the most deleterious and widespread (Brose, 2011; Crow, 1988; Lorimer, 1993; Lorimer et al., 1994). Generally, that problem correlates with site quality; competing/interfering vegetation is much more problematic on high productivity sites than on low productivity sites (Gould et al., 2005; Johnson et al., 2009; Ross et al., 1986; Weaver and Robertson, 1981). In fact, competing/interfering vegetation is often not considered an obstacle to regenerating mixed-oak forests on low-quality sites (Johnson et al., 2009).

An exception to the generality of low quality site – lack of competing/interfering vegetation may be the occurrence of mountain laurel (*Kalmia latifolia*) on such sites throughout the Appalachian Mountains of the eastern United States. This ericaceous shrub grows up to 4 m tall and broad, and has large, thick evergreen leaves. When multiple mountain laurels grow in close proximity to each other their branches intersect, creating a dense thicket. Such thickets can consist of thousands of stems/hectare and cover several hectares. Hardwood seedlings, especially oak seedlings, are usually scarce in mountain laurel thickets, making forest renewal an arduous, protracted process.

Mountain laurel may be one of a suite of ericaceous shrub species capable of becoming an obstacle to forest renewal (Royo and Carson, 2006). Elsewhere in the eastern United States, rosebay rhododendron (*Rhododendron maximum*) interferes with the establishment, survival, and growth of the seedlings of conifer and hardwood species in riparian zones and other mesic areas while black huckleberry (*Gaylussaccia baccata*) behaves similarly on xeric sites (Beckage et al., 2000; Chastain and Townsend, 2008; Clinton et al.,

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1994; Lei et al., 2002; Monk et al., 1985; Phillips and Murdy, 1985). In eastern Canada, sheep laurel (*Kalmia angustifolia*) has been shown to exert direct negative effects on the survival and growth of black spruce (*Picea mariana*) seedlings (Inderjit and Mallik, 1996; Yamasaki et al., 1998, 2002). Relative to sheep laurel and rosebay rhododendron, mountain laurel has not been studied extensively. Chapman (1950) conducted the earliest research on the shrub, a multi-year study done in Connecticut. He showed that mountain laurel was long-lived, at least 75 years, slow-growing (7–30 cm/year height growth), quite shade tolerant, and its thickets reduced understory insolation to less than 5% of full sunlight. In a follow-up study in Connecticut, Kurmes (1961) found that mountain laurel seed had its highest germination rates on moss and moist mineral soil, the shrub responded to increases in sunlight with increased height growth, and its thickets spread through mixed-oak forests via layering of its lowermost branches. More recently, ecophysiology research of mountain laurel reported that (1) the shrub had increased photosynthetic capacity and water use efficiency with increases in available sunlight, (2) its abundance was positively correlated with soil Ca:Al ratios less than 0.3 and to increasing soil acidity, (3) its evergreen foliage may sequester Mn, P, and Zn, and (4) its release of phenolic compounds may inhibit nitrogen mineralization (Huebner et al., 2014; Lipscomb and Nilsen, 1990a,b; Nilsen et al., 2001). Established and recent natural history research has shown mountain laurel thickets to be strongly associated with dry, exposed topographic positions and with gypsy moth (*Lymantria dispar*) defoliations (Chastain and Townsend, 2008; Clinton et al., 1994; Monk et al., 1985).

An interesting and unstudied aspect of mountain laurel thickets is their ecological history. Questions remain about when and under what conditions current mountain laurel thickets originated and developed as well as what are their likely future and the future of the surrounding forests. Dendroecological techniques can be used to address these and related questions by analyzing age structure and radial growth in relation to land-use history. In this study, I elucidate how three mountain laurel thickets and the surrounding mixed-oak forests began and developed through time. Specific research questions are: (1) What are the age structures of the thickets and the overstory trees? (2) When did both originate and what were the circumstances of their origins? (3) What has been the disturbance history of the thickets and overstory trees and how have they responded to the disturbances? and (4) What impacts are the thickets having on hardwood seedlings? Understanding the ecological history of mountain laurel thickets and their effects on hardwood seedlings will aid foresters and forest landowners in managing them so they do not become problematic to oak regeneration efforts.

2. Methods

2.1. Study sites

This study was conducted from 2001 to 2005 in three upland oak stands located across Pennsylvania (Fig. 1). The westernmost site (41°19′03″N, 79°02′21″W) was on Clear Creek State Forest (CCSF) while the easternmost site (41°18′27″N, 75°05′50″W) was on Delaware State Forest (DESF). The third site was in central Pennsylvania (40°42′59″N, 77°54′03″W) on the Rothrock State Forest (RRSF). Despite being 150–400 km from each other, the three study stands shared a number of characteristics. Each stand was 15- to 20-ha, situated on the upper slopes or summits of hills, had a stony loam soil, and an oak site index$_{50}$ of 16–20 m (Braker, 1981; Taylor, 1969; Zarichansky, 1964). Chestnut oak (*Quercus montana*) and northern red oak (*Quercus rubra*) were the most abundant oak species, but black oak (*Quercus velutina*), scarlet oak (*Quercus coccinea*), and white oak (*Quercus alba*) were also present. Associated tree species included blackgum (*Nyssa sylvatica*), pitch pine (*Pinus rigida*), red maple (*Acer rubrum*), serviceberry (*Amelanchier arborea*), and white pine (*Pinus strobus*). Canopy cover was not ubiquitous due to past canopy disturbances, but I visually estimated overstory stocking to be more than 70%. Mountain laurel dominated the understory plant community with its abundance ranging from individual shrubs to thickets covering a few hectares. Also present were other shrub species such as bear oak (*Quercus ilicifolia*), blueberry (*Vaccinium* spp.), huckleberry (*Gaylussacia* spp.), and sweet-fern (*Comptonia peregrina*). Herbaceous plant diversity was quite limited; it consisted of small areas of hay-scented fern (*Dennstaedtia punctilobula*) and scattered specimens of beetleweed (*Galax aphylla*), goat's rue (*Tephrosia virginiana*), trailing arbutus (*Epigaea repens*), and wintergreen (*Gautheria procumbens*). Hardwood seedlings were of the same species as the overstory trees and ranged in abundance from non-existent to ubiquitous.

Because these sites were 150–400 km apart, they differed in a number of characteristics. The CCSF site was in the Allegheny Plateau region while the DESF and RRSF sites were in the Pocono Plateau and Ridge/Valley regions, respectively (Schultz, 1999). Their weather varied with CCSF being the coolest and wettest, RRSF being the warmest and driest, and DESF was intermediate (Braker, 1981; Taylor, 1969; Zarichansky, 1964). The RRSF site was on a north aspect while the other two sites had southeastern aspects. The CCSF site was the highest, approximately 575 m, while DESF and RRSF were between 450 and 500 m. Their histories differed too; RRSF probably had been subjected to short-rotation timber harvesting for several decades due to its proximity to charcoal iron furnaces while the other two sites likely experienced just one or two timber harvests in the early 1900s (DeCoster, 1995; Eggert, 1994).

2.2. Sampling and lab procedures

In 2001 and 2002 at each site, I systematically established four 0.001-ha circular plots per hectare (84–100 plots per site) to uniformly inventory the understory. In these plots, I tallied all hardwood reproduction less than 3 m tall by species and height class using established sampling procedures (Marquis et al., 1992). Additionally, I visually estimated the cover of mountain laurel on the plot to the nearest 5%.

From the center of every-other understory plot, I used a 2.3 m prism to determine which nearby overstory trees more than 3 m tall were in a variable-radius plot. Selected trees were identified to species, measured for diameter to the nearest 2.5 cm at 1.4 m above the ground (dbh), and assigned to a canopy class (dominant, co-dominant, intermediate or suppressed) based on visual observation. For aging and radial growth analysis, I randomly chose four of these trees (two dominant or co-dominant and two intermediate or suppressed) in each overstory plot. If the selected tree was larger than 10 cm dbh, I extracted two increment cores from its bole at a height of approximately 30 cm above the ground. These cores were taken from the opposite sides of the tree and parallel to the contour so as to avoid any reaction wood that may distort the annual rings (Speer, 2010). If the selected tree was less than 10 cm dbh, then it was felled with a chain saw and a cross section cut from its base at ground level. Finally, I cut a cross section from the base of the mountain laurel (larger than 2.5 cm basal diameter) nearest each sampled overstory tree.

The sampling collected 690 cores and 759 cross sections from the three sites. In August 2002, a structure fire at the Forestry Sciences Lab in Irvine, Pennsylvania resulted in the loss of 324 cores and 513 cross sections. This loss was spread fairly evenly among the three sites; each was left with 96–119 cores and 101–

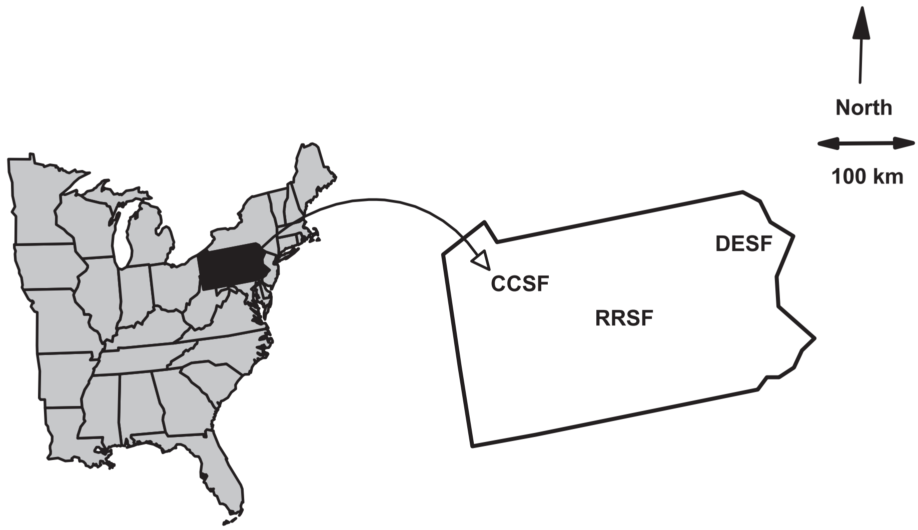

Fig. 1. The location of Pennsylvania in the eastern United States and the location of the three study sites (CCSF, DESF, and RRSF) within Pennsylvania.

108 cross sections. Management activities due to a related silviculture study at the three sites prevented any resampling to offset this loss.

The remaining cores were glued into core mounts and the cores and cross sections were air-dried for several weeks then sanded with increasingly finer sandpaper (120-, 220-, 320-, and 400-grit) to expose the annual rings. To identify the year of origin of each sample, I aged each core and cross section to the innermost ring or pith under a 40× dissecting microscope to determine a tentative establishment date. To arrive at a final establishment date for the cores, I made two adjustments. First, if the core did not contain the pith, I used a pith estimator (Villalba and Veblen, 1997; Speer, 2010) to determine how many annual rings were missed and adjusted the tentative establishment year back in time. No such adjustment was made to cores containing piths. Second, for all cores, I moved each tentative establishment date back five years, e.g., 1910 became 1905, to account for the time needed by the trees to grow to the 30-cm coring height (Brose, 2011). No adjustments were made to cross sections because they contained piths and were cut at ground level.

For each site, I visually inspected all the cores of chestnut oak (the most common tree species) and all the mountain laurel cross sections for defects and randomly selected 20 defect-free cores and 20 defect-free cross sections for radial growth analysis. These were skeleton plotted to identify signature years for crossdating to help recognize false or missing rings (Speer, 2010). After proper ages were verified for these cores and cross sections, their annual rings were measured to the nearest 0.02 mm with a Unislide "TA" Tree-Ring Measurement System (Velmex Inc., Bloomfield, NY). I used the COFECHA 2.1 quality assurance program (Grissino-Mayer, 2001; Holmes, 1983) to verify the crossdating. For the chestnut oak chronologies, I used the default settings in COFECHA, but for the mountain laurel chronologies I changed the segment length to examine from 50 years lagged by 25 to 20 years lagged by 10 because most of the mountain laurel chronologies were about 50 years long. Interseries correlations of the chestnut oak cores ranged from 0.495 to 0.603 for the three sites while the interseries correlations for the mountain laurel cross sections ranged from 0.340 to 0.386 for the three sites.

Previous dendroecology studies in the region involving chestnut oak used a negative exponential curve or linear regression as the standardization technique (Abrams et al., 1997; Mikan et al., 1994; Ruffner and Abrams, 1998). I initially tested both techniques on the individual chestnut oak chronologies using the ARSTAN program (Cook and Holmes, 1986). I found little difference in the results produced by these two approaches so I used the negative exponential curve to combine the individual oak chronologies of each site into stand-level chronologies. Standardization is necessary to remove the effects of differing tree ages among the samples as well as tree-to-tree variability due to microsite conditions (Speer, 2010).

No previous mountain laurel research involved radial growth analysis so there were no published methods on how to standardize the chronologies. However, regional dendroecology studies involving shade tolerant species used the negative exponential curve or linear regression in ARSTAN to standardize the chronologies (Abrams et al., 1998; Ruffner and Abrams, 2003). Therefore, I also used the negative exponential curve to standardize the individual mountain laurel chronologies so they could be combined into stand-level chronologies for each site.

Because this study may be the first one to use mountain laurel in a dendroecological analysis, my experiences of working with this species may be of value to other researchers. Viewing the annual rings in a cross section of mountain laurel was challenging. The wood was diffuse porous so seeing the ring boundaries was difficult. Furthermore, the wood varied in appearance from a light cream-colored hue to a darker, rose-colored tint with the former coloration making it especially difficult to see the annual rings. I tried several different liquids (coffee, tea, water, and red fox (*Vulpes vulpes*) urine) to accentuate the ring boundaries, but none of these worked as well as sanding the cross sections to a well-polished surface. Finally, mountain laurel on these sites was apparently insensitive to droughts resulting in complacent rings (little year-to-year variation in the width of the annual rings). Relative to the other diffuse-porous species encountered in this study, I would rank mountain laurel as more challenging than red maple and serviceberry to age, crossdate, and measure, but not as difficult as blackgum.

2.3. Data analysis

I organized the cores and cross sections into three species groups: xeric species, miscellaneous species, and mountain laurel. Xeric species included the oaks as well as pitch pine and the hickories. Miscellaneous species were all others, but was dominated by red maple and blackgum. Mountain laurel was a monospecific group. To determine when the species groups originated and their age structure, I created a history timeline for each site. Each timeline was from 1880 to 2000 and was divided into 5-year intervals, e.g., 1880–1884, 1885–1889. In each of these intervals, I tallied the cores and cross sections of each species group by their final establishment date. I used Smith's (1986) age class criteria to determine whether the three species groups were even-aged, two-aged, or uneven-aged. He defined even-aged as a distinct cohort of trees where the age difference between the youngest and oldest ones does not exceed 20% of the rotation length or longevity of the species. Similarly, two-aged means two cohorts and uneven-aged signifies three or more cohorts. For this study, I used 75 years as the lifespan of mountain laurel and 200 years as the lifespan for the oaks (Chapman, 1950; Burns and Honkala, 1990).

I used the JOLTS program (Holmes, 1999) and criteria developed by Lorimer and Frelich (1989) to identify major and moderate disturbances in the individual chestnut oak chronologies because this method was used in previous dendroecology studies involving chestnut oak (Abrams et al., 1997; Mikan et al., 1994; Ruffner and Abrams, 1998). A major disturbance consisted of more than a 100% increase in growth lasting at least 15 years. A moderate disturbance was an increase in growth of 50–100% for at least 10 years. These indicate events such as insect/disease outbreaks, timber harvests, severe wildfires, or windstorms that kill some overstory trees but allow the remaining ones to accelerate growth due to increased light, nutrients, and water.

Fire was an important forest floor disturbance until the early 1900s (Brose et al., 2014), so I examined all cores and cross sections for evidence of past fires by looking for external or internal scars. Scars in a cross section were dated by comparing them to adjacent unscarred annual rings and scars in a core were dated by comparing them to the other core extracted from the same tree. Because scars can be caused by means other than fires, I decided that three or more scars had to occur in the same year at the same site for them to be considered of fire origin. Fires were classified by seasonality based on criteria by Baisan and Swetnam (1990).

Because hardwood reproduction and mountain laurel were present to varying degrees in all plots at all three sites, I used regression analysis to determine whether or not the densities of hardwood seedlings were positively or negatively related to the degree of mountain laurel cover. I chose 15 seedlings per understory plot (≈14,300 per hectare) as the threshold to determine when mountain laurel cover was negatively impacting seedling densities based on SILVAH guidelines, a regional prescriptive silvicultural program (Marquis et al., 1992).

3. Results

3.1. CCSF site (Allegheny Plateau in northwestern Pennsylvania)

The mean basal area was 21.1 m^2/ha and the relative density, a measure of overstory stocking (Marquis et al., 1992), was 70%. Chestnut oak comprised 43% of the basal area, followed by red maple (20%) and northern red oak (17%). Three disjoint mountain laurel thickets occupied the understory. The thickets were dense and the individual shrubs tall. Mountain laurel cover ranged from 0% to 95% with a mean of 62%. Generally, these shrubs were 1–2 m tall. Hardwood reproduction averaged 17 seedlings per understory plot (≈16,200 per hectare) and oak reproduction dominated the seedling pool; 90% of the seedlings were oak. All seedlings were small, less than 15 cm tall.

The establishment timeline for the overstory trees and the mountain laurel thickets was from 1880 to 2000 (Fig. 2). The age structure of the trees was unimodal and even-aged. The miscellaneous and xeric trees established between 1880 and 1945. However, 84% of the oaks originated during a 15-year period, from 1900 to 1915, with peak establishment occurring in 1906. Peak establishment for the miscellaneous species was in 1909 with 54% of the red maples starting to grow within 10 years of that year. Since 1945, there has been virtually no recruitment of hardwood reproduction into the overstory canopy. The mountain laurel thickets were unimodal. A few mountain laurel shrubs began before 1945, but the vast majority originated during a 50-year period, from 1946 to 1995, with most establishing between during the 1960s and 1970s. Because the recruitment period (50 years) was almost as long as the species lifespan (75 years), I considered the mountain laurel thickets to be uneven-aged.

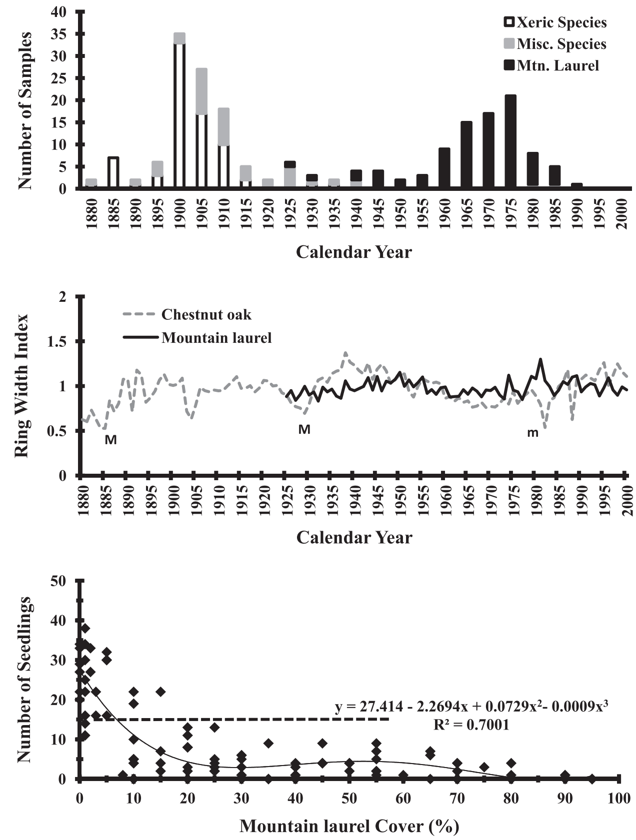

Fig. 2. The establishment timeline of the overstory trees and the mountain laurel shrubs (upper graph), radial growth chronologies of chestnut oak and mountain laurel (middle graph), and relationship between hardwood seedling density and mountain laurel cover (lower graph) at the CCSF study site. The uppercase and lowercase "m" in the middle graph mark the occurrence of major and moderate disturbances, respectively. The dashed line in the lower graph marks the minimum number of seedlings necessary to consider a sampling plot stocked as per SILVAH.

The radial growth chronology for chestnut oak spanned from 1880 and 2000 and the mountain laurel chronology covered the period from 1925 to 2000 (Fig. 2). The chestnut oak chronology showed steady growth punctuated by two major disturbances and one moderate disturbance. The first major disturbance was in the early 1880s and this coincides with the logging of the area. The next major disturbance occurred in 1926 and corresponds to the chestnut blight. The moderate disturbance was in 1982 when gypsy moth defoliated the area. Additionally, scarred cross sections and cores indicate a dormant-season fire in 1902 or 1903. The radial growth chronology of mountain laurel showed steady growth with occasional spikes of accelerated growth, most notably coinciding with the gypsy moth outbreak in 1982.

Seedlings were not uniformly distributed throughout the stand; they were concentrated in areas with little or no mountain laurel

(Fig. 2). According to SILVAH guidelines, only 23 understory plots were adequately stocked with hardwood seedlings. These plots averaged 26 seedlings (≈24,750 per hectare) and 4% mountain laurel cover. The other 77 understory plots averaged 4 hardwood seedlings (≈3800 per hectare) and 43% mountain laurel cover. Regression analysis revealed that the cover of mountain laurel explained 70% of the variability in hardwood seedling density.

3.2. DESF site (Pocono Plateau in northeastern Pennsylvania)

The overstory mean basal area was 18.4 m^2/ha and the relative density was 72%. Chestnut oak comprised 41% of the basal area, followed by red maple (22%), northern red oak (20%), and pitch pine (13%). One large mountain laurel thicket covered the entire site. The thicket was dense, cover ranged from 0% to 95% with a mean of 58%, and the individual shrubs were 1–3 m tall. Hardwood seedling densities averaged 6 stems per plot (≈5700 seedlings per hectare) and primarily consisted of red maple and blackgum. Oak seedlings averaged 1 per plot (≈950 per hectare). All the seedlings were less than 15 cm tall.

The establishment timeline was from 1880 to 2000 (Fig. 3). Within this time span, the xeric trees originated continuously from 1880 to 1945 while the miscellaneous species arose between 1896 and 1950. The overstory trees were multi-aged; most oaks and pines started growing in one of three distinct periods; 1891–1901, about 1914, and 1925–1936 while the maples established cohorts in the 1910s and 1925–1940. The mountain laurel thicket was uneven-aged. A few mountain laurel shrubs originated in the 1930s, but all others established between 1946 and 1995, especially from the mid-1960s to the mid-1980s.

The chestnut oak radial growth chronology covered the years from 1880 to 2000 (Fig. 3). During that time, the oak chronology showed four major disturbances occurring in 1885, 1912, 1930, and 1982. These most likely correspond to a timber harvest, chestnut blight, another timber harvest, and a gypsy moth defoliation, respectively. The mountain laurel radial growth chronology was from 1950 to 2000. In those years, growth generally increased steadily with intermittent spikes of growth until 1985 when a slow decline began. The growth spikes generally coincided with sudden drops in chestnut oak radial growth. I found no evidence of past forest fires.

Only 6 of the 96 understory plots were adequately stocked with seedlings (Fig. 3). On average, these plots contained 25 seedlings (≈23,800 per hectare) and had 12% mountain laurel cover. The remaining 90 understory plots averaged 4 seedlings (≈3800 per hectare) and 68% mountain laurel cover. Regression analysis indicated that mountain laurel cover explained 85% of the variability in hardwood seedling density.

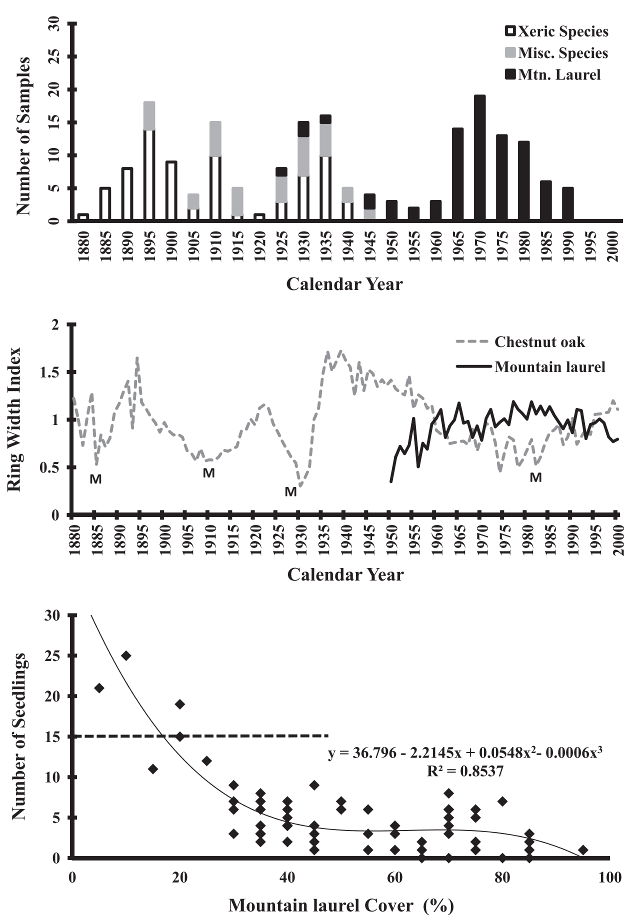

Fig. 3. The establishment timeline of the overstory trees and the mountain laurel shrubs (upper graph), radial growth chronologies of chestnut oak and mountain laurel (middle graph), and relationship between hardwood seedling density and mountain laurel cover (lower graph) at the DESF study site. The uppercase "M" in the middle graph mark the occurrence of major disturbances. The dashed line in the lower graph marks the minimum number of seedlings necessary to consider a sampling plot stocked as per SILVAH.

3.3. RRSF site (Ridge and Valley region in central Pennsylvania)

The overstory mean basal area was 24.6 m^2/ha and the relative density was 75%. Chestnut oak comprised 45% of the basal area, followed by red maple (16%), northern red oak (14%), and blackgum (11%). The mountain laurel occurred in several small scattered thickets and as numerous individual shrubs. Average cover was 23% with no plots having more than 50% cover. Mountain laurel height ranged from 1 to 3 m. Hardwood seedlings were numerous, well distributed, but universally small. Seedling densities averaged 19 stems per plot (≈18,100 per hectare). Oak reproduction accounted for 37% of the seedling population and a mix of black birch (*Betula lenta*), red maple, and serviceberry comprised most of the miscellaneous species component.

Almost all of the xeric and most miscellaneous overstory trees originated continuously from 1880 to 1955, giving the stand an uneven-age structure (Fig. 4). Within this period, no distinct cohorts were apparent although both species groups had their peak recruitment occur in the 1920s and 1930s. A cohort of black birch arose during the 1980s. The three oldest mountain laurels dated to 1936, but all others established since 1955 with most starting from the early 1970s to the mid-1980s. Consequently, the thickets have an uneven, unimodal age structure.

The chestnut oak radial growth chronology covers the period from 1880 to 2000 (Fig. 4). It showed four disturbances, three major and one moderate. The major disturbances occurred in 1888 (timber harvest), 1918 (chestnut blight), and 1992 (gypsy moth defoliation) while the moderate disturbance was in 1946 (timber harvest). The mountain laurel chronology commenced in 1955 and showed slow steady growth through 2000. In those 45 years, spikes in mountain laurel growth corresponded with declines in chestnut oak growth. As with DESF, I found no evidence of past forest fires at the RRSF site.

Seventy-three plots (86%) were adequately stocked with seedlings (Fig. 4). These stocked plots averaged 48 seedlings (≈45,700 per hectare) and 8% mountain laurel cover. The 13 understocked plots averaged 5 seedlings (≈4750 per hectare) and 25% mountain laurel cover. Mountain laurel cover explained approximately 38% of the variability in hardwood seedling density.

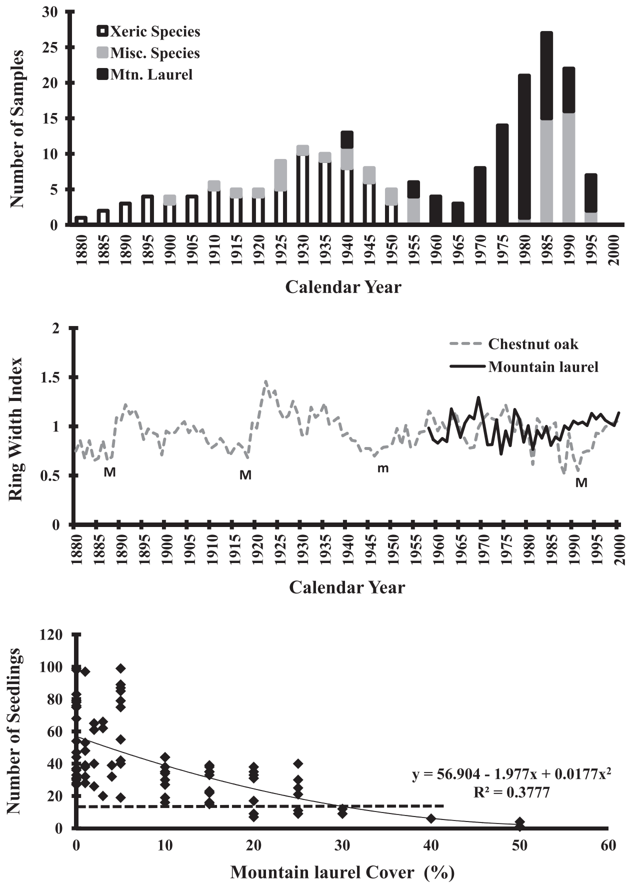

Fig. 4. The establishment timeline of the overstory trees and the mountain laurel shrubs (upper graph), radial growth chronologies of chestnut oak and mountain laurel (middle graph), and relationship between hardwood seedling density and mountain laurel cover (lower graph) at the RRSF study site. The uppercase and lowercase "m" in the middle graph mark the occurrence of major and moderate disturbances, respectively. The dashed line in the lower graph marks the minimum number of seedlings necessary to consider a sampling plot stocked as per SILVAH.

4. Discussion

One of the generalities of oak forest management is that regeneration difficulties become less problematic or nonexistent as site quality decreases (Gould et al., 2005; Johnson et al., 2009; Ross et al., 1986; Weaver and Robertson, 1981). Oaks, by virtue of several morphological and physiological characteristics, are better adapted to survive on sites whose productivity is limited by nutrient or water availability (Dey, 2002; Kolb and Steiner, 1990; Kolb et al., 1990; Lorimer, 1993). Consequently, oaks or their ecological analogues – the hickories and upland pines – often dominate low- to medium-quality sites as the edaphic constraints limit the competitiveness and long-term survival of most other tree species. However, this study clearly establishes a caveat to that generality; mountain laurel thickets stall forest renewal processes and threaten the perpetuation of oaks on sites where they should dominate and persist.

Each of the establishment timelines showed the same bimodal temporal pattern; oaks and other hardwoods regenerating and recruiting to the overstory canopy before 1950 and mountain laurel proliferating in the understory after 1950. In the pre-1950 portion of the timeline, the mixed-oak forests displayed even-aged, multi-aged, and uneven-aged structures depending on their specific disturbance histories. The CCSF overstory had an even-aged structure because the area was extensively logged and burned in the late 1800s and early 1900s (Briggs et al., 2004). At DESF, the overstory trees arose over a 90-year period, but many started in one of three distinct cohorts, 1891–1901, about 1914, and 1925–1936. These cohorts correspond to when the area was logged and chestnut blight occurred (Decoster, 1995). At RRSF, the oaks and other hardwood trees started over a 75-year period with no distinct cohorts being discernible although the 1920s and 1930s had increased oak establishment relative to the other decades. This age structure is most likely the result of intermittent small-scale timber harvesting over many decades (Decoster, 1995; Eggert, 1994).

Compared to the dissimilar age structures of the overstory trees, the age structures of the mountain laurel thickets were nearly identical at the three study sites, despite being 150–400 km apart. At each site, there were a few old mountain laurels that originated in the 1930s or 1940s, but the rest began growing after 1950 and they were established continuously until the late 1990s. Consequently, the mountain laurel thickets are uneven-aged and fairly new in existence. The oldest mountain laurels are approaching the 75-year lifespan reported by Chapman (1950) and are similar to results reported by Brose and Waldrop (2010) in the southern Appalachian Mountains. Each site had plentiful mountain laurel establishment in the 1960s and 1970s; two decades characterized by scant disturbance based on the steady or slowly declining radial growth chronologies of chestnut oak. Interestingly, these two decades had markedly different climates with droughts occurring in the 1960s and the 1970s having cool, wet summers (NCDC, 2015). This suggests that the lack of disturbance is important in the establishment and spread of mountain laurel. This agrees with Kurmes (1961) who found that mountain laurel regenerated best via layering of the lower branches. The absence of mountain laurel establishment and recruitment after 1995 is likely an artifact of the sampling procedures and probably does not represent an actual decrease. Because this was a dendrochronology-oriented study, I sampled mountain laurel larger than 2.5 cm basal diameter so that the cross sections could withstand processing in the lab and I avoided smaller diameter shrubs. Based on the observed presence of mountain laurel shrubs less than 2.5 cm basal diameter as well as mountain laurel seedlings, regeneration has not tapered off.

What caused the mountain laurel thickets to form? Five primary theories exist and four of them separate into two groups – prevention and facilitation. The most widely-accepted prevention theory is that periodic surface fires thwarted the formation of mountain laurel thickets by maintaining inhospitable seed beds and destroying any vegetative spread via layering of low branches (Chapman, 1950; Brose and Waldrop, 2010). Depending on location, forest fires were quite common throughout the Appalachian Mountains until the mid-1900s. On xeric upland sites, forest fires burned at a frequency of 1–2 fires per decade (Brose et al., 2014). Mountain laurel is quite flammable and easily top-killed by fire. The shrub readily sprouts post-fire, but the new shoots grow slowly, thereby allowing nearby hardwood reproduction ample time to grow past the developing shrub. In Pennsylvania, wildfire exclusion policies and practices made forest fires essentially nonexistent as an ecological process in the mixed-oak forests by the 1930s (DeCoster, 1995). The date coincides with the establishment of the oldest mountain laurel shrubs. Additionally, I found no evidence of fire at any of the sites after the 1920s.

Another prevention theory is that American chestnut (*Castanea dentata*) exerted an allelopathic influence over mountain laurel, thereby keeping it from proliferating. Vandermast and Van Lear (2002) showed that runoff from chestnut leaves inhibited the germination of rosebay rhododendron seeds so a similar effect on mountain laurel is possible. Prior to the early 1900s, American chestnut was the dominant tree species throughout the Appalachian Mountains, especially on xeric upland sites. Chestnut blight, caused by the fungus *Cryphonectria parasitica*, swept across

Pennsylvania between 1910 and 1930, virtually eliminating the once dominant species from the forest landscape (DeCoster, 1995). Without the controlling influence of American chestnut, the mountain laurel was free to proliferate and spread. In this study, all three sites had a substantial American chestnut component before the blight as evidenced by the presence of American chestnut sprouts in the understory and the demise of the American chestnut corresponds to the establishment of the oldest shrubs in the thickets.

The two facilitation theories focus on environmental factors that may have caused mountain laurel to proliferate and spread. One is that the increase in whitetail deer populations and the concurrent excessive browsing of forest understories have allowed mountain laurel to expand and fill the growing space. Mountain laurel is a non-preferred species by whitetail deer; they will only browse it under extreme conditions (Forbes and Bechdel, 1931; Forbes and Overholts, 1931). Pennsylvania has had a chronic deer problem since the 1930s and this has led to de pauperate forest understories (Frye, 2006). The unbrowsed mountain laurel colonized the available growing space resulting in the present-day thickets. Such a phenomenon of deer-facilitated colonization has been found in northern Pennsylvania where a suite of rhizamotous ferns have spread throughout many forest understories (Horsley et al., 2003).

In a similar model, atmospheric deposition has led to the spread of mountain laurel by increasing the acidity of the forest soils. Changes in soil acidity benefits species needing more acidic conditions (lower pH) and is detrimental to species needing neutral and higher pH soils. Pennsylvania forests have been subjected to atmospheric deposition for decades and the soils have increased in acidity (Bailey et al., 2005). Mountain laurel, like other ericaceous shrubs, thrives in acidic soils (Huebner et al., 2014), so its proliferation is due to improved soil conditions for its germination, survival, and growth. Like the previous three theories, the timing of atmospheric deposition in Pennsylvania matches well with the rise of the mountain laurel thickets in the mid-1900s.

The final theory is that mountain laurel thickets are not a new phenomenon, but just part of normal forest succession (Plocher and Carvell, 1970). Mountain laurel is a native species and thickets of the shrub are recorded in numerous historical writings of early explorers and settlers (Hulbert, 1910; Tome, 1854). The bimodal age structure of the three sites, hardwoods before 1950 and mountain laurel after 1950, may be an artifact of the longevity of the species and the sampling procedures. I may have found few mountain laurel shrubs more than 50 years old because these may have already died, decayed, and were no longer present to be sampled.

Of these five establishment theories, the last one seems unlikely. Mountain laurel probably existed at the study sites prior to the 1950s; but as individual shrubs and not as thickets. Had thickets existed, I should have found more mountain laurel predating the 1950s than I did because the shrub can live at least 75 years. The sudden, region-wide cessation of periodic fires in the early 1900s is also an unlikely reason for the rise of these mountain laurel thickets at these sites because fire was probably not a significant factor in their pre-1950 ecological histories. Each site had barriers such as nearby roads and wetlands that would have prevented fire spreading into them. Additionally, each had physical characteristics like a north aspect that would have made it difficult for them to sustain a fire. The sites' low probability of burning is supported by the fact that I found evidence of just one fire at one site. Of the remaining three theories (allelopathy by American chestnut, chronic deer overbrowsing, and soil acidification), it is impossible to make a determination from the results of this study. All three sites were subjected to loss of the American chestnut in the early 1900s, and decades of excessive deer browsing and atmospheric deposition throughout the 20th century. A complex, long-term study is needed to fully investigate and parse apart the contributions of these ecological events to the establishment of mountain laurel thickets.

How have the mountain laurel thickets developed through time? They have grown larger and denser by taking advantage of sporadic disturbances to the canopy. For at least the last 50 years, canopy disturbances such as partial timber harvests and environmental stresses like drought and gypsy moth defoliations have temporally increased insolation to the understory strata, causing surges in mountain laurel growth. This is apparent when comparing the growth chronologies of chestnut oak and mountain laurel. When oak growth dropped during the droughts and defoliations of the 1960s and 1980s, mountain laurel responded with increased growth. This is consistent with results published by several preceding studies (Beckage et al., 2000; Chastain and Townsend, 2008; Clinton et al., 1994).

What impacts are the mountain laurel thickets having on the regenerative process of these mixed-oak forests? Apparently the thickets have stopped or are at least contributing to the stalling of the oak regeneration process. Generally, mixed-oak forests on xeric sites have a persistent population of oak reproduction that is frequently replenished by acorn crops, i.e., an accumulating oak ecosystem (Johnson et al., 2009). This was clearly the case at these sites as the age structure graphs showed oaks successfully regenerating and recruiting into the canopies on a continuous basis from the mid- to late-1800s until the mid-1900s. That regeneration/recruitment ebbed and flowed through those decades based on each site's unique disturbance history, but it was fairly continuous. After 1950, all tree species cease to regenerate and recruit and this coincides with the advent of the mountain laurel thickets that presently dominate the understory. Since then, mountain laurel has proliferated while regeneration and recruitment of oaks and other hardwoods has virtually ceased. The sole exception to that pattern was in the 1980s when cohorts of black birch and red maple formed in the wake of heavy defoliation by gypsy moth at all three sites. Furthermore, the regression analysis of the seedling counts and the mountain laurel cover supports this conclusion.

At all three sites, as the percent cover of mountain laurel increased, the number of hardwood seedlings plummeted. Generally, in plots with less than 15% cover of mountain laurel, hardwood seedlings were sufficiently abundant to satisfy the seedling density requirements of SILVAH. But, at 20% mountain laurel cover at CCSF and DESF, seedling numbers fell below the SILVAH stocking threshold. At RRSF, 30% cover of mountain laurel was the point at which hardwood seedling numbers fell below the SILVAH stocking threshold. This negative relationship between mountain laurel cover and seedling densities was especially strong at CCSF and DESF, $r^2 \sim 0.70$ and 0.85, respectively, and fair at RRSF ($r^2 \sim 0.38$). The lack of a strong negative relationship between mountain laurel cover and seedling densities at RRSF is likely due to the area's high deer population. Selective browsing of seedlings by deer can create wide differences in seedling densities depending on the species present (Horsley et al., 2003). That phenomenon was evident at RRSF as less desirable black birch, red maple, and serviceberry seedlings were abundant and widespread while oak reproduction was scarce and patchy. Additionally, the hardwood seedlings that were present were all universally small. Nearly all of them were less than 15 cm tall.

What are the mechanisms by which mountain laurel reduces seedling establishment, survival, and growth? Three explanations are dense shading, nutrient sequestration, and allelopathy. Of these, dense shading is most likely the primary mechanism. The mountain laurel's evergreen foliage continually casts dense shade on the forest floor. Several studies show that mountain laurel and rhododendron thickets can reduce available sunlight to less than 5% (Clinton et al., 1994; Lei et al., 2002; Monk et al., 1985).

This scant amount of sunlight is insufficient for the seedlings of most hardwood species, including the oaks, to maintain a positive carbon balance (Dey, 2002; Johnson et al., 2009; Kolb and Steiner, 1990; Kolb et al., 1990). Consequently, seedlings die once they have exhausted the carbohydrates available from their seeds. Additionally, the thickets offer cover to small mammals and these consume seed and girdle seedlings (Royo and Carson, 2008). Nutrient sequestration is another means by which mountain laurel thickets may prevent regeneration of hardwoods. Mountain laurel roots are especially adept at absorbing and retaining several elements, especially phosphorus, essential for plant survival and growth so that they are not available for seedlings (Huebner et al., 2014; Nilsen et al., 2001). Similarly, mountain laurel may be allelopathic to the seedlings of some tree species. The shrub creates and exudes a suite of phenolic compounds and some of these may inhibit the germination of hardwood seed and the growth of hardwood seedlings. Mallik (1995) and Inderjit and Mallik (1996) demonstrated allelopathy between sheep laurel and black spruce so it is possible that a similar relationship exists between mountain laurel and one or more hardwood species. A comprehensive study is needed to ascertain the relative contributions of these three mechanisms to the virtual absence of hardwood seedlings in mountain laurel thickets.

The major conclusions of this study are likely correct – mountain laurel thickets are a recent and increasing phenomenon on xeric sites in the Appalachian Mountains and they are an obstacle to forest regeneration – because comparable results have been reported throughout the Appalachian Mountains (Beckage et al., 2000; Brose and Waldrop, 2010; Chapman, 1950; Chastain and Townsend, 2008; Clinton et al., 1994; Monk et al., 1985). However, these findings can be interpreted differently. For example, the bimodal age structure pattern of trees preceding mountain laurel may be due to differences in longevity between mountain laurel and the overstory tree species. The negative relationship between mountain laurel cover and hardwood seedling densities could be caused by an exogenous factor affecting both of them. An ongoing study will definitely answer the latter point, but the former can only be addressed by a comprehensive, long-term study. An additional finding with an alternative interpretation is the lack of fire, just one fire at one site in 1903. This may not mean that fire was an unimportant factor in the ecological histories of these three sites; it may be due to overlooking fires by requiring three scars in the same year as well as not obtaining cross sections from stems larger than 10 cm dbh. Again, a full-fledged fire history study would be needed to clarify that point.

5. Management implications

Presuming that the negative relationship between mountain laurel cover and seedling density found in this study is correct, then reducing the shrub's cover to less than 20–30% is necessary to either release existing oak reproduction or prepare for subsequent oak seedling establishment. Potential silvicultural treatments that may be suitable for reducing mountain laurel cover include chopping, herbicide application, prescribed fire, and timber harvesting. All of these have drawbacks. Chopping and herbicide application, either by hand or with machinery, would be expensive and limited by site conditions such as steep slopes and surface rocks. Also, chopping increases fuels and fire severity for at least 5 years (Waldrop et al., 2010) and the mountain laurel would sprout after the treatment. Prescribed fire may be less expensive and easier to apply than chopping and herbicides, especially on steep or rocky sites, but the mountain laurel would sprout post-fire so control would be short-lived and repeat burning a must. Additionally, mountain laurel burns hot and the fire intensity may kill trees and cause containment and safety issues. Timber harvesting would provide an economic income instead of a cost, but harvesting is prohibited in some locations plus the lack of seedlings would likely lead to a regeneration failure unless the site is planted. Of these, a timber harvest with an emphasis to crush the mountain laurel and disrupt the thickets seems like the most reasonable approach provided a harvest is not prohibited. In cases where harvesting is prohibited, the judicious and repeated application of prescribed fire may be a reasonable alternative. Clearly, a comparative study to examine the relative effectiveness of these treatments is needed.

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