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Reference Curves for Central Appalachian Red Spruce

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Abstract: Red spruce (*Picea rubens* Sarg.) was a prized timber species in West Virginia during the era of resource exploitation in the late 1800s and early 1900s. As a result, central Appalachian red spruce comprise a much smaller component of high-elevation stand composition and a greatly constricted presence across the region. Widespread restoration efforts are underway to re-establish red spruce across this landscape. However, without benchmarks to gauge growth rates and stand developmental patterns, it is unclear whether these efforts are successful. Our goal was to develop reference curves predicting centile height growth for understory red spruce ($\leq$7.6 m) across the region. We reconstructed the height growth patterns of over 250 randomly selected red spruce seedlings and saplings from 22 high-elevation stands in West Virginia. We also harvested 24 mature red spruce from the same stands to develop juvenile growth curves up to 7.6 m to compare understory growth rates of historical to contemporary rates from the reference curves. Our constructed reference curves showed height growth tended to peak between 10 and 30 years of age. Total heights ranged from 0.95 m to 6.85 m after 50 years. We identified two demographic populations in the mature red spruce trees. All the mature red spruce trees that established after 1890 exceeded the 97% growth centile by age 80. By contrast, only two trees from the pre-1890 population reached the same level by age 80. This work highlights the varied ascension pathways to the overstory for red spruce.

Keywords: *Picea rubens*; reference curves; height growth

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1. Introduction

Red spruce (*Picea rubens* Sarg.) was a coveted timber species in the early days of European settlement of the Central Appalachians. Estimates place pre-colonization forest extent between 200,000 and 600,000 ha in West Virginia or 4.1% to 12.3% of today's forested area [1,2]. Red spruce was subjected to exploitative logging and poor management practices in the 1800s and early 1900s. Wildfires that commonly followed harvests led to the destruction of much of the seed bank, seedlings, and organic soil in stands previously dominated by red spruce [3]. This favored the establishment of hardwood species [4], as a more open canopy led to reduced soil moisture during periods of summer drought and made spruce seedlings vulnerable to winter conditions in areas where dense spruce canopies had protected young trees [5]. Ultimately, red spruce was reduced to only 6 to 18% of its pre-colonization extent in the region [6].

Although its value as a major timber species has diminished, red spruce's value to the ecosystem and society is substantial. Red spruce stands provide habitat to vulnerable wildlife species [7], including the federally listed Cheat Mountain salamander (*Plethodon netting* Green) and formerly listed Virginia northern flying squirrel (*Glaucomys sabrinus fuscus* Miller). Red spruce trees line headwaters of prominent watersheds in the region, play a role in carbon sequestration [8], and cover some of the region's most scenic areas and tourist destinations.

Despite the depletion of red spruce throughout much of the Central Appalachian region, these forests have begun to recover [9–11]. Soil organic layers have developed to once again support red spruce reproduction, and in many stands, red spruce are now also encroaching on hardwood ecotones [8]. There are increased efforts to better understand the species and its life history specific to the Central Appalachian region. Regeneration, disturbance, climate change, and many other factors all play a large role in dictating the role of red spruce in high-elevation forest communities [7,12–17].

Restoration activities have undoubtedly improved red spruce establishment on many high-elevation sites throughout the region. However, the long-term success of these efforts is unknown since there are limited empirical data regarding height growth rates and ascension patterns for seedlings and saplings in the Central Appalachians. Growth rates for red spruce have been studied most commonly in the context of release treatments for saplings and small trees (e.g., [18]) or using growth simulations [15]. In general, growth rates are generally reported as averages across a population without necessarily reporting the range of growth rates. We are interested in understanding the development pathways for seedlings and quantifying the relative growth of individuals to better define height ascension pathways. Research has documented the successes (and failures) associated with silvicultural regeneration treatments (e.g., [19,20]). However, the vast amount of research regarding red spruce regeneration has been in unmanaged systems [10,14,21–23]. Similarly, many acres of red spruce have been planted throughout the southern range for restoration projects on forested and non-forested sites [24], but these efforts lack criteria to compare growth rates to natural systems.

Although their use is limited in ecology and forestry, reference curves are used to define centile growth rates and have widespread use in medical fields (e.g., the charts describing weight gain over time for infants in pediatrics). Applying this approach to trees is a newer concept [25]. Reference curves can be built using individual growth curves developed from stem analysis techniques using harvested seedlings and saplings.

Our objective is to provide a quantitative measure to evaluate the height growth of red spruce seedlings and saplings by constructing centile curves for height growth that can be used to compare growth rates across the Central Appalachian seedling and sapling population which can be used to assess regeneration and restoration goals. Secondly, we will use our reference curves to characterize growth rates of established overstory trees from the same region. By using the same stem analysis techniques, we can calculate growth rates of these mature trees when they were seedling and sapling-sized, which will allow us to document specific centiles for historical populations. These data will provide insight to how the current red spruce understory is growing relative to mature trees that represent "successful" individuals capable of ascension to the overstory.

2. Materials and Methods

Sampling was distributed across three counties in eastern West Virginia in summer 2019 (Figure 1). Using the random sample tool in Arc GIS [26], 100 potential sites were initially selected for study based on locations identified from a red spruce cover type layer (>10% spruce cover) superimposed over the outer boundary of the Monongahela National Forest [27]. From the 100 potential sites, we randomly selected twenty stands that after field verification contained >10% red spruce cover and had reasonable access. The sites were located within Tucker, Randolph, and Pocahontas Counties on the Monongahela National Forest. Two additional stands were located on Kumbrabow State Forest in Randolph Co., WV. The Kumbrabow sites were selected based on previous research on the forest [14], but specific sampling locations were randomly generated. Elevations across all stands ranged from 1000 m to 1482 m. Regionally, annual precipitation averages 156 cm [28], though some areas receive as much as 180 cm. Precipitation near the sample plots ranged from 122 to 168 cm annually [29]. The soils associated with red spruce and northern hardwood dominated stands contain well and moderately well drained inceptisols and spodosols [30]. Parent materials are often Pennsylvanian subperiod sandstone and shale [31].

Figure 1. Locations of red spruce sites across eastern Western Virginia.

Sampled locations contained overstory red spruce but in most cases also supported hardwood and other conifer species. Common associates included eastern hemlock (*Tsuga canadensis* (L.) Carr.), yellow birch (*Betula alleghaniensis* Britton), American beech (*Fagus grandifolia* Ehrh.), black cherry (*Prunus serotina* Ehrh.), Fraser magnolia (*Magnolia fraseri* Walt.), red maple (*Acer rubrum* L.), and sugar maple (*Acer saccharum* Marsh.). The historical land use and anthropogenic disturbances of these areas are typical of the region, with heavy cutting during the late 1800s through the early 1900s [18]. Fires often followed the harvesting, which altered the natural disturbance regimes (e.g., weather-related events such as blowdowns) of the region [32]. The age structure of each stand was variable and often multi-aged, based on the authors interpretation of stand structure and tree core data; however, detailed history and previous harvest data were largely unavailable.

In each stand, four randomly located points were identified for sampling using the random sample tool in Arc GIS. At each point, the closest damage-free understory spruce tree from each of three height classes (12 trees per stand) was selected and a range of measurements including dbh, total height, live crown height, and crown width measurements were recorded. Note that sampling was not proportional to tree counts by height class. Height classes were 0.1–2.6 m, 2.7–5.1 m, and 5.2–7.6 m. The sample tree was then cut, and depending on total tree height, cross-sections were collected at fixed increments along the bole: 0, 0.3, 0.6, 0.9, 1.37, 2.37, 3.37, 5.37, and 7.37 m from the ground. Trees in smaller height classes had cross-sections removed up to what their total height would allow.

In addition to the understory red spruce, one or two (at Kumbrabow State Forest) mature dominant/co-dominant, undamaged red spruce trees were harvested at each site to assess historical early growth patterns. At each plot, the closest tree to plot center was selected based on the criteria that it was in a dominant/co-dominant crown position and visually without damage to the lower portion of the bole that would preclude accurate aging. These trees were felled and cross-sections removed from the main stem using the same increments used for the understory trees.

All cross-sections were air-dried for several weeks then sanded using progressively finer sandpaper, finishing with 600 to 800 grit. Cross-sections were visually cross-dated using the list method described by Yamaguchi [33]. Disks were scanned at 2400 dpi (Epson Expression 12000XL, Indonesia; Epson Perfection V600, Japan) and uploaded into CooRecorder 9.01 software (Cybis Elektronik & Data AB; Saltsjobaden, Sweden). Tree ring measurement files were then assessed through COFECHA (Version 6.06P, Laboratory of Tree Ring Research, Univ. Arizona) separated by plot to statistically determine cross-dating accuracy. Flags or potential cross-dating issues were viewed and corrected when appropriate until a minimum satisfactory correlation value of 0.35 (which is the threshold for statistical significance for $p < 0.05$ for a chronology length of at least 44 years) was reached between each individual series and the master chronology for each plot [34]. Tree ring measurements from overstory mature trees could not be statistically cross-dated due to small sample size. As an alternative, two random radii were counted and reviewed for discrepancies [35]. A small number of understory samples and one overstory tree were removed prior to analysis due to the presence of injury, rot, or severe reaction wood that influenced accurate tree ring identification. A total of 252 understory and 23 mature red spruce trees were used in the final analyses.

The Carmean method was used to calculate height at ages between cross-sections [36]. This method assumes annual height growth between cross-sections is constant and that the cross-section was sampled in the middle of the year's height growth. From these data, growth rates between heights were determined and used to build height growth curves for individual trees using the equation:

$$H_{ij} = h_i + (h_i + 1 - h_i)/[2(r_i - r_i + 1)] + (j - 1)(h_i + 1 - h_i)/(r_i - r_i + 1)$$

where H_{ij} = estimated tree height at age of the jth ring, h_i is height at ith cross-section, r_i = number of rings at ith cross-section, and j = age transition between cross-sections.

Reference curves were developed for all height classes combined. The RefCurv software package (original version) [37] was used to carry out the lambda-mu-sigma (LMS) method [38]. A degree of freedom was set for each lambda, mu, and sigma using Bayesian information criterion (BIC) prior to using the Rigby and Stasinapoulos algorithm [39] to fit the curves in R 4.3.1 (R Core Team; Vienna, Austria). Prior to inputting data into the RefCurv program, an outlier analysis was carried out on the age distribution of all understory trees and on each individual height class. Data points beyond three standard deviations from the mean (less than 1% of all points) were removed to avoid individual trees heavily influencing portions of the curves.

3. Results

Among understory red spruce, as expected, taller seedlings/saplings were on average older than those in the shorter height classes. The range in mean age was 21 years. Average live crown height, dbh, crown width, and age increased by height class. Mean annual growth in the largest individuals was more than triple that of the smallest class (Table 1).

Table 1. Characteristics of understory red spruce (mean (+/−1 SD)) for the three height classes.

Height Class	N	Height (m)	Live Crown Height (m)	DBH (cm)	Crown Width (m)	Age (years)	Annual Height Growth (m)
1 (0.1–2.6 m)	83	1.22 (0.59)	0.53 (0.42)	1.17 (1.00)	0.68 (0.40)	29.8 (12.0)	0.04 (0.02)
2 (2.6–5.1 m)	85	3.47 (0.62)	1.50 (0.94)	3.84 (1.28)	1.27 (0.48)	42.1 (15.0)	0.09 (0.03)
3 (5.1–7.6 m)	84	5.87 (0.78)	2.74 (1.35)	7.08 (1.74)	1.83 (0.61)	50.7 (16.2)	0.13 (0.04)
All Classes	252	3.53	1.59	4.86	1.26	40.94	0.09

The height distribution by age varied greatly (Figure 2). For example, seedlings between 30 and 40 years-old varied in height from about 0.5 to over 7 m. Similarly, seedlings reached or approached 7 m heights by age 30 to over 100 years. However, these are endpoints, and do not describe growth patterns or trajectories among individual seedlings.

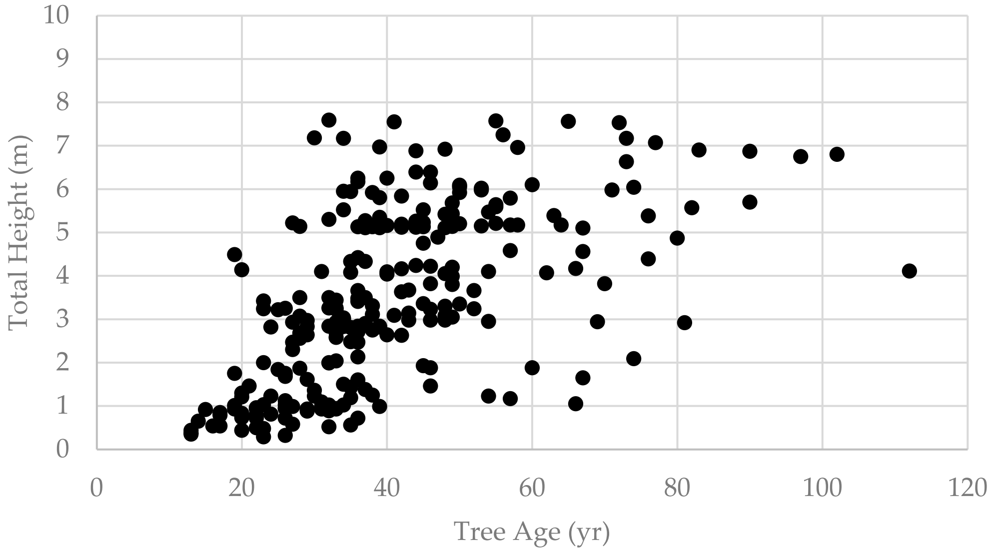

Figure 2. The total height of seedlings and saplings at the time of sampling.

Individual seedling height development is shown below (Figure 3). The 252 seedlings exhibited much overlap in growth patterns, with fewer individuals having much faster or slower growth. Using the RefCurv analysis program, seedlings across all height classes were combined into a comprehensive model for understory red spruce (Figure 4). The model fit was significant to an α = 0.0001 level. The upper centiles (75th through 97th percentiles) showed immediate differentiation in growth rates from the lower centiles. By year 10, the lower centiles (3rd through 50th percentiles) begin to differentiate. Growth rates were greatest between years 10 and 30 for centiles above the 50th. The lowest centiles displayed slow growth through 50 years. The range of heights modeled at 50 years was between 0.95 m (3rd percentile) and 6.85 m (97th percentile).

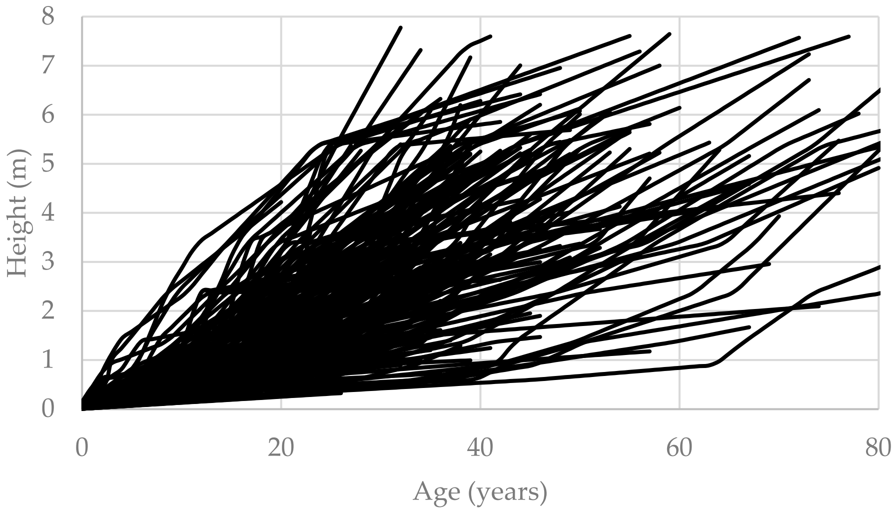

Figure 3. Individual growth patterns for 252 understory red spruce seedlings growing in the Central Appalachian region of West Virginia.

Sample size of overstory red spruce was insufficient and noncontiguous to properly model growth centiles. Twenty-three overstory trees were used to project individual age–height relationships to broadly compare how an older cohort grew during their seedling/sapling stages compared to the current understory cohort, which were modeled using the reference curves (Figure 5). The growth curves showed somewhat of a separation in growth rates between mature trees established before 1890, when large-scale logging occurred, and those established after 1890. Thirteen of the twenty-three mature individuals outperformed the 97th percentile in understory height growth by year 50, with two-thirds of those established pre-1890. Nine of the twenty-three mature trees remained below the 50th percentile of understory height growth at 50 years, but eventually reached a dominant or codominant position. The slowest growing individual did not display growth rates above the 10th percentile until after age 70.

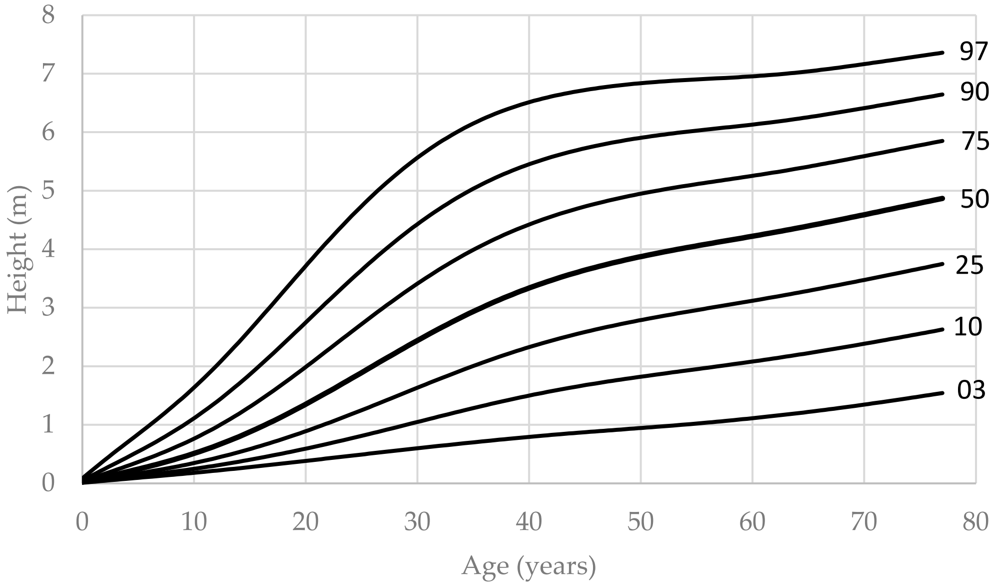

Figure 4. Centiles for red spruce height growth modeled in RefCurv [30]. The numbers to the right of each curve corresponds to the specific centile percent.

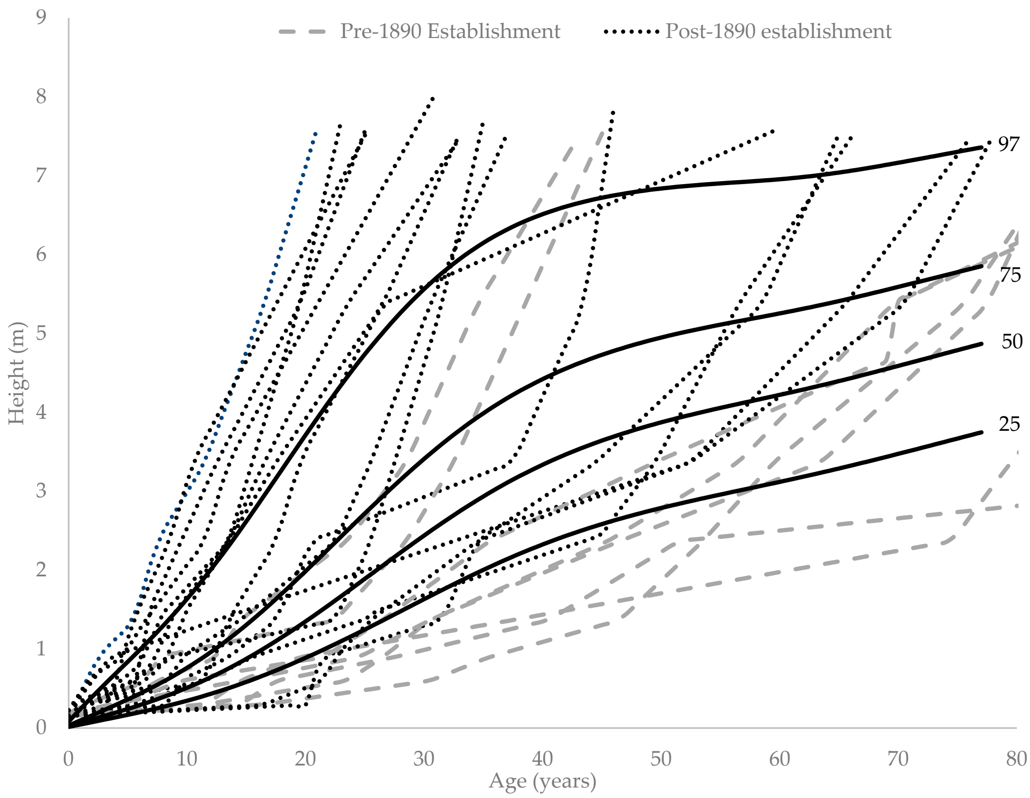

Figure 5. Centiles for height growth by age (solid lines, followed by corresponding centile) for all understory red spruce modeled in RefCurv [30] overlaid with early growth of 23 mature dominant and codominant red spruce separated by period of establishment.

4. Discussion

Red spruce is an important species in high-elevation Central Appalachian forests. Understanding its development and pathways into overstory canopy positions is important to guide silvicultural decision-making and evaluate restoration goals and establishment success. Height growth trajectories will also assist with understanding successional dynamics in mixed species stands that will eventually succeed to red spruce in the absence of natural disturbances and human logging [7].

Sampling of understory red spruce was separated into three height classes to capture a range of ages and height development in young trees. Although shorter height classes displayed a lower mean age, the range of ages across the three height classes was similar, highlighting the variability in growth rates of trees established during the same period (Table 1), which was likely due to microsite conditions within the stand. These microsites include altered conditions created by overhead light conditions and understory competition. In this study, the vast majority of the sampled understory stems were influenced by some form of competition. The most common species overtopping the sampled understory trees were other red spruce (39%), followed by red maple (21%), and yellow birch (15%) [40]. Many studies show suppressed red spruce trees positively responding to overhead competition removal treatments [18,41]. However, a challenge associated with prescribing release treatments is knowing when growth rates are stalled or lagging behind. Our reference curves provide a quantitative mechanism for assessing growth rates across the broad population of understory red spruce trees. Although red spruce is remarkably tolerant to shade [42], its height growth and hence stand development can be restrained due to shading. The reference curves show that height growth can differ by over 3 m in 20 years for upper and lower centile seedlings (Figure 4). Understanding various centiles for a certain age class will allow managers to make decisions regarding acceptability of growth rates ad potential need for release treatments.

The majority of seedlings sampled to create our reference curves were in locations without gaps or recent gaps. Only 7.5% of the sampled understory spruce trees occurred in gaps in the current stands [40]. Gaps averaged 41 m^2, which is comparable to the gap frequency and average size recorded by others in red spruce forests [14,15]. Seedlings growing under intact canopies or in small gaps typically have high turnover and slow growth rates, while larger gaps (>300 m^2) permit better growth [19]. The slower growth rates recorded for the red spruce seedlings in this study reflect competition from adjacent plants and light limitations associated with closed canopy forests [43], a common condition for forests on public lands due to the lack of harvesting [44]. However, these conditions are representative of most red spruce growing in the Central Appalachian region since about 90% of red spruce forests in the Central and Southern Appalachians is on public land [44], as were all the sites sampled in this study.

Some studies have shown as many as nine release events, averaging four per tree, leading to increased growth rates and ultimately overstory canopy positions, while other studies in West Virginia show 40% of seedlings had at least one release and an average age at release of 39 years [15]. Gap creation does result in success for individual red spruce. However, continuous open growth was generally absent for our understory red spruce seedlings (Figure 2). Although red spruce mortality has been widely studied through periods of overstory decline [45–48], it is less commonly researched in the seedling and sapling stages [32,39].

The widespread logging during the late 1800s and early 1900s reduced much of the red spruce range in West Virginia [5,49]. However, the logging activities during this time also spurred the regeneration of the many mature stands seen today. Our data show two distinct ascension pathways for early development in the mature trees (Figure 5). The open or free growth population that is largely characterized by the post-1890 trees, which likely experienced very open canopies and limited overhead competition. The other population, established pre-1890 spruce, developed prior to widespread logging in the region. They likely grew under at least partial overhead shading, and hence developed at slow rates.

In the absence of logging, stand replacing events are rare among this forest type, with disturbance limited to low- to moderate-severity events (e.g., windthrow, gaps associated with beech bark disease) [23]. However, without detailed site histories this cannot be confirmed.

When these mature spruce populations are compared to the reference curves developed from understory spruce seedlings and saplings, the ascension pathways are very evident. The fastest growing mature individuals outperformed the 97th centile for the understory trees almost immediately, indicating open growth or high resource availability from the time of establishment. The slowest growing individual matched the growth of the third centile for understory spruce at age 30. By age 50, more than one-half of the mature trees outperformed the 97th centile and no individual was below the 10th centile, suggesting the centiles shift as stand ages and individuals are not able to persist long enough to experience release into the overstory.

Still, many of sampled mature trees maintained growth rates consistent with lower centiles through age 50. This slower pathway to success is supported by other regional studies [15,43]. Red spruce has the remarkable ability to grow even when subjected to decades of suppression. Studies have shown red spruce can achieve roughly one-half its growth potential in openings with 25% open sky [50].

5. Conclusions

Red spruce has experienced an array of challenges in the Central Appalachians ranging from exploitative management practices to changes in climate and competition. Furthering our understanding of the species' growth pattern in the region can help inform management decisions to meet restoration goals. Understanding how successful trees developed in early stages of life can help verify which other young trees have similar potential to ascend into the upper canopy.

This study shows that understory red spruce can persist in the understory for decades without release. The successful mature trees established after 1890 grew much faster on average than our current understory trees. However, the mature trees that established prior to 1890 have growth patterns that are more similar to today's understory stems, which suggests there are many pathways available to this shade-tolerant species to ascend into the upper canopy. Our results showing two pathways for ascension to the canopy suggest that there is flexibility when designing restoration treatments for releasing existing red spruce and accelerating their accession to the canopy. Treatments can include a variety of canopy gap sizes. However, the successful development of the understory spruce seedlings will require additional releases in order to reach the upper canopy. Whether this can happen naturally is unclear, since the release events that allowed the pre-1890 stems to grow, were probably from much larger gaps than we see in our contemporary stands [23].

Future studies of red spruce growth should consider monitoring the microclimatic conditions of red spruce and spatially explicit measures of intra-specific (i.e., between red spruce) and inter-specific (i.e., between red spruce and other species) competition dynamics as this would help model recent trends in red spruce height growth trajectories. Additionally, although the height–age relationships for the reference curves were highly significant, practitioners would likely prefer using surrogates for age that could be more easily measured.

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Data Availability Statement: The data presented in this study are available on request from the corresponding author. The data are not publicly available due to ongoing research.

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