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Characterizing Red Spruce (*Picea rubens* Sarg.) Advanced Reproduction in an High Elevation Stand in West Virginia

Aaron Lutz

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**Characterizing Red Spruce (*Picea rubens* Sarg.) Advanced
Reproduction in an High Elevation Stand in West Virginia**

Aaron Lutz

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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Morgantown, West Virginia

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ABSTRACT

Characterizing Red Spruce (*Picea rubens* Sarg.) Advanced Reproduction in a High Elevation Stand in West Virginia

Aaron Lutz

Red spruce (*Picea rubens* Sarg.) has been a focal species in the high elevation areas of the central Appalachian Mountains to increase distribution into areas it occupied prior to extensive timber harvesting around the turn of the century. One area of interest is developing and improving management practices that mimic natural disturbance regimes that favor red spruce reproduction and encourage regeneration. The objectives of this study were to observe red spruce reproduction presence and characterize the local environmental conditions to better understand conditions favoring red spruce regeneration. Understory vegetation under closed canopy and in canopy gaps were characterized and tested for associations with red spruce reproduction. In addition, effects of gap attributes such as size, age, percent canopy cover, aspect, and seed source proximity on red spruce reproduction were examined. Red spruce reproduction was found to be taller under closed canopy conditions. Increased red spruce presence was associated with greater gap sizes, with higher probability of occurrence in gaps averaging $\geq 59.5 \text{ m}^2$. Positive height and seedling density associations were found between red spruce, eastern hemlock, and black cherry reproduction, and negative associations between red spruce and cucumbertree seedlings. Results of this study will be used to direct future red spruce regeneration efforts in high elevation sites in West Virginia.

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INTRODUCTION

Prior to European settlement, red spruce (*P. rubens*) was a major component of high elevation (762-1482 m) West Virginia forests covering an estimated 202,343 hectares across West Virginia (CASRI, 2011; Strausbaugh and Core, 1952). Accounts of lumbermen described expanses of uneven-aged, climax forests where the forest floors were covered with thick, moist humus layers, and dominated by large red spruce and eastern hemlock (Allard and Leonard, 1952). During the 1800's into the early 1900's, aggressive timber extraction operations and subsequent fires occurred throughout much of central Appalachia effectively reducing red spruce's dominance across much of the landscape. Currently, red spruce covers only 12-13% of its former extent prior to settlement (Adams and Stephenson, 1989; Pielke, 1981). These second-growth stands of red spruce are limited to higher peaks and ridges throughout the region (Adams and Stephenson, 1989) likely due to greater moisture availability and cooler temperatures (Nowacki and Wendt, 2010). In West Virginia, spruce forests are now considered some of the most endangered ecosystems in the United States (Christensen et al. 1996) and identified as the most important component of the high elevation forests in West Virginia (Morin and Widmann, 2010). In addition to its potential commercial importance, red spruce serves as a primary constituent in the endemic ecosystems found in this region. It provides habitat for a number of species including the federally listed Cheat Mountain salamander (*Plethodon nettingi*) and recently de-listed Virginia northern flying squirrel (*Glaucomys sabrinus fuscus*) (Rentch et al., 2010; Schuler et al., 2002). In recent years, there has been increasing interest in restoring red spruce to its pre-settlement range (Rentch et al., 2010; Rentch et al., 2016; Thomas-Van Gundy and Sturtevant, 2014).

Following the widespread timber harvesting and fires around the turn of the last century, natural expansion of red spruce forests has been slow. Following the early logging practices, mesic hardwoods were quick to inhabit these once spruce dominated cut over areas (Minckler, 1945) thereby excluding spruce regeneration.

Essential organic (O) and mineral (A) soil horizons were destroyed resulting in arid, hot soils, conditions which are inhospitable for spruce seed germination (Nowacki and

Wendt, 2010; Rentch et al., 2010). Over time, organic matter has accumulated, reestablishing the seedbed and improving water holding capacity; properties so essential for spruce regeneration (Nowacki et al., 2010; Pielke, 1981). Today, there is evidence of red spruce encroachment into hardwood stands, albeit slowly, showing the potential for spruce to naturally re-take these areas (Nowacki et al., 2010). Based on the presence and natural progression of red spruce, its high tolerance for shade, and the return of conducive growing conditions to larger areas of this region, silvicultural strategies could be developed to mimic natural processes that promote regeneration into historically red spruce dominated regions.

Natural disturbance plays a vital role in forest composition, structure (Brokaw, 1982; Busing, 2005; Pflugmacher et al., 2012; Runkle, 1981), and ecosystems (Edwards et al., 2014). Red spruce relies on small-scale disturbance, frequently in the form of canopy gaps to ascend into the overstory (Fraver and White, 2005; Wu et al., 1999). Dendrochronology research has shown most upper canopy red spruce trees have experienced at least one release event (Rentch et al., 2010; Wu et al., 1999). Some research suggests spruce restoration may be attainable through active management practices that simulate natural canopy disturbance, but that gap size or overstory density dictates regeneration success. Smaller openings (<100 m²) which increase light availability while retaining some shade from the overstory have been shown effective in maintaining seedling survival (Dumais and Prevost, 2016). Growth simulations suggest hardwood basal area reductions of 50%, could double red spruce basal area in as little as 20 years (Rentch et al., 2007; Schuler et al., 2002). Similarly, Sendak et al. (2003) increased spruce basal area by 22% over forty years using a three stage shelterwood treatment. In all cases, advanced reproduction was present in the understory.

In an effort to better understand factors influencing naturally occurring red spruce regeneration characteristics, this study was conducted on a high elevation forest dominated by yellow birch (*B. alleghaniensis*), maple (*Acer spp.*), and eastern hemlock (*T. canadensis*) with a red spruce component. This study was conducted to address the following objectives: (1) observe and compare site characteristics in areas where red spruce reproduction was present and absent; (2) identify the effects of other species

on red spruce reproduction within gaps; (3) determine effects of gap characteristics (gap size, canopy cover, aspect, orientation, number of gap makers, gap age, and seed source distance) on the presence or absence and reproduction of red spruce.

LITERATURE REVIEW

The focus of this study is to better understand the red spruce regeneration process within high elevation spruce/hardwood forests of the central Appalachian Mountains. To do this, understanding the ecological processes that occur in these unique forest systems is paramount. The explanations of subjects that follow are intended to provide a broad overview of some of the major factors involved in shaping forested ecosystems.

Disturbance

Disturbance regimes include, at a minimum, the timing (frequency) and effected area (scale) for landscapes. These regimes are the primary drivers of forest composition and structure (Pflugmacher et al. 2012; Runkle 1981; Brokaw 1985; Busing 2005), as well as the ecosystems contained within them (Edwards et al. 2014). Agents of disturbance can range from fire, wind, ice storms, drought, harvest, insect infestations, to disease outbreaks. Geographic location often dictates the agent, frequency, and magnitude of these disturbances (Cohen et al. 2016), varying in size from entire landscapes to the death of a single tree.

Frequency

Disturbance agents occur at particular frequencies described over a period of time and are often measured as return intervals. Wind induced disturbance affects forests across the country at varying frequencies. Estimates range from 1360 years between catastrophic stand replacing blowdowns in the Great Lakes region, to 24 year intervals between hurricane related windstorms in the southern Appalachian Mountains (Greenburg and McNab, 1997; Schulte and Mladenoff 2005).

Scale

Scale refers to the extent of the area affected by disturbance. The extent to which an area is disturbed can be large or fine scale and is dependent on the disturbance agent.

In the case of insect infestation and wildfire, magnitude can be shaped by the time and extent of the prior disturbance. In the west, where beetle induced mortality is most prevalent and tree densities are high, entire landscapes can be affected in a single outbreak event (Raffa et al., 2008). Years of drought conditions impose stress making them more susceptible to beetle attacks. In dense stands, the beetles easily able to move from tree to tree destroying the cambium and introducing vessel blocking fungus while building galleries in which to lay their eggs. Raffa et al. (2008) suggests that over 47 million hectares of pine forests have been affected by beetle outbreaks from 1998 to 2008 alone. In Maine, a fire in 1803 covered about 80,000 hectares and several years later, two separate fires occurring in 1825 burned approximately 42,000 hectares combined (Lorimer 1977). Winds cause disturbance at varying magnitudes and affect forests across all regions including hurricanes formed in the Atlantic, severe storms in the Pacific regions, and tornadoes that frequent the mid-west (Greenburg and McNab, 1998; Lorimer and Frelich, 1994; Sinton et al., 2000)

In the Appalachian Mountains, wind damage can range from fine to large scale. Small gaps created by windstorms averaging 200 m² were found to be the primary mode of forest regeneration in western Pennsylvania, Ohio, and the southern Appalachian Mountains (Runkle, 1981) affecting 9.5% of the land area (Runkle, 1982). Greenberg and McNab (1998) reported gaps ranging from 0.2-1.1 ha resulting from downbursts during hurricane Opal on the Bent Creek Experimental Forest in the Pisgah National Forest, North Carolina. A tornado event affected 400 hectares in an old-growth hemlock-beech stand in the Tionesta Scenic Area in Pennsylvania by causing extensive windthrow resulting in complete canopy removal (Peterson and Pickett 1991).

Records of pre-settlement forest conditions are available through township surveys conducted in the 18th and 19th centuries (Lorimer and Frelich 1994). In many of these land surveys, observations such as species composition, witness trees, and scale of disturbances were recorded providing valuable insight into pre-settlement forests. The frequency and magnitude in which disturbances occur often dictate species composition, and over time shape canopy complexity, and have a significant impact on age class distributions. Due to the extensive timber harvests around the turn of the

century, only small fractions of old-growth cohorts have been spared (Fraver and White 2005; Heinzelman 1973). Disturbances that occur within forests or across forested landscapes lead to changes in forest dynamics, succession trends, composition, microclimates, light availability, and growth resources (Bekker and Taylor 2010; Romer et al. 2007; Catovsky and Bazzaz 2002; Vilhar et al. 2015).

Gaps

A gap is often the result of the death of one or more canopy trees within closed-canopy forests (Brokaw and Busing, 2000; Runkle, 1982), and are integral in shaping forest structure and species composition (Whitmore, 1989). Gap characteristics, specifically size and portion of forest in gaps, vary among sites and are dependent upon disturbance regimes of the geographic location (Table 1). In the Great Smokey Mountains where the disturbance regime is lightning (fire), wind, and ice storms, Busing (2005) found that gaps accounted for an average of 9.5% of the forested area. To the north in the old growth red spruce stands of northern Maine, where the dominant disturbances are spruce budworm (*Choristoneura fumiferana*), spruce bark beetles (*Dendroctonus rufipennis*), and hurricanes, Fraver and White (2005) reported that the average gap size was 66 m² amounting to 26% of the study area occupied by gaps. Similarly, in the central Appalachian Mountains, Rentch et al. (2010) found beech bark disease was the common gap producer which averaged 53 m², but only accounted for 4.7% of the area.

Table 1 Previous research conducted on gap characteristics and dynamics.

Location	Forest Type	% in Gaps	Gap Size Range (m ²)	Mean Gap Size (m ²)	Source
Eastern US	Mesic	3.2- 24.4	50- 2009	----	Runkle, 1982
Ohio, US	Mixed hardwood	2.7	<25- 286	----	Cho and Boerner, 1990
Sweden	Spruce	31	9- 360	84.2	Qinghong and Hytteborn, 1991
Alaska, US	Western hemlock	8.7	<25- 274	37	Ott and Juday, 2002
Maine, US	Red spruce	26	8.5- 432	66	Fraver and White, 2005
Saxony, Germany	Norway spruce	7- 11	21- 2157	90.06	Huth and Wagner, 2006
Southern England	Beech	----	3- 241	69.87	Mountford et al., 2006
Quebec, Canada	Conifer and mixed hardwood	42	3- 698	70	Romer et al., 2007
Canary Islands	Evergreen	----	125- 268	174	Arevalo and Fernandez-Palacios, 2007
West Virginia, US	Red spruce/ northern hardwood	4.7	6.2- 276.4	53.4	Rentch et al., 2010
West Virginia, US	Mixed hardwood	2.7	6-963	98.6	Himes and Rentch, 2013

Canopy Gap Dynamics

When a gap forms (regardless of cause or extent), moisture availability, microclimate, nutrients, irradiance, soil properties, and growing space in and surrounding the disturbed site are modified resulting in gap partitioning (Rentch et al., 2016; Sleen et al. 2013; Vilhar et al., 2014; Yamamoto, 2000). Seedling recruitment and development responses to these environmental changes are defined by species specific growth requirements (Holladay et al., 2006; Narukawa and Yamamoto, 2001; Nowacki and Abrams, 1997; Rentch et al., 2010; Romer et al., 2007; Runkle, 2013). The concept of gap partitioning (Denslow, 1987) suggests that environments throughout the “gap understory mosaic” are utilized by vegetative species adapted to distinct growing conditions. This concept is based on the species-specific light requirements, growth rates, response to competition, substrate needs, temperature tolerances, moisture availability, and modes of seed dispersal. Seedlings germinate and successfully establish within areas of the gap that meet their specific needs and growing requirements (Couwenberghe et al., 2010; Denslow, 1980; Diaci et al., 2012; Grey et al., 2002; Mountford et al., 2006).

Light Regimes

Irradiance levels are a function of gap size. The larger a canopy opening is relative to its average canopy height, the more light will reach the forest floor (Clebsch and Busing, 1989; Dumais and Prevost, 2014). Lhotka et al. (2018), examined the effects of gap size on species composition and volume increases over fifty years in oak stands and found that species diversity and growth were significantly reduced in light limited small gaps (200 m²). The effects of gap size on regeneration species composition, survival, light availability, seedling density, and growth responses are well documented (Brokaw, 1985; Dumais and Prevost, 2016; Nakashizuka, 1984; Qinghong and Hytteborn, 1991; Rentch et al., 2016; Wu et al., 1999). Changes in irradiance have large impacts on seedling development and growth (Gilbert et al. 2001; Denslow 1987). Light regimes analyzed at several positions within gaps were reported to have higher light intensity in gap centers (Vilhar et al., 2015). From the center outward toward the gap edges, Vilhar et al. observed a gradient of light availability with the lowest occurring under closed

canopy. Ritter et al. (2005) observed changes of irradiance that were correlated with the sun's path in deciduous forests of Denmark. In the mornings variation in light distribution was low, but by midday through early evening, intensity was highest in the northern portions, and during the last four hours of daylight, light was most abundant in the eastern parts of the gap. Similarly, in the Douglas-fir (*Pseudotsuga menziesii*) stands in the Pacific Northwest, Gray et al. (2002) reported increased radiation levels in northern parts of gaps. As gap size was enlarged, there were substantial increases in light availability within central and southern portions.

Soil and Air Temperature

Within gaps, gradients in soil and air temperature are contingent upon location, gap size, and gap age. Variances in temperature are correlated with irradiance and follow trends associated with seasonal solar angles (Gray et al., 2002). Highest mean and maximum air temperatures occur in the central portions of the gap during the growing season when the sun is at its highest position (Gray et al., 2002; Wright et al., 1998). Consequently, during the first year of gap formation, mean and maximum soil temperatures are also highest in gap centers and extending to the north and south, with no significant difference following leaf drop (Ritter et al., 2005). This soil temperature pattern shifted in subsequent years due to high seedling densities in northern zones that likely created a barrier between sunlight and soil (Ritter et al., 2005).

Soil Properties

Soil physical and chemical properties such as soil water content, organic material, exposed soil, and nutrient availability are impacted by canopy gaps (Scharenbroch and Bockheim, 2007). Soil water content, organic material, and nutrient availability are contingent upon gap size. In the silver fir (*Abies alba*) stands of southern Italy, Muscolo et al. (2010) found that in medium gaps (410 m²), organic matter levels were lower when compared to small gaps (185 m²). This was attributed to faster decomposition rates resulting from elevated temperatures. Vilhar et al. (2014) reported similar results in fir/beech stands in Slovenia. In addition to deeper organic layers in small gaps and areas under closed canopy, they found higher organic matter around the partially shaded gap edges. Negative relationships between organic matter thickness and

nitrogen mineralization in gaps have been recorded in northern hardwoods-hemlock stands in the Great Lakes region where elevated soil temperatures promote microbial activity resulting in higher rates of decomposition (Scharenbroch and Brockheim, 2007).

Soil water content, by contrast can be highest in gaps and increasingly drier extending from the center into the closed canopy (Vilhar et al., 2014; Ostertag, 1998;) likely due to water uptake by canopy tree roots surrounding the gap (Gray et al., 2002)

Regeneration Patterns

Tree species vary in shade tolerance. Some species have low shade thresholds and cannot survive under any degree of shade: others prefer shaded conditions and are able to persist under low light conditions, and many others fall somewhere in between. Whitmore (1989) described trees as falling into one of two groups, climax species and pioneer species. Pioneer species tend to inhabit areas of disturbance with exposed soil (Yamamoto, 2000; Romer et al., 2007), and grow rapidly in large, light-rich gaps (Brokaw, 1985) often overtopping late successional climax species (Whitmore, 1989). This would suggest that competition may be greater in larger gaps or gap centers, where canopy openings permit more direct light to hit the forest floor (Brokaw and Busing, 2000; Diaci et al., 2012; Dumais and Prevost, 2016; Vilhar et al., 2014). In some studies however, established shade-tolerant seedlings can respond to the light regime change and grow into the canopy (Wu et al. 1999; Yamamoto 2000; Couwenberghe et al. 2010; Copenheaver et al. 2014). Pioneer seedlings have also been observed to experience higher mortality over time, thereby reducing competition for climax species to occupy gap center positions (Brokaw, 1985; Harcombe et al., 2002).

Mid-to shade-tolerant species are often able to inhabit areas of disturbance that many shade intolerant species cannot persist. In the beech (*Fagus spp.*) forests of England, Mountford et al. (2006), noted that beech seedlings and advanced reproduction densities were highest in gap edges despite lower light intensity. Higher concentrations of beech seedlings have also been found to occur across the northern portion of gaps attributed to partial shading by the overstory surrounding the southern edges of gaps (Ritter et al., 2005), while Gray et al. (2002) found the opposite. In Gray et al.'s

research, lower densities of reproduction were found in northern edges due to greater light intensity resulting in drier soils. Larger numbers of reproduction along these moderately shaded gap edges suggest that less ground vegetation and fewer pioneers may be beneficial to late successional species success (Vilhar, 2014). In small gaps where irradiance levels are lower compared to large gaps, pioneer species seedlings are occasionally found, but rarely persist (Brokaw, 1985). Dumais and Prevost (2016) found that inter-specific competition amongst climax species was significantly lower in small and medium gaps, but that red spruce had better height growth when some competition was present.

In a study on wave regeneration in fir forests of New England, Sprugel (1976) examined canopy tree mortality and regeneration cycles. Sprugel suggested that mortality of mature overstory firs occurred at the edges due to wind exposure, ice damage, and elevated evapotranspiration rates. As these trees die, regeneration is initiated and the cycle is repeated. These climax forests, he contends are in a constant state of change with new waves following 60-year intervals.

Forest Types and Associates

The high-elevation forest types found in the central Appalachian Mountains vary in species composition, primarily dictated by elevation, aspect, climate, and precipitation. Northern hardwoods are found on cool mesic sites with higher elevation, and can contain varying mixtures of red maple (*Acer rubrum*), sugar maple (*Acer saccharum*), American beech (*Fagus grandifolia*), eastern hemlock, yellow birch, red spruce, and black cherry (*Prunus serotina*). Eastern hemlock dominated stands are mixed with yellow birch, sugar maple, red maple, and beech and occur on moist sites, in coves and flats. The spruce forests occupy the highest elevation sites, generally on north and northeast aspects, where mean temperatures are cool and precipitation is high. Common associates are yellow birch, red and sugar maple, and black cherry. Each species however, has unique growing requirements and characteristics (Table 2).

Table 2 Characteristics and growth requirements of most prevalent species found and recorded on the study area located in Kumbrabow State Forest, West Virginia.

Species	Shade tolerance class	Good seed crops (yrs)	Reproduction	Seed Dissemination	Growth rate	Average Lifespan (yr)
<i>F. grandifolia</i>	Very tolerant	2-8	Seed, root suckers	Gravity, rodents, birds	Slow	300
<i>B. alleghaniensis</i>	Intermediate	2-3	Seed	Wind	Slow	150
<i>Acer saccharum</i>	Tolerant	2-5	Seed, stump sprouts	Wind	Slow to moderate	300
<i>Acer rubrum</i>	Tolerant	2	Seed, stump sprouts	Wind	Moderate	130
<i>M. fraseri</i>	Intermediate	4-5	Seed, stump sprouts	Gravity, animals	Fast	70
<i>M. acuminata</i>	Intolerant	4-5	Seed	Wind, gravity, birds	Fast	80
<i>P. serotina</i>	Intolerant	1-5	Seed, stump sprouts	Gravity, birds, mammals	Fast to moderate	100
<i>T. canadensis</i>	Very tolerant	2-3	Seed	Wind	Moderate	450
<i>P. rubens</i>	Tolerant	3-5	Seed	Wind, rodents	Moderate	350

Fagus grandifolia

American beech is found across the eastern United States and Mexico and considered to be a climax species. Common associates are sugar maple, yellow birch, American basswood, black cherry, eastern hemlock, red spruce, hickories, and oaks (Carpenter, 1974). Beech grows best on western aspects in deep, rich, well drained moist soils with high organic matter. Precipitation requirements are between 76 to 127 cm per year.

Due to its high shade tolerance, beech competes well under closed canopies (Rushmore, 1961). It is a monoecious tree containing male and female flowers and wind disseminated pollen, with good seed crops occurring every two to eight years (Morris et al., 2004). Seeds are a highly preferred food source for birds and rodents (Ward, 1961). Beech trees are also capable of vegetative reproduction, often stimulated by a disturbance or injury to the root system or main stem (Wagner et al., 2010). Beech bark disease is catalyst for this type of regeneration which can result in dense thickets of shade tolerant root suckers (Morris et al., 2004).

Betula alleghaniensis

Yellow birch's native range is as far north as Newfoundland, west across the lake states to Wisconsin, and extends south confined to high elevation sites along the Appalachian Mountains through to north Georgia. A mid-shade tolerant species, yellow birch grows well in moderately drained, deep, sandy loams (Post et al., 1969) on sites receiving an average of 114 cm of precipitation per year (Gilbert, 1960). As a climax species, it is most commonly found growing with American beech, eastern hemlock, red spruce, and white pine (Quigley and Babcock, 1969). Winged nutlets produced through sexual reproduction are wind disseminated and are viable for two to three years with good crop years occurring every other year (Houle, 1998). Yellow birch prefers exposed soil for seed germination often as a result of disturbance (Godman and Krefting, 1960), but are also highly successful at germinating on rotting stumps and logs as well as cracks in boulders (Gilbert, 1960). Sprouting from stumps of younger trees is also common. Seedling establishment and development of yellow birch has been shown to be most successful under 50% canopy cover conditions (Godman and Krefting, 1960).

Acer saccharum

Sugar maple native range is primarily in the hardwood forests of the eastern United States but can be found further west to the Dakotas and south to Oklahoma (USDA, 2017). Common associates are American beech, yellow birch, American basswood, black cherry, red spruce, and eastern hemlock (Kallio and Tubbs, 1980). Sugar maple thrives in a range of well drained soils and in the south, is typically found at higher elevations on cooler, less sun-exposed aspects. Sugar maples are polygamous

(Godman et al., 1990) and its fruit, samaras, are wind disseminated with some seed produced annually; good seed years occur every two to eight years. The seed can remain viable in the seed bank for up to five years. Sugar maple is long lived, shade tolerant, and resilient to browsing allowing it to remain in the understory for decades (Frelich & Lorimer, 1985). It responds well to small increases of light availability resulting from canopy disturbances, even after long periods of suppression (Holmes and Webster, 2010).

Acer rubrum

Red maple grows successfully in a range of climates occurring in the eastern United States into Canada, and as far west as Texas. It appears in an array of soil moisture conditions, but develops best in well drained, moist sandy loam soils. Not confined to cool high elevation sites, red maple grows well across its range making it a component of most forests and is commonly associated with over 70 different tree species. Like sugar maple, these trees are polygamous. Seed is disseminated by wind in early summer and has a germination rate of 46% (Hutnik and Yawney, 1961). Red maple is also a prolific sprouter, which could lead to changes in species composition through repeated partial harvest managed forests (Atwood et al., 2009).

Magnolia fraseri

Fraser magnolia (*Magnolia. fraseri*) has a limited range, confined to the southern Appalachian Mountains. Generally found on protected mesic sites, it grows well in moist fertile soils often at low densities. Common associates are striped maple (*Acer pensylvanicum*), sugar maple, American basswood (*Tilia americana*), American beech, yellow birch, hickories (*Carya spp.*), white ash (*Fraxinus americana*), yellow-poplar (*Liriodendron tulipifera*), cucumbertree, (*Magnolia acuminata*), blackgum (*Nyssa sylvatica*), black cherry, oaks (*Quercus spp.*), eastern hemlock, and red spruce. Its flowers are perfect and produce good seed crops only once every four to five years (Della-Bianca, 1990). The fraser magnolia has an intermediate shade tolerance and is commonly found to occupy canopy gaps made by eastern hemlock in the Great Smokey

Mountains (Barden, 1979). Stump sprouts are believed to be the origin of most mature Fraser magnolia that exist today (Della-Bianca, 1990).

Magnolia acuminata

Cucumbertree is found north to New York, as far west as Oklahoma, and extends into small pockets of Florida's western panhandle. It prefers well drained, moist, deep soils, and found on north and northeast aspects (Smith, 1990). Flowers are perfect and occur at branch tips. Seeds are contained within cones that ripen in late summer to early fall. Good seed years occur every four to five years with marginal seed years occurring annually (Smith, 1990). Dissemination of seed is through birds, wind, and gravity. In addition, cucumbertree can also regenerate through prolific stump sprouting. The trees intermediate shade tolerance and fast growth rate allows it to successfully compete with yellow-poplar and black cherry in mesic forests (Smith, 1990). Common associates are sugar maple, black cherry, oaks, yellow-poplar, and eastern hemlock.

Prunus serotina

Black cherry is widely distributed from northern Maine, west to Nebraska, Kansas, and Texas, extending south as far as central Florida. This species can be found on most sites with the exception of very wet and very dry sites. Black cherry grows best in moist fertile soils, on slopes with north and east aspects (Gatchell, 1971). The flowers are perfect and drupe fruit ripens late summer into early fall. Good seed crops occur every three to four years and produce moderate seed during intermediate years (Hough, 1960). The drupes are highly palatable and serve as a food source for a range of mammals and birds, primarily disseminated by gravity and animals. Black cherry also readily sprouts from stumps as a means of propagation. Young seedlings have intermediate shade tolerance but become shade intolerant as they grow into advanced stages of reproduction at two or three years of age. Under dense canopies, black cherry saplings have difficulty ascending into the canopy (Hough, 1990).

Tsuga canadensis

Eastern hemlock's native range extends as far north as New Brunswick and Nova Scotia, west to parts of Wisconsin, and as far south as north Georgia and Alabama, along the Appalachian Mountains. It prefers cool temps and adequate precipitation, conditions typical at higher elevations through its southern range. While eastern hemlock can be found growing on shallow rocky soils, it grows best in deep alluvial, fertile loams in cool valleys, coves, benches, and in hollows (Hough, 1960). Eastern hemlock is a very shade tolerant, slow growing tree living upwards of 800 years or more (Godman and Lancaster, 1990). Common associates are maples, birches, basswood, black cherry, red spruce, oaks, hickories, yellow-poplar, firs, and American beech. Hemlock is monoecious with separate flowers present on the same branch. Good seed and cone production years occur every other year, but viable seed is low (Godman and Lancaster, 1990). Seed is wind disseminated. Seedlings are highly palatable to white-tailed deer (*Odocoileus virginianus*) and heavy browsing has been attributed to low reproduction densities in the Great Lakes region (Frelich and Lorimer, 1985).

Picea rubens

In West Virginia, spruce is primarily found on poorly drained soils with high available water capacity, shallow (Nowacki and Wendt, 2010), acidic, and contain high amounts of organic matter (Adams and Stephenson, 1989). Spruce stands are limited to elevations over 1000 m (Rentch et al., 2010), where average annual air temperatures are under 8 C° and mean precipitation is over 140 cm (Nowacki and Wendt, 2010). While spruce dominates on peaks and ridges, it gradually transitions to a spruce-hardwood ecotone mid-slope, giving way to pure stands of mixed hardwoods. In the spruce- hardwood ecotone, red spruce reproduction is advancing down slope (Mayfield and Hicks, 2010); slowly regaining stands it once dominated. The sole mode of natural regeneration is through seed (Nowacki et al., 2010). Bumper seed crops occur every three to five years (White and Cogbill, 1992). Male and female flowers are present on the same tree, but on different branches (Hart, 1959). Seeds are wind disseminated up to 61 m and remain viable for up to one year (Sullivan, 1993). Seeds are highly sought-after food source and subject to predation (Blum, 1990) by a host of vertebrates.

Red spruce plantations in West Virginia have shown to be successful when thinned from below after 50 years and it has been suggested that supplemental planting to establish advanced reproduction may be a viable option (Hornbeck and Kochenderfer, 1998). A follow-up study on red spruce plantings in the wake of timber extraction in the early 1900s were reported to be the dominant tree species 65 years after reforestation efforts, comprising of over 60 percent of the stand volume (McNabb et al., 2010).

Microclimates found beneath closed canopy positions offer spruce competitive advantages and essential growing conditions. Under tree canopies, thermal loading is mitigated through light interception and soil moisture retention aided by thick O horizons and shade. These conditions are critical for spruce root systems which are generally shallow and susceptible to water stress (Greenwood et al., 2008). Newly fallen seed require a moist seedbed for successful germination (Baldwin, 1934). Moist humus layers, disturbed or exposed mineral soil, and coarse wood debris in advanced states of decay are suitable substrates (Dumias and Prevost, 2016; Weaver et al., 2009; Baldwin, 1934). Conversely, deep scarification can be detrimental to seedling recruitment (Prevost et al., 2010).

Canopy recruitment for red spruce can occur by growing within a large canopy opening and ascending into the canopy with no suppression period, or red spruce can exist as advanced reproduction and capitalize on multiple smaller, release events (Wu et al., 1999). Much to its advantage, red spruce is highly shade tolerant allowing it to persist in the understory for up to 100 years (Hart, 1959; Korstain, 1937). Consequently, growth is suppressed until a disturbance provides a period of release (Fraver and White, 2005). In old-growth spruce forests in the Smokey Mountains, Wu et al. (1999) observed an average of 1.43 and a maximum of 7 suppression periods before red spruce attained upper canopy positions.

Red Spruce Regeneration Methods

Red spruce can regenerate under low light conditions, which are typical of closed canopies. Increases in light availability for established advanced spruce reproduction

stimulate height and diameter growth (Korstian, 1937; Seymour, 1995), which can be accomplished through a variety of management techniques. Ultimately, management goals should determine the method used.

Even-aged silviculture is often used to manage red spruce where timber production is the goal, but site-specific attributes should be considered. Natural regeneration is the dominant method of stand establishment and adequate stocking should be in place before complete overstory removal (Frank and Bjorkbom, 1973). Conversely, Hughes and Bechtel (1997) found that while red spruce and balsam fir (*Abies balsamea*) reproduction decreased with increasing distances from clearcut edges, timing harvest so that it follows shortly after seed dispersal can be beneficial for stocking at greater distances from forest edges. As the overstory is removed, microclimates on the forest floor are altered with increasing rates of air and soil temperatures, as well as decreased soil moisture.

Watering-up effect occurs when overstory is removed. The sudden reduction of water uptake by overstory tree removal causes a rise in the water table (Pothier et al., 2003). These conditions can impair spruce's ability to germinate and establish and subsequently be outcompeted by other vegetation (Seymour, 1995). On a lowland site in Quebec, findings by Prevost and Gauthier (2012) suggest that in clear-cut sites where water is not a limiting factor and seedlings are protected from temperature extremes, red spruce can successfully regenerate. Shelterwood methods can be beneficial for mitigating harsh conditions, acclimating existing reproduction, and inhibiting competition thereby improving spruces regeneration success. Variations of the shelterwood method involving differences in rotation age, multi-staged overstory removal, and reserve tree retention (shelterwood with reserves), have resulted in mixed outcomes. In spruce-fir stands in Maine, Blum (1973) found that reproduction that established following overstory removal fared better than reproduction present prior to removals. Sendak et al. (2003) reported that the best red spruce regeneration was the result of a three-stage shelterwood.

Red Spruce Management Methods

Spruce regeneration can also be improved through thinning methods. Findings by Olson et al. (2014) suggest that relative density reductions of 33% through crown thinning increase red spruce reproduction of all size classes. In simulations, a 50% basal area thinning from above could increase red spruce volume by 100% over a 100-year period (Rentch et al., 2007).

The shallow root systems of red spruce should be considered when making decisions about harvest size and intensity. Windthrow is common for residual red spruce trees and basal area removals of over half the current basal area are not recommended (Blum, 1990). Two-aged and uneven-aged management can allow reserve trees to acclimate to changes in the new environment and adapt to become more windfirm (Seymour, 1995). Increasingly, red spruce management emulating natural disturbance regimes has become of interest. Fraver and White (2005) suggest that small scale canopy disturbance has allowed red spruce to maintain its dominance in Maine. Small and medium gaps (100 m²- 300 m²) have been shown to have the lowest seedling mortality and after ten years, the highest red spruce seedling densities (Dumais and Prevost, 2016). However, as reproduction develops into more advanced stages, the need for greater light availability increases to maintain optimum growth (Greenwood et al., 2008). Irregular shelterwood or expanding gap (e.g. *Femelchlag*) has also been used to mimic disturbance (Carter et al., 2017). These systems of planned gap creation maintain canopy complexity, indicative of climax forests. Continuous cover irregular shelterwood methods have been shown to increase red spruce relative densities and maintain species diversity over clear-cut treatments (Raymond and Bedard, 2017).

Disturbance-based Silviculture

Traditional forest management methods intended to maximize timber production have been used for decades but may be creating deficits in complex forest canopy structure, wildlife habitat, and species diversity (Lindenmayer et al. 2012; Lorimer 1977). Many spruce stands that were clearcut throughout West Virginia have naturally regenerated to even-aged stands, dominated by mixed hardwoods (Minckler, 1945; Thomas-Van Gundy and Sturtevant, 2014). In recent years, interest in developing alternative forest

management strategies has gained momentum. Variants of disturbance-based management are meant to mimic naturally occurring disturbance regimes in order to retain canopy complexity, climax species components, and sustaining ecosystems (Long, 2009). Management decisions should be based on disturbance regimes that occur in the region of interest with considerations to scope.

Dendrochronology

Within their annual growth rings, trees contain records of past environmental conditions, climate history, and disturbance events (Speer, 2010). Identifying tree ring signals can provide insight into these past conditions by analyzing fluctuations in ring widths from year to year or averages over time thereby reconstructing a history at large or fine spatial scales. Using dendrochronology to observe the effects of canopy disturbance on tree growth response has been well documented (Fraver and White, 2005; Hart et al., 2010; Lafon and Speer, 2002; Nowacki and Abrams, 1997; Rentch et al., 2010, 2002; Sleen et al., 2013; White et al., 2012; Wu et al., 1999). When a disturbance occurs, resource availability for surviving trees and saplings within the affected area increases. Higher exposures to light, reduced competition for nutrients, and higher soil moistures often result in higher growth rates (Nowacki and Abrams, 1997). Growth trends associated with age also affect ring width variability. Trees with larger diameters appear to respond with less intensity than smaller trees, simply due to the addition of new wood over larger surface areas (Speer, 2010). Considering the variability of climatic conditions and age, Nowacki and Abrams (1997) developed the percent growth change method to detect canopy disturbance (releases) while minimizing growth responses attributed to changes in climate. In this method, prior and subsequent ten-year mean ring widths are used to detect release and suppression periods. A 25% growth increase threshold was used to identify periods of release. In response, Fraver and White (2005) proposed the absolute increase method, simplifying the percent growth change approach as simply the difference between preceding ten-year means, and subsequent ten-year means. They argued, the method proposed by Nowacki and Abrams is overly sensitive, and results in false positive and false negative releases. Release thresholds are species-specific, accounting for rates of growth preceding the year in question.

One limitation to these growth averaging approaches is the inability to identify releases occurring during the ten-year windows at the beginning and end of each tree ring series. Comparisons have been made testing the accuracy of these growth averaging methods and time-series disturbance detection methods in hurricane impacted forests in New England by Trotsiuk et al. (2018). Trotsiuk et al. (2018) reported significantly higher temporal accuracies in the growth averaging approaches by Nowacki and Abrams and Fraver and White but that the absolute increase method may be most useful for applications involving large samples of single species. A combination of several methods was used to identify releases in second-growth spruce hardwood forests in West Virginia (Rentch et al. 2010). In addition to employing percent growth change and absolute increase methods, Rentch et al. (2010) also used visual inspection to identify releases that had occurred within the final ten years, where the methods described above, are unable to produce values.

METHODS

Study Area

Location

The study site is located along the western edge of the Allegheny Highlands within Kumbrabow State Forest in Randolph County, WV (Figure 1). Kumbrabow State Forest sits on Rich Mountain with elevations ranging from 914 m to 1198 m, and encompasses nearly 3834 hectares. The forest is managed using a multiple-use concept including recreation, watershed protection, commercial forestry and wildlife management. Located in the western portion of the Kumbrabow State Forest, the study site is bordered by Turkey Bone Road along the entire southern edge and covers 56.7 hectares.

Figure 1. Map of the study site location within West Virginia, and Kumbrabow State Forest.

History

Prior to the state's acquisition of the forest in 1934, Kumbrabow's forests were intensively logged for timber. Four timber companies operated from 1880-1920 and today, the old railroad grades still exist throughout the forest (WVDOF, 2002). Slash was left scattered across harvest sites providing fuel for the fires often ignited by the embers emitted from the coal-fired Shay engines as they removed the timber. These fires were often intense, burning valuable humus and organic layers down to mineral soils as well as the seed contained within the seed bed (Korstain, 1937).

In the late 1950s through the early 1960s limited timber harvests were conducted. The operations ended abruptly following a dispute between the contracted lumber company, other firms, and the state. It wasn't until 1975 that silvicultural plans were created to manage the forests and harvesting resumed in 1977 (WVDOF, 2018). Today, most of the overstory is even-aged with occasional legacy trees spared from the harvests at the turn of the century (Rentch et al., 2010).

Climate

Climate data were acquired from the US Climate Data in Pickens, West Virginia, located approximately 10 km west of Kumbrabow State Forest. Elevation at Pickens is 844 m, 240 m lower than the average elevation at the study site. The study site elevation ranges from 987 m to 1128 m with a mean elevation of 1084 m. Mean annual temperature is 9.31 °C, with a mean high of 25.6 °C during July and a mean low of –7.78 °C in January. Mean annual rainfall is 1683 mm and mean snowfall is 343.15 cm per year.

Soils

The primary soil types consist of Buchanan and Ernest (40%), Gaudineer-Simoda complex (21%), and Gilpin-Dekalb stony complex (13%) (Soil Survey Staff [Accessed 2018]). The Buchanan and Ernest series are composed of acid sandstone, quartzite, siltstone, and shale. These soils are generally poorly to moderately well drained and found on 0 to 50 percent slopes. Gaudineer-Simoda complex is extremely stony, and acidic as a result of high amounts of red spruce leaf litter. Parent materials are shale, siltstone, and sandstone and are found on slopes from 3 to 60 percent. The Gilpin-Dekalb stony complex is well drained and found on slopes ranging from 0 to 80 percent. Parent materials are acid siltstone, shale, brown acid sandstone, and sandstone. These soils are typical of high elevation sites for West Virginia.

Site Description

An inventory of the study site was conducted during the summer of 2017. Overall, the site contains 370.8 trees per hectare (TPH), and basal area of 33.7 m²ha⁻¹. The four major tree species are red maple, black cherry, eastern hemlock, and red spruce. Red maple is the dominant species, containing 28% of the basal area at 7.35 m² ha⁻¹. Black cherry makes up 27% of the basal area with 4.59 m²ha⁻¹, eastern hemlock 12% at 4.13 m²ha⁻¹, and red spruce 11% of basal area at 1.83 m²ha⁻¹.

The four most dominant ground cover species are intermediate woodfern (*Dryopteris intermedia*), native blackberry (*Rubus spp.*), greenbrier (*Smilax rotundifolia*), and stinging nettle (*Urtica dioica*). Additionally, beech bark disease has negatively affected a majority of the mature American beech (*Fagus grandifolia*) on the site, resulting in

prolific root suckering where dense thickets of beech reproduction dominate the understory.

Experimental Design

Defining Gaps

Due to the variability of gap characteristics, a gap criterion was established to allow for consistency and replication. A gap was defined as an opening caused by the death of one to ten canopy trees (Christensen and Franklin, 1987). Gaps thought to be created as a result of separate events occurring at different times, were counted as a single entity provided they were contiguous. Trees that contributed to or were solely responsible for gap creation are called gap makers. Trees believed to be responsible for gap creation had a minimum diameter at breast height (DBH) of ≥ 20 cm, were classified as gap makers (Qinghong & Hytteborn, 1991). Minimum gap area thresholds used in previous studies vary from over five to 2009 m² (Yamamoto, 2000; Stewart et al., 1991; Runkle, 1992). To study regeneration characteristics in older gaps nearing closure, minimum gap size threshold included in this study was 5 m². Within the gap area, if the tallest height of vegetation and regeneration in the opening exceed more than half the height of the surrounding dominant canopy, the gaps were classified as closed and considered non-gaps (Nakashizuka, 1984; Nakashizuka and Numata, 1982; Veblen, 1985).

Locating Gaps

Strip transects were created to provide unbiased sub-sampling of the study site. Transects were determined on a 20 m spacing to reduce large gap bias (Brokaw, 1982). Transects varied in length, ranging from approximately 20 m to 850 m in a north to south orientation, with length dependent on transect location within the study site. Each transect was assigned an identification number and randomly chosen using the random number generator. As each pre-determined transect was walked, only gap centers that fell within a 10 m zone on either side of the transect (Figure 2) fitting our gap definition (Runkle, 1992) were included.

Figure 2 Example of gaps in relation to transect. Gap A would not be included as it falls outside of the transect, but gaps B and C are included.

Gap Measurement

To determine gap size, a pair of perpendicular lines were established such that the first line was the longest that would fit in the gap (from edge of crown to edge of crown). The second line was the longest straight line (from edge of crown to edge of crown) perpendicular to the first line (Runkle, 1992). These lines were measured using measuring tape and recorded to the nearest half meter. Gap area was estimated using the formula for area of an ellipse (Runkle, 1982). Orientation of the gap was determined by recording the compass bearing of the longest line. For gaps too irregular to use the ellipse formula, the length of each line segment from the line intersection to the gap edge was recorded starting with the longest line. Here, gap size was calculated as the sum of the four quarter ellipses (Runkle, 1992).

Gap Observations

For each gap, the number of gap makers, species, area, aspect, elevation, percent canopy cover, red spruce seed source proximity, and azimuth were recorded and used for gap characteristic comparisons. Estimates of reproduction were made by counting and classifying all seedling regeneration ≥ 15 cm tall up to 2.54 cm DBH, within three 1 m radius sample plots along the longest initial gap measurement; from the dominant canopy edge to dominant canopy edge. Along the shorter perpendicular measurement, two one-meter radius plots were established at each dominant canopy edge (Figure 3).

In gaps where axes were over 7 m, 1-m radius sample plots along the axis were established at center, midpoint, and endpoint locations (Romer et al., 2007). A height classification was created to later determine species dominance (Table 3). Individuals of each species were tallied, and quantified into appropriate height class within each plot. Aggregate height was determined as the sum of height class for each species within each plot. Observations of understory herbaceous species contained within each gap (if any) included ocular estimates of height and percent ground cover.

Figure 3 Example of gap reproduction sample plots for gaps. Sampling layout for gaps less than seven meters long on the left, and layout on the right for gaps containing axes over seven meters.

Table 3 Reproduction height classification.

Height (cm)	Height Class
15-30	1
31-60	2
61-90	3
91-120	4
121-150	5
151-2.54 DBH	6

Importance Value

Importance values (IVI) for each species within each subplot were determined using counts and the height class classification as described earlier. Relative dominance was calculated as the sum of height classes within each species divided by the sum of height classes of all species within each subplot (Eq. 1).

$$\text{Relative dominance} = \frac{\sum \text{height}}{\sum \text{height, all species}} \quad (\text{Eq. 1})$$

Relative density was calculated as the sum of total individuals within each species divided by total individuals of all species (Eq. 2).

$$\text{Relative density} = \frac{\sum \text{individuals}}{\sum \text{individuals, all species}} \quad (\text{Eq. 2})$$

Importance value (0-2) was determined by the sum of relative dominance and relative density (Eq. 3).

$$\text{Importance value} = \text{Relative density} + \text{Relative dominance} \quad (\text{Eq. 3})$$

(A maximum importance value of two was obtained if only one species was found within a plot.)

Non-Gaps

For gap and non-gap comparisons, non-gap locations were determined from random waypoints. One, 1-m radius subplot was established on each coordinate. Within each plot observations of species, height class, counts, elevation, aspect, and groundcover species were recorded. From this, relative dominance, relative density, and importance values were calculated.

Aspect

Aspect was classified into three classes based on climate, soil conditions, and productivity differences. Study plots and gaps occurring on the hottest and driest aspects (S, SW) were classified as -1, the cooler and moister aspects of N, NE into class 1, and more neutral aspects (E, SE, W, and NW) classified as class 0 (Figure 4).

Figure 4 Aspect class delineation.

Seed Source Proximity

The distance between each study gap to the closest red spruce seed source was measured from gap center. A 360° observation was made to identify dominant red spruce over 12.6 cm DBH capable of producing seed (Heart, 1959), and within 61 m. Once located, the closest seed source distance was measured using a TruPulse laser. Each gap was divided into four quadrants (NE, SE, SW, and NW) and the location of the closest seed source within 61 m from gap center for each quadrant (if any) was marked using GPS. Distance and cardinal direction were recorded from the center of each gap. Proximity of seed source was based on red spruce potential wind dissemination distance of 61 m (Blum 1990).

Growth Response (tree ring analysis)

Tree ring analysis was used to determine approximate year of the disturbance (i.e. gap creation). Core samples were used to obtain gap influenced growth response of dominant, codominant, and suppressed from trees within gaps and those located on

gap edges. Due to the variability of gap age and diameters of trees within gaps, cores were taken at two different heights depending on diameter at breast height. Cores were taken at 1.4 m from trees ≥ 5 cm at DBH, and 0.2 m from trees < 5 cm at DBH (Rentch et al., 2010). To avoid ring width variation caused by reaction wood, all cores were extracted perpendicular to the slope fall line. Each core was mounted and sanded with progressively finer grit sandpaper. Red spruce and eastern hemlock required a 120, 220, 320, and 400 grit regimes, while yellow birch and maples required a final sanding with a 600-grit paper to effectively reveal annual rings. Most of the core sample ring widths were measured with the CooRecorder program (Cybis Co., 2018). Cores were digitally scanned using an Epson Perfection 4180 at 1200 DPI. Cores containing faint or highly suppressed rings, and thereby difficult to verify (some birch and maple) using CooRecorder, were dated using a microscope, a Velmex stage micrometer system, and J2X software (VoorTech Consulting, 2017). Ring width measurements in both programs were measured to the nearest .001 mm. Cross dating was verified using COFECHA (Grissino-Mayer, 2001). To identify the approximate date of disturbance, several methods were used. The percent increase method introduced by Nowacki and Abrams (1997) identifies dates of disturbance through a comparison of ten-year ring width means (Eq. 4).

$$\%GC = \frac{M_2 - M_1}{M_1} * 100 \quad (\text{Eq. 4})$$

Where %GC= percent growth change

M_1 = preceding ten-year mean (including the year of comparison)

M_2 = subsequent ten-year mean

The percent growth change method was created to reduce short term growth responses related to climate, and identify growth responses related to canopy disturbance. Two growth response thresholds were used to identify disturbance through this method; growth increases of $\geq 25\%$ for overstory trees (Nowacki and Abrams, 1997), and $\geq 100\%$ (Frelich and Lorimer, 1991) for saplings and gap fillers. To address concerns about the oversensitivity of the growth change method, Fraver and White's (2005) absolute increase method was used to help identify disturbance events. This method is a

modification of the percent growth increase where disturbances are identified using a species-specific threshold. Absolute increase is determined simply as the difference between the preceding ten-year average ring width and the subsequent ten-year average ring width (Eq. 5).

$$AI = M_2 - M_1 \quad (\text{Eq. 5})$$

Thresholds for canopy disturbance were 0.58, 0.74, and 0.52 for red spruce, eastern hemlock, and maples, respectively (Fraver and White, 2005)

For disturbances occurring within the past ten years, sapling growth responses were identified through observation of the cores. For these saplings, ring widths of $\geq 1\text{mm}$ per year with no decline in growth, were used to determine the gap age (Rentch et al., 2010). At least one or a combination of these three methods were used to estimate gap creation date.

Canopy Cover

The CanopyApp application was developed by Dexter Richards from the University of New Hampshire. Available for mobile phones with built in cameras, it was intended to replace traditional hand held densimeters and fish-eye cameras to estimate percent canopy accurately and more quickly. A user defined mask is created and calculates the number of pixels that meet the criteria. To capture the entire surrounding overstory, a clip-on XCSource 180° wide angle micro fish-eye lens was attached to a iPhone 5G camera lens. At each gap center, a picture was taken at 1.5 m from the ground and an estimation of canopy cover was generated using the CanopyApp.

Stand and Volume and Composition

Stand and volume composition for the site were estimated using the variable radius sampling method from 30 locations (BAF 20 prism). Merchantable height was estimated to a 20 cm top using a TruPulse laser for trees over 30 cm DBH. Board foot volume (Doyle) was calculated using Masavage-Girard form class 78 and converted to m^3 using a 0.0833 multiplier.

Statistical Analysis

A total of 210 gaps were identified and measured to determine mean gap area, gap area distribution, and area in gaps of the study site. Of those 210, 69 gaps (473 subplots) were randomly selected and used in the assessment of each of our objectives. In addition, 69 subplots from the center of each gap and 78 random plots (78 subplots) were established under closed canopy, across the site, and used to make spruce presence and absence comparisons for objective 1.

All continuous response variables were screened for normality using Shapiro-Wilk W test. Non-parametric association of spruce presence and type (gaps and non-gaps) while controlling for aspect were examined by the Cochran Mantel-Haenszel test (JMP PRO 2015, ver. 12.2).

GLIMMIX and logistic regression analysis were performed in SAS Version 9.4.

Effect of type, aspect, and type and aspect interaction on number of individuals, dominance, height, and IVI for each species were assessed using GLIMMIX procedure with negative binomial distribution and log link function.

Effects of type, aspect, and type and aspect interaction on red spruce relative dominance and relative density were analyzed using GLIMMIX procedure with beta distribution and logit link function for each species. Transformations on relative dominance and relative density were made as the beta distribution function requires data values between zero and one. Values of zero were increased by .00001, and values of one were reduced by .00001.

The analysis of correlations of total seedling density and aggregate height correlations with red spruce seedling density, height class, dominance, and IVI were performed using GLIMMIX procedure with negative binomial distributions using log link function. Stepwise logistic regression was used to assess relationships between total seedling density and aggregate height on red spruce presence.

To assess and identify the variables contributing to the presence and absence of red spruce reproduction in gaps, a logistic stepwise regression using a binary logit model was applied. Orientation, seed source bearing, shortest seed source distance, gap size, canopy cover, and elevation were used to identify impacts on red spruce reproduction presence. Only main effects were used with no interaction.

Effects tests to determine the effects of gap characteristics on red spruce characteristics were performed using GLIMMIX procedure. Effects on red spruce relative dominance and relative density were analyzed using a beta distribution and logit link function, and for all other red spruce characteristics, a negative binomial distribution using a log link function was used.

A second set of logistic regression with backward elimination was used for tests to evaluate the effects of number of individuals, height, and IVI variables on red spruce presence. These were performed separately with all species groups in three models.

Five final models were developed using effects showing correlation ($p = 0.05$). These final models used significant effects from subsequent analysis to determine red spruce presence, red spruce relative density, red spruce relative dominance, red spruce seedling density, and red spruce height. The final model used to determine effects of other tree characteristics and gap characteristics on red spruce presence was a stepwise linear regression model. The four remaining models used the GLIMMIX procedure with beta distribution using logit link function to predict red spruce relative dominance and red spruce relative density, and negative binomial distribution with log link function for predicting red spruce individuals and red spruce height. For all tests, statistically significant differences were tested at the $\alpha = 0.05$ level.

RESULTS

Gap Characteristics

Combined, the length of transects were 8.04 km totaling 16.1 ha. A total of 210 gaps were found, which represented 7% of the area measured. Of the 210 gaps, average gap size was 50.6 m² and ranged from 5 to 459 m² (Figure 5). In the 69 randomly selected study gaps, mean gap size was 59.5 m². In addition, canopy cover was recorded in study gaps and showed a normal distribution. Mean canopy cover was 68 percent and ranged from 34 to 92 percent (Figure 6).

Frequency distribution of gap area was right skewed with 41% of gaps 25 m² or smaller; 79% of gaps were 75 m² or smaller. Average gap makers per gap was 2.2 trees. The smallest gap was formed by two trees, and the largest gap was the result of eight gap makers. American beech was the most common gap maker species, making up 51% of the 438 gap makers recorded.

Figure 5 Gap size distribution and frequency.

Figure 6 Association of gap size and percent canopy cover.

Stand Characteristics

The study site contained 368 trees per hectare (TPH), 33.7m² basal area per hectare, and a total volume of 2604.3 m³ per hectare (Table 4). Most dominant overstory species included birches, red maple, eastern hemlock, and sugar maple, which accounted for 28%, 18%, 18%, and 12%, respectively. Birches, the most frequently occurring species accounted for 103 TPH, had the smallest average diameter of 37.1 cm, and only 16% of the total volume. Black cherries were the largest trees with an average diameter of 54.4 cm, and contained 21% of the volume. Red spruce made up 2%, or 7.4 TPH on average, had an average diameter of 48.8 cm, and accounted for 4% of volume.

Ground Cover

Of the ground cover species observed, the most dominant were intermediate woodfern (*D. intermedia*), broadleaf greenbrier (*S. rotundifolia*), native blackberry (*Rubus spp.*), and stinging nettle (*U. dioica*). Average coverage was 20%, 8%, 29%, and 26% for

Table 4 Summary of the stand, by species.

Species	Average DBH (cm)	Trees per hectare	Basal area (m ² /ha)	Volume (m ³ /ha)
American beech	37.4	29	1.5	59.8
black birch	34.4	32.3	2.1	89
black cherry	54.3	37.7	6.9	772.8
cucumbertree	49.3	3.4	.6	81.2
eastern hemlock	39.8	65.2	5.1	330.8
Fraser magnolia	45.4	12.8	1.8	131.9
sugar maple	37.9	44.8	3.1	184.3
red maple	47.2	65.2	7.7	637
red spruce	48.7	9	1.4	225.6
yellow birch	29.4	72.5	3.5	92.1
Total	42.4	370.8	33.7	2604.3

woodfern, greenbrier, blackberry, and nettle, respectively. There were no significant differences in coverage between gaps and non-gaps for any species. Woodfern was the most frequently occurring groundcover, and was present in 54% of non-gap plots and 75% of gaps. Rubus occurred on 17% of the 78 non-gap plots and 10% of the 69 gaps. Nettle was least common occurring in only 3% of non-gap plots and 4% of the gaps. Greenbrier groundcover occurred on 13% of non-gap plots and 7% of gaps. No groundcover was present in 14% of non-gap plots and 3% of gaps.

Gap Age Distribution

Tree cores were obtained from a subsample of the study gaps (49%) to determine approximate gap age. Thirty-nine percent of the cores were from red spruce, 33% from eastern hemlock, 11% from red maple and 17% from sugar maple. Tree diameters ranged from 2.5 to 53.6 cm DBH. In some cases, only one of the three tree species meeting the criteria for tree ring analysis was present, and in others up to four trees were available. The number of sample cores taken from each gap were determined based on diameter (≥ 2.54 cm DBH) and species (red spruce, eastern hemlock, an maple). Eleven gaps were dated using one core, 12 gaps using two cores, nine gaps using three cores, and four gaps using four cores. Dates were determined using one or more of the previously described methods. One gap age was determined based solely on visual inspection. Average gap age was 19.1 ± 6.84 years with the oldest gap dating back 37 years and the youngest gap, 3 years old. Most gaps were in the 11-15 and 21-25 year age classes, with each making up 29% of the total (Figure 7). Among the samples taken, mean release duration was 11 years and on average, experienced 1.8 releases. Seven trees showed no signs of suppression and three trees appeared to have never experienced release.

Reproduction Characteristics

In total, 69 gaps and 78 random non-gap plots were sampled for data collection. Eighteen species were found and recorded throughout the site. Black birch (*Betula lenta*), basswood (*Tilia americana*), Norway spruce (*Picea abies*), and pin cherry (*Prunus pensylvanica*), seedlings were found only in gaps, northern red oak (*Quercus rubra*) was found as a single individual on one non-gap plot.

Figure 7 Frequency of gap 5-year age class for the study site in Kumbrabow State Forest, WV (n=210)

Ten species with low representation included black birch, American basswood, mountain holly (*Ilex montana*), Norway spruce, pin cherry, witch-hazel (*Hamamelis virginiana*), white ash (*Fagus americana*), and northern red oak (Figure 8). Combined, these species comprised 8% of reproduction in gaps and 10% in non-gaps. Average reproduction characteristics on a per plot basis for each species indicated red maple had the highest seedling densities of 2.23 seedlings per plot. Relative density, aggregate height, dominance, relative dominance, and IVI were highest for American beech (0.22, 5.61, 1.82, 0.28, and 0.5, respectively) (Table 5).

Figure 8 Seedling composition in gaps and non-gaps, summarized

Red Spruce Presence

To address our first objective, we examined the effects of gap type and aspect on red spruce presence. Differences in red spruce presence within gaps and non-gaps was not significant ($p= 0.4207$) (Figure 9). At least one spruce was present in 36% of gaps and in 29% of non-gap plots. Conversely, in non-gaps, red spruce reproduction was significantly taller ($p= 0.0203$) and had higher relative dominance ($p= 0.0309$) (Table 6). No effects from aspect or the aspect and gap type interaction were found. Red spruce reproduction occurred on 32.4% of the total 147 combined sampled areas.

Table 5 Averages of species characteristics per plot

Species	Seedling Density	Relative Density	Aggregate Height	Dominance (avg height)	Relative Dominance	IVI
<i>Gaps</i>						
American beech	1.4	0.2	5.37	1.71	0.26	0.47
black cherry	0.23	0.03	0.28	0.08	0.02	0.05
cucumbertree	0.1	0.01	0.17	0.05	0.01	0.02
eastern hemlock	0.1	0.01	0.13	0.04	0.01	0.02
fraser magnolia	0.9	0.09	1.35	0.43	0.08	0.17
misc	0.09	0.02	0.16	0.07	0.02	0.05
red maple	2.61	0.13	3.23	1.03	0.1	0.24
red spruce	0.49	0.06	0.88	0.28	0.06	0.13
sugar maple	1.07	0.05	1.94	0.67	0.05	0.1
striped maple	0.94	0.07	1.8	0.56	0.07	0.14
yellow birch	1.84	0.15	3.28	1.04	0.15	0.31
<i>Non-gaps</i>						
American beech	1.53	0.24	5.82	1.91	0.29	0.53
black cherry	0.24	0.02	0.32	0.1	1.91	0.04
cucumbertree	0.13	0.02	0.23	0.07	0.02	0.04
eastern hemlock	0.06	0.01	0.06	0.02	0.00	0.01
fraser magnolia	0.26	0.02	0.28	0.09	0.02	0.04
misc	0.12	0.02	0.26	0.09	0.02	0.04
red maple	1.88	0.11	2.05	0.65	0.09	0.2
red spruce	0.64	0.17	1.74	0.56	0.18	0.36
sugar maple	1.45	0.09	1.78	0.49	0.06	0.15
striped maple	0.44	0.03	0.76	0.24	0.04	0.07
yellow birch	1.03	0.1	1.78	0.57	0.09	0.19

Figure 9 Effects of gap type on red spruce presence.

Table 6 Averages of red spruce characteristics in gaps, non-gaps, and aspect

	aggregate height	dominance	IVI
Gap type			
<i>gap</i>	0.88*	0.28*	0.13*
<i>non-gap</i>	1.74	0.56	0.36
Aspect			
-1	1.36	0.43	0.24
0	1.27	0.4	0.27
1	1.47	0.47	0.21

* Indicates significant differences between gap type at $\alpha = 0.05$

Additionally, the effects of other species on red spruce presence within gaps were analyzed. Effects used in this series of tests included all other seedling densities, height, and IVI. Black cherry seedling density and aggregate height had positive relationships with the presence of red spruce ($p = 0.0338$ and $p = 0.0375$, respectively)

(Figure 10). The probability of red spruce presence increased on plots as black cherry reproduction and height increased. No other species-specific effects were significant.

Red Spruce Seedling Characteristics

To address our second objective, the effects of other species on red spruce reproduction in gaps was tested. The seedling densities, aggregate height, and IVI of each species other than red spruce were tested for their effect on red spruce seedling density, relative density, aggregate height, dominance, and IVI.

Figure 10 Association of black cherry height and seedling density on red spruce presence within gaps.

Positive relationships between eastern hemlock aggregate height and red spruce seedling density and red spruce height were found ($p=0.0266$ and $p=0.0014$, respectively) (Table 7). In addition, there was a positive effect of eastern hemlock seedling density on red spruce aggregate height ($p=0.0055$).

The results showed a negative effect of cucumbertree seedling density on red spruce relative density and relative dominance ($p = 0.0184$ and $p = 0.0315$, respectively). Plots with greater cucumbertree reproduction had lower red spruce seedling density and decreased height. Increased cucumbertree aggregate height reduced red spruce relative density ($p = 0.0496$). Effect of black cherry IVI on red spruce relative density was significant ($p = 0.036$) and positive, that is, when black cherry IVI increased so did red spruce seedling relative density.

Effects of Canopy Gaps on Red Spruce

To satisfy the third objective, testing was done for effects of gap characteristic on red spruce presence. Effects used in the test were cardinal direction, number of gap makers, aspect, percent canopy cover, elevation, bearing, distance to seed source, gap size, and gap age. Tests showed gap size influenced red spruce presence ($p = 0.0072$) (Figure 11). In 25, 50, and 100 m² gaps, the probability of spruce presence was 50, 75, and 100%, respectively. No additional significant effects of gap characteristics on red spruce presence were found.

Similarly, gap characteristics had no influence on red spruce seedling density, relative density, aggregate height, dominance, relative dominance, and IVI.

Table 7 Summary table of effects ($Pr > F$) from other species characteristics on red spruce characteristics.

Effect	Red spruce characteristics ($Pr > F$)					
	Seedling density	Relative density	Aggregate height	Dominance	Relative dominance	IVI
Seedling density						
American beech	0.5639	0.7805	0.2910	0.5212	0.9104	0.9679
eastern hemlock	0.0848	0.5302	0.0055	0.1725	0.3651	0.5566
fraser magnolia	0.6993	0.9237	0.2929	0.6194	0.9349	0.7764
red maple	0.8535	0.0521	0.8713	0.9355	0.0865	0.6409
sugar maple	0.3414	0.1517	0.2636	0.4776	0.1967	NA ¹
yellow birch	0.4685	0.8749	0.7685	0.8024	0.9032	0.8817
black cherry	0.6787	0.2575	0.2675	0.5371	0.2310	0.7274
cucumbertree	0.8739	0.0184	0.8069	0.8903	0.0315	0.9613
misc.	0.7155	0.2744	0.2618	0.6456	0.3261	0.9329
striped maple	0.6055	0.0685	0.7979	0.8256	0.1090	.06645
Aggregate height						
American beech	0.5639	0.7805	0.2910	0.5212	0.9104	0.9679
eastern hemlock	0.0266	0.2113	0.0014	0.1353	0.1352	0.7435

¹ Sugar maple seedling density effect removed due to bimodal distribution and difficulty with optimization

Table 6 continued

fraser magnolia	0.8925	0.9614	0.646	0.8116	0.9833	0.9861
red maple	0.8779	0.1056	0.8429	0.9432	0.1684	0.5568
sugar maple	0.1767	0.1680	0.1096	0.3353	0.2214	0.6774
yellow birch	0.3256	0.8164	0.5641	0.7174	0.8819	0.8485
black cherry	0.9034	0.337	0.5023	0.6891	0.2814	0.8388
cucumbertree	0.8980	0.0496	0.7767	0.9459	0.0763	0.9693
misc.	0.9432	0.5410	0.6017	0.8234	0.6326	0.8945
striped maple	0.2142	0.0870	0.3723	0.5489	0.1461	0.8949
IVI						
American beech	0.7926	0.7062	0.9843	0.9124	0.5730	0.7140
eastern hemlock	0.5861	0.6352	0.4839	0.7660	0.5383	0.8356
fraser magnolia	0.9235	0.6226	0.6553	0.8492	0.7997	0.8769
red maple	0.4367	0.8841	0.6598	0.8610	0.7939	0.4448
sugar maple	0.3363	0.2653	0.1763	0.5632	0.2832	0.5205
yellow birch	0.3835	0.9275	0.6442	0.8933	0.8878	0.9128
black cherry	0.9471	0.0360	0.6558	0.8747	0.0524	0.9600
cucumbertree	0.8783	0.2421	0.6248	0.8363	0.3756	0.9165
misc.	0.4857	0.9355	0.2882	0.7030	0.9910	0.8205
striped maple	0.4875	0.4805	0.6463	0.8739	0.5469	0.8837

Figure 11 Effect of gap size on probability of spruce presence in intensive study gaps (orange circles represent where spruce was absent and green triangles represent where spruce was present).

Final Models

A series of four final models were developed by combining significant ($p < 0.05$) and weak ($p < 0.1$) effects on four attributes of red spruce (presence, relative density, relative dominance, and seedling density) found from previous tests. Only two metrics for red spruce had significant models.

The first model tested effects of black cherry height, black cherry IVI, gap size, distance to seed source, and total seedlings on red spruce presence. This model found a significant effect of gap size on red spruce presence ($p = 0.0072$) (Table 8).

Table 8 Final model testing for effects on red spruce presence.

Effect	Pr>ChiSq
Black cherry height	0.7608
Black cherry IVI	0.1095
Gap size	0.0072
Distance to seed source	0.0517
Total number of all seedlings	0.1227

The second model tested for effects of cucumbertree height, cucumbertree seedling density, red maple seedling density, striped maple height, striped maple seedling density, black cherry IVI, and distance to seed source on red spruce relative density. Significant effect of black cherry IVI was found for red spruce relative density ($p = 0.003$) (Table 9).

The third model was used to test effects of eastern hemlock seedling density and total individuals on red spruce seedling density. Significant effects of eastern hemlock seedling density on red spruce seedling density was found ($p = 0.0175$).

The fourth model tested for effects of eastern hemlock seedling density and height on red spruce height. No significant effects were found.

Table 9 Final model testing for effects on red spruce relative density.

Effect	Pr>F
Cucumbertree height	0.8239
Cucumbertree seedling density	0.4119
Red maple seedling density	0.4767
Striped maple height	0.698
Striped maple seedling density	0.4003
Black cherry IVI	0.003
Distance to seed source	0.077

DISCUSSION

The goal of this study was to characterize red spruce regeneration, deepening the understanding of its natural regeneration tendencies. The objective was to identify conditions in a high elevation spruce-hardwood stand in West Virginia that lead to increased red spruce abundance within central Appalachian high elevation stands. In this study, we were able to observe the conditions that favor spruce presence as well as those associated with important red spruce characteristics within an unmanaged, second-growth forest. Spruce regeneration in previous studies has been shown to establish under variable light conditions (Greenwood et al., 2008; Mayfield and Hicks, 2010; Potheir and Prevost, 2008) and respond positively to increases in light availability (Moores et al., 2007; Olson et al., 2014; Rentch et al., 2016). The relationship between spruce seedling establishment and seed source proximity has also been illustrated (Beach and Halpern, 2001; Cavallin and Vasseur, 2009; Hughes and Bechtel, 1997) suggesting higher seedling densities within shorter distances from seed sources.

Results of this study broadly align with findings from previous research and the observations made on our site.

Gap Size Distribution

There are a host of factors that contribute to the average gap size of a location. As stands mature, height and crown size increase. These increases lend to larger canopy openings as trees die from old age or disturbance events (Lorimer, 1989). Due to timber harvest activities up to the early 1900's, a majority of stands in central Appalachia are second and in some cases, third-growth stands. Due to smaller canopies, gaps in second growth forests are on average smaller (Clebsch and Busing, 1989). In red spruce forests, average gaps sizes range from 53.4 m² to 66 m² in second and old-growth stands, respectively (Fraver and White, 2005; Rentch et al., 2010). For this region, our gap size is comparable to some research (Rentch et al., 2010) and smaller on average to others (Himes and Rentch, 2013). Our findings may be attributed to the high proportion of beech gap makers suffering from beech bark disease. These trees experience mortality slowly and die standing. Often, these standing dead trees degrade over time inflicting less damage to surrounding trees thus, effecting smaller areas.

Red Spruce Presence

Red spruce presence significantly increased as canopy cover decreased. At 40, 60, and 80 percent canopy cover the probability of red spruce presence decreased from 95, 80, and 55 percent, respectively (Figure 12). Previous findings have found similar results that seedling recruitment and survival increases within canopy openings (Dumias and Prevost, 2016; Potheir and Prevost, 2008) and using irregular shelterwood management systems (Raymond and Bedard, 2017). Moores et al. (2007) reported sustained red spruce seedling growth responses $\leq 50\%$ canopy cover, while Raymond and Bedard (2017) found that a range of 15-55% transmitted light resulted in increases in reproduction densities and establishment. Results from our study suggest and support

other results that increased light availability, albeit moderate, is optimal for red spruce seedling establishment.

Figure 12 Association between red spruce presence and percent canopy cover.

Gap size was useful in predicting the presence of red spruce seedlings. Gaps averaging 59.5 m^2 were twice as likely to contain spruce seedlings than smaller gaps with a mean size of 26 m^2 . Similar positive associations between gap size and Norway spruce regeneration were also found in Sweden (Qinghong and Hytteborn, 1991). Dumias and Prevost (2016) reported that red spruce seedling densities were higher in small gaps ($<100 \text{ m}^2$) in comparison to large gaps. Results from these studies as well as ours, suggests that increases in light are helpful for establishing red spruce seedlings. Small openings in the canopy may not allow sufficient light levels to reach the forest floor and may close too quickly by way of lateral growth from trees surrounding the gap (Rentch et al. 2010). Conversely, large canopy openings can create unfavorable conditions that may inhibit seedling development and survival by

increased competition and extreme fluctuations in microclimate (Dibble et al., 1999; Dumias and Prevost, 2016; Raymond and Bedard, 2017; Vilhar et al., 2015). A study in Maine (Olson et al., 2014) showed that thinning treatments had significantly greater spruce-fir seedling densities compared to unthinned stands. Several studies suggest that perhaps the most effective way to establish red spruce regeneration is to start with small openings or light thinning of canopy trees, and to gradually increase the disturbed area by reducing overhead canopy as regeneration levels have reached management objectives (Frank and Bjorkbom, 1973; Olson et al., 2013; Raymond and Bedard, 2017; Westveld, 1953)

The weak relationship between red spruce presence and distance to seed source could be caused, in part, by physical barriers. In open conditions, red spruce seed can disseminate to distances of up to 61 m. However, trees in intact canopy positions are likely unable to disperse seed at greater distances due to interference by adjacent tree canopies.

The association between spruce presence and black cherry seedling density and aggregate height was unexpected, and perhaps not clearly explained. While light requirements for each species are different (very shade-tolerant and intolerant), black cherry can initially establish under lower light levels but require substantially more light after year two (Gatchell, 1971). The relationship between the species observed here may simply be a function of the similarity between seedling germination and establishment requirements with regard to light or seedbed moisture. Another possible explanation relates to the palatability of red spruce and black cherry reproduction. Neither species is preferred browse, sparing both species from higher seedling mortality (Horsley et al., 2003; Rentch et al., 2007). This may be useful in determining suitable spruce regeneration locations. Subsequent studies could further explore the relationship between red spruce presence and black cherry reproduction attributes to better understand this association.

Spruce Regeneration Characteristics

Results indicate a positive association with eastern hemlock seedling density on red spruce seedling height. In addition, aggregate height of eastern hemlock was positively

correlated with red spruce seedling densities. These relationships may be explained by the similarities in growing requirements and growth attributes of the two species. Mid-tolerant and shade tolerant tree species exhibit increased growth to increases in light by growing larger crowns resulting in greater leaf area (Jones and Thomas, 2007). As eastern hemlock and red spruce experience release from above (canopy disturbances), they respond by way of height and stem diameter increases (Jones et al., 2008; Rentch et al., 2007). Another explanation could be the eastern hemlock seedling distribution amongst red spruce seedlings. Eastern hemlock could be looked over by deer if seedlings are located within clusters of less palatable red spruce reproduction.

Fast growth rates characteristic of shade-intolerant species often out-compete and overtop slower growing trees, particularly in larger disturbed areas where light is abundant (Whitmore 1989). Our findings on the association of cucumbertree and red spruce seedlings suggest that greater densities and height of cucumbertree can cause a reduction in red spruce seedling density, relative dominance, and relative density. Intuitively this makes sense, as higher proportions of one will result in lower proportions of another, as does height relative to heights of all others.

Gap Type and Aspect Effects

Red spruce was affected by gap type. Red spruce seedlings had higher dominance, aggregate height, and IVI in non-gaps. The low light levels under closed canopy conditions are within red spruces shade tolerance, but a limiting factor to many competing shade intolerant species (Mayfeild and Hicks, 2010). The reduction of competition makes greater resources available to seedlings such as moisture, nutrients, and growing space (Couwenberghe, et al., 2010; Denslow, 1980; Grey et al., 2002). Conditions found under closed canopies offer ideal microclimates that in effect buffer red spruce seedlings from temperature extremes and water stress. This paired with red spruces ability to persist in low light conditions (Hart, 1969; Korstain, 1937) allows for more crown and root development, albeit slowly. It is also possible that gaps where large reproduction was reported, had experienced a prior release event (Wu et al., 1999). A canopy opening would have enabled seedlings to develop into advanced regeneration. While it is likely other species also colonized the gap during that time,

intolerant and mid-tolerant species experienced mortality following crown closure (Prevost and Raymond, 2012). The presence of advanced red spruce reproduction would suggest that management should be conducted in that location to further advance spruce into upper canopy positions.

Gap Age

Gap age showed no effects on red spruce attributes despite the detection of canopy release in growth ring observations. Mean gap age and range track other results for this forest type despite differences in age class distributions (Rentch et al. 2010). However, Rentch et al. (2010) reported higher frequencies in the 1-5 and 6-10 year gap age classes and lower occurrences of gaps over 25 years old. In contrast, results from this study show much lower occurrences of younger gaps and a higher frequency of older gaps. Within gaps, the variability of release dates between cores, or the lack of multiple cores for comparison made dating difficult in some cases. Gap age was determined using a combination of three methods that were not always in agreement. In these cases, position within the gap, species, and tree age were used to help make age determinations. Release detection methods using ten-year averaging approaches present issues in detecting releases that have occurred within the most recent ten years. The lack of association between gap age and red spruce reproduction in this study, do not offer insight into management intervals or frequency.

CONCLUSION

For forest managers, with goals to increase red spruce reproduction, management plans should be developed based on site-specific attributes. Red spruce on this central Appalachian high elevation site showed some patterns regarding natural seedling establishment and distribution. Gaps play an important role in natural red spruce regeneration. Red spruce reproduction was taller and showed higher importance on average, under closed canopy conditions due to reduced competition.

Gap size showed to be the most important factor in predicting the presence of red spruce. Small gaps, were significantly less likely to contain red spruce reproduction than large gaps.

Proximity to seed source may also be a contributing factor to red spruce presence. Distances within 15 m are increasingly likely to contain spruce seedlings at higher densities and greater relative dominance. Broadly, larger gaps located within a close distance to seed sources show potential for greater red spruce regeneration.

Relationships between red spruce reproduction characteristics and other species appeared to arise. The occurrence of higher black cherry seedling density and height may indicate suitable conditions and potential locations for red spruce regeneration. The probability of red spruce presence was higher in areas where black cherry is found, possibly because of a result of similar initial growth requirements shared by both species, because of reduced palatability, or a matter of coincidence. In addition, positive associations between eastern hemlock seedling densities and height and red spruce density and height seemed to emerge, similar to the relationship between black cherry and red spruce.

Cucumbertree seedling density and height appeared to negatively affect red spruce regeneration. Red spruce relative density and relative dominance decreased as cucumbertree density and height increased. Cucumbertree exhibits fast growth and has high light requirements, giving it the ability to outnumber and overtop smaller red spruce seedlings.

Management Strategy

Frank and Bjorkbom (1973) suggested that adequate stocking for spruce requires a minimum of one spruce on at least half of the plots sampled. This stand contained spruce on 49% of the total sample plots. The presence of gaps seems to be a primary driver of red spruce stocking, particularly gaps at least 59.5 m² within 15 m from a seed source. From a management perspective, gaps or overstory partial harvest replicating similar scope or intensity should be implemented to accelerate spruce regeneration. Maintaining partial shade by keeping or creating gap sizes of approximately 59.5 m², overstory partial harvest that retains between 30-65 percent canopy cover or a combination of these should limit shade intolerant tree and ground cover from inhabiting these management areas. Harvesting in this way will buffer potential and existing regeneration from environmental extremes by maintaining the critical microclimates that

red spruce regeneration requires. Sites selected for management should either contain established advanced red spruce regeneration, or contain sufficient black cherry and/or eastern hemlock regeneration within 15 m from an existing seed producing red spruce. Alternatively, existing gaps containing advanced red spruce regeneration could be expanded by thinning a desired area surrounding the gap. This expanding gap approach should be repeated as adequate stocking is reached to mimic the current area in canopy gaps (7%). The scope and intensity of harvesting should be dictated by harvesting cost and mimicking the current natural process existing on the desired management site.

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