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Detecting Balsam Woolly Adelgid Infestations Using Tree Rings

Morgan Leef

Thesis submitted to the West Virginia University Eberly College of Arts and Sciences in partial fulfillment of the requirements for the degree of

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Keywords: Balsam woolly adelgid, Dendrochronology, rotholz, traumatic resin canal, growth surge, defoliation, physiological drought

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Abstract

Detecting Balsam Woolly Adelgid Infestations Using Tree Rings

Morgan Leef

Balsam woolly adelgid (BWA), *Adelges piceae*(Ratzeburg), is a sap-sucking, exotic invasive insect that arrived in North America from central Europe around 1900. Since then, its range has expanded from New Brunswick, Canada to the southern Appalachian Mountains. It is a threat to all North American true-fir species, but populations can be controlled by cold continental winters. Adelgid feeding leaves noticeable traces on the wood tissue (“rotholz”) and causes a temporary positive radial growth response among affected trees. The purpose of this research was to determine dates of initial outbreaks, balsam fir radial growth change during outbreaks, and the relationship between cold winter temperatures and BWA outbreaks in the highlands of West Virginia. I used these two indicators on the wood tissue collected from tree cores from 14 balsam fir stands (*Abies balsamea*) and compared them to that of red spruce (*Picea rubens*) trees growing nearby. I also compared infestation dates with local climate records, to ascertain the relationships between infestations and winter air temperatures. I observed rotholz in 28% of the trees in all stands with the earliest evidence of occurrence at Upper Tract in 1952, four decades before BWA was first observed by the US-Forest Service at a Tucker County seed orchard. Using a host vs non-host model, I observed increases in growth caused by infestations particularly in 1987-1995 and 1998-2005. These periods are also periods of high rotholz occurrence. Periods of reduced infestation, as evidenced by normal or reduced growth and less rotholz, tend to occur following exceptionally cold winters. My results suggest that future monitoring of BWA should include tree core sampling for rotholz and growth increases in addition to exterior evaluation of trees. My results also suggest that as winters continue to warm, infestations may become more frequent and more severe.

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Introduction

Invasive species reduce biodiversity and incur costs on local economies (Pimentel, Zuniga, & Morrison, 2005). They cost the United States an estimated \$120 billion annually, and the cost of invasive insects likely exceeds \$4 billion a year (Pimentel et al., 2005). Exotic invasive insects not only destroy food crops, they threaten to eradicate many tree species in the United States, including species of ash, hemlock, spruce, and true fir. In the highlands of West Virginia, balsam fir (*Abies balsamea*) is currently threatened by balsam woolly adelgid (BWA, *Adelges piceae* Ratz.), an exotic invasive native to central Europe.

BWA likely crossed the Atlantic into North America via shipping around 1900, and entered southeastern Canada through Newfoundland and New Brunswick (MacAloney, 1935 and Balch, 1934). It has since expanded its range. By the early 1950s, BWA had spread from Maine to Vermont, New York, New Hampshire, Pennsylvania, West Virginia, Virginia, North Carolina, and Tennessee (Amman & Speers, 1965). In a separate incident around 1929, it was introduced on the west coast of the United States, notably in Oregon, Washington, and Idaho. On the west coast, BWA attacks pacific silver fir, grand fir, and subalpine fir. In southern Appalachia, the first infestation was recorded in 1955 at an unspecified location (Amman & Speers, 1965; Hain, 1988). The first detailed recording of infestation was reported in Canaan Valley in a seed orchard in 1992 (Amman & Speers, 1965; Cherefko, Fridley, Medsger, Woody, & Anderson, 2015).

In the primarily deciduous forests of eastern North America there is limited conifer cover, which makes balsam fir populations ecologically valuable. Balsam wood is often harvested for light framing construction, and is an important pulp wood resource (Bender, 1967). The resin that is

extracted from “blisters” on balsam fir bark has been used as an antiseptic in the past, and has been important in the manufacture of microscopic glass slides (Bender, 1967; IUCN, 2011). Balsam fir buds are an important winter food source for large mammals such as white-tailed deer in the United States, and moose in the northern United States and eastern Canada (Peek, 1974). Smaller mammals such as mice, voles, and squirrels also feed on seeds and buds (Cherefko et al., 2015).

Balsam fir mortality from BWA is caused by the chemical reaction that occurs because of balsam woolly adelgid feeding on the bole and the crown (Balch, 1934, 1952). Host trees typically respond to feeding by producing thicker bark, large-abnormally shaped cells, thick traumatic resin canals, and discolored wood tissue (Balch, 1952; Hain, 1988). The production of these abnormally large cells results in larger than normal ring widths and create large, dark colored annual rings, referred to as “rotholz” or redwood, for the duration of feeding. Rotholz tissue reduces the permeability of tracheid cells and inhibits the movement of water and nutrients through the stem and branches, simulating physiological drought (Balch, 1952; Greenbank, 1970; Hain, 1988). Infestation leaves noticeable damage around the feeding site, and as the tree continues to add annual rings, these scars remain. The intensity of infestation is dependent on geography and climate, as the adelgid can potentially reproduce year-round in warm and humid climates (Balch, 1952; Greenbank, 1970). Reproduction and population expansion are limited by cold winter temperatures (Amman, 1967; Balch, 1952; Greenbank, 1970).

The purpose of this study was to determine when balsam fir first showed signs of BWA infestation in the highlands of West Virginia, and to quantify the combined stresses of BWA and climate change on balsam fir populations. To accomplish this, I examined tree ring samples from balsam fir for damaged wood tissue and changes in radial growth patterns. West Virginia’s

balsam fir is co-dominant with red spruce in most stands. This allowed me to use red spruce as a non-host reference to compare radial growth patterns between spruce and balsam fir trees.

Research Questions

1. When did balsam fir first show signs of BWA infestation in West Virginia? Were trees from Canaan Valley and the sites in Pocahontas/Randolph counties infested during the same period? I hypothesized that:
 - a) Rotholz and abnormal cells, both definitive indicators of the presence of BWA, would be present on growth rings that formed prior to 1992.
 - b) Balsam fir ring width series would deviate from the patterns of red spruce after suspected outbreaks prior to 1992.
2. Have changes in winter temperatures since 1980 in the highlands of West Virginia allowed larger populations of BWA, causing longer periods of reduced radial growth in balsam fir? Based on PRISM climate records from 1980 to 1992, I hypothesized that:
 - a) Winter temperatures in the highlands of West Virginia were too cold to allow large overwintering BWA populations in years prior to 1992.
3. Do current monitoring techniques adequately quantify the extent of infestations and the timing and severity of BWA infestations? I hypothesized that:
 - a) Visually estimating BWA population sizes on the exterior of trees is not adequate to assess the extent of BWA infestation.

Balsam Fir (*Abies balsamea*)

Balsam fir (a.k.a. Canadian fir, Eastern fir, Canadian balsam) is one of two true fir species found in eastern North America, the other being Fraser fir (*Abies fraseri*), which replaces balsam fir in the highlands of North Carolina and Tennessee (Bakuzis, 1965; Balch, 1952). Balsam fir is the most widely distributed fir in North America, and makes up a large proportion of Canada's boreal

Figure 1: Balsam fir's range in North America. (Little's range)

forests (Balch, 1952; Hain, 1988). Balsam fir is most abundant in New England and southeastern Canada, but there are isolated stands in Iowa, Minnesota, and southern Appalachia. Its southernmost populations extend into the highlands of West Virginia and Virginia, before it is replaced by Fraser fir farther south. Balsam fir has retreated north over the last 10,000 years, and some have suggested that the southern remnants are relicts of the Pleistocene glaciation (Bakuzis, 1965; Jackson et al., 2000; Myers & Bormann, 1963; Oosting & Billings, 1951; Robinson & Thor, 1969). In West Virginia, balsam fir grows mainly in Tucker, Randolph, Pocahontas, and Grant counties (Core, 1934; Fulling, 1936). West Virginia's balsam fir are genetic variations of the northern balsam fir found in Canada and New England, and are sometimes referred to as Canaan fir (Stephenson & Adams, 1986). There is an ongoing debate as to whether the balsam fir in West Virginia is a genetic hybrid (*Abies intermedia*) between the balsam fir of New England and the Fraser fir of the mountains in North Carolina (Bakuzis, 1965; Core, 1934; Fulling, 1936).

Balsam fir grows best in cool areas, where there is abundant moisture. Optimal growth occurs in its range in eastern Canada, where it enjoys a mean annual temperature of 2-4° C, and 150-620

mm total annual precipitation (Bakuzis, 1965). For this reason, it can only be found at higher elevations in the south. Seedlings and mature trees experience excessive mortality if temperatures exceed 46-54° C, or if there is prolonged drought. Balsam fir typically does well in both organic and inorganic soils that form as a result of glaciation, usually including soils from the acidic Histosol, Inceptisol, and Spodosol orders. These soils have well defined A-horizons, and usually have a gray color, caused by leaching. They are commonplace in regions with ample precipitation, cooler temperatures, and abundant conifer populations (Fowells, 1965; Frank & Bjorkbom, 1973). In addition, balsam fir is a shade tolerant species, and can grow well under thick canopies. When growing in close proximity with red spruce, success may be limited by factors such as soil fertility, climate, and age. Competition will be strong in thickets of fir trees, or when growing adjacent to shade tolerant hardwoods (Frank & Bjorkbom, 1973).

Tree height ranges from 12-20 m, with a maximum diameter of 30-50 cm, and trees can live up to 200 years. Balsam fir has a narrow root system, and is highly susceptible to wind (Fowells, 1965). Balsam fir can easily be identified by its needles and cones (fir cones point towards the sky and do not hang like spruce or pines), which is a characteristic that is unique to true firs. Balsam fir can be differentiated from other fir species by its unique “blistered” bark (not always a reliable indicator, as bark varies from tree to tree). Fraser fir cones have bracts that protrude beyond the edges, while balsam fir cones do not (Bakuzis, 1965; Myers & Bormann, 1963).

On average, trees begin to produce seeds after about 20-30 years, though there have been recorded instances where trees as young as 15 years produced seeds (and even younger in some cases where the trees were only 2 m in height) (Bakuzis, 1965). Seed production cycles 2-4 years, and each cone will have approximately 135 seeds. Seed-fall begins in late summer, and peaks in early to mid-fall, and can continue throughout the winter. The age of the tree may

influence the viability of germination. A study in Michigan found that trees aged around 40 years produced seeds that were most likely to germinate, while older trees tended to have less germination (Fowells, 1965). Moisture and available light influence seed germination as well, but moisture is far more important.

Fir is not typically prized for structural integrity of its lumber, though it is commonly used in light framing construction. It has softer wood, and is susceptible to rotting (Ross & Service, 2010). However, it is a valuable wood pulp resource, and its resin is used in the manufacture of many products (*Paper*, 1918; Ross & Service, 2010). Before synthetic optics, balsam fir resin was invaluable in the manufacture of transparent epoxy and cement used in the manufacture of military optics and microscope mounting resin, and continued to see limited use into the 1960s (Bender, 1967). Balsam fir buds are an important winter food source for large mammals such as white-tailed deer in the United States, and moose in the northern United States and eastern Canada. Smaller mammals such as mice, voles, and squirrels also feed on seeds and buds. Certain species of hare use it as low-level cover, and beaver often use it in dam building (Cherefko et al., 2015).

Balsam Woolly Adelgid (*Adelges piceae*) - (Ratzeburg)

Figure 2: Image from (Ragenovich & Mitchell, 1966) – Ventral view of BWA in crawler stage.

Figure 3: BWA in dormant neosistentes stage. Photo acquired from <https://www.flickr.com/photos/sanmartin/31434461584/>.

BWA prefers to colonize true firs, and these species have varying susceptibility to BWA. In its native European forest ranges, adelgid feed on silver fir (*Abies alba*), which has coevolved and developed a resistance to the insect, and is not seriously harmed by it (Balch, 1952; Varty, 1956). The southernmost range of BWA in the United States is in the mountains of North Carolina and Tennessee, where it feeds on the most susceptible of the true firs, Fraser fir. In West Virginia, BWA's range consists of the highlands found in the Canaan Valley Wildlife Refuge, and the Monongahela National Forest, where it feeds on balsam fir.

North American BWA is a wingless, soft bodied, waxy insect that is not easily visible to the naked eye, with an overall length of 0.4 mm (crawler) to 0.8 mm (adult) (Balch, 1952). Adults typically have a purple or black color and are spherical in shape. Every year, adults produce the white woolly material, that surrounds its body, and some 100-250 amber colored eggs.

Depending on temperature, BWA can produce up to four new generations of offspring in a single year (from March to early November) (Balch, 1952; Greenbank, 1970; Hain, 1988). Current

temperatures in its range in southern Appalachia allow for 2-3 new generations annually, with more possibly at lower elevations (Amman & Speers, 1965).

Under native conditions in Europe, Adelgidae occur in five different forms, with a polymorphic lifecycle that occurs on both spruce and other conifers, but here in North America, the form that occurs on the primary host is not present (Balch, 1952). The primary host is always spruce, and other conifers (*Abies*, *Pinus*, *Tsuga*) are secondary hosts. The first form, *sexualis*, is a wingless, bisexual form that usually produces one egg on the primary host. Upon hatching, the *fundatrix*, the next wingless agamic form that overwinters on the primary host, then produces the *gallicola migrans*. The *gallicola* form then migrates to the secondary host, where it produces the *exsulis* or the *exsulis progrediens*. The *exsulis* form spawns the winged *sexupara*, that flies back to the primary host, to restart the cycle (Balch, 1952). In North America, BWA is anholocyclic, and all forms occur on the secondary host. Without the primary host, there are no winged males to complete the lifecycle, therefore North American populations of BWA are entirely female. The winged morph does occasionally occur but is exceedingly rare and cannot reproduce. As a result, North American BWA reproduce parthenogenically, where offspring are genetically identical to the parents. This means every individual can reproduce, with up to 250 eggs per individual. Populations grow exponentially, enhancing their ability to spread more rapidly. This can be advantageous for conservationists interested in combating BWA, because it is unlikely that North American BWA will ever develop a resistance to pesticides.

In North America BWA has several morphs in its lifecycle (all occur on *Abies*), and can overwinter during any of these stages (survival during certain stages depends upon temperature) (Balch, 1952). After hatching, the crawler emerges and has eyes, legs, and mouth parts (stylet). There is often confusion as to whether BWA is an *adelgid* or an *aphid*, but its lifecycle and lack

of mobility when feeding characterizes it as an adelgid. Aphids are free to move continuously around on the plant as they find different feeding positions, whereas adelgid are restricted once their stylets have been inserted (Greenbank, 1970). During the crawler stage, the adelgid is mobile and must find a suitable location to feed. Once it has found a suitable location, it will spend the rest of its life there. BWA are distributed and dispersed by wind, birds, small mammals, and by the transportation of wood products and firewood. Dispersal occurs during the egg and crawler stages, since adelgid cannot re-establish themselves after inserting their stylets. Once a suitable feeding location is found, the adelgid inserts its stylet and begins to feed. It is at this stage that BWA begins to produce the white woolly material to protect itself and begins to lay eggs. At this point, the adelgid enter the *neosistentes* stage, the only stage that can survive prolonged freezing winter temperatures. Individuals in any stage can survive below 0° C or higher, but individuals in the pre-dormant stages will die gradually in temperatures below 0° C and instantly in temperatures of -20° C (Amman, 1967; Balch, 1952; Greenbank, 1970). If larvae and crawlers are present below the snowline, they may survive in temperatures slightly lower than freezing. Adelgid that infest the crown are more vulnerable to cold temperatures, while adelgid that infest the trunk have several means of protection including snow and crevices in rough, rigid bark (protects against wind). Adelgid in the dormant stage can survive in temperatures below this if they are only exposed to these temperatures for short periods of time. *Neosistentes* have been known to survive temperatures of -40° C, but mortality was about 80% (Balch, 1952). For these reasons, long and harsh winters can limit population density and distribution (Balch, 1952; Berryman, 2013; Greenbank, 1970).

Impacts and Effects of BWA on Balsam Fir

The susceptibility of balsam fir to BWA varies regionally. Studies conducted in southeastern Canada and southern Appalachia suggest that BWA affects maritime and continental stands differently (Balch, 1934, 1952; Greenbank, 1970). This includes the intensity of infestation, the degree to which BWA spreads and reproduces, the rate of dispersal, the causes of tree mortality, and even the sustainability of stand populations of both hosts and BWA. The most important factors are minimum temperatures, and tree size. The size of the stand affects what part of the tree tends to be most severely infested, and this in turn determines how the tree reacts, and how long it takes to die or recover from infestation (Balch, 1952; Greenbank, 1970).

BWA infestation is typically present in both the crown and the stem of the host, and larger diameter trees are more likely to be heavily infested (Greenbank, 1970; Hain, 1988). Infestations in Fraser fir are typically concentrated on the bole, while for balsam fir, they are more concentrated in the foliage. Trunk infestations cause several responses from the host. When a crawler inserts its stylet, it salivates into the hosts bark, and it generates a hormonal response, causing abnormal cell division. The host also releases nutritious hormonal compounds, which makes the tree more suitable for feeding temporarily, and BWA populations increase more rapidly after the initial invasion. The abnormal cell division results in the formation of large parenchyma cells in the bark, and the cambium stimulates and produces excess phloem (Balch, 1952; Greenbank, 1970). This results in abnormally wide annual rings widths, large swollen cell walls, a larger proportion of late-wood, short and rounded tracheids surrounded by intercellular spaces, and higher lignin content, excess ray tissue, and resinosis (Balch, 1934, 1952; Hain, 1988; Mitchell, 1966; Smith, 1967). The abnormal tracheid cells that form are recognized as rotholz (German for redwood), which collectively form tissue with noticeable reddish/brown

color, and resemble compression wood (Figure 4, Figure 8)(Balch, 1952; Mitchell, 1966; Smith, 1967; Westing, 1968). Rotholz is almost always present around a feeding site, but is not always visible on the wood (Hain, 1988). The color can range from light to dark brown and is sometimes barely noticeable by the naked eye. These dense cells inhibit the conduction of water and nutrients through the xylem and phloem tissue and make the trunk brittle, making the tree more susceptible to wind damage or physical stress. Resin ducts may also form around the insertion point of the insect's stylets, where the number and size of parenchyma cells increases (Balch, 1952; Hain, 1988). After about a year, purple cork cells form around the parenchyma cells, and the parenchyma eventually disintegrates, and the void is filled with resin. Bark hardening also provides a temporary defensive barrier against infestation, because the bark becomes too hard and thick for adelgid to insert their stylets (Balch, 1952; Greenbank, 1970). In the branches and foliage, adelgid feeding results in what is referred to as gouting (Figure 5, Figure 6, Figure 7), where nodes and twigs become swollen after abnormal cell formation (Balch, 1952). When the nodes experience gouting, growth and needle production is curtailed, defoliation occurs, terminal growth is stunted, and the tree can effectively be starved to death, though this process can take years. In some cases, trees have been infested for 24 years before finally dying (rotholz was traced back 24 years, followed by narrow rings) (Balch, 1952).

Figure 4: Illustration of rotholz (red wood) from (Ragenovich & Mitchell, 1966)

Figure 5: Illustration of abnormally large cells with swollen cell walls causing gouting in nodules. (Balch 1952)

Tree morality from bole and branch infestation varies from stand to stand. Infestation in the crown causes a fiddle shape in the terminal leader of the tree, signaling stress. Infestation in mature trees is thought to reduce cone and seed production after 20-30 years, because buds are suppressed and cones may contain fewer seeds (Balch, 1952). Heavily infested trees may eventually become stressed to the point where they can no longer support large infestations, and mortality may occur about one year after the adelgid die off, if the damage has been severe. BWA is not only less likely to infest smaller diameter trees, but may be less lethal to smaller trees as well (Balch, 1952). Infestations are less common in trees younger than 15 years, and

*Figure 6: An example of branch gouting.
(Photo taken on the Balsam Fir Trail at
Canaan Valley Resort by Morgan Leef)*

*Figure 7: Gouting at the end of a twig. Photo
by: Jean-Paul Laplante, Natural Resources
Canada, Canadian Forest Service, Laurentian
Forestry Centre.*

more common for trees that are 25-35 years old (Balch, 1952; Greenbank, 1970; Mitchell, 1966). Adelgid populations are particularly dense on rapidly growing dominant and co-dominant trees, since vigorous trees provide more nutrients for the adelgid (Balch, 1952; Smith, 1967). After infestations, researchers found that host trees could recover from any extent of infestation (Amman & Speers, 1965; Balch, 1952).

Figure 8: Comparison of healthy (left) vs compressed (right) xylem tissue in grand fir, which shares the same effects as balsam fir. Note the rounded, thick walled cells. (Mitchell, 1966)

Dendrochronology

Dendrochronology involves analyzing information obtained from cross sections and core samples extracted from woody plants, by observing patterns in annual growth rings, and assigning dates to each individual growth ring, to form a series (Fritts, 1971). Series from multiple trees can be crossdated by comparing the variability in the ring-widths (Douglas, 1941).

Crossdating also allows the identification of false and partially absent rings (H. Fritts, 1971). Different variables affect the width of tree rings, including but not limited to climate, competition, moisture, local environmental factors, and the presence of endogenous and exogenous disturbance (Fritts & Swetnam, 1989; Fritts, 1971). Using tree ring widths and other ring properties, dendrochronologists have reconstructed past climate, fire history, and other historical events. Trees with more variability in ring widths are considered more sensitive, which usually includes trees growing at their ecological limits (H. Fritts, 1971). In temperate regions, these studies may become more difficult, as the rings may be more complacent (Stokes & Smiley, 1996).

Dendroecology, a sub-discipline of dendrochronology, utilizes dendrochronology to analyze the history of ecological processes. In this sub-field, researchers are concerned with different disturbances or temporal aspects of forest dynamics and how they affect tree ring-widths. Studies of disturbance caused by tree pathogens often employ a host vs non-host model. By comparing the growth rings between host and non-host tree species, it is possible to distinguish growth patterns influenced by climate, and growth patterns influenced by defoliating insects (Nash III, 1975; Swetnam & Lynch, 1989). This method was first used to study the effects of air pollution on tree growth by Nash *et al.*, but has since been used to study insect outbreaks.

$$R = \frac{SD_h}{SD_{nh}} (INDEX_{nh} - MEAN_{nh})$$

$$C = INDEX_h - R$$

R = rescaled index value for each year of the non-host series

SD = standard deviation for (nh – non-host) and (h – host) series

$INDEX$ = each index value of host and non-host

$$MEAN_{nh} = \text{mean of non-host series}$$

$$C = \text{corrected value for each year of host series}$$

This approach assumes that host and non-host species show similar responses to factors like climate. Under this premise, the non-host species should display normal or expected growth patterns, whereas the host species may not, allowing a comparison and detection of reduced, or in some cases, enhanced growth caused by the defoliating insect.

Climate Influence on Growth

Balsam fir is co-dominant with red spruce in most stands in West Virginia, and the two species show similar responses to temperature and precipitation. In Maine, Vermont, New Hampshire, New York, Pennsylvania, West Virginia, and Virginia, balsam fir is codominant with red spruce at high elevations, and Fraser fir shares the same role in North Carolina and Tennessee. Spruce-fir forests and their response to changing climate has been extensively studied in the past century, though results have been ambiguous. Studies conducted on spruce-fir stands in North Carolina (Grand Father Mountain/ Mt.Mitchel), New York (Whiteface Mountain), and Massachusetts found that red spruce and codominant firs have seen several periods of decline and recovery in the past century in response to climate change, air pollution, and tree pathogens (Johnson, Cook, & Siccama, 1988; Koo, Patten, Teskey, & Creed, 2014; McLaughlin, Downing, Blasing, Cook, & Adams, 1987; Ribbons, 2014; Scott, Siccama, Johnson, & Breisch, 1984; Soulé, 2011). In eastern North America, red spruce and the two-fir species of the region (balsam and Fraser fir) share similarities in their response to temperature at elevations above 900 m (Goelz, Burk, & Zedaker, 1999; McLaughlin et al., 1987; Oosting & Billings, 1951; Soulé, 2011).

Spruce-fir studies conducted in the northeast and southeast usually agree that spruce-fir stands were experiencing a decline in radial growth starting about 1960 and through 1980 (Goelz et al., 1999; Johnson et al., 1988; Scott et al., 1984; Soulé, 2011). The point of contention seems to be why spruce-fir stands have been in decline, and whether they still are and will continue to be in decline. Studies conducted by Siccama, Stephenson, Cook, and Adams concluded that spruce-fir species (particularly red spruce) decline unequivocally occurred from 1960 to 1980, because of atmospheric deposition of nitrogen and sulfate pollutants and a multi-year drought in the northern Appalachian Mountains (Johnson et al., 1988; McLaughlin et al., 1987; Stephenson & Adams, 1986). High concentrations of lower atmospheric ozone were also hypothesized to have a negative effect. They observed that red spruce basal area estimates in New York declined about 40-60% at high elevations (>900 m), and 60-70% at lower elevations (<900 m), while balsam fir basal area declined around 35% at higher elevations and was unchanged at lower elevations (Scott et al., 1984). Another study conducted by Johnson, Cook, and Siccama concluded that this could also have been the result of climate change, more specifically warmer, longer summers and earlier, colder winters (Johnson et al., 1988). The loss of codominant firs has also been attributed to red spruce decline, but this only causes mortality from exposure to wind, and not a decline in radial growth (Busing, 2004; Goelz et al., 1999; McLaughlin et al., 1987).

A more recent study conducted by Koo et al. (2014) suggests that after 1980, red spruce radial growth began to increase as temperatures increased, and atmospheric nitrogen and sulfate compounds decreased. In the Smokey Mountains in Tennessee, Koo et al. reported red spruce radial growth at high elevations (>1700 m) decreased by 10.8% when climate change interacted with a 10% increase in air pollution and increased by 8.4% with a 10% decrease in air pollution. At lower elevations (<1700 m), red spruce radial growth decreased 11.2% with a 10% increase in

air pollution, decreased by 8.9% with no change in air pollution, and decreased by 6.4% with a 10% reduction in air pollution. In agreement with Koo et al., Soulé 2011 observed that radial growth in red spruce increased from 1980 to 2007 at Grandfather Mountain, North Carolina. Soulé found that red spruce radial growth was significantly related to temperature, particularly minimum temperatures. Red spruce radial growth was positively correlated with increases in temperature, negatively correlated with days without precipitation, positively correlated with increases in atmospheric CO₂, and negatively correlated with increases in atmospheric nitrogen and sulfur pollutants (Soulé, 2011). Soulé concluded that Grandfather Mountain's annual temperature had increased by about 1.4° C since 1957, and that in combination with increased atmospheric pollution restricted red spruce growth until about 1980. After 1980, red spruce radial growth increased when those pollutants began to decrease in the atmosphere (Soulé, 2011). Goelz et al. observed similar results at Mount Rogers in Virginia, and Mount Mitchel in North Carolina (Goelz et al., 1999).

Ribbons (2014) conflicts with almost all the other studies, as she observed a negative trend in red spruce radial growth in the past three decades at lower elevation stands in Massachusetts. She found that red spruce radial growth had decreased between 1960 and 1980, but due to a multi-year drought and increasing temperatures (Ribbons, 2014). She also found that spruce radial growth had been positively correlated with precipitation before 1960, and negatively correlated after 1960 (presumably because of nitrogen and sulfate deposition). Her observations deviate from other studies, as she continued to see a decrease in radial growth after 1980, when atmospheric nitrogen and sulfate compounds decreased in the atmosphere. It is also worth noting that hardwood species like red maple (*Acer rubrum*), American beech (*Fagus grandifolia*), and yellow birch (*Betula alleghaniensis*) began to increase in importance as red spruce and balsam fir

decreased in importance, because those species are also present at balsam fir stands in West Virginia (Ribbons, 2014).

<i>Study</i>	<i>Location</i>	<i>Date Covered</i>	<i>+Temperature</i>	<i>Drought</i>	<i>+CO₂</i>	<i>+NO₂</i>	<i>+SO₂</i>	<i>+O₃</i>	<i>Exposure</i>
<i>Ribbons 2014</i>	Western Mass.	1960-2010	-	-	+	-	-	-	NA
<i>Goetz et al.</i>	Mt. Mitchell/Mt. Roger	1960-1998	+*	-	NA	-	-	-	-
<i>Stephenson & Adams</i>	West Virginia & Virginia	1960-1985	-	NA	NA	-	-	NA	NA
<i>Koo et al.</i>	Great Smoky Mountains	1960-1999	+*	-	+	-	-	-	NA
<i>Souté 2011</i>	GFM, North Carolina	1956-2007	+	-	+	-	-	-	NA
<i>McLaughlin et al.</i>	New York, New Hampshire, Vermont	1780-1985	-	-	NA	-	-	-	-
<i>Johnson et al.</i>	New York	1957-1981	-	-	NA	-	-	-	-
<i>Mathias & Thomas</i>	West Virginia	1900-2014	+	NA	+	-	-	NA	NA

*Table 1: Previous studies and their proposed causes of recent spruce-fir decline since 1960. A “+” indicates that the variable had a positive relationship with radial growth, and a “-” indicates that the variable had a negative relationship. *This was only true for stands at high elevations.*

In West Virginia, spruce-fir stands and their relationship to climate have been studied less, but there is documentation up to 2014. Stephenson and Adams observed that while balsam fir and red spruce radial growth decreased with increasing temperature, this was only true for trees at higher elevations (Adams, Stephenson, Blasing, & Duvick, 1985; Stephenson & Adams, 1986). In a more recent study, Mathias and Thomas observed an increase in red spruce basal area

increment as atmospheric SO₂ and NO_x decreased, and atmospheric CO₂ increased (Mathias & Thomas, 2018).

Methods

Study Area

The study area includes Canaan Valley, Dolly Sods, and the highlands of Randolph and Pocahontas Counties along the Alleghany Front in West Virginia. The study area is also completely contained within three of the four ranger districts in the Monongahela National forest (~ 371,906 ha), which is the largest expanse of public land in West Virginia, and spans several counties, primarily Greenbrier, Grant, Nicholas, Pendleton, Pocahontas, Randolph, Webster, and Tucker counties, with small sections in Preston and Barbour Counties (USDA, 2006).

Figure 9: Location of all balsam fir/red spruce chronologies in Canaan Valley, West Virginia. Every point represents one site where balsam fir and red spruce samples were collected. The inset map shows the location of the study area in West Virginia.

Canaan Valley (Tucker County, West Virginia) includes an estimated area of 14 ha, and resides in the highlands of the Cheat-Potomac Ranger District of the Monongahela National Forest,

where elevation ranges from 900-1000 m (Figure 9). Annual mean temperatures range from 2.2 - 14°C, and the area receives an average of 143 cm of precipitation per year (1980-2017) (PRISM Climate Group, 2011). It consists of wetlands and bogs that are drained by the Blackwater River. The valley is underlain by the sedimentary rock of the Greenbrier limestone, Pottsville sandstone, and Mauch Huck shale (WVGES 1968). The valley's wetland are also the largest inland freshwater wetland in the eastern United States (Fortney & Rentch, 2003). The late 19th and early 20th centuries saw widespread clear cutting and timbering, as well as massive burns, altering this unique ecosystem (Allard & Leonard, 1952). There was also a period of widespread livestock grazing that may have inhibited forest re-establishment in many areas. The sites in the southern region are located throughout the highlands of Pocahontas and Randolph Counties, in the Greenbrier and Marlinton-White Sulphur Springs Ranger Districts, where annual mean temperatures range from 1.7 to 13.7°C, and the area receives about 125 cm of precipitation annually (1980-2017) (PRISM Climate Group, 2011).

The highlands of Pocahontas and Randolph Counties once supported one of the most impressive ranges of fully grown spruce forests in North America, and perhaps the world (Allard & Leonard, 1952). Like much of West Virginia, the area was extensively logged in the 1880s. (Carvell, 1965). The establishment of the National Forest in 1920 was an attempt to counter the negative effects of this clearing, (i.e. sediment pollution of rivers, and deforestation) (Allard & Leonard, 1952). Beginning in 1930 the Civilian Conservation Corps were tasked with restoring forests and spruce and pine seedlings were replanted throughout the region (Carvell, 1965; Fortney & Rentch, 2003).

Most of the balsam fir stands sampled are close to roads, towns, or hiking trails, 10 of which are natural stands, and four are planted. The stands range from swamps to forests, and in some cases meadows, and have similar vegetation. The fir trees typically occur with several other tree and shrub species including yellow birch (*Betula alleghaniensis*), black cherry (*Prunus serotina*), black ash (*Acer negundo*), quaking aspen (*Populus tremuloides*), eastern hemlock (*Tsuga canadensis*), red spruce (*Picea rubens*), dotted hawthorn (*Crataegus punctata*), speckled alder (*Alnus incana*), choke cherry (*Prunus virginiana*), and occasionally sugar maple (*Acer saccharum*) (Bartgis, Byers, Fortney, Grafton, & Berdine, 2015; Bonner, Anderson, Rentch, & Grafton, 2009; Fortney & Rentch, 2003).

There are recorded BWA outbreaks in West Virginia dating back to 1955, but they do not detail the exact location, or the extent of the outbreak. In Canaan Valley, the first documented outbreak was detected by residents and confirmed by entomologists in 1992.

Figure 10: Location of all balsam fir/red spruce chronologies in Randolph and Pocahontas counties. Every point represents one site where balsam fir and red spruce samples were collected. The inset map shows the location of the study areas in West Virginia.

Lab and Field Methods

Sampling and Data Collection

I sampled a total of 14 balsam fir stands (4 planted and 10 natural) distributed across Tucker, Grant, Pocahontas, and Randolph counties in 2017 and 2018 (Figure 9 & 10, Table 2). All stands are located on property owned by CVNWR, Canaan Valley State Park, or the Monongahela National Forest. Four of the sites have been actively monitored for BWA infestation by the USDA Forest Service since 2014. At these sites, the Forest Service tagged up to 30 balsam fir trees >10 cm DBH, and I sampled their tagged trees where possible. In some cases, tagged trees were either dead, dying (rotting), or too difficult to sample, so I selected mature (diameter at breast height (DBH) of 20 cm or greater) replacement trees that were nearby. At sites without pre-tagged trees, I extracted two increment cores at 1.37 m from 30 balsam fir trees varying in health and size. I also recorded signs and symptoms of infestation including: DBH, estimated percent of live foliage, presence of bole or branch infestation, and the presence of the fiddle shaped crown. To estimate stand density, I collected the species, DBH, status (live or dead), and distance of the five nearest trees with a DBH of 10 cm or greater. I also sampled two cores from at least ten mature red spruce trees from each site to compare radial growth of balsam fir with a non-host species.

Table 2: Site ID, location, elevation (in meters), and land ownership of each site in the study area. All land was owned by the Monongahela National Forest, Blackwater Falls State Park, Canaan Valley State Park, or the Canaan Valley National Wildlife Refuge.

<u>SITE</u>	<u>SITE ABB.</u>	<u>LAT.</u>	<u>LONG.</u>	<u>ELEVATION (M)</u>	<u>LAND OWNERSHIP</u>
BALSAM FIR TRAIL	BFT	39.11899	-79.4934	945	BWF State Park (planted)
BEAVER DAM RUN	BDR	38.83829	-79.643	902	Mon NF (planted)
BLISTER RUN SWAMP	BRS	38.60044	-79.8516	1145	Mon NF
COURTLAND ROAD	COR	39.08327	-79.4228	963	CV NWR
DEER RUN TRAIL	DRT	39.01541	-79.4619	990	CV State Park
DOLLY SODS WILDERNESS	DOL	39.01961	-79.3796	1125	Mon NF
FREELAND ROAD	FRE	39.0255	-79.4278	987	CV NWR
MALLOW LAKE	MAL	39.08625	-79.4372	980	CV NWR
MARLINGTON/SCENIC HW.	MSH	38.20188	-80.234	1254	Mon NF (planted)
MIDDLE VALLEY TRAIL	MVT	39.11692	-79.3583	964	CV NWR
ROUTE 32/MANOR ROAD	RMR	39.06417	-79.4481	993	CV NWR (planted)
SEWER PLANT	SEW	39.03521	-79.4622	987	CV State Park
UPPER TRACT	UPT	39.17146	-79.3529	972	CV NWR
VOLUNTEER FIRE DEPT.	VFD	39.05124	-79.458	989	CV State Park

Sample Preparation and Measurement

Increment core samples were mounted on wooden blocks and sanded with progressively finer grit sandpaper (220, 400, and 600 grit) to reveal cellular structure under magnification (Speer, 2010; Stokes & Smiley, 1996). All mounted samples were then crossdated using skeleton plots (Stokes & Smiley, 1996). I measured each sample using a sliding stand Velmex measuring system (Velmex, East Bloomfield, NY, USA) and a Leica M80 microscope to 0.001mm and entered the measurements into a Tellervo server (Laboratory of Tree-Ring Research University of Arizona, Tucson, AZ). I used the statistical crossdating software tool COFECHA (Holmes, 1983) to quality check crossdating. Once all samples were crossdated and measured, I recorded the presence or absence of rotholz and traumatic resin canals for every ring in each sample. Traumatic resin canals appear as dark rows of resin-filled intercellular spaces surrounded by epithelial cells that occur proximal to a ring boundary (Figure 11). These occur after several years of severe BWA infestations but can also occur in rings with no signs of rotholz (Balch,

1952; Hain, 1988). Rotholz rings were identified as abnormally large, dark rings with high proportions of latewood and altered cellular structure (Figure 11). Rotholz rings were differentiated from compression wood by observing swollen, rounded cells surrounded by intercellular space.

Figure 11: Illustration of samples with rotholz and resin canals

Fir and Spruce Climate Relationship

I detrended balsam fir and red spruce ring width series with a modified negative exponential curve using the dplR package in R (R Core Team, 2018; R Studio Team, 2015),(A. Bunn, 2018; A. G. Bunn, 2008). I created balsam fir and red spruce mean value chronologies for each site by averaging (Tukey's biweight robust mean) the yearly ring width values from all the series at each

site. To determine whether red spruce was an appropriate non-host species, I assessed the relationship between a suite of climate variables (minimum and maximum monthly temperature, total precipitation (monthly), and monthly mean Palmer Drought Severity Index) and each site chronology (fir and spruce) using the *treeclim* package in R Studio (Zang & Biondi, 2015). The *treeclim* package computes the Pearson correlation coefficients and their bootstrapped confidence intervals between monthly climate data and chronology indices (fir and spruce). I also assessed these relationships at a regional scale, where time series for grids were combined into two regional time series, by averaging the values from all grids within each region. All sites surrounding Canaan Valley (BFT, COR, FRE, DRT, DOL, MAL, MVT, RMR, SEW, UPT, and VFD) were combined into the “north” region, and the sites in Monongahela National Forest (BDR, BRS, and MSH) were combined into the “south” region. For temperature (minimum, maximum, and mean) and precipitation (total monthly) variables, I used the 4 km resolution PRISM (PRISM Climate Group, 2004) dataset extracting those grids which contained my study sites. For PDSI (Palmer Drought Severity Index), I used division 4 of West Virginia (National Oceanic and Atmospheric Administration, 2019). Correlation coefficients were calculated on monthly climate variables from the previous May to the current September of the growing season (1980 to 2016).

Outbreak Identification Analysis

To identify outbreaks of BWA in balsam fir, I identified periods of growth enhancement in balsam fir that were absent from red spruce and then compared those growth 'surges' with the frequency of rotholtz and traumatic resin canal occurrence by year at each site. I then compared the synchrony of outbreaks detected using growth and anatomy with three years of USDA Forest Service field observations of BWA outbreaks in five of the stands I sampled.

Growth Correction

After assessing the climate relationships between fir and spruce at each site, I 'corrected' each balsam fir series by removing the variability in the spruce chronology for that site from each balsam fir index series. I used a modified version of the dfoiatR package in R (Guiterman 2019), which emulates the functions of the Fortran program OUTBREAK, (Holmes & Swetnam, 1996). OUTBREAK uses the chronologies from host and non-host species to highlight periods of growth suppression caused by defoliating insects such as gypsy moth or spruce bark beetle. Growth signals caused by climate and other exogenous factors are removed from the host series to generate a GSI (growth suppression index):

$$GSI(i) = H(i) - \left(\frac{SD_h}{SD_{nh}} (meanNH - NH(i)) \right)$$

GSI = "Growth Suppression Index"

Figure 12: Four-step illustration of the corrected chronology calculation on each site. a.) Plot of the standardized, detrended chronology of each species. b.) Plot of the corrected non-host chronology and host chronology. c.) Plot of the corrected host chronology or site mean growth suppression index ($\bar{x}$ GSI). d.) Plot of the site mean normalized GSI ($\bar{x}$ nGSI) where areas highlighted with red bars indicate outbreaks.

Following the calculation of GSI, values for each series are standardized to generate a normalized growth suppression index (nGSI). Since OUTBREAK was originally designed to detect defoliation events by finding periods of reduced annual growth and that design endured in *dfoliatR*, I modified the package to detect periods of elevated growth “surges” present in every series.

Growth surges were defined based on the following criteria: 1.) increases in growth > 1.28 standard deviations above the mean nGSI value (nGSI threshold), 2) periods of at least 4 consecutive years with nGSI > 0 (prior to or following the initial flag event > 1.28), 3) inclusion of 1 year periods of growth reduction prior to or after the maximum growth increase (bridge event). These criteria are similar to the defaults that were used in previous studies on insect defoliation that utilized OUTBREAK to reconstruct defoliation events (Axelson, Smith, Daniels, & Alfaro, 2015; Speer, Swetnam, Wickman, & Youngblood, 2001), though in this case detections are based on elevated, as opposed to suppressed, growth. To assess an outbreak that affects multiple trees in a stand, the percentage of series with growth surges are tallied for every year in each site. Years with at least 25% of series displaying surge status are flagged as potential outbreaks and highlighted with red bars overlaying the sites’ mean nGSI (Figure 12).

Climate and BWA Outbreaks

Based on laboratory experiments (Amman, 1967; Balch, 1952; Greenbank, 1970), I expect that cold winter temperatures would reduce BWA infestations and the extent of growth surges in balsam fir. To measure the relationship between BWA infestation and recent temperature

variability, I compared the nGSI from the north and south regions to daily temperature data (PRISM Climate Group, 2004). I combined series from both regions and created regional normalized growth suppression indices in which I tabulated the percentage of trees that were defoliated based on the same criteria used in the outbreak reconstructions. While winter temperatures in West Virginia are not low enough to kill adelgid in the dormant stage, periods of freezing temperatures lasting five days or longer would be enough to kill all adelgid in the crawler stage that reside above the snowline and reduce susceptible adelgid in the dormant stage (Amman, 1967; Balch, 1952; Greenbank, 1970). I also summarize (mean) the climate data by region and calculated the frequency of winter freeze events, defined as daily $T_{max} < 0$ persisting for five days or more. I compared this to the regional nGSI from 1981 to 2016. This period was chosen since the daily climate data from West Virginia starts in 1981, and most outbreaks occurred after that year.

Comparison to Field Observations

From 2014-2016, the US Forest Service performed a field survey of BWA population on five sites in Tucker County (FRE, MAL, MVT, SEW, and VFD) in early spring. They visually estimated the size of BWA populations on the bole of tagged trees which they revisited each year. Trees were assigned to one of four classes: no BWA observed (none), lightly infested (light), moderately infested (moderate), or heavily infested (heavy). I compared my nGSI values and rotholtz frequency for each of the trees that the USFS observed. The occurrence of traumatic resin canals was excluded from this part of the analysis, since they did not occur during the year of the survey.

Results

Tree-Ring Data

I collected 676 balsam fir, and 243 red spruce cores from 14 balsam fir stands in West Virginia (Table 1) to construct chronologies for each species at each site. I also constructed two regional chronologies from samples collected at sites that were separated by elevation and geographic space. The “north” region was constructed from the 11 sites that surround Canaan Valley, and the “south” region was constructed from 3 sites in the highlands of Randolph and Pocahontas Counties.

The mean length of the balsam fir chronologies was 62 years (range = 44 - 84 years) (Table 3). The mean length of the red spruce chronologies was 103 years (range 42 - 268 years). Mean interseries correlations for balsam fir and red spruce were similar, though slightly lower for balsam fir likely due to BWA infestation (mean of 0.424 and 0.500 respectively). Both species displayed evidence that the radial growth from the previous year had a strong influence on the radial growth of the current year. The balsam fir lag-1 autocorrelations ranged 0.571 to 0.824 and averaged 0.687, and the red spruce lag-1 autocorrelations ranged 0.639 to 0.906 and averaged 0.750.

Table 3: Interseries correlation, the number of dated cores, the length of the ring record (inner most ring to outer most ring of oldest samples), and the first-order auto-correlation (correlation between ring values lengths of the previous year (t-1) and the current year (t)(AC)) for each species at each of the 14 sites.

SITE	INTER SERIES COR.		NO. OF DATED CORES		RECORD LENGTH		AC	
	ABBA	PCRU	ABBA	PCRU	ABBA	PCRU	ABBA	PCRU
BDR	0.396	0.549	31	19	1966-2016	1911-2017	0.824	0.853
BFT	0.487	0.547	48	26	1943-2017	1829-2017	0.581	0.744
BRS	0.449	0.407	24	3	1946-2016	1925-2016	0.788	0.894
COR	0.425	0.443	58	10	1945-2016	1930-2017	0.707	0.684
DOL	0.344	0.504	16	20	1944-2016	1922-2017	0.818	0.906
DRT	0.359	0.443	60	26	1965-2016	1749-2017	0.725	0.789
FRE	0.479	0.534	59	9	1961-2017	1941-2017	0.677	0.704
MAL	0.499	0.438	58	11	1949-2017	1936-2017	0.571	0.651
MSH	0.557	0.549	59	20	1973-2017	1975-2017	0.688	0.699
MVT	0.430	0.514	29	8	1932-2016	1941-2016	0.581	0.798
RMR	0.450	0.660	59	20	1964-2016	1968-2017	0.686	0.639
SEW	0.339	0.472	60	21	1952-2016	1922-2017	0.750	0.730
UPT	0.413	0.465	55	22	1944-2017	1920-2017	0.655	0.677
VFD	0.302	0.484	60	28	1973-2016	1924-2016	0.574	0.733

Climate Characteristics

I calculated Pearson correlation coefficients between mean chronologies and four climate variables (minimum and maximum temperature, total monthly precipitation, and PDSI) for each site. Pearson correlation coefficients indicated that balsam fir and red spruce are similarly influenced by climate, but there was more agreement between the species for temperature and less agreement for total monthly precipitation (Figure 13 – Figure 27). The most common significant correlations occurred for minimum and maximum temperatures for previous and current June. There were no consistent significant correlations between balsam fir and total monthly precipitation or PDSI, but there were consistent significant correlations for total monthly precipitation and red spruce mean chronologies during the summer months.

Figure 14: (BFT) Pearson Correlation Coefficients of site by site growth vs each climate variable plotted side by side (1980 – 2016) for both balsam fir (red) and red spruce (blue). Bars with bold gray borders indicate significant values ($p < 0.10$)

Figure 15: (BRS) Pearson Correlation Coefficients of site by site growth vs each climate variable plotted side by side (1980 – 2016) for both balsam fir (red) and red spruce (blue). Bars with bold gray borders indicate significant values ($p < 0.10$)

Figure 16: (COR) Pearson Correlation Coefficients of site by site growth vs each climate variable plotted side by side (1980 – 2016) for both balsam fir (red) and red spruce (blue). Bars with bold gray borders indicate significant values ($p < 0.10$)

Figure 17: (DOL) Pearson Correlation Coefficients of site by site growth vs each climate variable plotted side by side (1980 – 2016) for both balsam fir (red) and red spruce (blue). Bars with bold gray borders indicate significant values ($p < 0.10$)

Figure 18: (DRT) Pearson Correlation Coefficients of site by site growth vs each climate variable plotted side by side (1980 – 2016) for both balsam fir (red) and red spruce (blue). Bars with bold gray borders indicate significant values ($p < 0.10$)

Figure 19: (FRE) Pearson Correlation Coefficients of site by site growth vs each climate variable plotted side by side (1980 – 2016) for both balsam fir (red) and red spruce (blue). Bars with bold gray borders indicate significant values ($p < 0.10$)

Figure 20: (MAL) Pearson Correlation Coefficients of site by site growth vs each climate variable plotted side by side (1980 – 2016) for both balsam fir (red) and red spruce (blue). Bars with bold gray borders indicate significant values ($p < 0.10$)

Figure 21: (MSH) Pearson Correlation Coefficients of site by site growth vs each climate variable plotted side by side (1980 – 2016) for both balsam fir (red) and red spruce (blue). Bars with bold gray borders indicate significant values ($p < 0.10$)

Figure 22: (MVT) Pearson Correlation Coefficients of site by site growth vs each climate variable plotted side by side (1980 – 2016) for both balsam fir (red) and red spruce (blue). Bars with bold gray borders indicate significant values ($p < 0.10$)

Figure 23: (RMR)Pearson Correlation Coefficients of site by site growth vs each climate variable plotted side by side (1980 – 2016) for both balsam fir (red) and red spruce (blue). Bars with bold gray borders indicate significant values ($p < 0.10$)

Figure 24: (SEW)Pearson Correlation Coefficients of site by site growth vs each climate variable plotted side by side (1980 – 2016) for both balsam fir (red) and red spruce (blue). Bars with bold gray borders indicate significant values ($p < 0.10$)

Figure 25: (UPT) Pearson Correlation Coefficients of site by site growth vs each climate variable plotted side by side (1980 – 2016) for both balsam fir (red) and red spruce (blue). Bars with bold gray borders indicate significant values ($p < 0.10$)

Figure 26: (VFD) Pearson Correlation Coefficients of site by site growth vs each climate variable plotted side by side (1980 – 2016) for both balsam fir (red) and red spruce (blue). Bars with bold gray borders indicate significant values ($p < 0.10$)

Figures 27-28: Pearson Correlation Coefficients of regional growth vs each climate variable plotted side by side (1980 – 2016) for both species for the regional chronologies (North – Canaan Valley (top) / South – Highlands of Pocahontas & Randolph Counties (bottom)). Bars with bold gray borders indicate significant values ($p < 0.10$)

Rotholz Record and Outbreak Reconstructions

The rotholz record extends from 1952 to 2016, with peak occurrence from 1988 to 1994, 1999 to 2003, and 2007 to 2013. Rotholz occurrence prior to 1988 was rare but did occur in several sites throughout the study area, particularly DRT, MVT, SEW, and UPT.

My outbreak reconstructions suggest that BWA outbreaks occurred during three different periods across the study area since 1980, mainly between 1987 and 1995, 1998 and 2005, and 2009 and 2011. Not all sites experienced outbreaks during these periods simultaneously, but there were synchronous outbreaks across many of the sites during the same periods. All sites except MSH (Figure 37) and UPT (Figure 41) recorded prolonged periods of high nGSI values throughout the 1990's through the year 2000. At MSH, nGSI values began to increase after 2000, and nGSI values spiked at UPT beginning around 2010. All sites except DOL and BRS recorded an outbreak period starting around 2007, peaking in 2010, and continuing until about 2013. Since 2013, nGSI at BDR, COR, DOL, DRT, MAL, and VFD have been declining, in some cases far below any nGSI value recorded previously. BFT, BRS, FRE, MSH, MVT, SEW, and UPT also experienced decline in 2013, but this decline did not continue. RMR was the only site that recorded increasing nGSI values prior to and following 2013.

Rotholz occurrence did not always occur simultaneously with high nGSI values at all sites. The strongest synchrony between high nGSI and rotholz years occurred at BDR (Figure 29), BRS (Figure 31), COR (Figure 32), DRT (Figure 34), and SEW (Figure 40). Other sites (FRE (Figure 33), MVT (Figure 38), RMR (Figure 39)) that had high rotholz occurrence had a lag period between spikes in nGSI values and rotholz. Rotholz occurrence peaked in 2000 and 2010 across

all sites. Traumatic resin canals were rare across all sites, but when resin canals did occur, they were always coincident with rotholz occurrence.

Figure 29: BDR normalized growth suppression index/corrected chronology, the percent of live samples that displayed signs of rotholz or resin canals, and the percentage of trees flagged as having a surge.

Figure 30: BFT normalized growth suppression index/corrected chronology, the percent of live samples that displayed signs of rotholz or resin canals, and the percentage of trees with a surge.

Figure 31: BRS normalized growth suppression index/corrected chronology, the percent of live samples that displayed signs of rotholz or resin canals, and the percentage of trees with a surge.

Figure 32: COR normalized growth suppression index/corrected chronology, the percent of live samples that displayed signs of rotholz or resin canals, and the percentage of trees with a surge.

Figure 33: DOL normalized growth suppression index/corrected chronology, the percent of live samples that displayed signs of rotholz or resin canals, and the percentage of trees with a surge.

Figure 34: DRT normalized growth suppression index/corrected chronology, the percent of live samples that displayed signs of rotholz or resin canals, and the percentage of trees with a surge.

Figure 35: FRE normalized growth suppression index/corrected chronology, the percent of live samples that displayed signs of rotholz or resin canals, and the percentage of trees with a surge.

Figure 36: MAL normalized growth suppression index/corrected chronology, the percent of live samples that displayed signs of rotholz or resin canals, and the percentage of trees with a surge.

Figure 37: MSH normalized growth suppression index/corrected chronology, the percent of live samples that displayed signs of rotholz or resin canals, and the percentage of trees with a surge.

Figure 38: MVT normalized growth suppression index/corrected chronology, the percent of live samples that displayed signs of rotholz or resin canals, and the percentage of trees with a surge.

Figure 39: RMR normalized growth suppression index/corrected chronology, the percent of live samples that displayed signs of rotholz or resin canals, and the percentage of trees with a surge.

Figure 40: SEW normalized growth suppression index/corrected chronology, the percent of live samples that displayed signs of rotholz or resin canals, and the percentage of trees with a surge.

Figure 41: UPT normalized growth suppression index/corrected chronology, the percent of live samples that displayed signs of rotholz or resin canals, and the percentage of trees with a surge.

Figure 42: VFD normalized growth suppression index/corrected chronology, the percent of live samples that displayed signs of rotholz or resin canals, and the percentage of trees with a surge.

Figure 43: Rotholz occurrence from 1950 to 2016 for all samples combined. Bars represent the percentage of cores with rotholz, and the line represents sample depth for each year.

Climate Analysis

To detect possible relationships between recent changes in temperature and balsam fir growth, I compared regional outbreak reconstructions to the frequency of cold events. I expected years with many cold events (5 or more consecutive days with high temps < 0) would have low or decreasing nGSI values in the following year, and the opposite effect during years with fewer cold events. In Canaan Valley (Figure 44), this pattern occurred consistently up to about 2000, where nGSI values were lower than average until 2005, and there were few cold events. The pattern continued in Canaan Valley after 2005. In the Poca/Rand region (Figure 45), the pattern

occurs consistently from 1980 to 2016.

Figure 44: Regional nGSI plotted over an annual count of cold runs (consecutive days with temperatures below 0°C) in Canaan Valley (North Region)

Figure 45: Regional nGSI plotted over an annual count of cold runs (consecutive days with temperatures below 0°C) in Poca/Rand (South Region)

Comparison to Field Observations

I compared my outbreak reconstructions to data collected by the USDA Forest Service at five of our sites from 2014-2016. I expected trees that were categorized as not infested (None) or lightly infested (Light) to have lower nGSI values and rotholz occurrence than trees that were categorized as moderately or heavily infested. Trees categorized as not infested or lightly infested recorded low nGSI values (< 1.28 SD above the mean), but the lightly infested trees had lower nGSI values and rotholz occurrence than the trees that were not infested at all sites except SEW from 2014-2016. At FRE (Figure 49), the trees categorized as not infested had higher rotholz occurrence than all other categories.

Figure 46: Mean nGSI for each BWA size class plotted above proportion of USFS trees with/without rotholz (2014-2016) in FRE.

Figure 47: Mean nGSI for each BWA size class plotted above proportion of USFS trees with/without rotholz (2014-2016) in MAL.

Figure 48: Mean nGSI for each BWA size class plotted above proportion of USFS trees with/without rotholz (2014-2016) in MVT.

Figure 49: Mean nGSI for each BWA size class plotted above proportion of USFS trees with/without rotholz (2014-2016) in SEW.

Figure 50: Mean nGSI for each BWA size class plotted above proportion of USFS trees with/without rotholz (2014-2016) in VFD.

Discussion

Climate Summary

Balsam fir and red spruce in this study showed little agreement in their growth response to different climate variables influencing them. Significant correlations between mean chronologies and temperature, precipitation, and PDSI were sporadic, and showed little consistency outside the month of June. Previous studies that examined the agreement of climatic effects on spruce-fir systems concluded that eastern North America's spruce and fir species react to climate similarly when they grew at low elevations (<900 m)(Adams et al., 1985; Stephenson & Adams, 1986). At higher elevations, there was more variation (Soulé, 2011; Stephenson & Adams, 1986). All sites in my study area reside at elevations greater than 900 m, with the highest being 1252 m, which may explain the divergence. Another study that examined how red spruce growth had been affected by recent changes in atmospheric composition observed weak relationships between red spruce growth and climate variables outside June and July (Mathias & Thomas, 2018). In my study area, I had limited options for non-host comparison species, and red spruce grew alongside balsam fir across all sites.

Rotholz Record

At UPT, samples that I examined had evidence of rotholz as early as 1952, which is three years earlier than outbreaks reported in other studies, but only a few trees I sampled were old enough to display these signs during that period (Amman, 1966; Amman & Speers, 1965). Rotholz appeared again a decade later in samples from four other sites (DRT, MAL, SEW, UPT) which displayed signs of rotholz occurrence from 1960 to 1963 (Figure 52-55). After 1975, rotholz occurrence steadily became more common across all sites until about 2013 (Figure 43).

Rotholz if identified correctly, is a definite indicator of BWA infestation as there is no other known cause of rotholz in balsam fir (Amman, 1970; Balch, 1952; Westing, 1968). In moderate to severe outbreaks, rotholz is a reliable indicator, but extracting a core with rotholz damage is left to chance, as it occurs locally, and not always along the entire circumference of the stem. Rotholz has been used extensively as an indicator of BWA infestation in past studies that examined many different species of fir including Fraser fir, grand fir, subalpine fir, and balsam fir (Amman & Speers, 1965; Balch, 1952; Mitchell, 1966), but in these studies, the researchers often sampled entire tree cross sections, thereby killing the trees.

Traumatic resin canal occurrence is not limited to BWA feeding, but it often appeared between the latewood of rotholz years and the earlywood of the following year in trees thought to be severely infested. Traumatic resin canals are rare in balsam fir, but they can be caused by other types of tissue damage. Traumatic resin canals were too infrequent across the study area to assess any relationships between their occurrence and infestation intensity. In other studies, traumatic resin canals alone were not used as indicators of BWA infestation, but instead used as additional supporting evidence (Balch, 1952; Hain, 1988; Smith, 1967). However, traumatic resin canals have been used as infestation indicators for other species of defoliators, such as spruce bark beetle (DeRose, Bekker, & Long, 2017).

One disadvantage I encountered in this study was the brevity of the balsam fir ring record, as the oldest balsam fir samples were only 90 years old, and only a few of these older trees are alive today. This not only made crossdating more difficult, but it reduced the number of live samples that could record outbreaks during earlier decades. A second disadvantage I encountered is that I analyzed samples extracted from surviving trees. I could not sample dead trees, as balsam fir wood rots and decays quickly. Even in many of the older trees I was able to sample, I could not

reach pith because the heartwood had decayed. The possibility remains that there may have been trees that recorded outbreaks but did not survive them.

Outbreak Identification

When I compared the corrected chronologies to the rotholz dates, I expected to find that years with high rotholz occurrence would also record higher than normal nGSI values. This was often the case for the most severely infested sites, but it did not occur for all sites. Each site recorded varying degrees of outbreaks and rotholz occurrence, but outbreaks occurred during the same periods. Sites that had large proportions of young trees (20-30 ring years) often had a lag period between peak rotholz occurrence and spikes in nGSI values (FRE, MSH, RMR, VFD). The older sites (majority of trees 30-50 ring years) displayed more agreement between peak rotholz occurrence and peak nGSI (BDR, DRT, SEW). This indicates that the age of the stand, and therefore stand vigor, not only influences the severity of outbreaks, but agreement between rotholz dates and spikes in nGSI. Previous studies observed that severe infestations often occur when the majority of trees are 30-50 years, when trees are most vigorous, and provide the best conditions for adelgid feeding (Balch, 1952; Smith, 1967). Again, there is some degree of uncertainty, since I examined a relatively short record of surviving trees.

Older sites displayed signs that outbreaks were constant since the initial outbreak (DRT, MAL, SEW), where increases and decreases in rotholz occurrence and nGSI values occurred in unison. This could be due to BWA populations reaching maximum carrying capacity during years of high rotholz occurrence and high nGSI values, followed by the host's inability to support increases in BWA populations, which would result in a steep decrease in BWA population, rotholz occurrence, and nGSI simultaneously. This phenomena of BWA population

overabundance leading to population crashes was studied in depth in eastern Canada (Balch, 1952; Greenbank, 1970), where researchers observed that some trees had survived decades of severe infestations. We have not yet determined the threshold of infestation that leads to tree mortality, but it would be insightful to assess rotholz occurrence and nGSI values of recently deceased trees.

Climate Analysis

When I analyzed the rotholz dates and nGSI values, I observed that outbreaks have become more frequent and severe over the past 60 years. I expected low nGSI values to occur simultaneously with years that had many cold events (5-consecutive days of average temperatures of 0°C or below) and high nGSI values during years with few cold events. Instead, decreases in nGSI occurred one year after years with more cold events than in previous years. I observed this pattern in the Pocahontas/Randolph region, as the years with many cold events (1986, 1996, 2010-2011) recorded large decreases in nGSI in the following year, and periods with few cold periods often coincided with nGSI spikes (Figure 45). This pattern was also evident in the Canaan Region (Figure 44) until about 2000, where there were several years with few cold events and low nGSI. This indicates that low winter temperatures do have a negative influence on BWA population size and therefore reduce outbreak intensity, which was also evident in previous studies (Amman, 1967; Balch, 1952; Greenbank, 1970). However, infestations often persisted through years with many cold events, further reinforcing the fact that temperatures in West Virginia do not get low enough, or low temperatures do not persist long enough to completely eradicate overwintering BWA populations. Separate factors that influence stand health could also influence the intensity of infestations, as the health of the stand reflects the abundance of adelgid populations since they rely on healthy, vigorous trees for nutrition and carrying capacity.

Comparison to Field Observations

There was little agreement between the nGSI and rotholz data and the USFS assessments (Figures 46-50). In four of the five sites, I observed high rotholz occurrence, while the Forest Service classified the trees as not infested, or lightly infested. Trees categorized as not being infested often had higher nGSI values than trees that were categorized as lightly or moderately infested. The VFD stand had the most agreement, as the trees classified as lightly infested recorded low rotholz occurrence and nGSI values. This could be due to the timing of the annual assessments, since they were often conducted in the early spring. This may be too early in the year to assess peak infestation, which likely occurs during the summer months when temperatures are warmer. It is for these reasons that analyzing nGSI and rotholz occurrence may be better indicators of infestation than field observations since it can be difficult to observe severe canopy infestations from the ground. Canopy infestations gout branch nodules and curtail needle production (which would shorten ring widths) (Balch, 1952; Smith, 1967). These types of infestations may be detected by examining shorter ring widths that occur after known stem outbreaks.

Conclusions

Rotholz and nGSI data I collected throughout the highlands of Tucker, Randolph, and Pocahontas Counties indicate that BWA outbreaks occurred much earlier than previously thought. According to my data, outbreaks occurred as early as 1952, which is three years earlier than even the least detailed recorded outbreak in all of West Virginia, which is recorded in 1955, and much earlier than the most widely accepted date in 1992. This outcome is consistent with

various arrival dates in eastern North America. Outbreaks were recorded in Maine around 1900 and in Virginia and North Carolina in 1955. It is reasonable to assume that the highlands of West Virginia served as part of BWA's dispersal corridor south into Southern Appalachia and the Smokey Mountains. Based on my data, I can also reasonably conclude that BWA was present in Canaan Valley prior to sites in the Pocahontas/Randolph region, as I recorded outbreaks in Canaan Valley much earlier. This also confirms that BWA likely moved south over the past century through West Virginia.

I can also conclude that temperature, stand age, and stand vigor are important factors in BWA outbreak severity. One of the least infested sites MSH (Figure 37), which was also the southernmost site, had the highest elevation (1254 m), winters with more cold periods (Figure 47), and the youngest trees on average (Table 3). At higher elevations where winters are too cold, BWA may struggle to maintain large populations. This phenomenon may explain why BWA has only recently (1988 - present) developed large populations in Canaan Valley, since the area has been experiencing fewer cold periods annually (Figure 47).

The timing of cold periods may also influence BWA dispersal and population size, as temperatures in the high elevation sites are still not cold enough to kill adelgid in the dormant phase. The cold periods would only succeed in containing BWA populations when they are in the mobile stage of their lifecycle, since temperatures just below freezing are enough to kill adelgid in this stage. In the high elevation stands, BWA may have failed to establish populations large enough to sustain further population growth before cold winters wipe them out, and only small numbers of adelgid make it to the dormant stage where they can successfully overwinter.

Lastly, while some stands seem like they will not survive the next severe outbreak, others show no signs of succumbing to outbreaks. In the rotholz and nGSI records, there are many trees that

have survived two or more severe infestations over a period of 30 years. This seems to indicate that BWA alone may not be enough to kill entire stands of balsam fir. BWA typically infests trees when a tree is experiencing maximum vigor, which is 30-40 years, and rarely infests immature trees. It is the introduction of additional threats such as drought, deer over browsing, or competition with other tree species that may tip the balance and wipe out balsam fir stands. Deer threaten to limit balsam fir regeneration, since they browse trees while they are still young and relatively immune to BWA infestation (Cherefko et al., 2015; Michael, 1992). Drought becomes a threat when trees are heavily infested, since BWA infestation simulates drought stress, and the tree becomes vulnerable to any additional stress. Otherwise, BWA may ravage balsam fir populations as they reach maturity, but if trees are able to produce seeds, fir populations may sustain themselves. Climate change and warmer annual temperatures may pose a greater threat to balsam fir, especially if they become drought stressed and warmer winters fail to contain large BWA populations.

Appendix

Figure 51: Full nGSI/rotholz/outbreak record for BFT (1970-2016).

Figure 51: Full nGSI/rotholz/outbreak record for DRT (1950-2016).

Figure 53: Full nGSI/rotholz/outbreak record for MAL (1950-2016).

Figure 54: Full nGSI/rotholz/outbreak record for SEW (1955-2016).

Figure 55: Full nGSI/rotholz/outbreak record for UPT (1950-2016).

Outbreak history for each site. These were calculated using the nGSI values per sample in all sites. (Outbreak periods with a mean (mean of flagged outbreak period) nGSI <0.75 are considered minor, >0.75 and <1.28 are moderate, and values >1.28 are severe)

Figure 56: Outbreak history and severity of samples collected from BDR from 1980 to 2016.

Figure 57: Outbreak history and severity of samples collected from BFT from 1980 to 2016.

Figure 58: Outbreak history and severity of samples collected from BRS from 1980 to 2016.

Figure 59: Outbreak history and severity of samples collected from COR from 1980 to 2016.

Figure 60: Outbreak history and severity of samples collected from DOL from 1980 to 2016.

Figure 61: Outbreak history and severity of samples collected from DRT from 1980 to 2016.

Figure 62: Outbreak history and severity of samples collected from FRE from 1980 to 2016.

Figure 63: Outbreak history and severity of samples collected from MAL from 1980 to 2016.

Figure 64: Outbreak history and severity of samples collected from MSH from 1980 to 2016.

Figure 65: Outbreak history and severity of samples collected from MVT from 1980 to 2016.

Figure 66: Outbreak history and severity of samples collected from RMR from 1980 to 2016.

Figure 67: Outbreak history and severity of samples collected from SEW from 1980 to 2016.

Figure 68: Outbreak history and severity of samples collected from UPT from 1980 to 2016.

Figure 69: Outbreak history and severity of samples collected from VFD from 1980 to 2016.

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