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Central Appalachian Understory Red Spruce (Picea rubens Sarg.) Growth Rates and Allometric Relationships

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Central Appalachian Understory Red Spruce (*Picea rubens* Sarg.) Growth Rates and Allometric Relationships

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Thesis submitted

to the Davis College of Agriculture, Natural Resources, and Design

at West Virginia University

In partial fulfillment of the requirements for the degree of

Master of Science in Forestry

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ABSTRACT

Central Appalachian Understory Red Spruce (*Picea rubens* Sarg.) Growth Rates and Allometric Relationships

Joseph Gray

Red spruce (*Picea rubens*) was a prized timber species in West Virginia during the era of resource exploitation in the late 1800s and early 1900s. Consequently, Central Appalachian red spruce has faced large reductions in range and changes in stand composition. This region is relatively underrepresented in literature partially due to these constrictions. Investigating how stem growth occurs in young individuals can fill in some of our gaps in understanding the species and aid in restoration efforts. We sampled an array of high elevation sites on federal and state lands in West Virginia to analyze understory spruce growth and allometric relationships. We compared these relationships to those found in other regions in the range of red spruce. Stem analysis was carried out on understory trees. Results were applied to build reference curves to model growth percentiles for the young trees. Growth rates tend to peak between 10 and 30 years of age. Heights range from 0.95 m to 6.85 m after 50 years. Results allow for comparison of growth rates to the cohort of understory red spruce regionally. Nonlinear analysis was carried out on allometric measures on the same cohort of red spruce. Diameter at breast height was found to be a somewhat reliable predictor of total height as well as crown width. Total height was less reliable when predicting crown width. None of the three measures were found to be reliable for predicting tree age as may be expected with a shade tolerant species.

ACKNOWLEDGEMENTS

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INTRODUCTION

Red spruce was a coveted timber species in the early days of European settlement in the Central Appalachian region. These forests were refugia on the highest peaks in the Alleghany Mountains after the last glaciation event. Estimates place pre-colonization forest extent between 200,000 and 600,000 hectares in West Virginia (Hopkins 1899; Stausbaugh and Core 1952). Exploitative logging practices in the 1800s and early 1900s extracted red spruce from the landscape at an unsustainable rate. Wildfire often followed resulting in the loss of some remnant trees and organic soil layers.

Current estimates place red spruce forests at 6-18% of its former range in West Virginia (Griffith and Widmann 2003). The species no longer dominates much of its past domain. Pure stands of spruce are constricted further to high peaks and protected areas. Northern hardwoods now grow in conjunction with red spruce in many of the exploited stands of the past. Differences in soil, microclimate, competition, and disturbance now play a role in the development of young spruce. Other anthropogenic factors, some of which are more widely studied than others, also affect development. Climate change, forest pests, and acid rain have all played a role in a documented decline in the entirety of red spruce's range throughout much of the 1900s.

Red spruce habitat has begun to recover in the last 100 years. Accounts of the previous era mention impressive stands of pure red spruce climax forests notorious for their deep organic layer. Soil layers have developed to once again support regeneration in many stands. Spruce has encroached on hardwood ecotones (Rollins 2010, Nowacki et al. 2010, Mayfield and Hicks 2010). Deforested high elevation stands have regrown in some areas. There are increased efforts put forward to study and 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 better understanding this unique species (Adams et al. 1985; Schuler et al. 2002; Beane and Rentch 2015; Lutz 2018; Rentch 2007).

The importance of red spruce to West Virginia cannot be overstated. The species supports unique wildlife communities including the federally listed Cheat Mountain salamander and formerly listed Northern Virginia flying squirrel. Spruce forests cover some of the state's most scenic areas and tourist destinations. The species plays an important role in the identity and history of Central Appalachia as it supported the settlement of new towns and development of infrastructure. Red spruce may play an important role in mitigating climate change effects through carbon sequestration. Red spruce lines the headwaters of many of the region's most prominent watersheds. Timber value is generally restricted to niche markets in the region, but its value to the ecosystem is substantial.

In order to achieve a better understanding of red spruce and how it grows in the Central Appalachians, it is necessary to understand how it grows during seedling and sapling stages.

Restoration efforts should have clear goals or parameters by which success is measured. Once we understand what growth rates have been successful in the past, we can apply that knowledge to present cohorts of young trees if conditions are believed to be similar. Red spruce can persist for decades in the understory of a stand. Knowing the development patterns of successful mature individuals may allow managers to understand which individuals have a reasonable chance at succeeding in the future.

This study addresses the following goals and objectives:

(1) To model the height growth patterns of understory red spruce growth.
(2) To compare the current height growth of understory red spruce to successful mature spruce when they themselves were growing in the understory.
(3) To gain a further understanding of allometric relationships in understory red spruce with a future goal of identifying characteristics of trees that have a chance to successfully ascend to the forest canopy.

These are some of the areas of research that may be necessary to understand how Central Appalachian red spruce will exist in years to come. This project can contribute to the conglomerate of studies carried out with the goal of preserving and increasing some of West Virginia's most celebrated ecosystems, red spruce forests.

LITERATURE REVIEW

Red Spruce

<u>Silvics</u>

Red spruce (*Picea rubens*) is a shade tolerant, monoecious medium-sized conifer. Flower buds emerge on the previous year's shoot growth and open in May. Cones develop from July until the following spring maturing in September and October. Cones are only fully open for a few days during which they are receptive to pollen (Youngblood and Safford 2008). Good seed years occur every 3 to 8 years with lighter crops common during interim years (Hart 1965). Seeds are primarily wind dispersed travelling as far as 300 feet (Walter 1967; Randall 1974). Seed drops in the fall and can germinate soon after but more often in the following spring and summer. In strong years 60 to 80 percent of seed is viable (Koristian 1937). Viability rarely extends beyond one year after seed fall due to drying (Frank 1970). Seed is commonly predated by small mammals (Blum 1990; Abbott and Hart 1960; Hart et al. 1968). Mineral soil that maintains moderate temperatures is a preferred medium due to moisture availability (Hart 1965). Other forms of reproduction outside of seed germination (e.g., vegetative reproduction) are rare (Gordon 1976).

Reproduction establishes well in shaded areas with as little as 10% direct sunlight although seedlings grow optimally at levels greater than 50% once established and heights of 15 cm are reached (Frank and Bjorkbom 1973). Growth can be exceptionally slow until light is increased through disturbance. Regeneration is more common on cool and moist north and east facing slopes where exposure to sunlight is decreased (Baldwin 1933). Growth medium is a major determinant for seedling survival. Leaf litter moisture fluctuations may reduce survival compared to a bryophyte layer which provides adequate moisture and nutrients (Dibble 1999).

Saplings can vary greatly in age and are influenced heavily by direct sunlight. Trees can reach heights of 7 meters in 20 years if open growth is experienced (Hart 1965). Seed production can begin as early as 15 years of age but is more likely to occur in mature individuals (Frank and Bjorkbom 1973, Korstian, 1937). Trees can take longer than 100 years to reach biological maturity. Smaller crowns yield slower growth (Hart 1959, Hart 1965). Mature red spruce can reach heights up to 35 meters in the southern portions of its range but is restricted to a medium sized tree in the northeast reaching heights of 18-23 meters. (Burns and Honkala 1990). The species is long-lived with recorded individuals reaching 400 years of age (Hart 1965).

Red Spruce grows well in moist, cool environments. Sites experiencing wet growing seasons and cold winters create favorable conditions for the species (Saunders 1983). The species is shallow rooting making it susceptible to windthrow. Acidic soils between a pH of 4 and 6 are preferred and compounded by its own leaf litter (Frank and Bjorkbom 1973). Well and moderately-well drained inceptisols and spodosols are common soil orders that support red

spruce (Jenkins 2002). Sandstone and shale are common parent materials in the Central Appalachians (Price 1968). Soils can be rocky depending on topography and location. Red spruce stands are commonly characterized by a deep humus layer with high moisture holding capacity (Frank and Bjorkbom 1973).

Due to its shallow rooted nature (Greenwood et al., 2008) leaving it susceptible to windthrow, small gap openings from single trees or small groups of trees serve as the main disturbance in red spruce stands (Eager and Adams 1992, Fraver and White 2005). Response to release can occur after many years of suppression (Burns and Honkala 1990). Multiple releases are often needed to allow ascension into the canopy (Wu et al. 1999, Rentch et al. 2010) and many understory trees have already undergone one or more releases (Rentch et al. 2007). Small gaps have shown greater success in implemented treatments (Dumais and Prevost, 2016). Shelterwood treatments and thinning from above are common treatments to mimic natural disturbance (Sendak et al. 2003, Rentch et al. 2007, Carter et al., 2017). Mean gap size in spruce and spruce-hardwood stands has been recorded from around 50 square meters in the Central Appalachians (Rentch et al. 2010; Lutz 2018) to 66 square meters in the Northeast (Fraver and White 2005).

Red spruce can grow in pure stands but commonly grows in association with a number of other tree species. It is considered shade-tolerant (Burns and Honkala 1990). The Society of American Foresters recognizes red spruce as a major component of Red Spruce-Yellow Birch, Red Spruce-Sugar Maple-Beech, Red Spruce-Balsam Fir, and Red Spruce-Fraser Fir forest types, although it grows in a number of other forest types as a lesser component. Associated species in West Virginia include eastern hemlock (*Tsuga canadensis*), yellow birch (*Betula alleghaniensis*), American beech (*Fagus grandifolia*), black cherry (*Prunus serotina*), red maple (*Acer rubrum*), and sugar maple (*Acer saccharum*) (Rentch et al. 2016). Associated fauna include the formerly federally listed Virginia northern flying squirrel and the federally threatened Cheat Mountain Salamander endemic to red spruce stands of West Virginia (Schuler et al. 2002).

Red Spruce Range

Red Spruce is endemic to the eastern United States and Canada. Its range is commonly split into three distinct regions: the northeast, the central Appalachians, and the southern Appalachians. The northeast region is the most contiguous and encompasses most of New England and stretches into Canada as far north as the Maritime Provinces, west into portions of Ontario, and south into pockets of Pennsylvania. The Central Appalachian populations become more isolated and restricted to high elevations primarily in West Virginia but also Pennsylvania, western Maryland, and Northern Virginia. The southern Appalachian population is constricted to high elevations in western North Carolina, eastern Tennessee, and southwest Virginia (Burns and Honkala 1990). The Central Appalachian population shows several distinctions from the other regions. Red spruce stands tend to occur at or above 1067 meters (Hicks and Mudrick 1994) which is a lower elevation compared to the Southern Appalachians. Spruce-fir stands that can be

found in the Northeast and Southern Appalachians are uncommon in the Central Appalachians (Stephenson and Clovis 1983). Spruce budworm and spruce bark beetles are notably absent from the region.

Red Spruce in the Central Appalachians

Pollen records indicate spruce forests were present in the Central Appalachians 12,000 years ago following the northern retreat of the Wisconsin glaciation and tundra-like conditions in the region. As *Tsuga* and several hardwood genera began to appear around 10,000 years ago, *Picea* dropped from pollen records indicating a movement to higher elevations as climate warmed. *Picea* once again appeared in the record less than 5,000 years ago as *Tsuga* notably became absent likely reducing interspecies competition (Watts 1979, Rollins 2010). The range of red spruce in the region has been relatively consistent for 6,000 years (Jacobson et al. 1987) or has possibly increased due to cooler and wetter conditions (Delcourt and Delcourt 1984).

Documentation of the region's forests are somewhat absent during early European settlement. Journal entries and logging records can be used to gain some understanding of composition and conditions; although their accuracy cannot be confirmed. In fact, some errors can be used to highlight just how unreliable observations of the period were. Misidentification and exaggeration are said to run rampant through these accounts (Bailey and Ware 1990, Clarkson 1964). Loggers of the era were unable to provide ecological descriptions of spruce forests, although size of mature trees were recorded as large as two meters in diameter (Clarkson 1964, Allard and Leonard 1952). Virgin spruce stands in high elevations were likely pure stands with a simple understory composition of shade tolerant tree and shrub species (Allard and Leonard 1952). Lower elevations yielded mixed composition containing black cherry, American beech, sugar maple, eastern hemlock, yellow birch, and balsam fir (*Abies balsamea*) as well as pin cherry (*Prunus pensylvanica*) in times following disturbance (Allard and Leonard 1952).

European expansion into West Virginia in the late 1800s decimated many areas of the Central Appalachians previously deemed inaccessible. Estimates approximate between 200,000 hectares of red spruce forest prior to this period up to 600,000 hectares including mixed stands (Hopkins 1899; Stausbaugh and Core 1952). The use of steam powered railroads and logging equipment increased productivity and transport for logging operations (Clarkson 1964). Red spruce was a favored species. Widespread clearcuts followed in order to extract timber and clear land for agriculture. Wildfire was common after clearcutting resulting in the destruction of much of the seed bed and seedlings in stands previously dominated by spruce as well as organic soil beneath (Lewis 1998). Subsequent conditions favored the establishment of hardwood species (Thomas-Van Gundy and Sturtevant, 2014). Open canopy conditions allowed faster growing understory species to overtake any remaining spruce regeneration. The resulting hardwood overstory produced unfavorable conditions for spruce. A more open canopy retained less moisture in months of summer drought and made seedlings vulnerable to winter conditions in areas where dense spruce canopy had protected young trees (Adams and Stephenson 1989).

Recent reports estimate 12,000 hectares of red spruce forest remaining in West Virginia, somewhere around 6-18% of the original area (Griffith and Widmann 2003). A recent report shows 62,000 hectares available for management of red spruce and spruce-hardwood communities, although some sites are more suited more northern hardwoods (Moore 2011).

Public land has become a stronghold for the remaining red spruce in West Virginia. Established in 1920, the Monongahela National Forest has acquired additional units of land throughout the twentieth century to reach its current size. Its highest elevations encompass the majority of the range of red spruce forest in West Virginia (Griffith and Widemann 2003). These sites often have a history of logging and burning which interrupted natural disturbance regimes of the region (Thomas-Van Gundy and Strager 2012). Understory ages vary within most stands indicating continuous establishment. Site index varies by elevation and soil types as noted by Flegal (1999) in surveys of Pocahontas County. Stand age is variable by location with many originating between 1890 and 1930 from clear-cut harvests and some containing residuals from the mid-1800's (Rentch et al. 2016). Kumbrabow State Forest atop Rich Mountain in Randolph County, West Virginia is another example of historical decline and present-day management of red spruce. Established in 1934 after enduring decades of logging and wildfire, the forest represents similar conditions to much of the region's red spruce stands. Prior to its acquisition by the state in 1934, the Midland Corporation utilized the area for timber harvest. At least four major sawmills sourced timber from the forest while operating a spur railroad line for removal. Fires followed these harvests. Additional harvests occurred throughout the 1950's and 1960's prior to establishing silvicultural prescriptions in 1975. Seven harvests occurred between 1977 and 2001 averaging 80 hectares in size. Much of the current management focuses on promoting shade-tolerant species including red spruce as the current stands display an even-aged distribution dominated by hardwoods (WVDOF 2002).

A more recent decline in growth in the Central Appalachians has been noted although the cause is not certain. Adams et al. (1985) and Schuler et al. (2002) both noted a decline in growth for red spruce in the region with the latter finding the period lasting around 60 years beginning in the 1930s. Mielke et al. (1986) found concerning rates of mortality in West Virginia spruce stands during the same period. Although several anthropogenic stressors have been discussed, climate change has become a leading concern for red spruce in the region (Johnson et al 1988, Hamburg and Cogbill 1988, Beane and Rentch 2015, Mathias and Thomas 2018). Current models indicate a loss of over half of the region's suitable red spruce habitat within the next 5 years and potentially all suitable habitat by 2080 (Beane and Rentch 2015) likely leaving remnant stands at only the highest elevations. Even so, some communities dominated by red spruce have undergone recent expansion in ecological status and have extended into the ecotone while increasing in number of stems (Rollins 2010, Nowacki et al. 2010, Mayfield and Hicks 2010) showing a level of resilience in the population.

Based on historic records and modern studies, the composition of interspecies competition is not extremely different after periods of logging and decline. Allard and Leonard

(1952) noted two types of red spruce forests; high elevation stands containing pure spruce and lower elevations where spruce began to mix with northern hardwood species and eastern hemlock. Today a similar distinction can be found. Unfortunately, it is unknown what portion of the canopy spruce filled and at what elevation these mixed stands existed in the past to compare to today's structure. Common associates between the two eras include eastern hemlock, American beech, yellow birch, red maple and black cherry (Lutz 2018, Pauley 1989, Adams and Stephenson 1989, Allard and Leonard 1952, Hopkins 1899).

Stem Analysis

<u>The History of Stem Analysis</u>

Stem analysis is a method used to examine tree cores or cross-sections to learn about how it grew throughout its life. The technique utilizes growth rings to obtain ages at different heights of the tree. Records of stem analysis in the United States date back to the late 1800s (Mlodiansky 1898). The process can reconstruct both radial and height growth throughout the life of a tree by measuring diameter and height of cross-sections or cores extracted incrementally along the bole. Early adopters used tree height and diameter measurements to determine volume and height development. A practical issue arises when estimating height at an age between sampled cross-sections, even more so when several age transitions occur. Multiple methods to correct for this, each with different assumptions, have been reported in the literature. Some were found more accurate than others. For example, Dyer and Bailey (1987) found Carmean's (1972) method, which assumes height growth between cross-sections is constant and that the cross-section sampled occurs in the middle of the year's growth, as the most accurate method when tested against both older (Mlondiansky 1898; Graves 1906) and modern methods (Lenhart 1972; Newberry 1978). Kariuki (2002) found that a tree annual radial growth method can outperform other methods, assuming annual radial growth percentage is associated with annual height growth percentage, at the cost of more labor and equipment for analysis. Even so, Carmean (1972) and Lenhart's (1972) methods are still deemed acceptable.

<u>Site Index Using Stem Analysis</u>

Currently, stem analysis is a common method employed for developing site index curves, although estimates are less accurate than using data from permanent or temporary sample plots (Allen and Burkhart 2015). Site index calculated from stem analysis will often underestimate the height of young trees yielding an overestimation of future growth in a stand due to the assumption that growth is free of suppression at all ages (Magnussen and Penner 1996). As a shade tolerant species with the ability to persist under suppression for many years, red spruce is a poor candidate for the traditional method of calculating site index. Griffin et al. (1970) used polymorphic site index curves to account for this in even-aged stands. Seymour and Favian (2001) found by substituting areas of suppression with an adjusted age, which is the number of

years resulting in equal radial growth under non-suppressed conditions, site index calculations in shade tolerant species become more accurate. Otherwise studies involving shade tolerant species' site index will be limited to even-aged pure stands. Earlier methods simply substituted diameter for age on the site index curve (McLintock and Bickford 1957).

<u>Other Uses</u>

Stem analysis is not limited to site index studies. It is a method that can help answer applied and practical questions in the field. Zenner (2012) used the method to answer if dominant oaks were ever shorter than direct competitors. LeBlanc (1990) notes that detailed stem analysis is costly, but indices can be derived to model whole stem growth in trees where a single core is taken at breast height. Stem analysis has yielded tree-specific stem profile models (Yang 2009) as well as taper equations from both destructive (Larsen 2017) and standing tree analysis (Westfall and Scott 2010). Stem analysis provides detailed data about tree growth resulting in a variety of equations and models at the cost of the sampled resource. Alternatively, labor is saved overall by reducing entries into a plot to carry out many measurements over the lifetime of a tree.

Reference Curves

Reference curves are frequently used in the medical field to assess growth and development of a cohort. Centiles can be modelled from the distribution of the measurement of interest and plotted against age. An individual can then be assessed using the distribution's centiles to quantitively compare them to their peers (Ulijaszek et al. 1998). The lambda-mu-sigma (LMS) method can be used to normalize a data set prior to plotting reference curves (Cole 1990). Similarly reference curves have been applied to other cohorts outside of the medical field. A number of studies have developed reference curves for the body mass index (BMI) of wildlife species (Nesbitt 2008; Curry 2020; Mech 2006). Vickers et al. (2017) used reference curves to assess tree performance in young oak stands. To date these methods have yet to be applied to shade-tolerant species including red spruce. Managers are interested how the development of seedlings occur in their stands as well as how it compares to other stems in the region. Reference curves may give us the opportunity to answers these questions.

OBJECTIVES

This study modelled the understory development of red spruce in the Central Appalachians, specifically West Virginia. The primary objective was to identify the variation in understory individuals and quantify the rates at which they grew with future objectives including developing applied management strategies using this information. Specific goals included: 1) to model the height growth patterns of understory red spruce growth; 2) to compare the current height growth of understory red spruce to successful mature spruce when they themselves were growing in the understory; 3) to gain a further understanding of allometric relationships in

understory red spruce with a future goal of identifying characteristics of trees that have a chance to successfully ascend to the forest canopy.

METHODS

Study Area

Sampling was distributed across three counties in eastern West Virginia. Twenty plots containing red spruce were located within Tucker, Randolph, and Pocahontas Counties on the Monongahela National Forest, and two additional plots located on Kumbrabow State Forest in Randolph County (Figure 1). The red spruce forests sampled were near the highest points of the region between 1000 m and 1482 m in elevation.
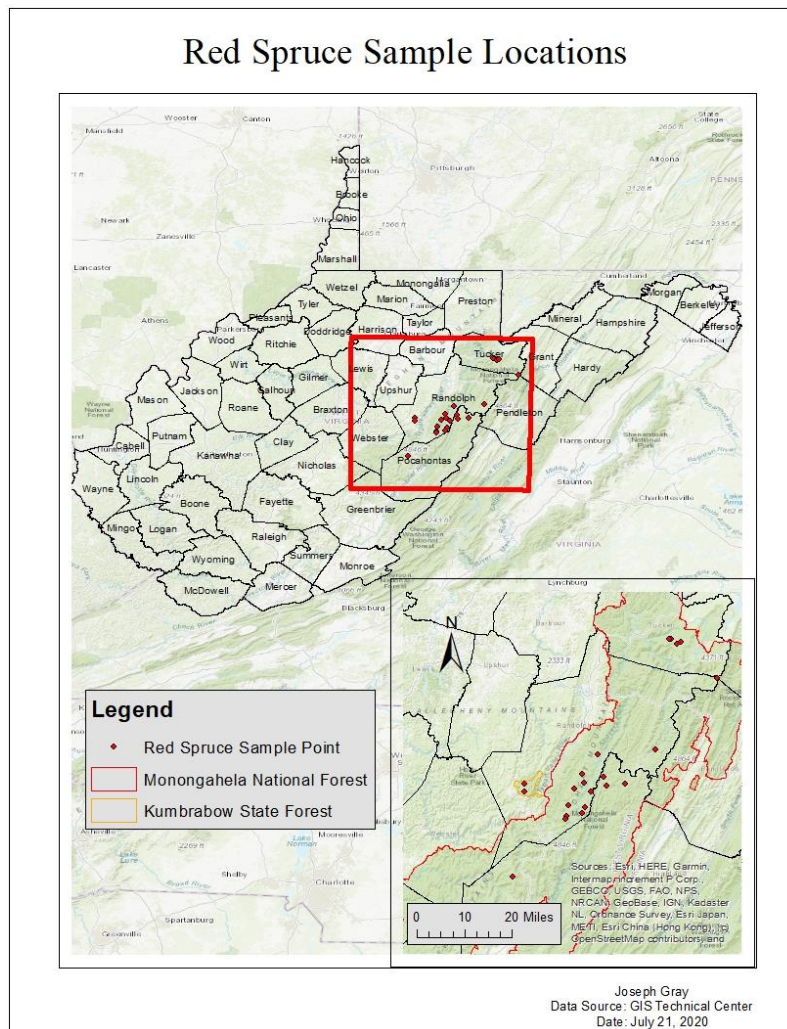
Figure 3: Red Spruce plot locations in the Monongahela National Forest and Kumbrabow State Forest.

Sampling locations were strongly dominated by red spruce but also contained hardwood and other conifer species. Common associates included eastern hemlock, yellow birch, American beech, black cherry, Fraser magnolia (*Magnolia fraseri*), red maple, and sugar maple. The historical landuse and anthropogenic disturbances of these areas are typical of the region. These areas were clear-cut during the late 1800s through the early 1900s (Rentch et al. 2016). Fires often followed the harvesting, which interrupted the natural disturbance regimes of the region (Thomas-Van Gundy et al. 2007). Some of these stands now contain a few individuals that originated from the mid-1800s, but the majority of the understory trees have ages that are quite varied, indicating continuous establishment.

Site index ranges from 42 to 65 feet at a base age of 50 depending on elevation and soil type as noted by Flegal in surveys of Pocahontas County (1999). The soils associated with red spruce and northern hardwood dominated stands contain well and moderately well drained inceptisols and spodosols (Jenkins 2002). Parent materials are often Pennsylvanian subperiod sandstone and shale (Price 1968). Soils are rocky and acidic partially attributed to red spruce organic matter.

Regionally, annual precipitation averages 156 cm (Rentch et al. 2016, NCDC 2020), while some areas receive as much as 180 cm. Precipitation near the sample plots ranged 122 to 168 cm annually. Average daily temperatures are highest in July, ranging between 16.1 ⁰C and 17.7 ⁰C, and lowest in January between -3.1 ⁰C and -4.8 ⁰C (PRISM, Oregon State University).

Sampling Techniques

<u>Plot Selection</u>

Using the West Virginia GIS Technical Center's data (2013) for red spruce cover in West Virginia, the potential range of the species within the state was superimposed over the Monongahela National Forest boundary in ArcMap 10.6. One hundred fifty random points (plots) were generated for consideration. From these points, 100 sites containing red spruce overstory trees were sampled for a companion site index project (Yetter 2020). A subset containing 20 sites was selected for this study.

Kumbrabow State Forest plots were selected from two sites known to contain a dominant red spruce overstory component. Two mature dominant or codominant red spruce were sampled at each plot. Rather than cutting a mature tree for destructive sampling, recent windthrown trees were selected for stem analysis. The stands are undisturbed in recent years making the pattern of windthrow natural if not somewhat random, although the degree of randomness is related to site factors including slope and soil depth, influencing which trees are more likely to succumb (Eager and Adams 1992).

At each sample point location, the first mature red spruce encountered moving clockwise from a random bearing from plot center was felled, except at the Kumbrabow sites as discussed. Once felled, disks were removed from the stem at specific locations and used to reconstruction growth patterns. The specific locations and processing techniques were the same as for seedling and sapling trees described below.

The understory seedling and sapling layer was sampled at each location. For each site, 36 potential sampling locations were delineated in ArcMap 10.6 (Figure 3). Four locations were randomly selected. Due to different stand sizes, the distance between subplots differed among sites, ranging from 25 and 90 m.
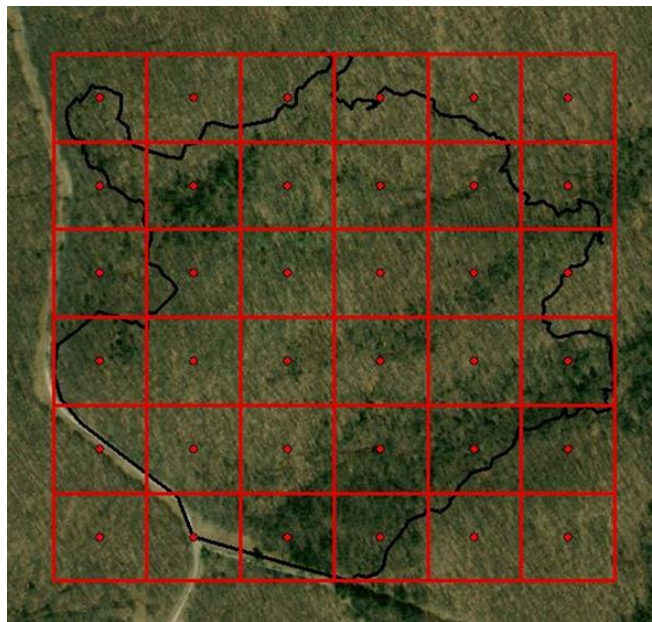
Figure 4: A six-by-six grid overlaid on Kumbrabow Site 1 used for subplot selection.

Twelve understory red spruce were sampled at each site (3 per subplot). At each subplot, an individual red spruce was harvested for each of three height classes: 0.1 m to 2.6 m, 2.6 m to 5.1 m, and 5.1 to 7.6 m. The closest tree in each height class was sampled at each of the four designated subplots in the stand. A total of 288 understory red spruce trees were destructively sampled.

Cross-sectional disks were cut at 0 m or as close to the ground as possible, 0.3 m, 0.6 m, 0.9 m, 1.37 m (breast height), 2.37 m, 3.37 m, 5.37 m, and 7.37 m (Figure 3). Most sampled trees did not include all possible cross-sections since their total height was below the height of the cross-sections. Total height, height to live crown, diameter at breast height, and crown diameter major and minor axis were all recorded. Additionally, aspect, percent slope, and presence of a gap or overtopping species were recorded.
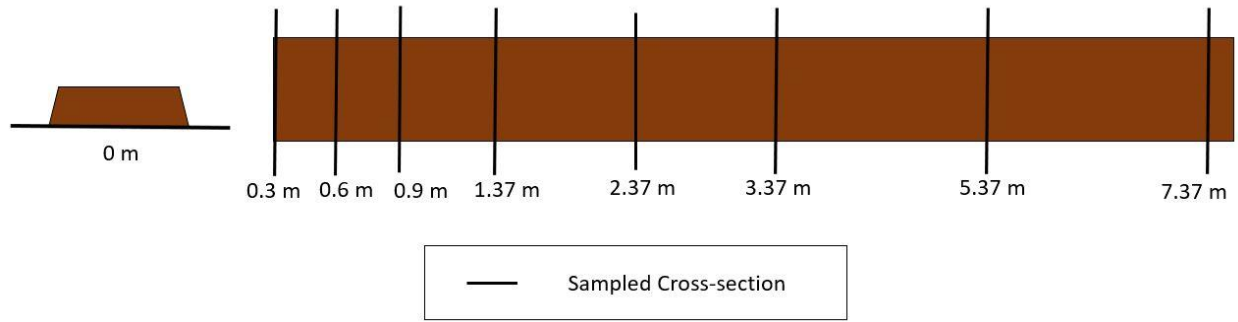
Figure 5: Cross-sections taken from destructively sampled red spruce.

Stem Analysis

Cross-sections were air-dried for several weeks then sanded using progressively finer sandpaper finishing with 600 to 800 grit. Disks were scanned at 2400 dpi (Epson Expression 12000XL and Epson Perfection V600) and uploaded into CooRecorder 9.01 software (Cybis Elektronik & Data AB; Saltsjobaden, Sweden) prior to visually cross dating using the list method described by Yamaguchi (1991). Files were then assessed through COFECHA (Version 6.06P) separated by plot to statistically determine cross-dating accuracy. Flags or potential mistakes were viewed and corrected when appropriate until a minimum satisfactory master correlation value of 0.35 was reached. Overstory samples could not be statistically cross-dated due to small sample size. As an alternative, two random transects were counted and reviewed for discrepancies (Stokes and Smiley 1968). A small number of samples were removed prior to analysis due to the presence of injury, rot, or severe reaction wood that influenced accurate ring identification. Five of nine cross-sections taken from mature spruce in the Monongahela National Forest were sanded and aged for the companion site index project and shared with this study (Brown et al. unpublished).

The Carmean method (1972) was used to calculate height at ages between cross-sections. 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 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 inner ring

h_i = height at ith crosscut

r_i = rings at ith crosscut

j = age transition between cross-sections

Data Analysis

Reference Curves

      Reference curves were used to develop separate growth standards for height by age among the three height classes for the understory red spruce and a composite set of curves for all height classes. The RefCurv software package (Winkler et al. 2019) was used to carry out the lambda-mu-sigma (LMS) method. This method utilizes the Box-Cox Cole Green distribution to penalize splines of the three parameters for which it is named in order to normalize their distributions throughout the range of ages present. A degree of freedom is set for each lambda, mu, and sigma using Bayesian information criterion (BIC) prior to using the Rigby and Stasinapoulos algorithm (Stasinopoulos et al. 2017) to fit the curves in R (R Core Team; Vienna, Austria). Higher degrees of freedom provide a more flexible curve to fit the data. Simple models will have lower degrees of freedom. Although this procedure is fairly standard in the medical field, it is less prominent in the natural sciences. Vickers et al. (2017) carried out similar work to model young stands in the Missouri Ozarks.

      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. Individual mature tree growth histories were then overlaid to compare growth to the centiles for each understory height class.

Analysis of Allometric Relationships

      Nonlinear analysis was used to model allometric relationships in JMP 14 (SAS Institute Inc.; Cary, NC). Diameter at breast height was used to predict tree height and crown width, while height was used to predict crown width. Deviations in polynomial, sigmoid, and exponential fits were compared. Akaike information criterion (AIC) was used to determine the best model for each relationship. Visual confirmation was necessary to check if the best model in terms of AIC score did not overpredict changes where data were absent. Equivalence analysis was used to assess significant differences between height classes. Simple regression was attempted prior to nonlinear analysis but the assumptions of normality of errors and homoscedasticity of errors were not met. Data transformations attempted failed to achieve normality as well. Similar nonlinear analysis was carried out to determine if any of the three measures (DBH, height, age) could reliably predict tree age.

Suppression and Releases

      Number of releases were calculated using percent growth change in the second cross-section (0.3 m) of each sample as described by Rentch et al. (2007). Radial means were calculated in rolling 10-year averages. A 100% increase in radial increment indicated a release in understory samples (Lorimer and Frelich 1989). Periods of suppression were then identified as time between release events.

RESULTS

Characteristics of the dataset

A total of 252 understory red spruce trees were used in final analyses. Understory red spruce were growing on sites with average slopes of 9.9 percent, while the most common aspect was north facing. The most common overtopping species was red spruce (39%), followed by red maple (21%) and yellow birch (15%). At the time of sampling 7.5% of the trees were located within a gap with an average area of 41 m^2. Most understory trees had never experienced a release. Table 1 highlights allometric differences between samples of different height classes. As expected, the taller samples were on average older than those in the shorter classes but the range in mean age was only 11 years. Every measurement taken produced higher means for the larger height class. Mean annual growth in the largest individuals was more than triple that of the smallest class.

Table 1: Summary statistics for the three height classes of understory red spruce including results for all classes combined

Height Class	N	Mean Height (m)	Mean Live Crown Height (m)	Mean DBH (cm)	Mean Crown Width (m)	Mean Age (years)	Annual Height Growth (m)
1 (0.1-2.6 m)	83	1.22	0.53	1.17	0.68	29.8	0.04
2 (2.6-5.1 m)	85	3.47	1.50	3.84	1.27	42.15	0.09
3 (5.1-7.6 m)	84	5.87	2.74	7.08	1.83	50.71	0.13
All Classes	252	3.53	1.59	4.86	1.26	40.94	0.09

Reference Curves

Understory Trees

Reference curves built for height class 1 (Figure 4) show almost immediate differentiation in the 90th and 97th percentiles compared to lower centiles where differences become more apparent around 20 years. Modelling growth to 50 years of age showed heights spanning from 0.67 m (3rd percentile) to 2.48 m (97th percentile). Growth appears to level off with no indication of an age where widespread release occurs for any of the centiles. The LMS degrees of freedom producing the best Bayesian Information Criterion (BIC) score (-651.9) were 0, 3, and 0 respectively. The fit of the model was significant to a 0.0001 level (Appendix 5).

Reference curves built for height class 2 (Figure 4) display more immediate differences between several of the upper centiles (75th, 90th, and 97th percentiles). All centiles increase in growth rate between ages 10 and 20 years. This increase is more pronounced in the upper centiles. Growth begins leveling off after 20 years of age. At 50 years of age, the model ranges in

heights between 1.28 m (3rd percentile) and 4.52 m (97th percentile). The LMS degrees of freedom producing the best BIC score (4628.8) were 0, 5, and 4 respectively. The fit of the model was significant to a 0.0001 level (Appendix 6).

Reference curves built for height class 3 produced the widest range of results. Differences in height and growth rates are apparent for most centiles after 10 years. Growth rates were highest between 10 and 30 years of age for the upper centiles (75th, 90th, and 97th percentiles). Growth rate remained fairly constant for the 50th percentile. Lower centiles (3rd, 10th, and 25th percentiles) display constant growth until age 30 where growth rate begins to increase. At 50 years the model ranges in heights from 1.58 m (3rd percentile) to 7.25 m (97th percentile). The LMS degrees of freedom producing the best BIC score (10075.6) were 0, 0, and 3 respectively. The fit of the model was significant to a 0.0001 level (Appendix 7).

All height classes were compiled to model a comprehensive set of reference curves for understory red spruce. The upper centiles (90th and 97th percentiles) showed immediate differentiation in growth rates from the lower centiles. The 50th and 75th percentiles showed faster growth compared to the lowest centiles by year 10. The lowest centiles (3rd, 10th, and 25th percentiles) were similar in growth until year 20. Growth rates were largest between year 10 and 30 for centiles above the 50th percentile before beginning to level around year 40. The lowest centiles displayed fairly constant slow growth through 50 years. The model displays a range of height between 0.95 m (3rd percentile) and 6.85 m (97th percentile) at 50 years. The LMS degrees of freedom producing the best BIC score (16791.5) were 0, 5, and 3 respectively. The fit of the model was significant to a 0.0001 level (Appendix 8). Lambda, sigma, and mu values are reported in the appendices (Appendix 1-4) along with age and height values for each individual centile curve.
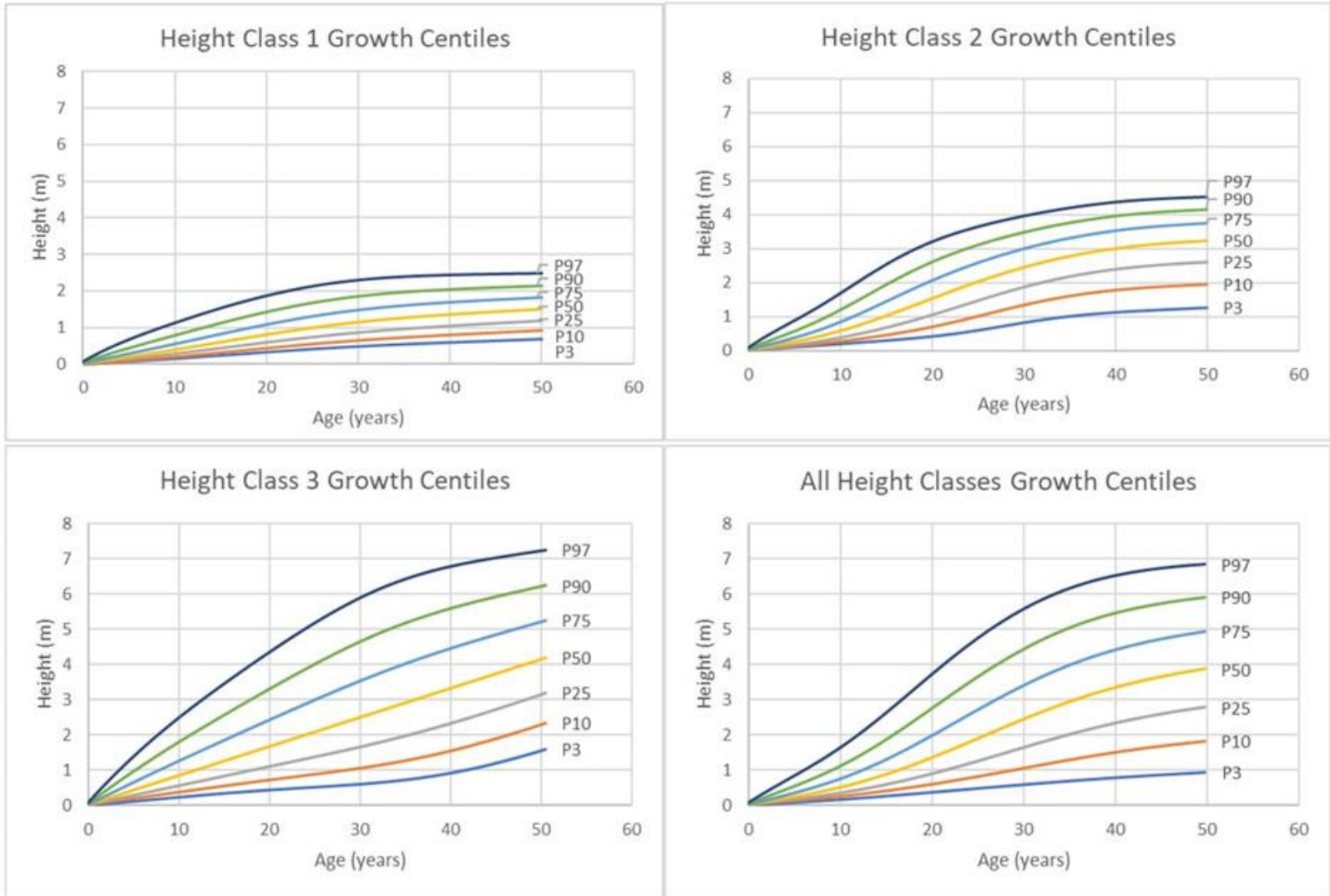
Figure 6: Height class centiles for red spruce modelled in RefCurv (Winkler 2017).

Mature Tree Overlay

Sample size of overstory red spruce was insufficient and noncontiguous to properly model growth centiles. Twenty-four overstory trees were used as individual overlays to broadly compare how an older cohort grew in a seedling/sapling stage compared to the current understory cohort. Further analyses showed somewhat of a separation in growth rates between mature trees established before and after the year 1900. Fifteen of the twenty-four mature individuals outperformed the 97th percentile in understory height growth by year 50. Among the mature trees 7 of 24 were never slower growing than the 97th percentile of the understory trees. Eight of 24 mature trees remained below the 50th percentile of understory height growth at 50 years but eventually still reached a dominant or codominant position. The slowest growing individual did not display growth rates above the 10th percentile until after age 70.
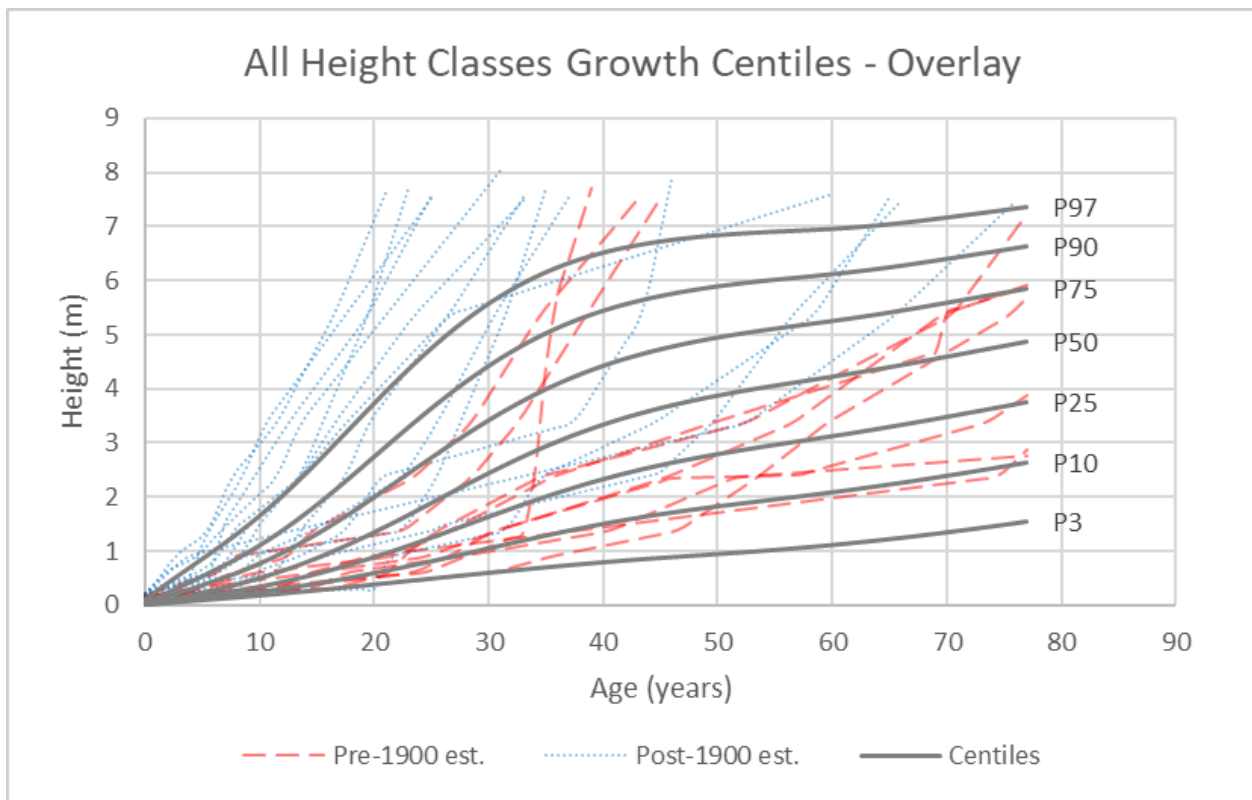
Figure 5: Centiles for height growth by age for all understory red spruce modelled in RefCurv (Winkler et al. 2017) overlaid with early growth of 24 mature dominant and codominant red spruce separated by period of establishment.

Nonlinear Analysis

     JMP was used to model allometric relationships in understory red spruce. Of the 9 combinations of measurements considered only 3 were modelled based on having significant relationships. Three models were produced using nonlinear analysis. Diameter at breast height (DBH) was used to predict total tree height, DBH was used to predict crown width, and total tree height was used to predict crown width. Multiple fits were assessed and graphed to determine which was best using AIC score. Models with nonsignificant parameters were removed. Nonlinear analysis was also used to predict age using DBH, crown width, and total height respectively.

The following equations were found to be among the top preforming nonlinear models for one or more of the allometric and age relationships:

     Linear: Height = intercept + slope * DBH

     Quadratic: Height = intercept + slope + quadratic * DBH^2

     Gompertz 3P: Height = asymptote * exp (-exp (-growth rate (DBH – inflection point)))

     Linear: Crown Width = intercept + slope * DBH

     Exponential 2P: Crown Width = scale * exp (growth rate * DBH)

     Lorentzian Peak: Crown Width: (peak value * growth rate^2) / ((DBH – critical point)^2 + growth rate^2)

     Linear: Crown Width = intercept + slope * DBH

     Quadratic: Crown Width = intercept + slope + quadratic * DBH^2

     Gaussian Peak: Crown Width = peak value * exp (-(0.5 * ((Height – critical point) / growth rate)^2))

     Linear: Age = intercept + slope * DBH

     Exponential 2P: Age = scale * exp (growth rate * DBH)

     Linear: Age = intercept + slope * Height

     Exponential 2P: Age = scale * exp (growth rate * Height)

     Gaussian Peak: Age = peak value * exp (-(0.5 * ((Height – critical point)/growth rate)^2))

     Linear: Age = intercept + slope * Crown Width

     Exponential 2P: Age = scale * exp (growth rate * Crown Width)

     Gaussian Peak: Age = peak value * exp (-(0.5 * ((Crown Width – critical point)/growth rate)^2))

<u>Allometric Relationships</u>

<u>Diameter at Breast Height Predicting Height</u>

Diameter at breast height used to predict total tree height was the strongest relationship found, resulting in an R^2 value of 0.79. The relationship was best represented using a Gompertz (3P) fit resulting in an AIC score of 439.1 followed closely by quadratic and linear fits. Although a Gompertz (3P) fit had a lower AIC score, it may overpredict the relationship overtime. Both quadratic and linear fits had only slightly lower R^2 values but much lower AIC weights. The linear fit predicts a more expected relationship beyond the data points available.

Table 2: Summary of the three best performing nonlinear models developed for the DBH predicting height relationship.

Model	AIC	AIC Weight	BIC	SSE	MSE	RMSE	R-Square
Gompertz 3P	439.091	0.893	451.994	103.401	0.536	0.732	0.794
Quadratic	443.363	0.105	456.266	105.679	0.548	0.740	0.789
Linear	452.070	0.001	461.779	111.661	0.576	0.759	0.778
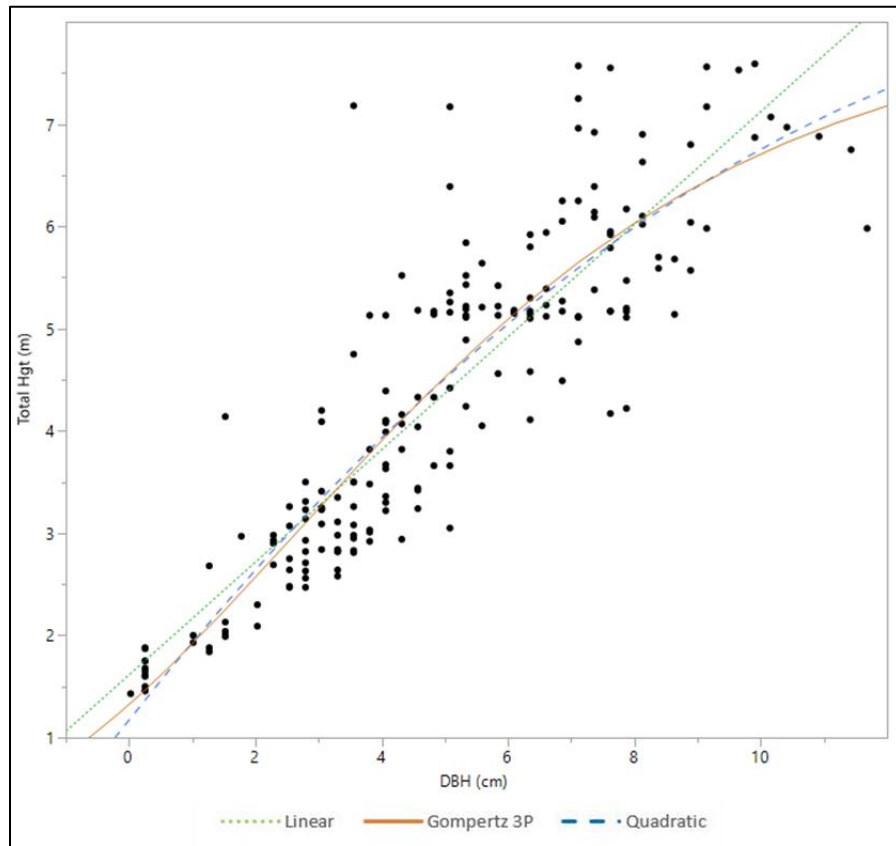
Figure 6: The top three nonlinear models produced using diameter at breast height to predict tree height in understory red spruce.

Table 3: Model parameters for the three best performing models for the DBH predicting height relationship.

	Parameter	Estimate	Std Error	Wald ChiSquare	Prob > ChiSquare	Lower 95%	Upper 95%
Linear	Intercept	1.614	0.116	192.845	<.0001	1.386	1.842
	Slope	0.551	0.021	677.996	<.0001	0.509	0.592
Quadratic	Intercept	1.174	0.175	45.119	<.0001	0.831	1.517
	Slope	0.778	0.072	117.815	<.0001	0.637	0.918
	Quadratic	-0.022	0.007	10.924	0.001	-0.035	-0.009
Gompertz 3P	Asymptote	8.069	0.589	187.713	<.0001	6.914	9.223
	Growth Rate	0.228	0.030	56.200	<.0001	0.169	0.288
	Inflection Point	2.594	0.338	58.765	<.0001	1.931	3.257

Diameter at Breast Height Predicting Crown Width

Diameter at breast height used to predict crown width displayed a significantly weaker relationship ($R^2 = 0.5$). An exponential (2P) relationship was the best fit producing an AIC score of 241.6. Linear and Lorentzian fits were modelled producing similar R^2 values and AIC weights. A linear fit is expected when modelling this relationship. The other models produce less likely scenarios beyond the data points.

Table 4: Summary of the three best performing nonlinear models developed for the DBH predicting crown width relationship.

Model	AIC	AIC Weight	BIC	SSE	MSE	RMSE	R-Square
Exponential 2P	241.566	0.401	251.276	38.148	0.197	0.443	0.499
Lorentzian Peak	241.981	0.326	254.884	37.824	0.196	0.443	0.503
Linear	242.328	0.274	252.037	38.296	0.197	0.444	0.497
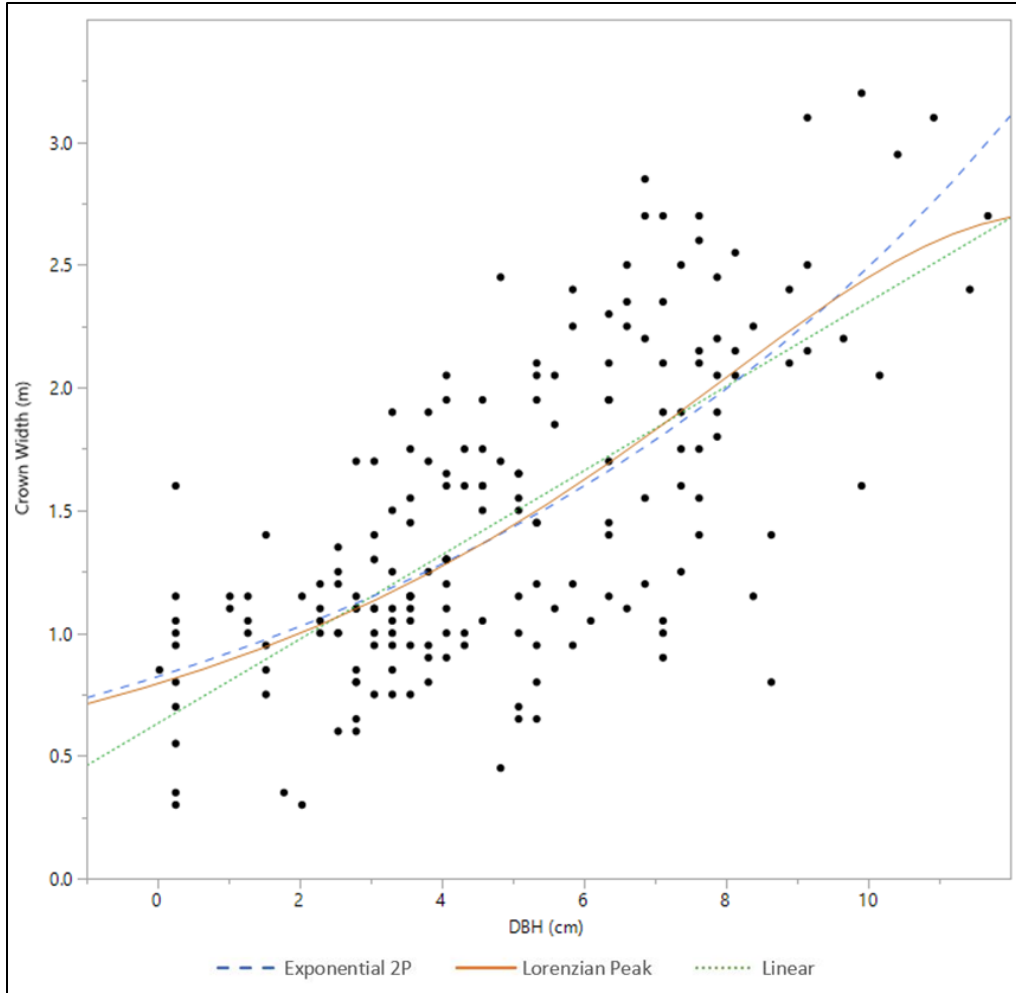
Figure 7: The top three nonlinear models produced using diameter at breast height to predict crown width in understory red spruce.

Table 5: Model parameters for the three best performing models for the DBH predicting crown width relationship.

	Parameter	Estimate	Std Error	Wald ChiSquare	Prob > ChiSquare	Lower 95%	Upper 95%
Linear	Intercept	0.632	0.068	86.170	<.0001	0.498	0.765
	Slope	0.172	0.012	191.914	<.0001	0.147	0.196
Exponential 2P	Scale	0.822	0.045	337.514	<.0001	0.734	0.910
	Growth Rate	0.111	0.008	196.530	<.0001	0.095	0.126
Lorentzian Peak	Peak Value	2.713	0.363	55.884	<.0001	2.002	3.425
	Growth Rate	8.147	0.825	97.550	<.0001	6.531	9.764
	Critical Point	12.676	1.697	55.819	<.0001	9.351	16.002

Height Predicting Crown Width

Total height was used to predict crown width producing a Gaussian Peak model with a R^2 value of 0.53. The model achieved an AIC score of 343.3 outperforming quadratic and linear variations. This was the second weakest of the three modelled allometric relationships. The quadratic model only produced a slightly higher AIC score (343.3) and an identical R^2 value compared to the best fitting model. A linear relationship is expected when modeling this relationship despite the AIC scores produced using the understory red spruce data.

Table 6: Summary of the three best performing nonlinear models developed for the height predicting crown width relationship.

Model	AIC	AIC Weight	BIC	SSE	MSE	RMSE	R-Square
Gaussian Peak	343.281	0.492	357.236	55.778	0.224	0.473	0.530
Quadratic	343.336	0.478	357.292	55.791	0.224	0.473	0.530
Linear	348.878	0.030	359.369	57.500	0.230	0.480	0.516
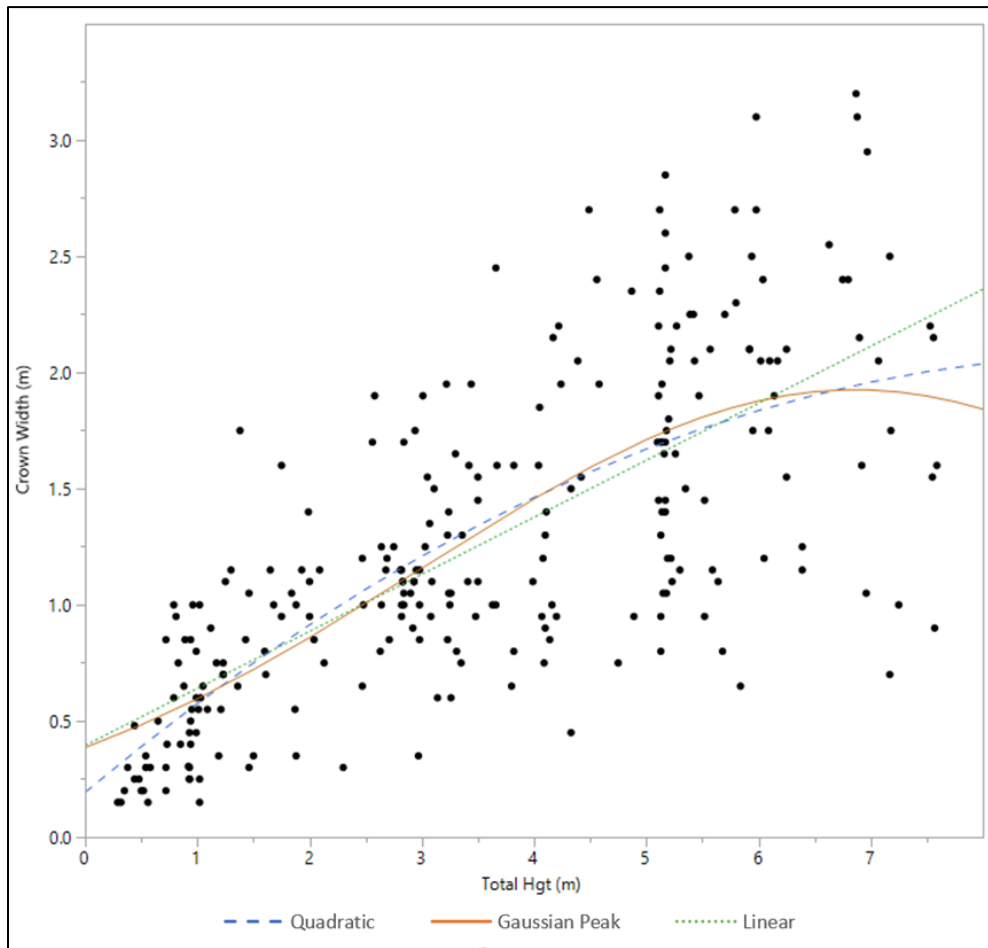
Figure 8: The top three nonlinear models produced using tree height to predict crown width in understory red spruce.

Table 7: Model parameters for the three best performing models for the height predicting crown width relationship.

	Parameter	Estimate	Std Error	Wald ChiSquare	Prob > ChiSquare	Lower 95%	Upper 95%
Linear	Intercept	0.395	0.061	41.784	<.0001	0.275	0.515
	Slope	0.245	0.015	266.285	<.0001	0.216	0.275
Quadratic	Intercept	0.193	0.095	4.158	0.041	0.008	0.379
	Slope	0.404	0.059	46.509	<.0001	0.288	0.520
	Quadratic	-0.022	0.008	7.631	0.006	-0.037	-0.006
Gaussian Peak	Peak Value	1.926	0.079	590.037	<.0001	1.770	2.081
	Critical Point	6.862	0.526	170.131	<.0001	5.830	7.893
	Growth Rate	3.825	0.382	100.313	<.0001	3.077	4.574

Age Prediction

Diameter at Breast Height Predicting Age

Diameter at breast height was used to predict age in understory red spruce. The top models produced were exponential (2P) and linear fits. They produced similar R^2 values (0.29) as well as AIC scores although an exponential fit was deemed best. This relationship only explained around 29% of the variation in age using diameter. The scatterplot (Figure 9) shows large variations in ages in trees of a similar diameter highlighting varying year of suppression. Only two models could be produced with significant parameters for this relationship.

Table 8: Summary of the two best performing nonlinear models developed for the DBH predicting age relationship.

Model	AIC	AIC Weight	BIC	SSE	MSE	RMSE	R-Square
Exponential 2P	1583.478	0.745	1593.187	35880.695	184.952	13.600	0.299
Linear	1585.623	0.255	1595.333	36275.668	186.988	13.674	0.292
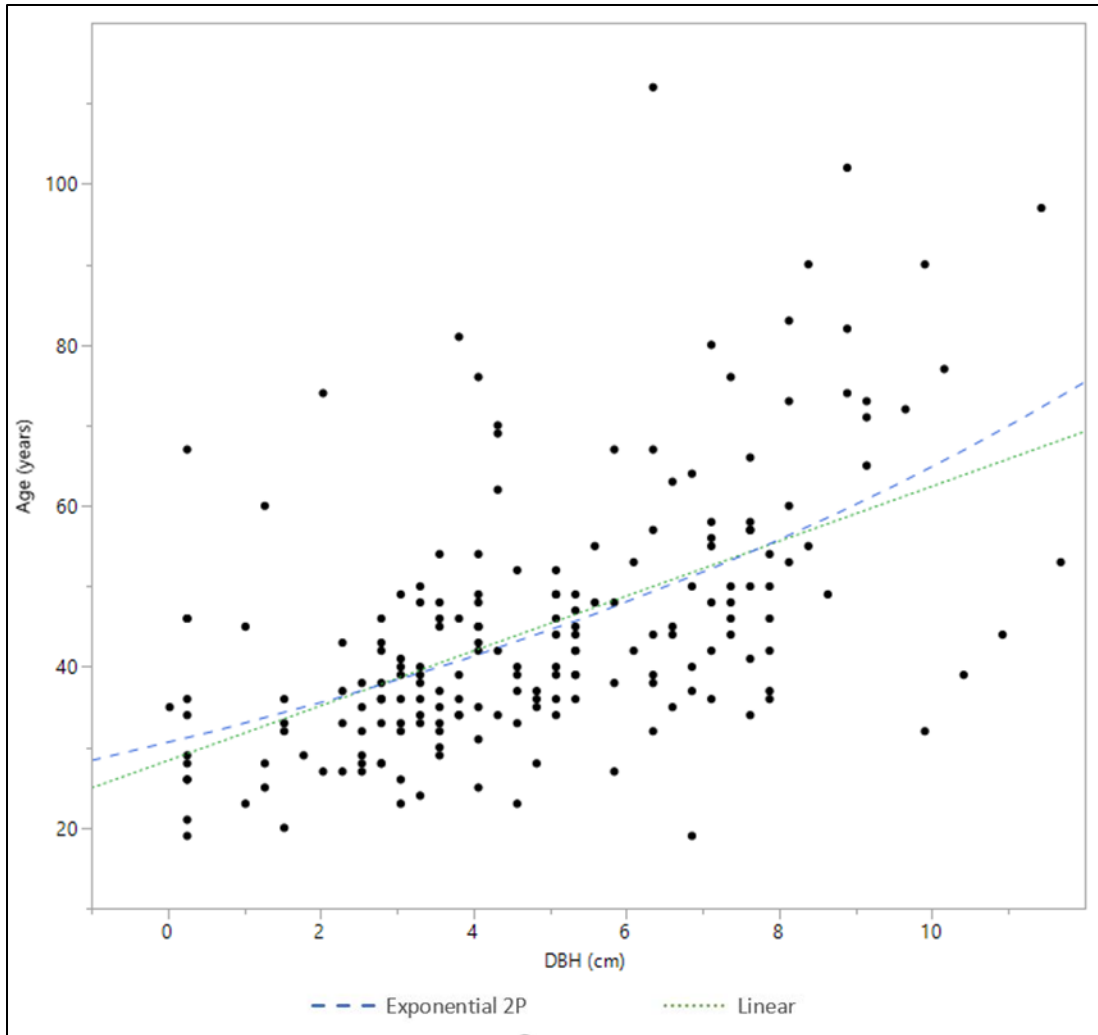
Figure 9: The top two nonlinear models produced using diameter at breast height to predict age in understory red spruce.

Table 9: Model parameters for the two best performing models for the DBH predicting age relationship.

	Parameter	Estimate	Std Error	Wald ChiSquare	Prob > ChiSquare	Lower 95%	Upper 95%
Linear	Intercept	28.348	2.095	183.163	<.0001	24.243	32.454
	Slope	3.408	0.381	79.870	<.0001	2.660	4.155
Quadratic	Scale	30.575	1.591	369.548	<.0001	27.458	33.693
	Growth Rate	0.075	0.008	86.659	<.0001	0.059	0.091

Height Predicting Age

Tree height was used to predict age in understory red spruce. A linear fit received the best AIC score (2042.1) followed by a Gaussian peak fit and an exponential (2P) growth model. Similar R^2 values were produced ranging from 0.329 to 0.339 resulting in only around 33% of the variation in age being explained by height. The scatterplot (Figure 10) again shows large variations in ages among trees of a similar height. The trees collected for data analysis met minimum heights of 0.1 m. Extrapolation below these heights, prior to establishment (15 cm), may not be accurate as biologically the relationship should be constrained to the origin.

Table 10: Summary of the three best performing nonlinear models developed for the height predicting age relationship.

Model	AIC	AIC Weight	BIC	SSE	MSE	RMSE	R-Square
Linear	2042.141	0.642	2052.632	47623.995	190.496	13.802	0.329
Gaussian Peak	2043.952	0.259	2057.908	47576.055	191.068	13.823	0.330
Exponential 2P	2045.882	0.099	2056.373	48336.231	193.345	13.905	0.319
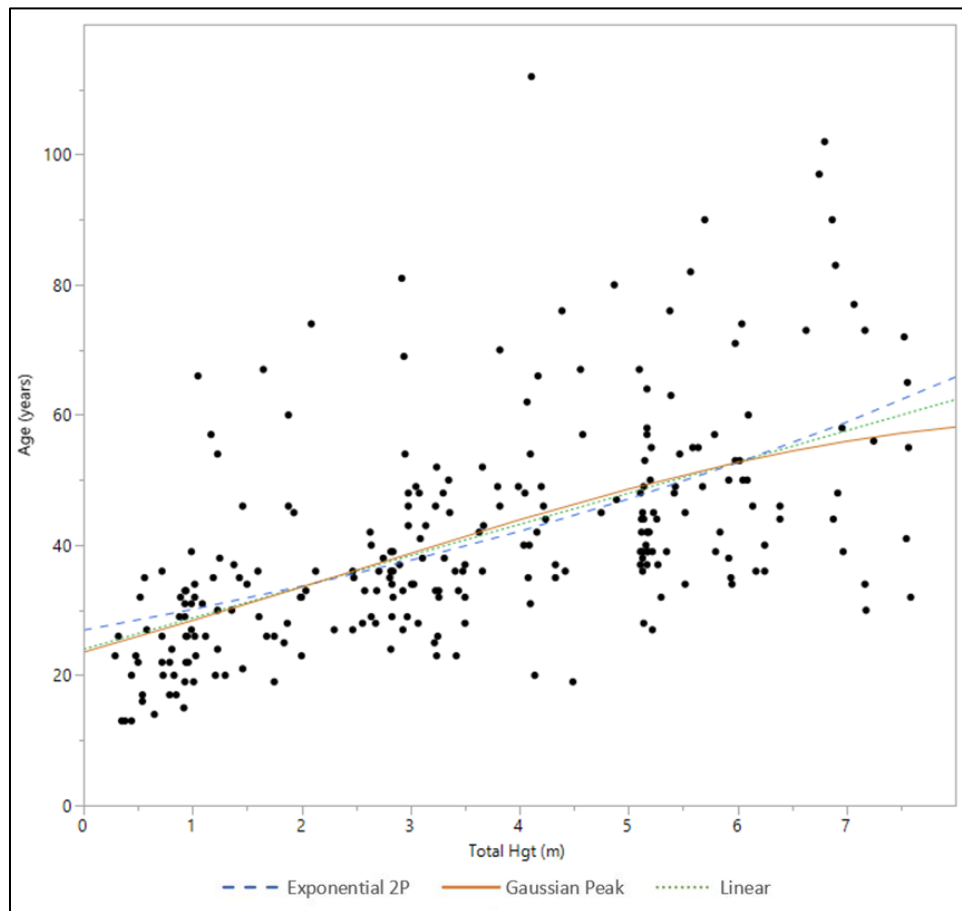
Figure 10: The top three nonlinear models produced using tree height to predict age in understory red spruce.

Table 11: Model parameters for the three best performing models for the height predicting age relationship.

	Parameter	Estimate	Std Error	Wald ChiSquare	Prob > ChiSquare	Lower 95%	Upper 95%
Linear	Intercept	24.007	1.758	186.482	<.0001	20.562	27.453
	Slope	4.796	0.433	122.758	<.0001	3.948	5.644
Exponential 2P	Scale	26.938	1.388	376.579	<.0001	24.217	29.659
	Growth Rate	0.112	0.011	109.922	<.0001	0.091	0.133
Gaussian Peak	Peak Value	59.201	8.435	49.255	<.0001	42.668	75.734
	Critical Point	9.298	2.756	11.380	0.001	3.896	14.701
	Growth Rate	6.848	1.779	14.820	0.000	3.362	10.335

Crown Width Predicting Age

Finally, crown width was used to predict age in understory red spruce. Similarly, low R^2 values of 0.293 – 0.302 were produced for the three best preforming models. A linear fit was deemed best based on the lowest AIC score of 2052.1 compared to the exponential (2P) and Gaussian peak fits. Still only 30% of the variation in age was attributed to crown size in the linear fit. The scatterplot (Figure 11) displays large variations in crown sizes for trees of similar age.

Table 12: Summary of the three best performing nonlinear models developed for the crown width predicting age relationship.

Model	AIC	AIC Weight	BIC	SSE	MSE	RMSE	R-Square
Linear	2052.117	0.655	2062.608	49547.095	198.188	14.078	0.302
Gaussian Peak	2054.360	0.213	2068.316	49582.140	199.125	14.111	0.302
Exponential 2P	2055.327	0.132	2065.819	50182.350	200.729	14.168	0.293
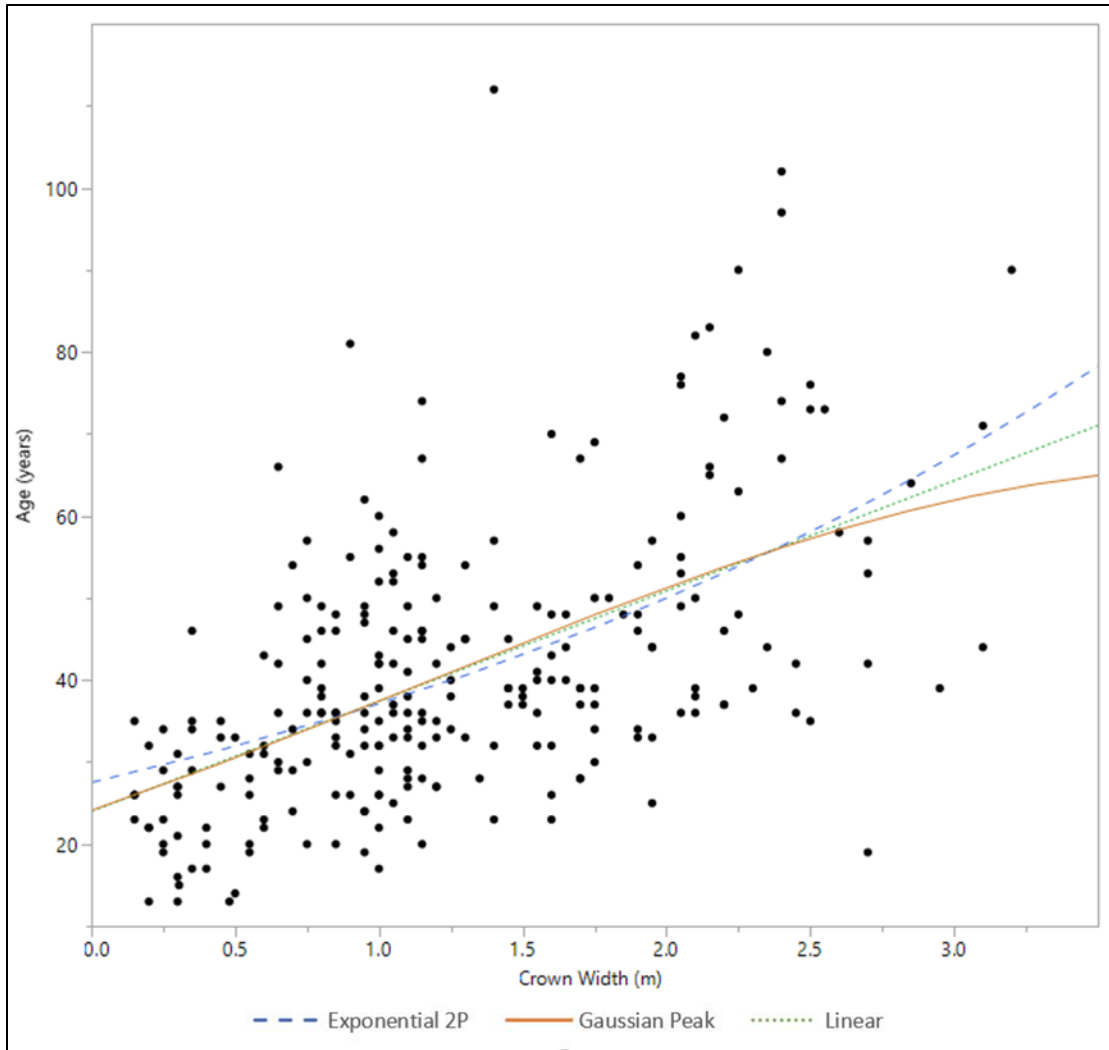
Figure 11: The top three nonlinear models produced using crown width to predict age in understory red spruce.

Table 13: Model parameters for the three best performing models for the crown width predicting age relationship.

	Parameter	Estimate	Std Error	Wald ChiSquare	Prob > ChiSquare	Lower 95%	Upper 95%
Linear	Intercept	23.980	1.855	167.100	<.0001	20.345	27.616
	Slope	13.444	1.292	108.290	<.0001	10.912	15.976
Exponential 2P	Scale	27.506	1.370	403.048	<.0001	24.821	30.191
	Growth Rate	0.299	0.029	108.420	<.0001	0.243	0.355
Gaussian Peak	Peak Value	65.981	13.691	23.226	<.0001	39.147	92.815
	Critical Point	4.002	1.445	7.666	0.006	1.169	6.835
	Growth Rate	2.820	0.848	11.066	0.001	1.158	4.481

Regional Comparisons

Diameter at Breast Height Predicting Height

Nonlinear analysis was carried out on diameter at breast height predicting tree height. Separate linear fits were used on samples larger and smaller than three inches in diameter to compare the relationship with the Curtis-Arney (Curtis 1967; Arney 1985) equations used in the Forest Vegetation Simulator (FVS) parameterized for red spruce using the NE variant. Two equations are utilized creating a separation at 7.62 cm (3 inches) between larger and smaller trees. The linear relationship developed using sampled understory red spruce differed only slightly for trees below 7.62 cm in diameter. The slope in the predicted Curtis-Arney line has a larger slope and smaller intercept compared to the actual data. The relationship in trees with diameters larger than 7.62 cm shows larger differences. The predicted line using the Curtis-Arney equation displays a much larger slope and smaller intercept compared to the actual data. Sampled red spruce underperformed compared to the Curtis-Armey equations. The sample size for trees above three inches in diameter (n =28) is much smaller compared to those less than 3 inches (n = 224) possibly influencing the differences.
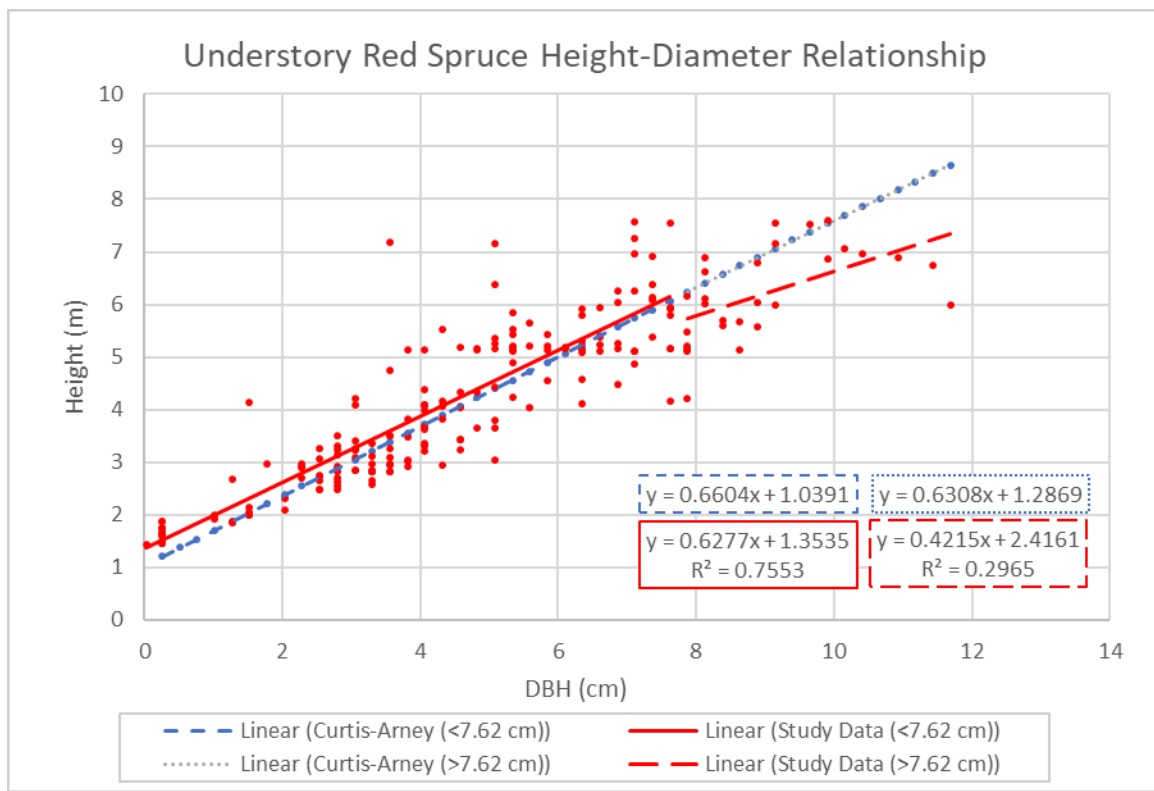
Figure 12: Comparison of diameter at breast predicting tree height using the Curtis-Arney equations and the linear models developed for understory red spruce in this study.

<u>Diameter at Breast Height Predicting Crown Width</u>

        Another comparison was carried out on the allometric relationship using diameter at breast height to predict crown width. A power equation developed by Bechtold (2003) from plots across the range of red spruce in the United States was compared to the linear equation developed using the sampled understory red spruce. The local equation consistently produced slightly larger crown widths (about 0.5 m larger) compared to the equation from Bechtold. The difference in the lines decreased with larger diameters. Using a power equation on the understory red spruce data, only 35% of the variation in crown width could be explained by diameter size. The linear fit, one of the best models, compared to nonlinear analysis, improved the R^2 value (0.497).
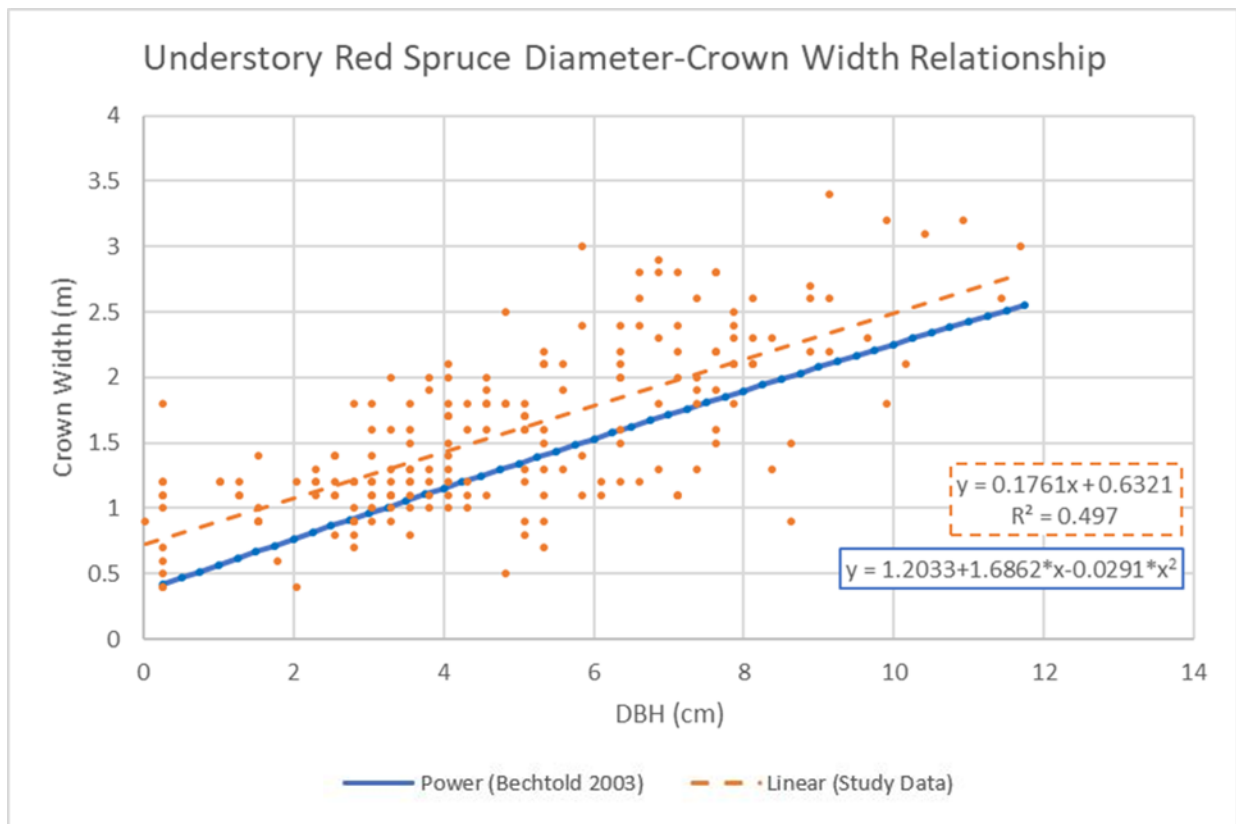
Figure 13: Comparison of diameter at breast height predicting crown width using the equation developed by Bechtold (2003) and the linear model developed using understory red spruce data from this study.

DISCUSSION

Reference Curves

<u>Understory Height Classes</u>

Sampling of understory red spruce was separated into three height classes to capture the variation in young trees prior to ascension into the canopy. Although shorter height classes displayed a lower mean age, the age range across the three height classes was similar, which suggested that trees established during the same period were having different growth rates likely attributed to their location in the stand. Growth rates are influenced by a number of factors including competition. Sampled trees were most commonly found under mature red spruce and a variety of northern hardwoods. Red spruce is long lived but its canopy and associated soils may produce more suitable microclimates for young trees to outlast faster growing hardwoods (Baldwin 1933; Dumias and Prevost 2016; Greenwood et al. 2008). Northern hardwoods can compete with understory red spruce (Cogbill and White 1991), but yield gaps more frequently (Rentch et al. 2010).

Although red spruce mortality has been widely studied through periods of decline (Mielke 1986; Johnson et al. 1988; McLaughlin et al. 1987; Hamburg and Cogbill 1988), it is less commonly researched in the seedling and sapling stages (Busing and Wu 1990; Dumais et al. 2019). Centiles produced for height class 1 displayed the least variation in height compared to the other classes. Only the 3rd and 10th percentiles in height class 1 displayed shorter heights than the lowest centile in height class 2. Given that this is survivor-only data, most of these individuals are likely to experience mortality prior to advancing to the next height class. The reference curves do indicate that a small portion of seedlings are able to persist with slow growth. This is supported by Busing and Wu's (1990) work with red spruce in the Southern Appalachians where mortality in small trees was 0.7% annually. The 50th percentile in height class 1 yields a similar height to the 3rd percentile in height class 3. Around half of the trees in height class 1 are therefore able, yet may be unlikely, to persist into height class 3, albeit as the slowest growing in that class. Even the 97th percentile in height class 1 only produces similar height to the 10th percentile in height class 3 at 50 years. This suggests that the range of individuals in height class 1 have a chance to reach height class 3 but a majority are likely to experience mortality prior to release into the overstory. Given the observed rates in the Southern Appalachians annually (Busing and Wu 1990), a large majority of these individuals would succumb to mortality prior to 50 years of age.

Height class 2 produces a range of heights greater than height class 1 after 50 years. The fastest growing centile (97th percentile) produces similar heights to average trees (50th percentile) in height class 3. Only the 3rd percentile in height class 2 yields a shorter tree than the 3rd percentile in height class 3. This indicates the ability of nearly all trees in height class 2 to advance into height class 3 prior to mortality. This would suggest lower mortality rates in larger trees when comparing height class 2 to height class 1 where the lowest 10 percent of trees were

unable to advance into the next class. This drop in mortality as red spruce increases in size is supported by the literature (Busing and Wu 1990). Even so, both smaller height classes show the ability to persist in the understory with slow growth which is expected in shade-tolerant species like red spruce.

Height class 3 displays the most variation in height obtained after 50 years in its centiles. Higher centiles display more vertical in growth indicating unimpeded conditions. Still growth slows as 50 years are modelled. Very few of the understory spruce trees that were sampled occurred in gaps, which would likely support the decline in growth until future release events. It is possible that growth rates will increase again with a release event, but this class was the largest sampled and any additional release would likely begin approaching lower canopy layers. The absence of faster growth rates in height classes 1 and 2 may be a product of the recent lack of disturbance in red spruce habitat on public lands in the region. Most sites appeared to only display sporadic windthrow. This theory of lack of disturbance is supported by the small number of samples taken from gaps during the study and is consistent with other datasets (Lutz 2018; Rentch et al. 2007).

Mature Tree Overlay

A goal of this study was to compare early growth in successful red spruce to growth in understory red spruce today. A limited sample size for dominant and codominant red spruce precluded the development of significant growth centile models. These trees were instead overlaid on centiles built using all sampled understory height classes.

The variation in height growth among mature spruce was larger than any understory height class centiles. The fastest growing individuals outperformed the 97th percentile of the composite model immediately indicating open growth or different resource availability from the time of establishment. The slowest growing individuals barely outperformed the 10th percentile for understory spruce. This may indicate that only the slowest growing understory samples, below the 10th percentile, are not able to persist long enough to experience release into the overstory. Fifteen of twenty-four individuals outperformed the 97th percentile by year 50. 75% of mature trees outperformed the 97th percentile by year 80 meaning most trees with a chance of success will be released by that age. Still 25% of successful trees will persist in the understory beyond that point. This slower pathway to success is supported by other regional studies (Rentch et al. 2007; Rentch et al. 2016; Wu et al. 1999). Gap creation that produced a canopy release resulted in success for individual red spruce. However, continuous open growth was absent in these cases (Wu et al. 1999).

A distinct pattern can be seen in the sampled mature spruce. Fifteen individuals displayed more open growth when young while 9 individuals experienced slower growth. These differences in growth are likely attributed to competition and disturbance in the stand early in their life history. Trees were separated based on year of establishment. Seven of 10 trees established prior to 1900 were slower growing. Eleven of 14 trees established after 1900

experienced what appears to be open growth. This difference in growth pattern by year of establishment could be a product of logging. Most red spruce in the region was logged in the late 1800s with fewer remnant stands being logged in the early 1900s. This would make it more likely that trees established prior to 1900 had a canopy overhead in their youth. Later releases could be attributed to their stands being logged. These trees were likely too small for harvest and left as residuals. Trees established after 1900 may have been located in cut over areas from time of establishment producing open growth conditions. Without detailed site histories this cannot be confirmed but used as a possible explanation of the differences in growth.

Nonlinear Analysis

Allometric Relationships

The height-diameter relationship was by far the strongest of any allometric relationship that was assessed. The height of understory red spruce can be predicted by a diameter measurement with reasonable accuracy. Crown relationships were less predictable. Using diameter or height to predict crown width produced an R^2 value lower than what may be expected for many species. Red spruce is unique in its ability to persist for long periods in the understory. Most individuals are under varying degrees of stress including that induced by low light levels. Small crowns are able to sustain individuals until a release or mortality event occurs. Due to varying degrees of stressors and light conditions it becomes hard to predict crown size with a single, easily attained measurement. Similar difficulties were noted for other shade-tolerant species, both regionally in the Appalachians and beyond in tropical species (Dawkins 1963; Shallenberger et al. 1986; Hemery et al. 2005). Red spruce in early stages of life may not be an ideal candidate to use allometric relationship as predictors. Practically, the strength of the height-diameter relationship could at least be used to quickly obtain a height estimate.

Using Allometric Measurements to Predict Age

Ideally a specific growth rate could be identified in past successful individuals and compared to a young trees growth rate today to identify good candidates for management efforts. The 24 destructively sampled red spruce spanned the range of understory growth rates present today. Unfortunately, this does not allow us to identify trees that have a high probability of reaching the canopy. Inversely, this does not rule out most understory trees from doing so, although we understand that most will not reach the canopy based on mortality studies (Busing and Wu 1990). A common thread in many past successful individuals is an early period of sustained, rapid growth meaning younger trees reaching taller heights in the understory quickly have a good chance to advance into taller height classes. Evidence for this theory of younger trees more successfully responding to release is supported by findings that the response of older individuals declines with age (Brix and van den Driessche 1977). Therefore, identifying age in understory trees could allow us to focus resources on the best individuals. The practical issue of identifying age without destructively sampling then becomes the goal. An easily obtainable

measurement in the field helping us identify tree age would be of use in management to allocate resources to individuals more likely to succeed in years to come.

Using diameter at breast height, height, and crown width to predict age proved to be difficult. Diameter at breast height predicting age was the strongest identified relationship explaining around 40% of the variation in age with diameter. This is still a weak relationship. The relationship becomes more unpredictable as age increases. Red spruce seedlings can survive for extended periods of time, even with very little diameter growth (Hart 1965). This feature leads to the same challenges when comparing height-age and crown diameter-age relationships where the R^2 values are even lower. These are the difficulties faced when modelling growth for a shade-tolerant species like red spruce. It is likely that this species is not a good candidate for models involving annual growth in the understory.

Regional Comparisons

When using a growth model an important question to ask is how the model was developed. This includes the time period, the sites, and the sampled trees used to develop said model. Since red spruce was depleted in the Central Appalachians prior to many models being developed, it is likely that current literature does not accurately represent how the species behaves in the region. Additional anthropogenic factors including climate change, disturbance, and pollution could impact the species as well. It is important to identify if red spruce in West Virginia aligns with widely used models. And if not, we may be able to develop a more regionally specific alternative for management purposes.

Two additional models for red spruce growth were identified in the literature. The Forest Vegetation Simulator (FVS) program developed by the USDA Forest Service (Dixon et al. 2008) models the height-diameter relationship using the Curtis-Arney (Curtis 1967, Arney 1985) equations. Trees below 7.62 cm in diameter performed nearly identical to the predicted equation. Deviations began to occur in trees above that 7.62 cm diameter split. Sampled red spruce underperformed the equation. These differences may be explained when considering differences in site conditions in larger diameter trees. Individuals experiencing competition and low light levels may continue to add diameter growth at disproportionate rates compared to height growth. Additionally, sample size for trees above a 3-inch diameter was significantly smaller than below that split. A larger sample size could plausibly produce a different result. Additional investigation into Curtis and Arney's work revealed the equation form was developed using western Douglas-fir stands. Although shade-tolerant species were used, the conditions deviate significantly from red spruce stands of the Central Appalachians. For these reasons the accuracy of predictions are more impressive.

The second model compared was developed by Bechtold (2003) using FAI data. He used trees that spanned 24 eastern states including the whole range of red spruce in the United States. Only open grown trees were eliminated to create a sample representative of stand grown trees. Only trees above 12.7 cm in diameter were measured. This varies from conditions used in our

study. Red spruce samples were obtained from the understory and no individual met a 12.7-cm diameter. The underperformance of the data when comparing to the model is likely explained by these differences in methodology.

CONCLUSION

Red spruce has experienced an array of challenges in the Central Appalachians ranging from exploitative practices to changes in climate and competition. Furthering our understanding of how the species develops in the region can help inform management decisions to meet restoration goals. More concrete measures of success are necessary to evaluate our efforts. Understanding how successful trees developed in early stages of life can help quantify which other young trees that have similar potential to ascend into the upper canopy. Additionally, identifying young trees with the allometric measures to meet this quantified success is necessary in management.

This study suggests that understory red spruce today can persist in the forest floor for decades without release or can experience growth matching that of most competitors given the right conditions. Development today is similar to many successful individuals that established prior to the turn of the twentieth century which span most percentiles produced in analysis. Development after that point was revealed to be more rapid. It is apparent that faster growth is more likely to result in a successful tree, but slow growing individuals are able to experience release to reach the same fate. There are multiple pathways for these shade-tolerant individuals to reach the canopy.

Diameter at breast height was found to be the most reliable predictor of tree height and crown width. The relationship between height and crown width was slightly weaker. Predicting age with any of these measures was found to be unreliable. Difficulty in age prediction in shade-tolerant understory red spruce is a result of the variation seen in trees of the same sizes. Given the range of successful development, these allometric measures may not be necessary for selecting an individual with the ability to release in the future. Developed equations were found to underperform allometric predictors used in literature. It is possible that a different methodology may be necessary to predict these relationships regionally.

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APPENDICES

Appendix 1: The lambda, sigma, and mu values for the centiles modelled for height class one where "x" is age in years and "P" is percentile.

Height Class 1

x	mu	sigma	nu	P3	P10	P25	P50	P75	P90	P97
0.000	0.018	0.580	-0.381	0.007	0.010	0.013	0.018	0.028	0.044	0.076
0.505	0.037	0.577	-0.370	0.015	0.019	0.026	0.037	0.056	0.088	0.148
1.010	0.055	0.574	-0.359	0.022	0.029	0.039	0.055	0.084	0.130	0.217
1.515	0.074	0.570	-0.348	0.030	0.038	0.051	0.074	0.112	0.171	0.283
2.020	0.092	0.567	-0.337	0.037	0.048	0.064	0.092	0.139	0.212	0.346
2.525	0.111	0.563	-0.326	0.045	0.058	0.077	0.111	0.166	0.252	0.406
3.030	0.129	0.560	-0.315	0.052	0.068	0.090	0.129	0.193	0.291	0.464
3.535	0.148	0.557	-0.304	0.059	0.077	0.103	0.148	0.220	0.330	0.520
4.040	0.166	0.553	-0.293	0.067	0.087	0.117	0.166	0.247	0.368	0.575
4.545	0.185	0.550	-0.282	0.074	0.097	0.130	0.185	0.273	0.405	0.627
5.051	0.203	0.547	-0.271	0.082	0.107	0.143	0.203	0.300	0.442	0.678
5.556	0.222	0.544	-0.259	0.090	0.117	0.156	0.222	0.326	0.479	0.728
6.061	0.241	0.540	-0.248	0.097	0.127	0.170	0.241	0.353	0.515	0.777
6.566	0.260	0.537	-0.237	0.105	0.137	0.183	0.260	0.379	0.550	0.824
7.071	0.279	0.534	-0.226	0.113	0.147	0.197	0.279	0.406	0.586	0.871
7.576	0.298	0.531	-0.215	0.121	0.158	0.211	0.298	0.432	0.621	0.916
8.081	0.317	0.528	-0.204	0.128	0.168	0.225	0.317	0.459	0.656	0.961
8.586	0.337	0.525	-0.193	0.136	0.179	0.239	0.337	0.486	0.691	1.005
9.091	0.356	0.521	-0.182	0.144	0.190	0.253	0.356	0.512	0.726	1.049
9.596	0.376	0.518	-0.171	0.153	0.200	0.268	0.376	0.539	0.761	1.092
10.101	0.396	0.515	-0.160	0.161	0.211	0.282	0.396	0.566	0.796	1.135
10.606	0.416	0.512	-0.149	0.169	0.223	0.297	0.416	0.593	0.830	1.177
11.111	0.437	0.509	-0.138	0.178	0.234	0.312	0.437	0.621	0.865	1.219
11.616	0.457	0.506	-0.127	0.186	0.245	0.327	0.457	0.648	0.899	1.261
12.121	0.478	0.503	-0.115	0.195	0.257	0.343	0.478	0.675	0.934	1.301
12.626	0.499	0.500	-0.104	0.203	0.268	0.358	0.499	0.703	0.968	1.342
13.131	0.519	0.497	-0.093	0.212	0.280	0.373	0.519	0.730	1.002	1.382
13.636	0.541	0.494	-0.082	0.221	0.292	0.389	0.541	0.758	1.036	1.422
14.141	0.562	0.491	-0.071	0.229	0.303	0.405	0.562	0.785	1.069	1.461
14.646	0.583	0.488	-0.060	0.238	0.315	0.421	0.583	0.813	1.103	1.499
15.152	0.604	0.485	-0.049	0.247	0.327	0.436	0.604	0.840	1.136	1.537
15.657	0.625	0.483	-0.038	0.256	0.339	0.452	0.625	0.867	1.169	1.574
16.162	0.646	0.480	-0.027	0.265	0.351	0.468	0.646	0.894	1.201	1.611
16.667	0.667	0.477	-0.016	0.274	0.363	0.484	0.667	0.921	1.233	1.647
17.172	0.688	0.474	-0.005	0.283	0.375	0.500	0.688	0.948	1.265	1.682

17.677	0.709	0.471	0.006	0.292	0.387	0.516	0.709	0.974	1.296	1.716
18.182	0.730	0.468	0.017	0.300	0.399	0.532	0.730	1.000	1.326	1.750
18.687	0.751	0.466	0.028	0.309	0.411	0.548	0.751	1.026	1.357	1.783
19.192	0.771	0.463	0.040	0.318	0.423	0.563	0.771	1.052	1.386	1.815
19.697	0.792	0.460	0.051	0.327	0.435	0.579	0.792	1.077	1.415	1.846
20.202	0.812	0.457	0.062	0.335	0.447	0.594	0.812	1.102	1.444	1.877
20.707	0.832	0.455	0.073	0.344	0.459	0.610	0.832	1.126	1.472	1.906
21.212	0.851	0.452	0.084	0.352	0.470	0.625	0.851	1.150	1.499	1.935
21.717	0.871	0.449	0.095	0.361	0.482	0.640	0.871	1.174	1.525	1.963
22.222	0.890	0.447	0.106	0.369	0.493	0.655	0.890	1.197	1.551	1.990
22.727	0.909	0.444	0.117	0.378	0.504	0.670	0.909	1.220	1.577	2.016
23.232	0.928	0.441	0.128	0.386	0.516	0.685	0.928	1.242	1.601	2.041
23.737	0.946	0.439	0.139	0.394	0.527	0.699	0.946	1.264	1.625	2.066
24.242	0.964	0.436	0.150	0.402	0.538	0.713	0.964	1.285	1.648	2.089
24.747	0.982	0.434	0.161	0.409	0.548	0.727	0.982	1.306	1.671	2.111
25.253	0.999	0.431	0.172	0.417	0.559	0.741	0.999	1.326	1.693	2.133
25.758	1.016	0.428	0.183	0.425	0.569	0.755	1.016	1.346	1.714	2.153
26.263	1.032	0.426	0.195	0.432	0.580	0.768	1.032	1.365	1.734	2.173
26.768	1.049	0.423	0.206	0.440	0.590	0.781	1.049	1.384	1.754	2.192
27.273	1.064	0.421	0.217	0.447	0.600	0.794	1.064	1.402	1.772	2.209
27.778	1.080	0.418	0.228	0.454	0.610	0.807	1.080	1.419	1.790	2.226
28.283	1.095	0.416	0.239	0.461	0.619	0.819	1.095	1.436	1.808	2.242
28.788	1.109	0.413	0.250	0.467	0.629	0.831	1.109	1.453	1.824	2.257
29.293	1.124	0.411	0.261	0.474	0.638	0.843	1.124	1.468	1.840	2.272
29.798	1.138	0.408	0.272	0.481	0.647	0.854	1.138	1.484	1.856	2.285
30.303	1.151	0.406	0.283	0.487	0.656	0.866	1.151	1.499	1.870	2.298
30.808	1.164	0.404	0.294	0.493	0.664	0.877	1.164	1.513	1.884	2.310
31.313	1.177	0.401	0.305	0.499	0.673	0.887	1.177	1.527	1.898	2.321
31.818	1.190	0.399	0.316	0.505	0.681	0.898	1.190	1.540	1.910	2.332
32.323	1.202	0.396	0.327	0.511	0.689	0.908	1.202	1.553	1.923	2.342
32.828	1.213	0.394	0.339	0.517	0.697	0.918	1.213	1.565	1.934	2.351
33.333	1.225	0.392	0.350	0.523	0.705	0.928	1.225	1.577	1.945	2.359
33.838	1.236	0.389	0.361	0.528	0.713	0.938	1.236	1.588	1.956	2.367
34.343	1.247	0.387	0.372	0.533	0.720	0.947	1.247	1.600	1.966	2.375
34.848	1.257	0.385	0.383	0.539	0.728	0.957	1.257	1.610	1.975	2.382
35.354	1.267	0.383	0.394	0.544	0.735	0.966	1.267	1.621	1.984	2.388
35.859	1.277	0.380	0.405	0.549	0.742	0.974	1.277	1.630	1.993	2.394
36.364	1.287	0.378	0.416	0.554	0.749	0.983	1.287	1.640	2.001	2.399
36.869	1.297	0.376	0.427	0.559	0.756	0.992	1.297	1.649	2.009	2.405
37.374	1.306	0.374	0.438	0.564	0.763	1.000	1.306	1.658	2.017	2.409
37.879	1.315	0.371	0.449	0.569	0.770	1.008	1.315	1.667	2.024	2.414

38.384	1.324	0.369	0.460	0.574	0.777	1.016	1.324	1.676	2.031	2.418
38.889	1.332	0.367	0.471	0.578	0.783	1.024	1.332	1.684	2.037	2.422
39.394	1.341	0.365	0.482	0.583	0.790	1.032	1.341	1.692	2.044	2.425
39.899	1.349	0.363	0.494	0.588	0.796	1.040	1.349	1.700	2.050	2.429
40.404	1.358	0.360	0.505	0.592	0.802	1.047	1.358	1.707	2.056	2.432
40.909	1.366	0.358	0.516	0.597	0.809	1.055	1.366	1.715	2.062	2.435
41.414	1.374	0.356	0.527	0.601	0.815	1.062	1.374	1.722	2.068	2.438
41.919	1.381	0.354	0.538	0.606	0.821	1.070	1.381	1.729	2.073	2.440
42.424	1.389	0.352	0.549	0.610	0.827	1.077	1.389	1.736	2.078	2.443
42.929	1.397	0.350	0.560	0.615	0.833	1.084	1.397	1.743	2.083	2.445
43.434	1.404	0.348	0.571	0.619	0.840	1.092	1.404	1.750	2.089	2.448
43.939	1.412	0.346	0.582	0.624	0.846	1.099	1.412	1.757	2.093	2.450
44.444	1.419	0.344	0.593	0.628	0.852	1.106	1.419	1.763	2.098	2.452
44.949	1.426	0.342	0.604	0.633	0.858	1.113	1.426	1.770	2.103	2.454
45.455	1.433	0.340	0.615	0.637	0.864	1.120	1.434	1.776	2.108	2.456
45.960	1.441	0.338	0.626	0.641	0.870	1.127	1.441	1.782	2.113	2.459
46.465	1.448	0.336	0.637	0.646	0.876	1.134	1.448	1.789	2.117	2.461
46.970	1.455	0.334	0.649	0.650	0.882	1.141	1.455	1.795	2.122	2.463
47.475	1.462	0.332	0.660	0.655	0.888	1.148	1.462	1.801	2.126	2.465
47.980	1.469	0.330	0.671	0.659	0.894	1.155	1.469	1.807	2.131	2.467
48.485	1.476	0.328	0.682	0.664	0.900	1.162	1.476	1.814	2.135	2.469
48.990	1.483	0.326	0.693	0.668	0.906	1.169	1.483	1.820	2.140	2.471
49.495	1.490	0.324	0.704	0.673	0.912	1.176	1.490	1.826	2.145	2.474
50.000	1.497	0.322	0.715	0.678	0.919	1.183	1.497	1.832	2.149	2.476

Appendix 2: The lambda, sigma, and mu values for the centiles modelled for height class two where "x" is age in years and "P" is percentile.

Height Class 2

x	mu	sigma	nu	P3	P10	P25	P50	P75	P90	P97
0.000	0.022	0.515	-0.623	0.010	0.013	0.016	0.022	0.033	0.052	0.096
0.768	0.056	0.519	-0.578	0.026	0.032	0.041	0.056	0.083	0.130	0.234
1.535	0.091	0.523	-0.533	0.041	0.051	0.066	0.091	0.134	0.207	0.363
2.303	0.126	0.527	-0.487	0.056	0.070	0.090	0.126	0.185	0.285	0.485
3.071	0.161	0.531	-0.442	0.071	0.089	0.116	0.161	0.238	0.362	0.602
3.838	0.198	0.535	-0.397	0.085	0.108	0.142	0.198	0.293	0.441	0.716
4.606	0.236	0.539	-0.352	0.099	0.127	0.168	0.236	0.349	0.522	0.828
5.374	0.277	0.543	-0.307	0.114	0.147	0.195	0.277	0.408	0.605	0.942
6.141	0.319	0.547	-0.261	0.128	0.167	0.224	0.319	0.470	0.691	1.057
6.909	0.364	0.551	-0.216	0.143	0.188	0.254	0.364	0.536	0.782	1.175
7.677	0.411	0.555	-0.171	0.158	0.210	0.286	0.411	0.605	0.877	1.297

8.444	0.462	0.558	-0.126	0.172	0.233	0.320	0.462	0.679	0.977	1.423
9.212	0.516	0.560	-0.081	0.188	0.257	0.355	0.516	0.757	1.081	1.552
9.980	0.573	0.562	-0.036	0.203	0.281	0.393	0.573	0.839	1.189	1.683
10.747	0.633	0.563	0.010	0.218	0.307	0.433	0.633	0.925	1.299	1.816
11.515	0.696	0.563	0.055	0.234	0.333	0.474	0.696	1.014	1.413	1.950
12.283	0.762	0.562	0.100	0.249	0.361	0.518	0.762	1.106	1.529	2.083
13.051	0.831	0.560	0.145	0.265	0.389	0.563	0.831	1.200	1.645	2.215
13.818	0.902	0.557	0.190	0.281	0.419	0.611	0.902	1.297	1.761	2.344
14.586	0.976	0.552	0.235	0.297	0.450	0.661	0.976	1.394	1.876	2.469
15.354	1.051	0.546	0.281	0.313	0.482	0.712	1.051	1.492	1.990	2.590
16.121	1.127	0.539	0.326	0.330	0.516	0.766	1.127	1.589	2.101	2.705
16.889	1.205	0.530	0.371	0.347	0.551	0.821	1.205	1.686	2.209	2.815
17.657	1.284	0.521	0.416	0.365	0.588	0.878	1.284	1.782	2.314	2.919
18.424	1.363	0.510	0.461	0.384	0.626	0.937	1.363	1.876	2.414	3.018
19.192	1.442	0.499	0.507	0.403	0.666	0.997	1.442	1.968	2.511	3.110
19.960	1.522	0.488	0.552	0.425	0.707	1.059	1.522	2.058	2.603	3.196
20.727	1.600	0.475	0.597	0.447	0.751	1.121	1.600	2.146	2.691	3.276
21.495	1.678	0.463	0.642	0.471	0.796	1.185	1.679	2.231	2.775	3.352
22.263	1.755	0.450	0.687	0.498	0.844	1.250	1.756	2.314	2.855	3.423
23.030	1.831	0.438	0.732	0.526	0.892	1.315	1.832	2.393	2.931	3.489
23.798	1.906	0.425	0.778	0.556	0.942	1.380	1.907	2.470	3.003	3.551
24.566	1.979	0.413	0.823	0.588	0.993	1.445	1.981	2.545	3.073	3.610
25.333	2.050	0.402	0.868	0.621	1.045	1.510	2.053	2.616	3.139	3.666
26.101	2.120	0.390	0.913	0.655	1.097	1.574	2.123	2.686	3.202	3.719
26.869	2.188	0.379	0.958	0.690	1.149	1.637	2.191	2.752	3.262	3.769
27.636	2.253	0.369	1.003	0.725	1.200	1.698	2.257	2.816	3.320	3.818
28.404	2.316	0.360	1.049	0.760	1.251	1.759	2.320	2.878	3.376	3.864
29.172	2.377	0.351	1.094	0.795	1.301	1.817	2.382	2.937	3.429	3.908
29.939	2.436	0.343	1.139	0.829	1.349	1.874	2.441	2.994	3.480	3.951
30.707	2.492	0.335	1.184	0.863	1.396	1.928	2.498	3.048	3.529	3.992
31.475	2.546	0.328	1.229	0.894	1.440	1.980	2.553	3.101	3.576	4.032
32.242	2.597	0.322	1.275	0.924	1.483	2.030	2.605	3.150	3.621	4.070
33.010	2.646	0.316	1.320	0.953	1.523	2.077	2.655	3.198	3.664	4.106
33.778	2.692	0.311	1.365	0.980	1.562	2.122	2.702	3.243	3.705	4.141
34.545	2.736	0.306	1.410	1.005	1.598	2.165	2.746	3.286	3.744	4.174
35.313	2.777	0.302	1.455	1.028	1.631	2.205	2.789	3.327	3.780	4.206
36.081	2.815	0.299	1.500	1.050	1.663	2.243	2.829	3.365	3.815	4.236
36.848	2.851	0.296	1.546	1.070	1.692	2.278	2.866	3.401	3.848	4.264
37.616	2.885	0.293	1.591	1.088	1.719	2.311	2.902	3.435	3.879	4.290
38.384	2.916	0.291	1.636	1.105	1.744	2.342	2.935	3.468	3.908	4.315
39.152	2.945	0.289	1.681	1.121	1.767	2.371	2.966	3.498	3.935	4.338

39.919	2.972	0.287	1.726	1.135	1.789	2.398	2.995	3.526	3.961	4.360
40.687	2.996	0.286	1.771	1.148	1.808	2.423	3.022	3.552	3.984	4.380
41.455	3.018	0.285	1.817	1.161	1.826	2.446	3.047	3.576	4.006	4.398
42.222	3.038	0.285	1.862	1.173	1.843	2.467	3.070	3.598	4.026	4.414
42.990	3.056	0.285	1.907	1.184	1.858	2.487	3.092	3.619	4.044	4.429
43.758	3.072	0.285	1.952	1.195	1.872	2.505	3.112	3.638	4.061	4.442
44.525	3.087	0.285	1.997	1.205	1.886	2.521	3.130	3.655	4.076	4.454
45.293	3.099	0.285	2.043	1.215	1.898	2.537	3.147	3.671	4.089	4.465
46.061	3.110	0.286	2.088	1.225	1.909	2.551	3.162	3.686	4.102	4.474
46.828	3.120	0.287	2.133	1.234	1.920	2.564	3.177	3.699	4.113	4.482
47.596	3.128	0.288	2.178	1.243	1.930	2.577	3.190	3.712	4.123	4.490
48.364	3.135	0.290	2.223	1.253	1.940	2.589	3.203	3.724	4.133	4.497
49.131	3.141	0.292	2.268	1.262	1.949	2.600	3.215	3.735	4.143	4.504
49.899	3.147	0.294	2.314	1.272	1.958	2.611	3.227	3.746	4.153	4.511
50.667	3.151	0.296	2.359	1.282	1.967	2.621	3.239	3.758	4.162	4.518
51.434	3.155	0.299	2.404	1.292	1.977	2.632	3.251	3.769	4.172	4.526
52.202	3.159	0.302	2.449	1.302	1.986	2.643	3.263	3.780	4.182	4.534
52.970	3.162	0.306	2.494	1.313	1.996	2.654	3.275	3.792	4.192	4.542
53.737	3.165	0.310	2.539	1.324	2.006	2.665	3.287	3.804	4.203	4.551
54.505	3.168	0.314	2.585	1.336	2.017	2.676	3.299	3.816	4.214	4.561
55.273	3.170	0.318	2.630	1.348	2.028	2.688	3.312	3.828	4.225	4.570
56.040	3.172	0.322	2.675	1.361	2.040	2.700	3.325	3.841	4.237	4.581
56.808	3.174	0.327	2.720	1.375	2.052	2.713	3.338	3.854	4.249	4.591
57.576	3.176	0.332	2.765	1.389	2.065	2.726	3.351	3.868	4.261	4.602
58.343	3.178	0.338	2.811	1.403	2.078	2.739	3.365	3.881	4.274	4.613
59.111	3.179	0.343	2.856	1.418	2.092	2.753	3.379	3.895	4.287	4.624
59.879	3.180	0.349	2.901	1.434	2.107	2.767	3.393	3.908	4.299	4.635
60.646	3.182	0.355	2.946	1.450	2.121	2.781	3.408	3.922	4.312	4.647
61.414	3.183	0.361	2.991	1.466	2.137	2.796	3.422	3.936	4.325	4.658
62.182	3.184	0.368	3.036	1.483	2.152	2.811	3.437	3.950	4.338	4.670
62.949	3.184	0.375	3.082	1.500	2.168	2.826	3.452	3.964	4.351	4.681
63.717	3.185	0.381	3.127	1.518	2.185	2.841	3.467	3.978	4.363	4.692
64.485	3.185	0.388	3.172	1.535	2.201	2.857	3.482	3.992	4.376	4.703
65.253	3.186	0.396	3.217	1.553	2.218	2.873	3.497	4.006	4.389	4.714
66.020	3.186	0.403	3.262	1.572	2.236	2.889	3.512	4.020	4.401	4.725
66.788	3.187	0.411	3.307	1.590	2.253	2.905	3.527	4.034	4.413	4.736
67.556	3.187	0.418	3.353	1.609	2.271	2.921	3.542	4.047	4.426	4.746
68.323	3.187	0.426	3.398	1.628	2.288	2.938	3.557	4.061	4.438	4.757
69.091	3.187	0.434	3.443	1.647	2.307	2.955	3.572	4.075	4.450	4.768
69.859	3.188	0.443	3.488	1.666	2.325	2.971	3.588	4.089	4.463	4.778
70.626	3.188	0.451	3.533	1.685	2.343	2.988	3.603	4.103	4.475	4.789

71.394	3.189	0.460	3.579	1.705	2.362	3.005	3.619	4.117	4.487	4.800
72.162	3.189	0.469	3.624	1.724	2.381	3.023	3.634	4.131	4.500	4.811
72.929	3.190	0.478	3.669	1.744	2.400	3.040	3.650	4.145	4.512	4.821
73.697	3.190	0.488	3.714	1.764	2.419	3.057	3.665	4.159	4.524	4.832
74.465	3.191	0.497	3.759	1.784	2.438	3.075	3.681	4.173	4.537	4.843
75.232	3.192	0.507	3.804	1.804	2.457	3.092	3.697	4.186	4.549	4.853
76.000	3.192	0.517	3.850	1.824	2.476	3.110	3.712	4.200	4.561	4.864

Appendix 3: The lambda, sigma, and mu values for the centiles modelled for height class three where "x" is age in years and "P" is percentile.

Height Class 3

x	mu	sigma	nu	P3	P10	P25	P50	P75	P90	P97
0.000	0.021	0.654	-0.028	0.006	0.009	0.014	0.021	0.033	0.049	0.074
1.030	0.106	0.650	-0.012	0.032	0.046	0.069	0.106	0.165	0.245	0.364
2.061	0.191	0.647	0.005	0.056	0.083	0.123	0.191	0.295	0.437	0.643
3.091	0.276	0.643	0.021	0.081	0.120	0.179	0.276	0.425	0.625	0.911
4.121	0.361	0.639	0.037	0.106	0.157	0.234	0.361	0.554	0.809	1.170
5.152	0.446	0.635	0.054	0.130	0.194	0.289	0.446	0.681	0.989	1.419
6.182	0.531	0.631	0.070	0.154	0.231	0.345	0.531	0.808	1.166	1.660
7.212	0.616	0.627	0.086	0.178	0.268	0.400	0.616	0.933	1.339	1.893
8.242	0.701	0.623	0.102	0.201	0.305	0.456	0.701	1.057	1.509	2.118
9.273	0.786	0.619	0.119	0.225	0.342	0.512	0.786	1.181	1.676	2.337
10.303	0.871	0.614	0.135	0.248	0.379	0.568	0.871	1.303	1.840	2.549
11.333	0.956	0.610	0.151	0.271	0.416	0.625	0.956	1.425	2.002	2.755
12.364	1.041	0.607	0.168	0.293	0.452	0.681	1.041	1.546	2.161	2.956
13.394	1.126	0.603	0.184	0.315	0.489	0.738	1.126	1.666	2.319	3.153
14.424	1.211	0.600	0.200	0.337	0.526	0.794	1.211	1.786	2.474	3.347
15.455	1.296	0.597	0.217	0.358	0.562	0.850	1.296	1.906	2.629	3.538
16.485	1.381	0.594	0.233	0.379	0.597	0.907	1.381	2.025	2.782	3.726
17.515	1.466	0.591	0.249	0.398	0.633	0.963	1.466	2.144	2.934	3.911
18.545	1.551	0.589	0.266	0.418	0.668	1.019	1.551	2.262	3.085	4.095
19.576	1.636	0.587	0.282	0.436	0.702	1.075	1.636	2.380	3.235	4.276
20.606	1.720	0.585	0.298	0.454	0.737	1.131	1.720	2.498	3.384	4.455
21.636	1.805	0.583	0.315	0.471	0.770	1.187	1.805	2.616	3.532	4.631
22.667	1.890	0.581	0.331	0.487	0.804	1.242	1.890	2.733	3.678	4.804
23.697	1.975	0.579	0.347	0.503	0.838	1.299	1.975	2.849	3.822	4.974
24.727	2.060	0.576	0.363	0.519	0.872	1.355	2.060	2.964	3.964	5.140
25.758	2.145	0.574	0.380	0.535	0.906	1.412	2.145	3.078	4.103	5.300
26.788	2.230	0.571	0.396	0.551	0.940	1.469	2.230	3.191	4.239	5.455
27.818	2.315	0.567	0.412	0.568	0.976	1.527	2.315	3.303	4.372	5.604

28.848	2.400	0.563	0.429	0.586	1.013	1.586	2.400	3.412	4.500	5.746
29.879	2.485	0.558	0.445	0.604	1.051	1.646	2.485	3.520	4.624	5.881
30.909	2.570	0.553	0.461	0.625	1.091	1.707	2.570	3.625	4.743	6.008
31.939	2.655	0.546	0.478	0.647	1.132	1.770	2.655	3.728	4.858	6.126
32.970	2.740	0.539	0.494	0.671	1.176	1.835	2.740	3.829	4.967	6.237
34.000	2.825	0.532	0.510	0.698	1.223	1.901	2.825	3.927	5.071	6.339
35.030	2.910	0.524	0.527	0.728	1.272	1.969	2.910	4.023	5.170	6.434
36.061	2.995	0.515	0.543	0.760	1.324	2.039	2.995	4.117	5.263	6.520
37.091	3.080	0.505	0.559	0.796	1.380	2.111	3.080	4.208	5.352	6.600
38.121	3.165	0.495	0.576	0.836	1.438	2.185	3.165	4.296	5.437	6.673
39.152	3.250	0.485	0.592	0.879	1.499	2.260	3.250	4.383	5.517	6.739
40.182	3.335	0.474	0.608	0.926	1.563	2.338	3.335	4.467	5.594	6.800
41.212	3.420	0.463	0.624	0.976	1.631	2.417	3.420	4.550	5.667	6.857
42.242	3.505	0.452	0.641	1.030	1.701	2.497	3.505	4.631	5.737	6.909
43.273	3.590	0.441	0.657	1.088	1.774	2.580	3.590	4.710	5.804	6.958
44.303	3.675	0.430	0.673	1.149	1.849	2.663	3.675	4.788	5.869	7.005
45.333	3.760	0.418	0.690	1.214	1.927	2.748	3.760	4.866	5.933	7.049
46.364	3.845	0.407	0.706	1.281	2.007	2.834	3.845	4.942	5.995	7.091
47.394	3.930	0.396	0.722	1.352	2.089	2.921	3.930	5.017	6.056	7.132
48.424	4.015	0.385	0.739	1.426	2.174	3.009	4.015	5.092	6.116	7.173
49.455	4.100	0.375	0.755	1.503	2.260	3.098	4.100	5.167	6.176	7.213
50.485	4.184	0.364	0.771	1.582	2.347	3.187	4.185	5.241	6.235	7.253
51.515	4.269	0.354	0.788	1.664	2.436	3.277	4.270	5.314	6.294	7.293
52.545	4.354	0.344	0.804	1.748	2.526	3.368	4.355	5.388	6.352	7.334
53.576	4.439	0.335	0.820	1.834	2.618	3.459	4.440	5.461	6.411	7.375
54.606	4.524	0.325	0.837	1.922	2.710	3.551	4.525	5.534	6.470	7.416
55.636	4.609	0.316	0.853	2.011	2.803	3.642	4.610	5.608	6.529	7.458
56.667	4.694	0.308	0.869	2.102	2.898	3.735	4.694	5.681	6.589	7.501
57.697	4.779	0.299	0.886	2.195	2.992	3.827	4.779	5.754	6.649	7.545
58.727	4.864	0.291	0.902	2.288	3.088	3.919	4.864	5.828	6.709	7.590
59.758	4.949	0.283	0.918	2.383	3.183	4.012	4.949	5.902	6.770	7.636
60.788	5.034	0.276	0.934	2.479	3.279	4.104	5.034	5.976	6.831	7.683
61.818	5.119	0.268	0.951	2.575	3.376	4.197	5.119	6.050	6.893	7.731
62.848	5.204	0.261	0.967	2.672	3.472	4.290	5.204	6.124	6.956	7.780
63.879	5.289	0.255	0.983	2.769	3.569	4.382	5.289	6.199	7.019	7.831
64.909	5.374	0.248	1.000	2.866	3.665	4.475	5.374	6.274	7.083	7.883
65.939	5.459	0.242	1.016	2.964	3.761	4.567	5.459	6.349	7.148	7.936
66.970	5.544	0.236	1.032	3.062	3.858	4.659	5.544	6.424	7.214	7.990
68.000	5.629	0.230	1.049	3.159	3.954	4.751	5.629	6.500	7.280	8.045
69.030	5.714	0.225	1.065	3.257	4.050	4.843	5.714	6.577	7.347	8.102
70.061	5.799	0.220	1.081	3.355	4.145	4.934	5.799	6.653	7.414	8.160

71.091	5.884	0.215	1.098	3.452	4.241	5.026	5.884	6.730	7.483	8.219
72.121	5.969	0.210	1.114	3.549	4.336	5.117	5.969	6.807	7.552	8.279
73.152	6.054	0.205	1.130	3.645	4.430	5.207	6.054	6.885	7.622	8.340
74.182	6.139	0.201	1.147	3.741	4.524	5.298	6.139	6.963	7.693	8.403
75.212	6.224	0.197	1.163	3.836	4.618	5.388	6.224	7.041	7.764	8.467
76.242	6.309	0.193	1.179	3.931	4.711	5.478	6.309	7.120	7.836	8.532
77.273	6.394	0.189	1.195	4.026	4.804	5.568	6.394	7.199	7.909	8.597
78.303	6.479	0.185	1.212	4.119	4.896	5.657	6.479	7.278	7.982	8.664
79.333	6.564	0.182	1.228	4.213	4.988	5.747	6.564	7.358	8.056	8.732
80.364	6.648	0.178	1.244	4.305	5.080	5.836	6.649	7.438	8.131	8.801
81.394	6.733	0.175	1.261	4.398	5.171	5.924	6.733	7.518	8.206	8.871
82.424	6.818	0.172	1.277	4.489	5.261	6.013	6.818	7.598	8.282	8.941
83.455	6.903	0.169	1.293	4.581	5.352	6.101	6.903	7.679	8.358	9.012
84.485	6.988	0.166	1.310	4.672	5.442	6.189	6.988	7.760	8.434	9.084
85.515	7.073	0.164	1.326	4.762	5.532	6.277	7.073	7.841	8.511	9.157
86.545	7.158	0.161	1.342	4.852	5.621	6.365	7.158	7.922	8.589	9.230
87.576	7.243	0.159	1.359	4.942	5.711	6.453	7.243	8.004	8.667	9.303
88.606	7.328	0.156	1.375	5.032	5.800	6.541	7.328	8.085	8.744	9.377
89.636	7.413	0.154	1.391	5.122	5.889	6.628	7.413	8.167	8.823	9.452
90.667	7.498	0.151	1.408	5.212	5.978	6.716	7.498	8.249	8.901	9.526
91.697	7.583	0.149	1.424	5.301	6.067	6.803	7.583	8.330	8.979	9.601
92.727	7.668	0.147	1.440	5.391	6.156	6.891	7.668	8.412	9.058	9.676
93.758	7.753	0.145	1.456	5.481	6.245	6.978	7.753	8.494	9.137	9.752
94.788	7.838	0.143	1.473	5.571	6.334	7.065	7.838	8.576	9.216	9.827
95.818	7.923	0.141	1.489	5.661	6.423	7.153	7.923	8.658	9.295	9.902
96.848	8.008	0.139	1.505	5.751	6.512	7.240	8.008	8.740	9.373	9.978
97.879	8.093	0.137	1.522	5.841	6.602	7.328	8.093	8.822	9.452	10.053
98.909	8.178	0.135	1.538	5.932	6.691	7.415	8.178	8.904	9.531	10.129
99.939	8.263	0.133	1.554	6.023	6.781	7.503	8.263	8.986	9.610	10.204
100.970	8.348	0.131	1.571	6.114	6.870	7.591	8.348	9.068	9.689	10.280
102.000	8.433	0.129	1.587	6.206	6.960	7.678	8.433	9.149	9.767	10.355

Appendix 4: The lambda, sigma, and mu values for the centiles modelled for all height classes where "x" is age in years and "P" is percentile.

			All Classes							
x	mu	sigma	nu	P3	P10	P25	P50	P75	P90	P97
0.000	0.022	0.554	-0.395	0.009	0.012	0.015	0.022	0.032	0.050	0.083
0.778	0.055	0.556	-0.372	0.023	0.029	0.039	0.055	0.083	0.127	0.208
1.556	0.089	0.558	-0.349	0.036	0.047	0.063	0.089	0.134	0.203	0.330

2.333	0.123	0.560	-0.326	0.050	0.065	0.086	0.123	0.185	0.280	0.449
3.111	0.158	0.563	-0.303	0.063	0.082	0.110	0.158	0.236	0.356	0.565
3.889	0.192	0.565	-0.280	0.076	0.100	0.134	0.192	0.288	0.432	0.680
4.667	0.228	0.567	-0.258	0.089	0.117	0.158	0.228	0.341	0.510	0.794
5.444	0.264	0.570	-0.235	0.102	0.135	0.183	0.264	0.395	0.589	0.908
6.222	0.302	0.572	-0.212	0.114	0.153	0.208	0.302	0.451	0.670	1.024
7.000	0.341	0.575	-0.189	0.127	0.171	0.234	0.341	0.510	0.754	1.143
7.778	0.382	0.578	-0.166	0.141	0.190	0.262	0.382	0.571	0.841	1.265
8.556	0.425	0.580	-0.143	0.154	0.210	0.290	0.425	0.636	0.932	1.391
9.333	0.470	0.583	-0.120	0.168	0.230	0.320	0.470	0.703	1.028	1.522
10.111	0.518	0.585	-0.097	0.182	0.251	0.351	0.518	0.774	1.128	1.658
10.889	0.568	0.588	-0.074	0.196	0.273	0.384	0.568	0.849	1.232	1.799
11.667	0.621	0.590	-0.051	0.211	0.296	0.419	0.621	0.928	1.342	1.945
12.444	0.677	0.592	-0.028	0.226	0.319	0.455	0.677	1.011	1.456	2.096
13.222	0.735	0.594	-0.005	0.241	0.344	0.493	0.735	1.097	1.575	2.252
14.000	0.796	0.595	0.018	0.257	0.369	0.532	0.796	1.188	1.698	2.412
14.778	0.860	0.596	0.041	0.273	0.396	0.573	0.860	1.282	1.826	2.575
15.556	0.927	0.597	0.064	0.289	0.423	0.616	0.927	1.379	1.957	2.742
16.333	0.996	0.598	0.087	0.305	0.451	0.661	0.996	1.480	2.091	2.911
17.111	1.067	0.598	0.110	0.321	0.479	0.707	1.067	1.584	2.228	3.082
17.889	1.141	0.597	0.133	0.338	0.509	0.754	1.141	1.690	2.366	3.253
18.667	1.217	0.597	0.156	0.355	0.539	0.803	1.217	1.799	2.507	3.424
19.444	1.295	0.595	0.179	0.371	0.570	0.854	1.295	1.909	2.649	3.595
20.222	1.375	0.594	0.202	0.388	0.602	0.906	1.375	2.021	2.791	3.764
21.000	1.457	0.592	0.225	0.405	0.634	0.959	1.457	2.134	2.933	3.932
21.778	1.539	0.589	0.248	0.422	0.668	1.013	1.539	2.249	3.075	4.097
22.556	1.624	0.586	0.271	0.439	0.701	1.069	1.624	2.363	3.216	4.258
23.333	1.709	0.582	0.294	0.456	0.736	1.126	1.709	2.478	3.355	4.416
24.111	1.794	0.578	0.317	0.473	0.771	1.183	1.794	2.592	3.492	4.570
24.889	1.880	0.574	0.340	0.490	0.806	1.241	1.880	2.706	3.627	4.719
25.667	1.967	0.570	0.363	0.507	0.842	1.300	1.967	2.818	3.759	4.863
26.444	2.053	0.565	0.386	0.523	0.879	1.360	2.053	2.930	3.888	5.002
27.222	2.139	0.560	0.409	0.540	0.915	1.420	2.140	3.039	4.013	5.136
28.000	2.225	0.554	0.432	0.557	0.953	1.480	2.225	3.147	4.135	5.264
28.778	2.310	0.549	0.455	0.573	0.990	1.540	2.310	3.253	4.253	5.386
29.556	2.394	0.543	0.477	0.590	1.027	1.600	2.394	3.356	4.367	5.502
30.333	2.477	0.538	0.500	0.606	1.065	1.660	2.477	3.456	4.476	5.613
31.111	2.558	0.532	0.523	0.622	1.102	1.720	2.558	3.553	4.581	5.717
31.889	2.637	0.526	0.546	0.638	1.139	1.779	2.638	3.647	4.681	5.815
32.667	2.715	0.520	0.569	0.654	1.176	1.837	2.715	3.738	4.777	5.908
33.444	2.790	0.514	0.592	0.670	1.213	1.894	2.791	3.826	4.868	5.994

34.222	2.864	0.508	0.615	0.685	1.249	1.951	2.865	3.910	4.954	6.075
35.000	2.935	0.503	0.638	0.700	1.285	2.006	2.937	3.990	5.035	6.150
35.778	3.004	0.497	0.661	0.716	1.321	2.060	3.006	4.067	5.112	6.220
36.556	3.070	0.491	0.684	0.730	1.355	2.112	3.073	4.141	5.184	6.285
37.333	3.133	0.486	0.707	0.745	1.389	2.164	3.137	4.210	5.252	6.344
38.111	3.194	0.481	0.730	0.760	1.423	2.213	3.199	4.277	5.316	6.399
38.889	3.253	0.476	0.753	0.774	1.455	2.262	3.258	4.340	5.375	6.449
39.667	3.309	0.471	0.776	0.787	1.487	2.308	3.315	4.399	5.431	6.495
40.444	3.362	0.466	0.799	0.801	1.517	2.353	3.369	4.456	5.483	6.538
41.222	3.413	0.462	0.822	0.814	1.547	2.397	3.421	4.509	5.532	6.576
42.000	3.462	0.457	0.845	0.827	1.576	2.439	3.471	4.560	5.577	6.612
42.778	3.508	0.453	0.868	0.839	1.603	2.479	3.519	4.608	5.620	6.644
43.556	3.552	0.449	0.891	0.852	1.630	2.518	3.565	4.653	5.659	6.673
44.333	3.594	0.445	0.914	0.863	1.656	2.555	3.608	4.696	5.697	6.701
45.111	3.634	0.442	0.937	0.875	1.681	2.591	3.650	4.737	5.731	6.725
45.889	3.672	0.439	0.960	0.887	1.705	2.626	3.690	4.775	5.764	6.748
46.667	3.708	0.435	0.983	0.898	1.729	2.659	3.728	4.812	5.795	6.769
47.444	3.743	0.432	1.006	0.909	1.752	2.691	3.764	4.847	5.823	6.788
48.222	3.776	0.429	1.029	0.920	1.774	2.722	3.800	4.880	5.850	6.805
49.000	3.807	0.427	1.052	0.931	1.795	2.752	3.833	4.912	5.875	6.821
49.778	3.837	0.424	1.075	0.942	1.816	2.782	3.866	4.942	5.899	6.835
50.556	3.866	0.421	1.098	0.953	1.837	2.810	3.897	4.970	5.922	6.848
51.333	3.894	0.419	1.121	0.965	1.857	2.837	3.927	4.998	5.943	6.860
52.111	3.920	0.417	1.144	0.976	1.877	2.864	3.957	5.024	5.962	6.871
52.889	3.946	0.414	1.167	0.988	1.897	2.891	3.985	5.049	5.981	6.881
53.667	3.970	0.412	1.190	1.000	1.917	2.917	4.013	5.073	5.999	6.890
54.444	3.994	0.410	1.212	1.013	1.937	2.942	4.040	5.097	6.016	6.898
55.222	4.018	0.408	1.235	1.025	1.957	2.967	4.066	5.120	6.033	6.906
56.000	4.040	0.406	1.258	1.039	1.977	2.992	4.092	5.142	6.049	6.913
56.778	4.063	0.404	1.281	1.052	1.997	3.017	4.118	5.164	6.065	6.921
57.556	4.085	0.402	1.304	1.066	2.017	3.042	4.143	5.186	6.080	6.929
58.333	4.108	0.400	1.327	1.080	2.037	3.067	4.169	5.208	6.096	6.937
59.111	4.130	0.398	1.350	1.095	2.058	3.092	4.194	5.230	6.113	6.945
59.889	4.152	0.396	1.373	1.110	2.079	3.117	4.220	5.252	6.129	6.955
60.667	4.175	0.394	1.396	1.126	2.100	3.142	4.246	5.275	6.147	6.965
61.444	4.198	0.392	1.419	1.142	2.121	3.168	4.272	5.298	6.164	6.976
62.222	4.221	0.391	1.442	1.158	2.143	3.194	4.299	5.322	6.183	6.988
63.000	4.244	0.389	1.465	1.175	2.166	3.221	4.326	5.346	6.203	7.002
63.778	4.269	0.387	1.488	1.192	2.189	3.248	4.354	5.372	6.224	7.016
64.556	4.293	0.386	1.511	1.210	2.212	3.275	4.382	5.397	6.245	7.032
65.333	4.318	0.384	1.534	1.228	2.235	3.303	4.411	5.424	6.267	7.049

66.111	4.343	0.383	1.557	1.247	2.259	3.331	4.440	5.451	6.290	7.066
66.889	4.369	0.381	1.580	1.266	2.284	3.359	4.470	5.478	6.314	7.085
67.667	4.395	0.380	1.603	1.285	2.309	3.388	4.500	5.506	6.338	7.104
68.444	4.421	0.379	1.626	1.305	2.334	3.417	4.530	5.535	6.363	7.124
69.222	4.448	0.377	1.649	1.325	2.359	3.447	4.560	5.563	6.388	7.145
70.000	4.475	0.376	1.672	1.345	2.385	3.476	4.591	5.592	6.413	7.165
70.778	4.501	0.374	1.695	1.366	2.411	3.506	4.622	5.621	6.439	7.186
71.556	4.528	0.373	1.718	1.387	2.438	3.536	4.653	5.650	6.464	7.208
72.333	4.555	0.372	1.741	1.409	2.464	3.566	4.684	5.679	6.490	7.229
73.111	4.582	0.370	1.764	1.431	2.491	3.596	4.715	5.708	6.516	7.251
73.889	4.610	0.369	1.787	1.453	2.518	3.627	4.746	5.737	6.542	7.273
74.667	4.637	0.367	1.810	1.475	2.546	3.657	4.777	5.766	6.568	7.294
75.444	4.664	0.366	1.833	1.498	2.573	3.687	4.808	5.795	6.594	7.316
76.222	4.691	0.365	1.856	1.521	2.601	3.718	4.838	5.824	6.619	7.338
77.000	4.718	0.363	1.879	1.544	2.628	3.748	4.869	5.853	6.645	7.360

Appendix 5: Statistical output produced by RefCurve for the best fitting model for height class 1.

		Estimate	Std. Error	t-value	Pr(> |t|)
Mu Coeff.	**Intercept**	0.00534	0.00107	4.99	6.46E-07
	pb(x, median df)	0.04024	0.00042	95.69	<2.00E-16
Sigma Coeff.	**Intercept**	-0.5439	0.0268	-20.3	<2.00E-16
	pb(x, sigma df)	-0.0118	0.00144	-8.195	4.00E-16
Nu Coeff.	**Intercept**	-0.3812	0.05125	-7.439	1.40E-13
	pb(x, nu df)	0.02193	0.00333	6.589	5.40E-11

Appendix 6: Statistical output produced by RefCurve for the best fitting model for height class 2.

		Estimate	Std. Error	t-value	Pr(> |t|)
Mu Coeff.	**Intercept**	-0.0456	0.00109	-41.98	<2.00E-16
	pb(x, median df)	0.07686	0.00051	151.25	<2.00E-16
Sigma Coeff.	**Intercept**	-0.5698	0.02307	-24.7	<2.00E-16
	pb(x, sigma df)	-0.0122	0.00106	-11.5	<2.00E-16
Nu Coeff.	**Intercept**	-0.6229	0.05077	22.34	<2.00E-16
	pb(x, nu df)	0.05885	0.00263	22.34	<2.00E-16

Appendix 7: Statistical output produced by RefCurve for the best fitting model for height class 3.

		Estimate	Std. Error	t-value	Pr(> |t|)
Mu Coeff.	**Intercept**	0.02118	0.00137	15.42	<2.00E-16
	pb(x, median df)	0.08247	0.00063	131.86	<2.00E-16
Sigma Coeff.	**Intercept**	-0.2755	0.0208	-13.25	<2.00E-16
	pb(x, sigma df)	-0.0144	0.0006	-23.98	<2.00E-16
Nu Coeff.	**Intercept**	-0.028	0.04319	-0.649	5.16E-01
	pb(x, nu df)	0.01583	0.00188	8.422	<2.00E-16

Appendix 8: Statistical output produced by RefCurve for the best fitting model for all height classes.

		Estimate	Std. Error	t-value	Pr(> |t|)
Mu Coeff.	**Intercept**	-0.2157	0.00069	-310.6	<2.00E-16
	pb(x, median df)	0.08849	0.00037	236.9	<2.00E-16
Sigma Coeff.	**Intercept**	-0.4694	0.01284	-36.55	<2.00E-16
	pb(x, sigma df)	-0.0064	0.00051	-12.42	<2.00E-16
Nu Coeff.	**Intercept**	-0.3953	0.02664	-14.84	<2.00E-16
	pb(x, nu df)	0.02953	0.00131	22.59	<2.00E-16