2021

White Pine Blister Rust Distribution in New Hampshire 1900-2018: Exploring the Impacts of an Exotic Pathogen on Forest Composition and Succession

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WHITE PINE BLISTER RUST DISTRIBUTION IN NEW HAMPSHIRE 1900-2018: EXPLORING THE IMPACTS OF AN EXOTIC PATHOGEN ON FOREST COMPOSITION AND SUCCESSION

A Dissertation

Presented to the Faculty of
Antioch University New England

In partial fulfillment for the degree of

DOCTOR OF PHILOSOPHY

by

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August 2021

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This dissertation, by Janine Marr,
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Antioch University New England
in partial fulfillment of requirements for the degree of

DOCTOR OF PHILOSOPHY

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ABSTRACT

WHITE PINE BLISTER RUST DISTRIBUTION IN NEW HAMPSHIRE 1900-2018: EXPLORING THE IMPACTS OF AN EXOTIC PATHOGEN ON FOREST COMPOSITION AND SUCCESSION

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White pine blister rust (WPBR) has been affecting New Hampshire's white pines for more than a century, yet no data exist on the long-term effects of the non-native disease on the state's forests, particularly with respect to the regeneration and sustainability of white pine, and forest succession. This study aimed to address the gaps in the literature by exploring: 1) the current distribution, incidence, and severity of WPBR in New Hampshire; 2) the application of two historical hazard ratings models, one climatic, and one biotic; and 3) the long-term effects of the disease on forest composition, structure, and succession. Historical blister rust maps were used to select research sites for a comparison between pine stands that had blister rust, and pine stands that were infection-free when mapped (1929-1976) by the NH Blister Rust Control Program. One hundred sites in 50 towns were revisited in the spring of 2018. This research included the development and application of: 1) a WPBR canker severity index for white pine; 2) a disease-disturbance model for WPBR; and 3) a forest succession trajectory for forests disturbed by WPBR. Results suggested that 1) WPBR incidence had increased since a 1998 statewide study; 2) native *Ribes* populations were well-distributed throughout the state; 3) *Ribes* that infected white pines were less likely to be within the historical 300-yard protection zone; 4) the historical hazard models were outdated, particularly in relation to New Hampshire's climate; and 5) WPBR can aid natural successional processes to influence forest structure and succession. This research connected historical data with the present to improve our understanding of the relationship between WPBR and forest succession in a changing climate. During this process, several knowledge gaps were identified for future research. This dissertation is available in open access at AURA, http://aura.antioch.edu/ and OhioLINK ETD Center, https://etd.ohiolink.edu/etd.

Keywords: white pine blister rust, *Cronartium ribicola*, forest succession, New Hampshire

Dedication

This dissertation is dedicated to individuals and organizations from the past, the present, and the future who:

- researched the "blasenrost" of the pines and the "filzrost" of the *Ribes* to identify the different stages of the disease, white pine blister rust;
- served the Blister Rust Control Program, working long hours in the swamps, poison ivy, heat, and mosquitoes, in a nationwide attempt to save our white pines;
- financed the eradication efforts on their pine plantations, forests, and lands and/or offered their diseased pines for use in demonstration areas and public outreach;
- remember the story of the most expensive forest epidemic in U.S. history;
- work to develop white pine cultivars resistant to the deadly disease;
- enjoy a true story that spans nearly 120 years, combining forest science, pathology, ecological history, politics and economics, resilience, and climate change;
- will be inspired by this research and choose to build upon it.

It is only through the connection between the past and the present, and the many lessons learned, that we can address the impacts of an exotic disease on our valued white pine.

> It is obvious that blister rust will always be with us; and in order to keep it under control, it is necessary to keep *Ribes* out of white pine areas…unless we can successfully maintain control on areas which have been protected, the tremendous effort which has been put forth to save the white pine will be largely wasted (Martin, 1928, p. 45).
> From: The blister rust control problem in the Eastern United States. In *Report of the Proceedings of the Fourteenth Annual Blister Rust Control Conference Held in Providence Rhode Island, November 19-20, 1928* (pp. 43–46).

Acknowledgements

This dissertation was a team effort. Special thanks are extended to everyone who assisted and supported my research, both directly, and indirectly:

- The blister rust agents and researchers who provided the historical background and data;
- Kyle Lombard, NH Forest Health Specialist, who taught me to recognize white pine blister rust in trees of various ages and sizes;
- Dr. Isabel Munck, Plant Pathologist, U. S. Forest Service, who shared my excitement for locating sporulating cankers in the field, and who appreciated the edible currant;
- My Dissertation Committee, who contributed their unique perspectives and support to create a truly one-of-a-kind study;
- Brian Nelson Burford, State Archivist, who enthusiastically allowed me access to the state's historical blister rust maps collection;
- To the landowners who allowed me to conduct research on their forest lands decades after the last *Ribes* eradication;
- Roger Ayotte, wildlife tracker turned blister rust scout, who drove countless hours with me across the state to search for *Ribes*, often encountering ticks instead;
- Dr. Alesia Maltz, who supported my interests in environmental history and currant jelly;
- Dr. Abigail Abrash-Walton whose encouraging words made me believe I can;
- Staff at Antioch University New England who assisted me in the library, student services, and the environmental studies department;
- Family and friends who allowed me to be out-of-contact when I needed to write.

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Abstract

White pine blister rust (WPBR) has been infecting the five-needled white pines in New Hampshire for more than a century, yet the disease does not concern the forest managers of today as it did in the past. By 1965, the decline in *Ribes* presence and reduced incidence on white pine allowed many land managers to conclude that the epidemic had ended and that WPBR was no longer a threat to one of the state's most valuable timber resources. The national blister rust control program ended in the 1960s and the New Hampshire program ended in the 1970s. By 1980, attention had turned to other insect and disease pests in the forests of New Hampshire. Since then, few WPBR studies have been published to update landowners and the forest industry on the presence and distribution of WPBR in New Hampshire. This chapter provides a review of the WPBR life cycle through the seasons on both the perennial host white pine, and the telial host, *Ribes*. A history of the blister rust control program in New Hampshire is offered for insight into the monumental effort put forth by landowners and the workers of the NH Blister Rust Control Program to save the white pine trees. The chapter concludes with an outline of this dissertation that explores the long-term impacts of a non-native pathogen on the white pine forests of New Hampshire.

Keywords: white pine blister rust, *Cronartium ribicola*, NH Blister Rust Control Program, *Ribes*

White Pine Blister Rust in New Hampshire: An Introduction

The subject of this dissertation was the distribution of white pine blister rust (WPBR) in New Hampshire and its impacts on white pine, forest composition, and succession. I chose this subject to advance our understanding of an exotic plant disease that has been adapting to New Hampshire's climate and environment for more than a century. My research built upon nearly 120 years of scientific and anecdotal data for New Hampshire and the Northeast. My interdisciplinary approach combined historical ecology, silviculture, plant pathology, disturbance theory, succession theory, and climate science. I incorporated historical blister rust maps, created by the NH Blister Rust Control Program, to identify white pine stands from the past (1929-1976) and revisit them in 2018 to determine if pine was still a component. I also wanted to see if WPBR still existed in the historically-infected stands, and if it had developed in stands that were free of infection when they were mapped by the NH Blister Rust Control Program.

My research evolved from both curiosity and fear as I watched the discolored trunks of my young pine trees erupting with what resembled cheese popcorn. The orange-yellow powdery spores were a sign of the WPBR disease that girdled the young saplings and killed them in just a few years. What could I do as a landowner to protect my white pines from this deadly disease? I found no current research on WPBR in New Hampshire or the Northeast. Most of the published literature referred to western studies or historical reports from the nationwide epidemic in the early 1900s. I wondered if other landowners shared my concerns. What percentage of our pine trees have died from WPBR in recent years compared to the years of the epidemic? What long-term effects has WPBR had on New Hampshire's forests? Was the disease adapting to climate change? These were some of the many questions I wanted to answer. In this chapter, I shared what I've learned about WPBR, its history in New Hampshire, and its life cycle, which is dependent upon a relationship between: 1) an exotic pathogen with specific climatic needs for infection; 2) an early successional tree valued as a commercial forest product; and 3) *Ribes*, a native and naturalized alternate host with berries consumed by wildlife and humans.

White Pine Blister Rust Life Cycle

White pine blister rust has been in the United States since the late 1800s (Spaulding, 1914), and in New Hampshire since 1900 (Newman & Filler, 1930). White pine blister rust is a rust fungus caused by *Cronartium ribicola* J.C. Fisch, a pathogen that is exotic to North America and native to central Siberia and Asia (Hummer, 2000). The pathogen is heteroecious, requiring two hosts to complete its life cycle (Pettis, 1909). In the Northeast, susceptible five-needled white pines (Hoff, Bingham, & McDonald, 1980), including New Hampshire's important timber species, eastern white pine (*Pinus strobus* L.), serve as the perennial host, while *Ribes* species (gooseberries and currants) are the known alternate hosts to date. In the western states, *Ribes*, *Pedicularis*, and *Castilleja* species serve as alternate hosts of WPBR (McDonald, Richardson, Zambino, Klopfenstein, & Kim, 2006; Zambino, Richardson, & McDonald, 2007). While some diseases target weak, declining, or damaged trees, WPBR can girdle and kill healthy trees, and trees with vigorous growth (Boyce, 1938). Familiarity with the WPBR life cycle is important for three reasons explored in this research: 1) for understanding why some New Hampshire forests are heavily-infected and others have not developed the disease; 2) when developing hazard ratings for white pine management in areas where both white pine and *Ribes* co-exist; and 3) for exploring the potential impacts of a changing climate on the WPBR pathosystem, its individual components, and stages of disease progression as forests succeed.

The five-stage WPBR life cycle begins when a windborne basidiospore from an alternate host attaches to a pine needle. The developing infection travels from the needle to the branch, then towards the main stem of the tree, killing the infected needle and branch (Schwandt, Kearns, & Byler, 2013) (Figure 1.1). When the infection reaches the main stem, it forms a perennial canker that spreads outward until the stem is completely girdled and dies (Schoettle & Sniezko, 2007); a lethal stem canker in the upper portion of the tree will cause death to the crown above the canker (Schoettle & Sniezko, 2007; Schwandt et al., 2013; Smith & Hoffman, 2000), while stem cankers on the lower bole can kill a small tree in three years, or a mature tree in 10-20 years (Martin & Spaulding, 1949). A non-lethal branch canker that dies before reaching the main stem will not kill the tree (Burns, Schoettle, Jacobi, & Mahalovich, 2008), but will kill the branch that may have produced cones (Maloney, Vogler, Jensen, & Delfino Mix, 2012). Signs of the disease on white pines include spore-producing pycnia, aecia, and telia; symptoms include needle spots, discolored bark around a canker, and branch flagging (Cleaver, Burns, & Schoettle, 2017). Five-needled white pines in all size classes are susceptible to WPBR (Benedict, 1981).

1) Needle infection expands into branch towards main stem; 2) branch dies; 3) main stem infection expands and girdles tree; 4) tree dies.

Figure 1.1. Progression of WPBR from infected needle to tree mortality. Photos by Janine Marr.

Damage to the alternate *Ribes* host is minimal and confined to dead tissue spots on the leaves that senesce in the fall; however, when heavily-infected, a shrub may shed its leaves prematurely

(Hummer & Dale, 2010); *R. cynosbati* is especially prone to disease-induced shedding in the Northeast (Zambino, 2010).

The life cycle of WPBR consists of two spore stages on white pine and three on the alternate host (Figure 1.2). Pycniospores (spermatia) are the first spore stage on the white pine and appear in water-like droplets (pycnia) where the discolored bark was infected the previous year (Hirt, 1964). They serve as the sexual reproduction stage of the disease and are disseminated by insects to other cankers (Schwandt et al., 2013; Zeglen, Hunt, & Cleary, 2009). The sweet pycnial drops are occasionally eaten by porcupines, squirrels, mice (Lombard & Bofinger, 1999), snails (Spaulding, 1922), and gypsy moth caterpillars (Gravatt & Posey, 1918; Martin, Sheals, & Stene, 1920).

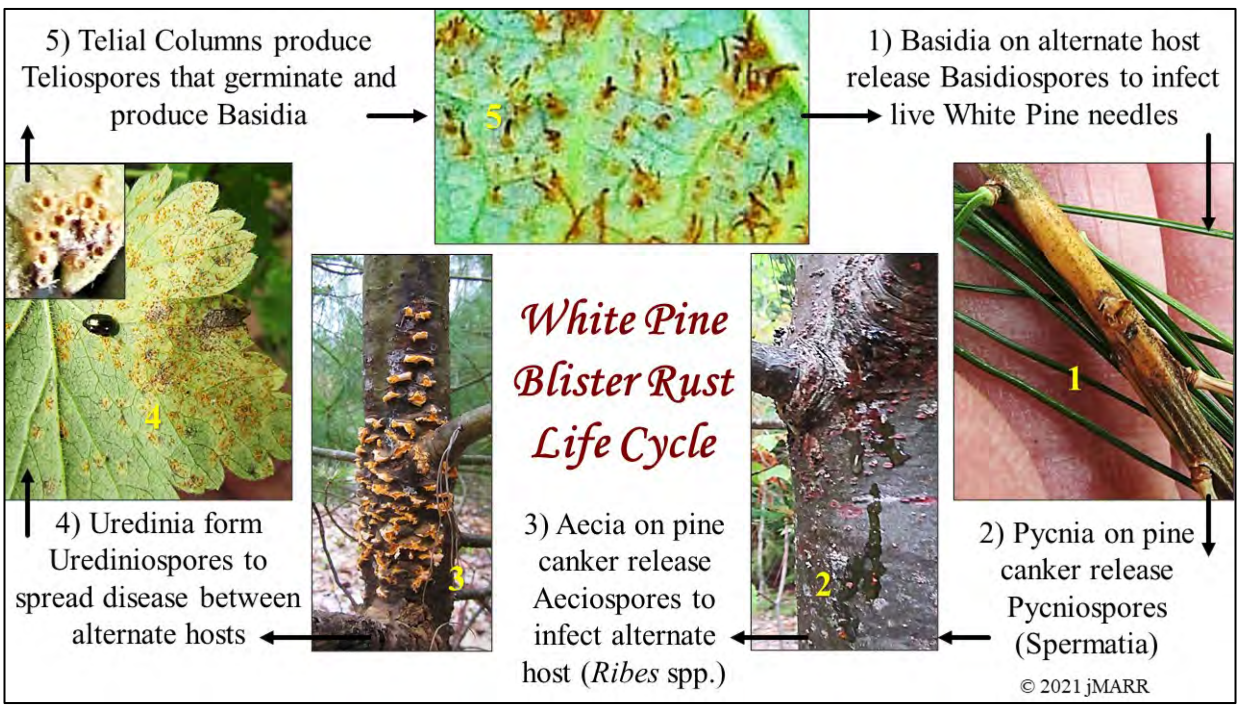

Figure 1.2. White pine bister rust life cycle. Photos by Janine Marr.

If fertilization is successful, aecial blisters erupt from the bark the following spring and release aeciospores that travel by wind (Schwandt et al., 2013). Aeciospores may travel distances that range from a few feet to 300 miles depending upon topography and wind currents (Muir & Hunt, 2000). In New Hampshire, aeciospores are released in May and June to infect *Ribes*.

Within a month of becoming infected, a *Ribes* plant will develop uredinia on the undersides of the leaves; their purpose is to produce urediniospores that travel by wind, rain, and insects to infect other *Ribes* (Newcomb, Upper, & Rouse, 2010). The uredinial stage spreads WPBR to other *Ribes* patches in the landscape throughout the summer months (Motty, 2004).

During the summer, as early as mid-July in New Hampshire, urediniospores begin the last two stages of the WPBR life cycle on *Ribes*. The urediniospores produce telial columns with teliospores. The teliospores germinate and produce basidia, upon which basidiospores develop, usually when the weather cools in September. Basidiospores, which are very sensitive to ultra-violet light and desiccation (Williams, 1989), are very short-lived; they require 48 hours of 98% humidity and air temperatures between 60 degrees and 68 degrees Fahrenheit for germination and pine infection to occur (Van Arsdel, 1961). Hirt (1935) reported that with optimal climate conditions, teliospores could germinate and produce basidia upon which basidiospores grow. The basidiospores could then travel through the air up to 1/3 mile to attach to a pine needle. The entire process could occur in 11 hours and 23 minutes (Hirt, 1935). Once the basidiospores are dispersed by the wind and infect pine trees, the disease cycle begins again.

History of White Pine Blister Rust Control Program in New Hampshire

The first confirmation of WPBR on *Ribes* in the United States occurred in September of 1906 at the New York Experimental Station in Geneva, New York, where 48 plantation varieties were infected (Stewart, 1907). The first evidence that WPBR had infected white pines in the United States was observed in 1909 by Dr. Perley Spaulding, a pathologist for the Bureau of Plant Industry, who personally inspected imported white pines at a Marlow, New Hampshire plantation and found infected trees (Spaulding, 1911). That same year, an emergency bulletin was prepared to alert the forest industry about recommended eradication measures. Recommendations included: 1) monitoring plantings of white pine through 1911; 2) removing all *Ribes* within 100 yards of imported pines; and 3) monitoring all cultivated *Ribes* for WPBR and destroying all infected plants by burning (Atwood, 1909). Those recommendations announced the beginning of the costliest control efforts for a forest disease in American history, with more than $100 million invested by 1959 (Benedict, 1981). The Blister Rust Control Program, operating under the Bureau of Plant Industry since 1915, was transferred to the U.S. Forest Service in 1953 and discontinued in 1965 (Benedict, 1981). The national program's demise was due to its success and its failure: it effectively reduced WPBR in the Northeast by eliminating the highly-susceptible cultivated black current as an alternate host; and it demonstrated that the cost of the programs in the Midwest and West were excessive where WPBR remained uncontrolled (Benedict, 1981).

In New Hampshire, *Ribes* eradication began in 1917 through cooperative efforts by the state forestry department and the Bureau of Plant Industry (NH Forestry Commission, 1922) as six-man crews (Newman & King, 1927) manually pulled *Ribes* plants from white pine areas. In 1918, New Hampshire became the first state to establish an organized control program with towns and individuals to protect the state's pines from WPBR (Simmonds, 1952); Edmund Filler, head of the Northeast Regional Blister Rust Control Program, wrote the first *Ribes* eradication manual for the Northeast at the New Hampshire State Forester's office in Concord (Benedict, 1981); and towns began appropriating money for control work (NH Forestry Commission, 1922). A 1919 forest survey indicated that New Hampshire had 1,020,750 acres of merchantable timber, of which 27% was white pine, although Cheshire, Merrimack, Belknap, Hillsborough, Strafford, and Rockingham counties reported 54% to 80.6% of their merchantable timber as white pine (NH Forestry Commission, 1922). In 1920, the program removed 2,061,996 wild and 21,288 cultivated *Ribes* from 49 towns (NH Forestry Commission, 1922) to protect the white pine timber resources (N.H. Forestry and Recreation Commission, 1946).

Control efforts were expanded throughout New Hampshire's white pine region, while new treatment options were tested. On January first, 1922, a state quarantine went into effect that prohibited the shipment of all gooseberries and currants within and to New Hampshire (State of New Hampshire Department of Agriculture, 1922). A chemical experiment in Brentwood, Exeter, and Kensington compared the use of Atlacide, sodium chlorate, and diesel oil on *Ribes* in a swamp, meadow, and roadside application, and demonstrated that the oil was applied more easily and quickly, covered more of the *Ribes* leaves, and remained on the leaves longer, killing them completely (Swain, 1931). However, herbicide use was reserved for the most troublesome areas where *Ribes* were hard to reach, or too numerous to pull by hand efficiently. By 1948, the most popular and cost-effective herbicides used to control *Ribes* were 2,4-D acid and 2,4,5-T isopropyl ester (Offord, Moss, Benedict, Swanson, & London, 1952). In 1952, 2,4,5-T was used to remove over 100,000 skunk currants from 20.25 acres in New Hampshire; so much time and manual labor were saved using the chemical that it was recommended for regular control work (Simmonds, 1952).

Ribes eradication was a successful measure for controlling WPBR in the Northeast (Benedict, 1981; Bingham, 1963; Ostrofsky, Rumpf, Struble, & Bradbury, 1988); by 1952, the Rochester and Keene districts were virtually *Ribes*-free (Simmonds, 1952). Random statewide surveys conducted in 1952 reported WPBR incidence ranging from 0-10% in 66.4% of the plots, 10.1-40% in 32.4% of the plots, and incidence levels over 40% for just 12% of the plots. The results of a 1962-1963 U.S. Forest Service survey indicated that the average incidence for WPBR in New Hampshire was 1.1% (Marty, 1965), suggesting that *Ribes* regeneration was controlled and WPBR was no longer a threat (Benedict, 1981). In 1965, when the U.S. Forest Service discontinued the national program, the NH Office of Blister Rust Control began operating under the state's Forest Insect and Disease Program (State of New Hampshire, 2019). In 1980, with the retirement of the state leader, the NH Blister Rust Control Program officially ended.

One major contribution of the NH Blister Rust Control Program was the creation of the blister rust scout map. Developed for the 1923 field work season in Merrimack County, the scout map divided each town into blocks that were bounded by roads, town lines, water bodies, etc.; each block illustrated the location of brooks, trails, stone walls, forest stands, *Ribes* patches, cellar holes, and pine infections (Newman & King, 1927). By 1927, the map was used to document control work throughout the state (Figure 1.3).

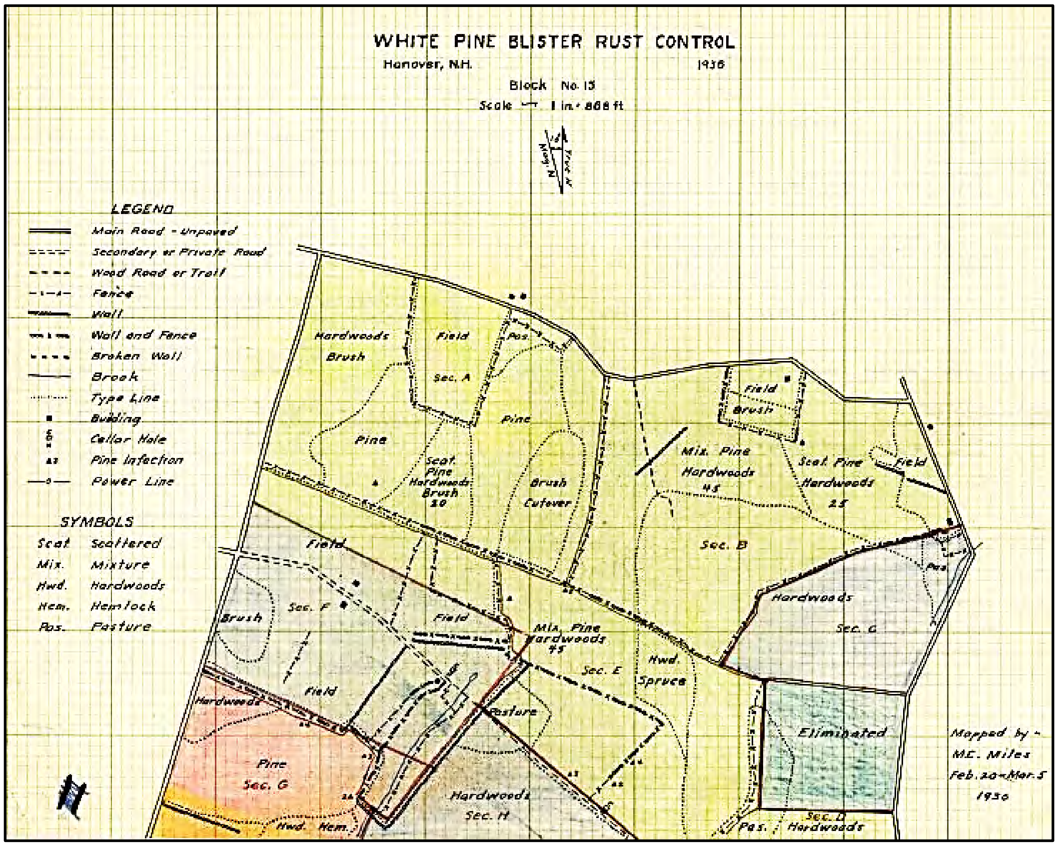

Figure 1.3. Blister rust scout map of Hanover, NH, Block 15, section 1, 1938. (Miles, 1938). Courtesy of NH Blister Rust Control Archives.

The original map was reused for each subsequent working of an area unless an area had changes due to land conversion or development, at which time the area was remapped. These blister rust maps provided historical documentation of the WPBR pathosystem and forest composition in New Hampshire, and therefore, were the basis for this research.

Research Overview

The purpose of this research was to explore the long-term effects of an exotic pathogen on the white pine forests of New Hampshire. Historically, research on the disease was focused on cause and control. Recent studies documented WPBR distribution and incidence levels. To date, no published study of WPBR in New Hampshire or the Northeast has ever approached WPBR research from a long-term perspective. No studies revisited pine stands with historical infection to see if the stands were resilient or altered by the disease. Long-term effects of WPBR on forest regeneration, composition, succession, and sustainability, if found, would provide valuable information for the management of white pine and the control of the disease.

Data for this study was collected from a variety of time periods and sources. The blister rust maps were used to determine the historical locations of white pine forests for observations in 2018. The maps were used for data purposes, including location of WPBR infections, white pine percentages, stand ages, and *Ribes* locations. The industry publication, *The Blister Rust News*, and documents from the archives of the NH Office of Blister Rust Control provided additional anecdotal data, including WPBR incidence levels in various New Hampshire counties.

The research sites, selected from the blister rust maps, represented the diversity of land management and land ownership in New Hampshire, and included land owned by private individuals, conservation commissions and municipalities, and businesses (Figure 1.4). Altogether, 44 sites were privately-owned (blue); 32 sites were owned by federal, state, or local governmental agencies (yellow); and 24 sites were owned by commercial or non-profit businesses (green).

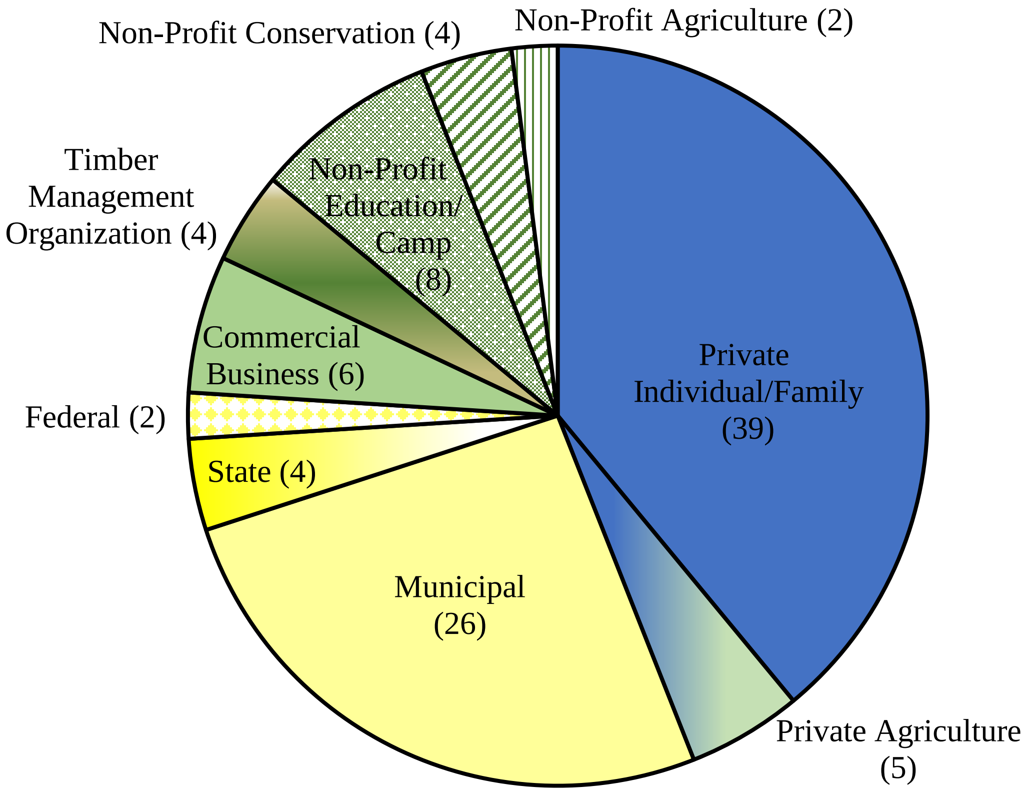

Figure 1.4. Private, municipal, and business ownership of 100 research sites in 2018.

The research sites were used to collect data for three separate yet related topics: 1) past and present WPBR incidence; 2) the use of hazard ratings to predict areas where WPBR was most likely to occur; and 3) the effects of past, present, and long-term WPBR infection of white pine on forest composition, structure, succession, and white pine sustainability. Additional details for each chapter follow.

Dissertation Chapters

My dissertation contains five chapters: an introduction; three chapters with separate but interconnected studies; and a conclusion.

In Chapter Two, I explored the distribution, incidence, and severity of WPBR in New Hampshire in 2018. My purpose was to understand: 1) where the disease was in 2018; 2) the impacts of WPBR on white pine forests; 3) whether trees in some climatic regions of the state were more vulnerable to the disease than others; and 4) how to create a baseline of WPBR incidence for future research. This study combined both historical ecology and forest pathology. I used the historical blister rust maps to select research sites that were positive for WPBR when they were mapped, and research sites that had no WPBR when they were mapped to compare past and present conditions of white pine health and disease presence. I combined field data collected during the spring of 2018 with anecdotal data and maps from the NH Blister Rust Control Program archives and the historical monthly journal, *The Blister Rust News*.

Chapter Three incorporated incidence data from Chapter Two to compare two historical hazard models designed to predict areas of the state with conditions favorable for WPBR establishment. I questioned the accuracy of each historical model for predicting locations most favorable to WPBR infection in 2018. I also explored if the models, using current climatic and biotic data, reflected current conditions in today's climate and forests. I combined historical ecology and climate science to assess the accuracy of the hazard models.

Chapter Four explored the impacts of WPBR on forest composition and succession after more than a century of the disease's presence in New Hampshire's forests. I questioned if WPBR: 1) affected forest composition and structure by acting as a thinning agent (Boyce, 1938); 2) disrupted ecosystems by impacting the natural successional trajectory of white pine forests over time (Kinloch Jr., 2003); and 3) threatened white pine sustainability as a species. White pine and *Ribes* have adapted to disturbances that open the canopy and disturb the soil (Zambino, 2010). In this chapter, WPBR was viewed as a disturbance (Loehman et al., 2018) and an example for my disease-disturbance model. I combined field data from 2018 with silvicultural recommendations in this chapter that was framed in disturbance and succession theory. Based upon the results of this research, I introduced a model that depicted the disturbance impacts of WPBR upon the successional trajectory of New Hampshire forests.

Chapter Five summarized my research findings, recommendations, and implications for future research. I reviewed my key findings on WPBR incidence, hazard models, and forest succession. I discussed the need for additional studies on WPBR in the Northeast and the development of management tools, such as a white pine climate vulnerability index. I showed how this research filled gaps in the literature and demonstrated the value of incorporating historical data to create an initial baseline for framing current research. My research results showed how a forest changed naturally from forest succession, and unnaturally from an exotic pathogen. This chapter reiterated the value of viewing exotic diseases as disturbance agents, which, along with logging and climate change, affect the succession and sustainability of white pine forests in New Hampshire, the Northeast, and North America.

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Chapter Two: White Pine Blister Rust in New Hampshire--Distribution, Incidence, and Severity in 2018

Abstract

Nearly 40 years after the cessation of New Hampshire's blister rust control program, white pine blister rust (WPBR) persists, killing susceptible eastern white pines (*Pinus strobus* L.), particularly in the regeneration size classes. Since 1998, very little research has been conducted on WPBR in New Hampshire to update management strategies for white pine health. This study revisited white pine stands historically mapped by the New Hampshire Blister Rust Control Program from 1929 to 1976. The objectives were to: 1) create a map of WPBR distribution in 2018; 2) compare 2018 incidence levels with those reported in a 1998 study; and 3) create a WPBR severity index for use in future studies. One hundred historically-mapped pine stands were observed during the spring of 2018 for stand composition, site characteristics, and WPBR presence and severity. Key findings included: WPBR was distributed throughout the state but was more prevalent in regions where it was first introduced more than a century ago; and WPBR incidence increased since 1998, but remained below epidemic levels for most stands. Infection and disease severity were highest in the seedling and sapling size classes, supporting previous research in New Hampshire and Maine. *Ribes cynosbati*, believed to have caused historical infections, was infected in 2018; however, *Ribes* presence within 300 yards of white pine was not indicative of WPBR infection. Additional research may clarify how WPBR has managed to persist for more than a century in some New Hampshire locations.

Keywords: white pine blister rust, *Cronartium ribicola*, NH Blister Rust Control Program, eastern white pine, *Pinus strobus*, *Ribes*, New Hampshire, incidence, distribution, severity index

White Pine Blister Rust in New Hampshire: The 2018 Distribution, Incidence, and Severity

White pine blister rust (WPBR) is a disease of five-needled white pines (*Pinus* subgenus *strobus*). The disease is caused by the fungal pathogen *Cronartium ribicola* Fisch., native to the central region of Siberia (Hummer, 2000; Yokota, 1983). In North America, the disease infects, girdles, and kills susceptible white pines of all ages, although the greatest damage is to young trees under age 30 (Martin, Gravatt, & Posey, 1921). The alternate telial hosts, *Ribes* (gooseberries and currants), and *Pedicularis* and *Castilleja* species in western states, are unharmed (McDonald, Richardson, Zambino, Klopfenstein, & Kim, 2006; Mulvey & Hansen, 2011; Zambino, Richardson, & McDonald, 2007). Since 1888 or earlier (Spaulding, 1914), the health and sustainability of all five-needled white pine species in North America have been threatened by WPBR, most notably whitebark pine (*Pinus albicaulis* Engelm.), (Shanahan et al., 2016) and limber pine (*Pinus flexilis* James), (Schoettle, 2016). The combination of WPBR, mountain pine beetle infestations, fire suppression, and climate change have reduced the populations of whitebark and limber pines in North America; in Canada, they are listed as endangered species (Alberta's Species at Risk Program, 2015; Sniezko, 2016). In the United States, whitebark pine was selected as a candidate for the threatened or endangered species list (U.S. Fish and Wildlife Service, 2016), while limber pine was listed as a "Species of Special Management Concern" in the Rocky Mountain National Park (Schoettle, Burns, Cleaver, & Connor, 2019). In New Hampshire, WPBR has affected the health of eastern white pine (*Pinus strobus* L) for more than a century (Filler, 1925; Foster, 1930; Newman, 1945; Spaulding, 1922).

Pathologists confirmed the introduction of WPBR to New Hampshire at the beginning of the 20th century (Newman, 1923; Spaulding, 1922). By comparing the growth stage of a WPBR canker with the age of the wood on which it was found (Martin, 1944), pathologists estimated the year of infection. In Littleton, WPBR infection was traced to white pine nursery stock imported from England to Lyndonville, Vermont around 1900 (Foster, 1930). In 1909, cankers on white pines in Cheshire and Hillsborough counties were dated to 1901 (Newman, 1945). By 1910, WPBR was established in at least three southern and western New Hampshire counties (Filler, 1925; Newman, 1945; Spaulding, 1922). By 1919, WPBR infection had been found in at least one town in every New Hampshire county (Figure 2.1 and Appendix A-1); and by 1920, the disease had spread throughout the state's white pine region (Appendix B-1) that encompassed all of the state except the northernmost portion of Coos County (Spaulding, 1922), (Table 2.1). While the disease continued to spread, the blister rust crews removed *Ribes* from the landscape; in 1919, the crews eradicated 1,659,936 wild and 21,171 cultivated *Ribes* in 49 towns; the following year, 2,061,996 wild and 22,206 cultivated *Ribes* were removed from 54 towns in an effort to save the state's valuable white pine (State of NH Forestry Commission, 1920).

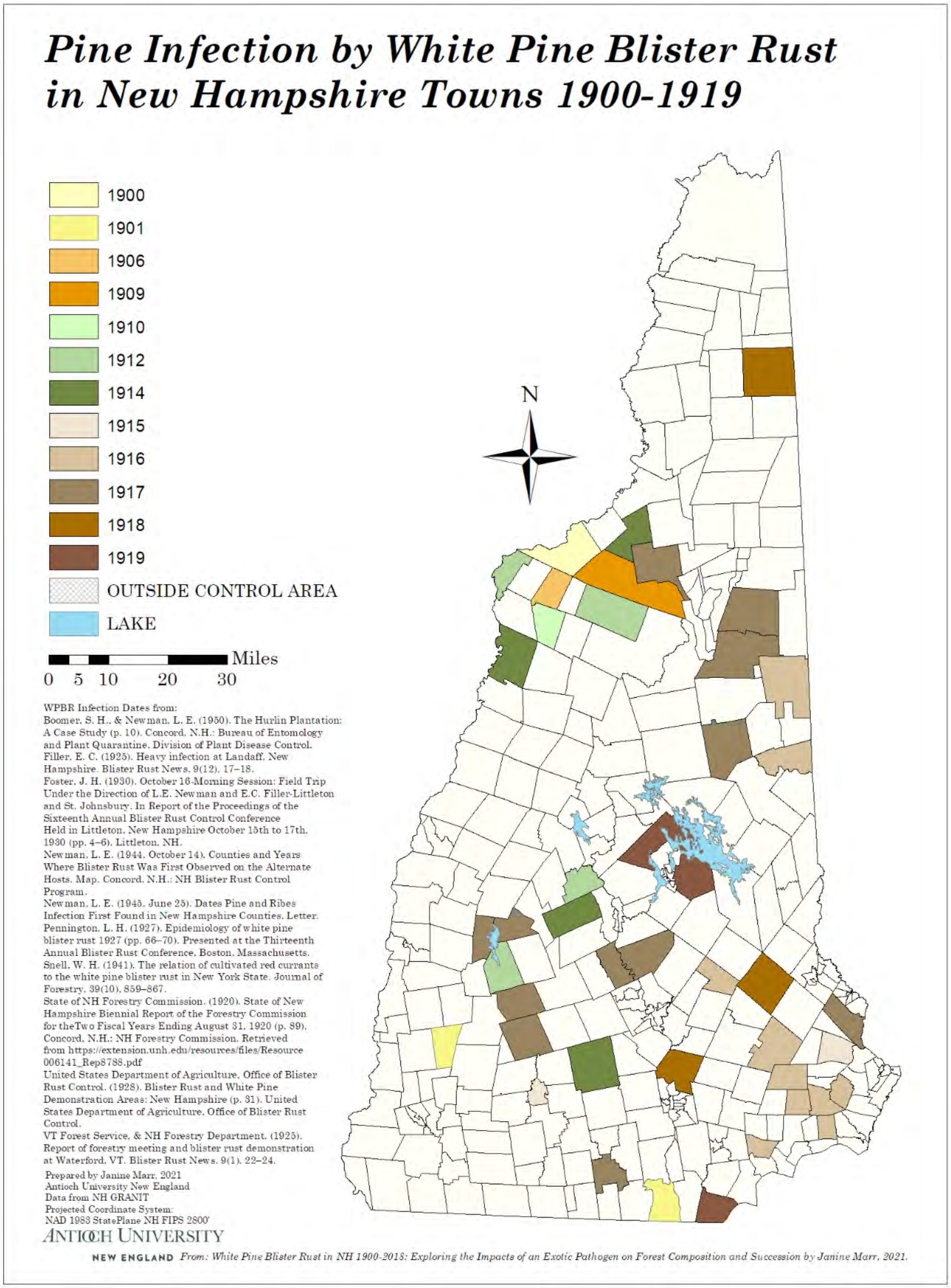


Figure 2.1. Early WPBR infections in New Hampshire towns, 1900-1919.

Table 2.1

Early History of WPBR in New Hampshire

Year	Event	Reference
1900	Littleton (Grafton County) infection traced to white pines imported from England to Lyndonville, VT.	Foster (1930)
1901	WPBR cankers formed on eastern white pines (*Pinus strobus* L.) in Cheshire County.	Newman (1945)
1909	WPBR confirmed on *Ribes* in Hillsborough County.	Newman (1945)
1914	Disease spread beyond cultivated red & black currants to native pasture gooseberry (*R. cynosbati* L.) & skunk currant (*R. glandulosum* Grauer).	Spaulding (1922)
1915	First infections in Strafford and Rockingham counties confirmed.	Spaulding (1922)
1915-1916	First official mention of WPBR in NH in biennial report of Forestry Commission	State of New Hampshire Forestry Commission (1924)
1916	WPBR established in entire white pine region of New Hampshire.	Spaulding (1922)
1917	NH law passed that required all landowners within areas designated by state forester to remove & destroy all *Ribes* and infected pines.	Secretary of State (1917)
1917-1980	*Ribes* eradicated or treated with chemicals by NH Blister Rust Control Program. Discontinued in 1980 (K. Lombard, personal communication, 2018).	State of New Hampshire Forestry Commission (1920)
1922	All towns in Belknap & Strafford counties had infected pine; 16 towns in Grafton County reported ≥ 25% of all white pine infected.	NH Forestry Commission (1922)
1926	Official control area designated in NH to prohibit the shipment of *Ribes* south of Stratford & Erroll. Possession of any *Ribes* within control area prohibited.	Pierce (1926)

Early surveys of WPBR incidence, defined as the percentage of the white pine population with infection, indicated that New Hampshire's northern region from Littleton to Lancaster was most heavily infected and incidences often ranged from 70-100% (United States Department of Agriculture, 1928). In 1998, the same Littleton to Lancaster region had a mean incidence of 7.2%; (Lombard & Bofinger, 1999). Since 1998, no research has been conducted specifically on the distribution, incidence, and severity of WPBR in New Hampshire.

The few published studies on WPBR in New England confirm that WPBR still exists (Bergdahl & Teillon, 2000; Lombard & Bofinger, 1999; Munck, Tanguay, Weimer, Villani, &

Cox, 2015; Ostrofsky, Rumpf, Struble, & Bradbury, 1988), but its impacts upon white pine after a century of naturalization remain unknown. This study was conducted to explore the long-term impacts of WPBR on white pine stands in New Hampshire. I used a historical ecology framework to build upon past research conducted in New Hampshire. Data from multiple points in time were compared with 2018 data to explore how WPBR distribution and incidence have changed since New Hampshire's white pine region was mapped by the NH Office of Blister Rust Control. Objectives included: mapping WPBR distribution in 2018 to determine if WPBR persisted in historically-infected stands; comparing 1998 and 2018 incidence levels to reveal patterns in WPBR persistence; and creating a baseline of WPBR distribution, incidence, and severity for future research purposes.

Methods

A field survey was conducted to record the presence of WPBR cankers as evidence of the disease during the spring of 2018 when sporulating cankers were most visible. One hundred research sites were selected from white pine stands mapped by the New Hampshire Blister Rust Control Program from 1929-1976. The research sites were located in each of New Hampshire's two provinces as defined by climate, geology, hydrology, and potential natural vegetation (Cleland et al., 2007): 1) the Adirondack-New England Mixed Forest Province, characterized by mountains and glacial features in western and northern New Hampshire; and 2) the Northeastern Mixed Forest Province, with a varied topography, warmer climate, and longer growing season in the Seacoast and Lakes Region (Janowiak et al., 2018).

Study Design

Fifty towns were randomly selected from the 226 towns in the historic control area (Appendix B-1). Towns were selected from the 1979 New Hampshire Blister Rust Control map, which indicated the status of the control work at the end of the program (Avery, 1980), (Appendix B-2). The fifty towns were chosen equally from two groups: 25 of the 52 towns rated high-hazard in 1979 and actively managed for WPBR; and 25 of the 129 towns rated low-hazard in 1979 that no longer required regular control work (Table 2.2, Figure 2.2). Forty-five towns had not yet received a hazard rating in 1979 and therefore, were not selected for this study.

Table 2.2

Fifty Towns Selected for 2018 New Hampshire WPBR Study

High Hazard		Low Hazard	
Acworth	Haverhill	Alexandria	Hinsdale
Alton	Lebanon	Andover	Keene
Barnstead	Littleton	Antrim	Lyndeborough
Barrington	Loudon	Belmont	New Boston
Bath	Lyme	Bristol	New London
Brookfield	Moultonborough	Candia	Raymond
Canaan	New Durham	Claremont	Sullivan
Canterbury	Pembroke	Danbury	Sunapee
Charlestown	Strafford	Deering	Swanzey
Concord	Thornton	Dublin	Troy
Cornish	Tuftonboro	Dunbarton	Warner
Enfield	Wakefield	Grantham	Weare
Hanover		Hebron	

Note. Hazard ratings assigned to NH towns in 1979; Avery (1980).

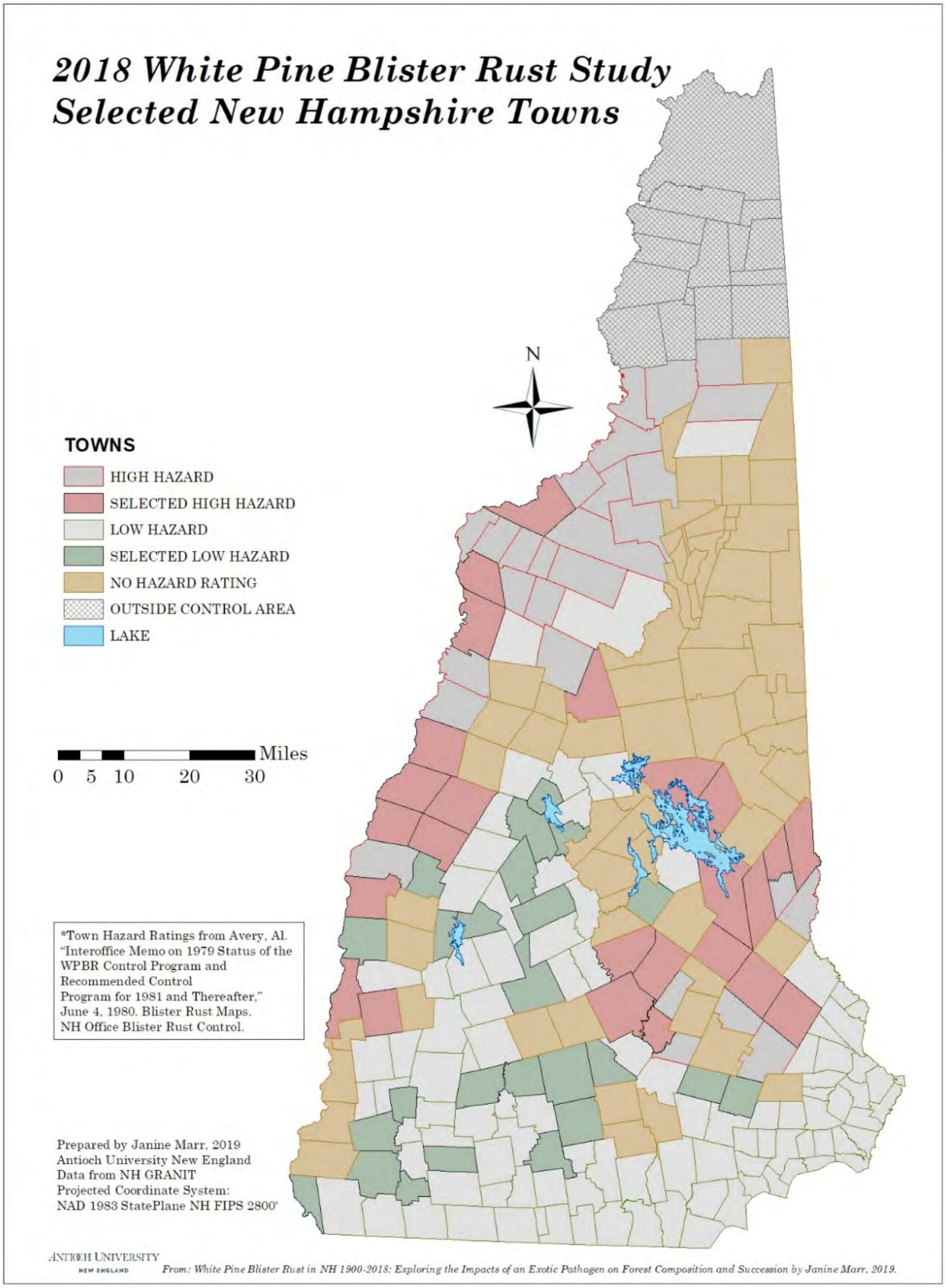


Figure 2.2. Map of 50 towns selected for 2018 WPBR research in New Hampshire.

Two forest areas approximately five acres in size were selected in each town: one represented a historic pine stand with infection; the second represented a pine stand where no infection was mapped (Figure 2.3). I randomly selected a block from the blister rust maps of a town and then selected two stands from the same block, when possible, to reduce differences in topography and climate. If the stands were not at least 300 yards apart (per historical WPBR regulations for white pine management), other stands were selected. Google Earth Pro (version 7.3.1.4507) images were used to confirm the stands were forested in 2018.

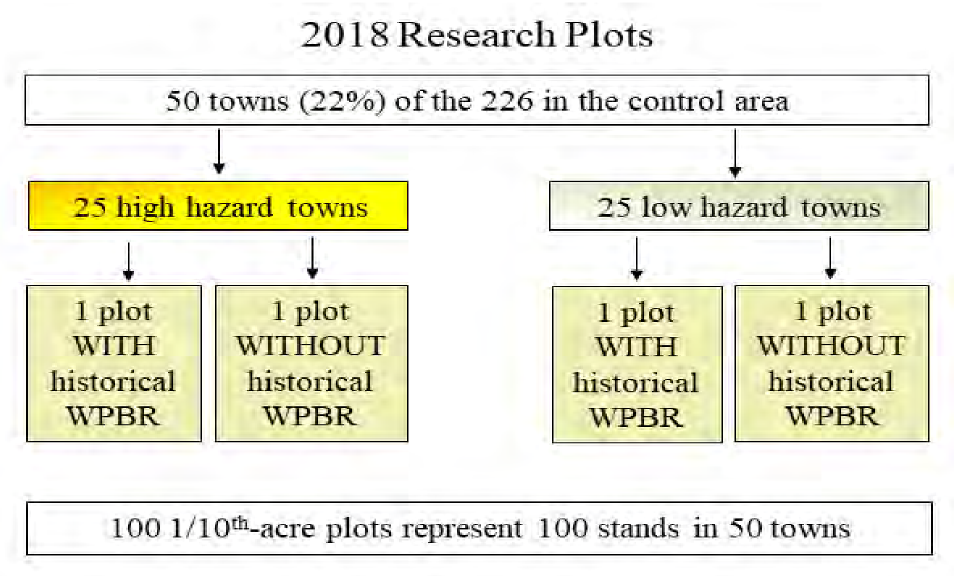


Figure 2.3. 2018 research plots were stratified by hazard rating and infection history.

Sampling occurred in one 1/10th-acre circular plot within each stand per town. One plot was placed in the approximate location of a triangle that marked WPBR infection on the historical blister rust map, and one was located in a pine stand without infection that was at least 300 yards from any triangle on the map. Three hundred yards was the distance chosen for sampling independence as it offered an opportunity to evaluate the historically-documented and traditionally-accepted recommendations for maintaining a 200-300 yards *Ribes*-free zone for white pine in regions where WPBR was present (Detwiler, 1920; Spaulding, 1922). The map below demonstrates the selection process (Figure 2.4). The triangle circled in red (in the map's center) was chosen as the plot within a young pine stand with historical infection. A second young pine stand was selected to the southeast to represent a stand without WPBR (circled in red); the stand was at least 300 yards from other WPBR infection. Measurements from the nearest roads, stone walls, streams, and cellar holes on the historical blister rust maps were used to approximate the plot locations on the 2018 Google Earth map.

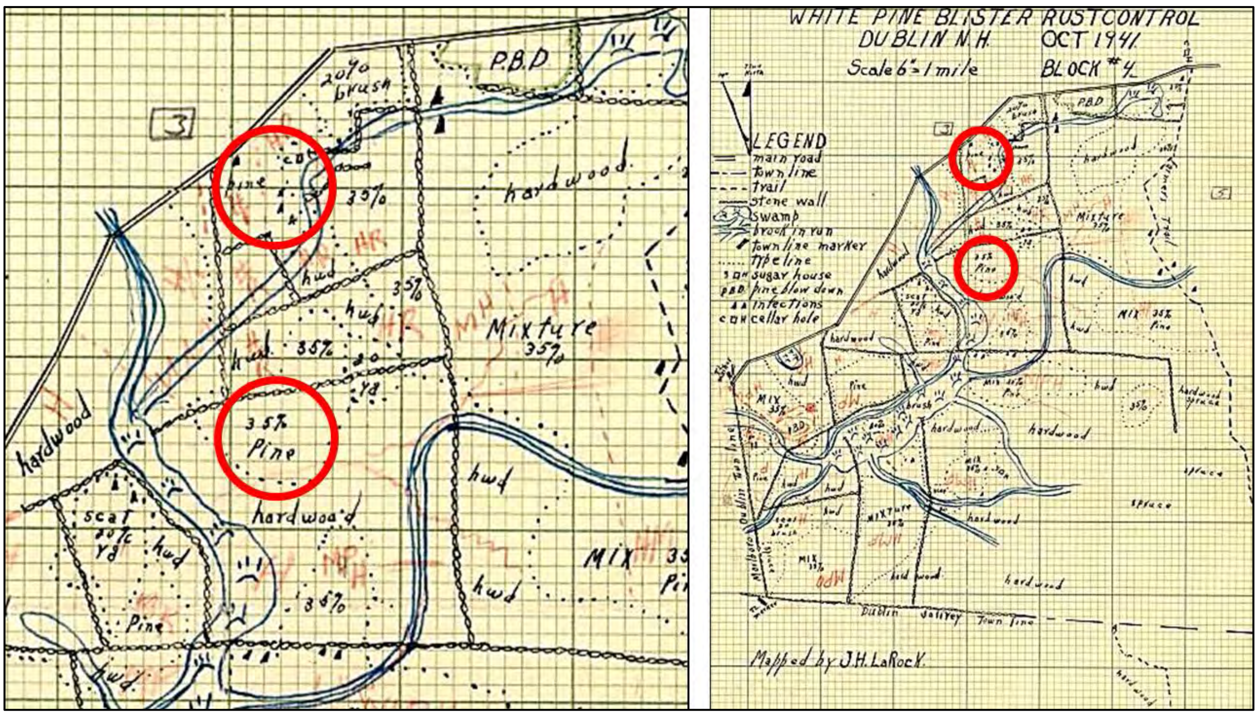


Figure 2.4. Plot selections using historical blister rust map for Dublin, NH (LaRock, 1941). Courtesy of NH Blister Rust Control Archives.

In addition to placing research plots for sampling independence, they were also located where no disturbances such as fire (e. g. Marlow Fire of 1941) or hurricane blowdown (e. g. 1938 Hurricane) had been historically mapped, and where no active or recent logging (<10 years) occurred (per Google map imagery and landowner confirmation). Each plot was placed onto the Google Earth map to confirm that they were at least 300 yards apart; the coordinates were then loaded into ArcGIS (10.6) for mapping; the GPS coordinates were imported into a Garmin GPSMAP 60CSx for locating on the ground. Each plot was visited once for observations between May 1 and June 3, 2018 when cankers were actively releasing aeciospores.

Sampling Methods

Data collected in the field at each plot included site and stand features: elevation; aspect; topographic position (valley, lower slope, mid-slope, upper slope, ridge) (Jenness, 2006); percentage canopy cover; tree species and size classes; *Ribes* presence and evidence of WPBR infection, and the presence and severity of WPBR cankers. All standing trees in each plot were tallied by species, live or dead, and diameter at breast height (DBH) 4.5 feet above the ground using a Biltmore stick. All white pines, alive or dead, with evidence of WPBR infection (aecial cankers and scars, including bark discoloration and swelling around the cankers), were included in the WPBR data to assess the stand-level impact of the disease (Ostrofsky et al.,1988); however, dead trees that had no bark or easily recognizable WPBR cankers were recorded as non-WPBR deaths. Active, inactive (non-sporulating), and dead cankers and scars (Phelps & Weber, 1969) were recorded for WPBR identification (Figure 2.5).

Figure 2.5. Active (left), non-sporulating (middle), and dead WPBR cankers (right). Photos by Janine Marr.

Building upon previous research in western states that measured WPBR severity based upon canker presence and location on each tree (Burns, 2006: Smith & Hoffman, 2000), I developed a numerical scale for branch and stem cankers that represented the canker placement in relation to the main stem (Smith & Hoffman; 2000), and the percentage of main stem girdled (Table 2.3). A value of zero indicated that no cankers were present. The highest value, five, was assigned to cankers that had girdled at least 50% of the main stem; death was imminent and could be attributed to WPBR (Pike, Robison, Maynard, & Abrahamson, 2003). Trees with branch and stem cankers were assigned a severity rating for the stem canker (Ostrofsky et al., 1988). Stem cankers were measured by visually examining the circumference of the cankered stem (and discolored bark at the outer edge of the infection) to determine if <50% or ≥50% had been girdled.

Table 2.3

White Pine Blister Rust Severity Ratings

Severity	Description	Canker Distance from Stem
0	None	No cankers visible
1	Low	Branch canker > 24" from bole
2	Moderate	Branch canker 6-24" from bole
3	Serious	Branch canker < 6" from bole
4	Severe	Stem canker girdled < 50% of bole
5	Lethal	Stem canker girdled 50-100% of bole

Ribes presence was recorded using three spatial scales: within the 1/10th acre plot; < 300 yards of the center of the plot; and > 300 yards of the plot's center. *Ribes* and early invasives such as bush honeysuckle (*Lonicera* spp.) were the prominent species that had leafed out when the field research was conducted, making *Ribes* location and identification easier (Figure 2.6). After *Ribes* were recorded as present or absent within the plot, the area was surveyed by walking in circles around the plot in 50-foot increments from the plot's center, beginning with 50 feet from the plot's edge, then 100 feet, 150 feet, etc., until the area around the plot up to 1000 feet had been searched for *Ribes*. *Ribes* found on the way to or from the plot were also recorded. A GPS point was taken with a Garmin GPS64Sc at each *Ribes* location to verify distance from a plot's center and for mapping. A photograph was taken of each *Ribes* patch to assist with identification as needed. The presence of urediniospores on the underside of the leaves, indicating WPBR infection, was also noted.

Figure 2.6. A patch of skunk currant (*Ribes glandulosum*) Deering, NH, May, 2018. Photo by Janine Marr.

Data Analysis

Trees were divided into four size classes in each plot for analysis using the size classifications in the NED-3 program (version 3.0.7.1) (Twery & Thomasma, 2019) (Table 2.4).

Table 2.4

NED-3 Size Class Definitions

Size Class	Diameter at Breast Height (DBH) in Inches
Saplings	1-4.5
Poles	4.6-10.5
Small Sawtimber	10.6-16.5
Medium Sawtimber	16.6-23.5
Large Sawtimber	≥ 23.6

Note. From Twery & Thomasma (2019).

The distribution of WPBR in 2018 was mapped using ArcGIS 10.6-10.8. White pine blister rust incidence was recorded for each stand as the percentage of infected live white pines (Smith, Resler, Vance, Carstensen, & Kolivras, 2011; Smith, Shepherd, Gillies, & Stuart-Smith, 2013), and the percentage of live and dead white pines with observed WPBR cankers. Town, county, and regional incidence were based on the proportion of infected pines to total pines for each grouping at the plot level. The 2018 data were analyzed at the town scale to compare with historical reports of WPBR infection during the height of the epidemic in 1922. The 2018 data were also analyzed at the regional scale to compare with a statewide study from 1998, nearly 20 years after the NH Blister Rust Control Program ended, in which pine stands were sampled in 50 towns and the results were reported by region (Lombard & Bofinger, 1999). Chi-square tests were used to determine: 1) if location, size class, infection history, or *Ribes* presence was associated with infection incidence; and 2) if a relationship existed between size class categories (seedling, sapling, pole, and timber (as determined by tree diameter measurements) and WPBR severity.

Results

A total of 2154 living and dead white pines in all diameter size classes were examined throughout the 100 stands. White pine blister rust cankers were observed on 11.1% of all white pines and 14.7% of the 1476 living pines.

White Pine Blister Rust Distribution and Incidence

Disease presence and distribution in 100 NH stands. In 2018, WPBR infection was observed in 36 of the 100 stands located in 27 of the 50 towns selected for this study. All 100 stands had grown white pine historically, and 50 of the stands were infected when mapped by the NH Office of Blister Rust Control; however, no relationship was found between infection history and WPBR presence in 2018: $X^2(2, N = 100) = 2.51, p = 0.29$. Thirty-two of the 50 stands with no historical infection were again free of WPBR in 2018 (Figure 2.7).

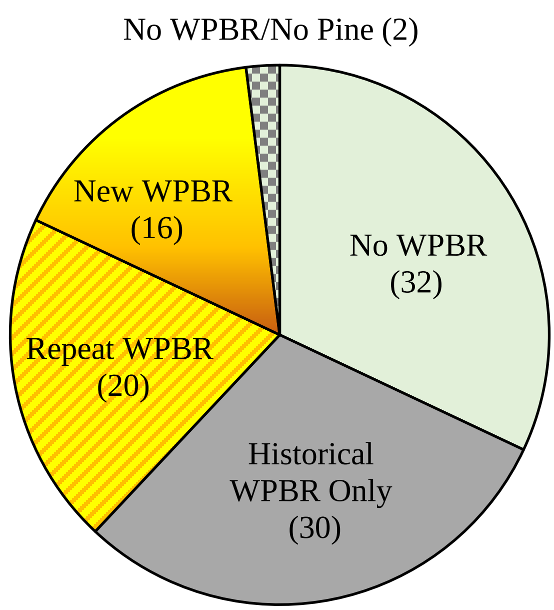


Figure 2.7. Infection status for 100 New Hampshire stands in 2018 by WPBR history.

A map with WPBR presence from 1929-1976 and 2018 showed that the 32 stands with WPBR were well-distributed throughout the state (Figure 2.8).

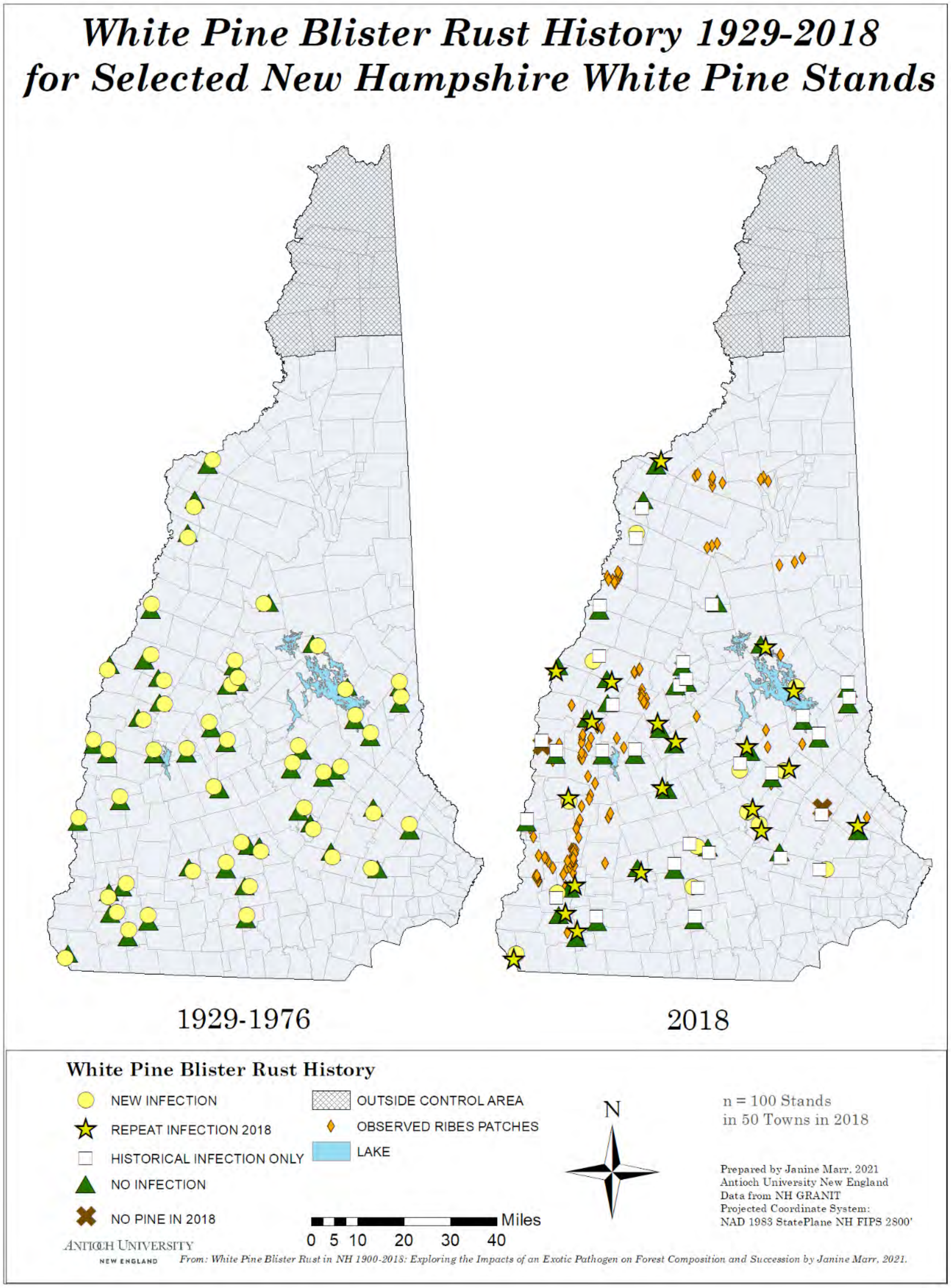
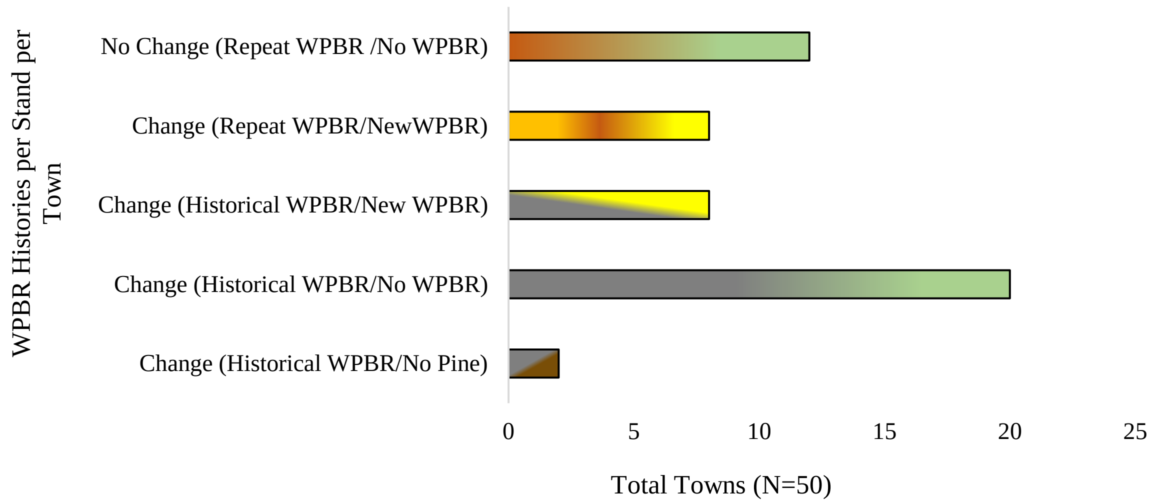


Figure 2.8. WPBR history in 100 stands observed in 2018 and 2018 *Ribes* presence.

Disease presence and distribution in 50 NH towns. In 2018, 14 of the 50 selected towns had no change in infection status from when they were mapped (1929-1976). In those 14 towns, the stand with historical infection was again infected in 2018 (repeat infection), and the stand with no historical infection had no WPBR in 2018 (Figure 2.9). Twenty towns with historical infection had no WPBR in 2018; two towns had no WPBR and no white pine.



Note. No Change (repeat WPBR + no WPBR): Stand with historical WPBR infected 2018; stand with no historical WPBR still without WPBR in 2018.
Change (repeat WPBR + new WPBR): Stand with historical WPBR infected 2018; stand with no historical WPBR had (new) infection in 2018.
Change (historical WPBR + no WPBR): Stand with historical infection no WPBR in 2018; stand with no historical WPBR not infected in 2018.
Change (historical WPBR + new WPBR): Stand with historical infection not infected in 2018; stand with no historical WPBR infected in 2018.
Change (historical WPBR + no pine): Stand with historical infection no WPBR in 2018; stand with no historical WPBR no pine in 2018.

Figure 2.9. Changes in WPBR stand presence for 50 New Hampshire towns in 2018.

In 2018, eight towns experienced WPBR infection in both stands, suggesting that the distribution of WPBR had expanded in those towns during the past several decades. The towns with an expanded presence of WPBR were Acworth, Barnstead, Canaan, Concord, Hinsdale, Moultonborough, Pembroke, and Tuftonboro (Figure 2.10).

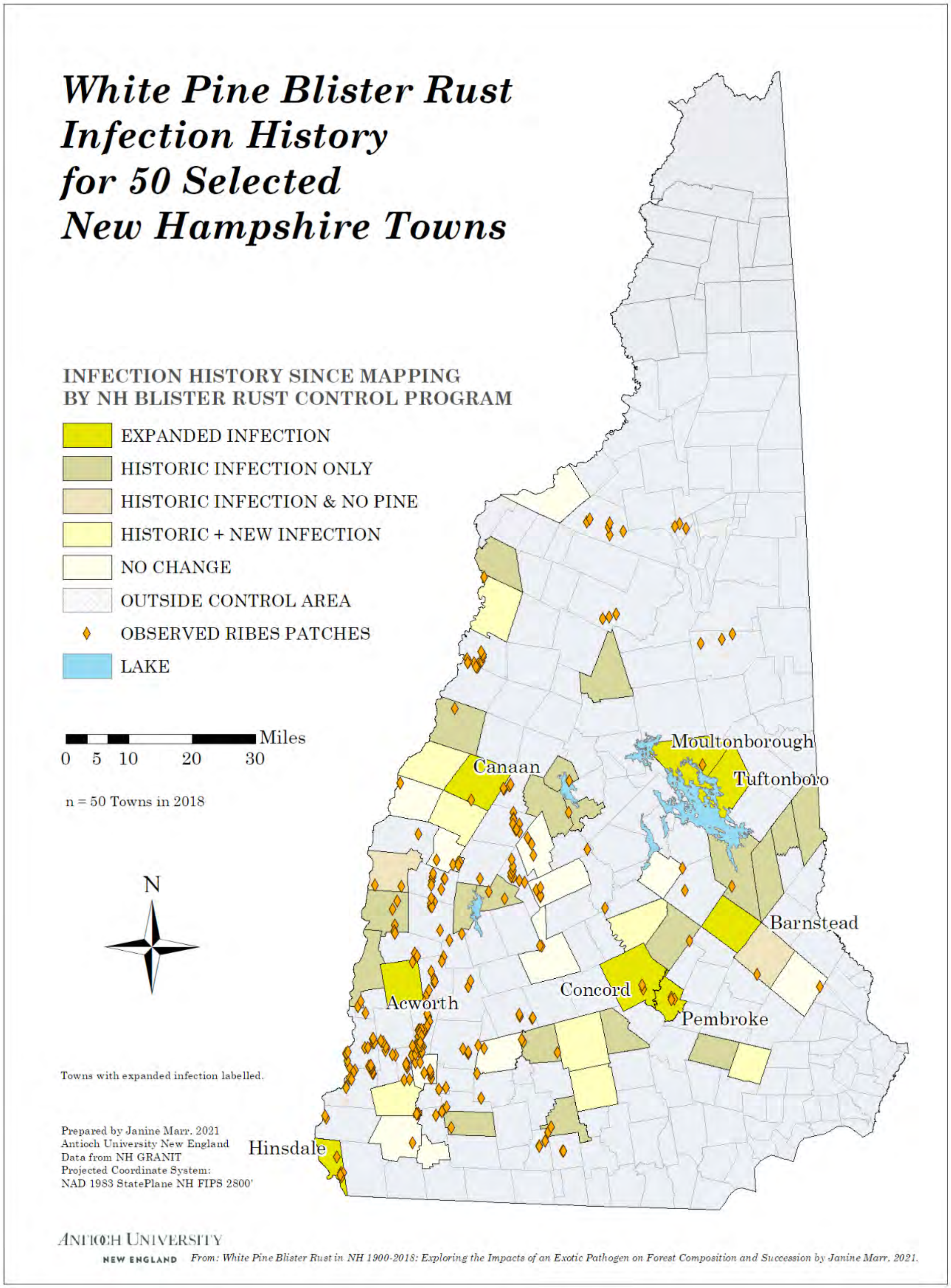


Figure 2.10. WPBR presence since mapping for surveyed stands and 2018 *Ribes*.

Disease incidence in 50 NH towns. In 2018, WPBR incidence ranged from 0-85.7% for living white pines and 0-40.9% for all white pines at the town scale (Table 2.5). White pine blister rust was not observed in 22 towns.

Table 2.5

Incidence of WPBR in New Hampshire Towns in 2018

Town	WPBR % Live Pines	WPBR % Live + Dead Pines	Town	WPBR % Live Pines	WPBR % Live + Dead Pines
Hanover (n=24)	85.7	33.3	Swanzey (n=100)	2.5	2
Warner (n=81)	58.3	38.3	Andover (n=61)	2.1	1.6
Tuftonboro (n=159)	46.6	40.9	Grantham (n=86)	1.4	1.2
Littleton (n=58)	37.2	29.3	Alexandria (n=12)	0	0
Barnstead (n=64)	28.8	26.6	Alton (n=42)	0	0
Hinsdale (n=33)	28.6	24.2	Bath (n=41)	0	0
Acworth (n=73)	26.8	27.4	Bristol (n=26)	0	0
Concord (n=83)	20	18.1	Brookfield (n=25)	0	0
New Boston (n=88)	13.8	18.2	Candia (n=38)	0	0
Weare (n=67)	13.6	11.9	Charlestown (n=2)	0	0
Keene (n=41)	9.1	7.3	Claremont (n=14)	0	0
Barrington (n=51)	8.7	5.9	Cornish (n=1)	0	0
Canterbury (n=28)	8.3	7.1	Deering (n=5)	0	0
Raymond (n=31)	8.3	3.2	Dublin (n=8)	0	0
Sullivan (n=35)	8	5.7	Dunbarton (n=46)	0	0
Lebanon (n=19)	7.1	5.3	Hebron (n=18)	0	0
Antrim (n=35)	6.7	2.9	Loudon (n=25)	0	0
Moultonborough (n=119)	6.7	2.5	Lyme (n=23)	0	0
Haverhill (n=20)	6.3	5	Lyndeborough (n=8)	0	0
Danbury (n=21)	6.3	4.8	New Durham (n=19)	0	0
Belmont (n=56)	6.3	1.8	New London (n=21)	0	0
Pembroke (n=105)	5.8	5.7	Strafford (n=2)	0	0
Enfield (n=48)	5.3	6.3	Sunapee (n=52)	0	0
Troy (n=44)	4.3	4.5	Thornton (n=44)	0	0
Canaan (n=44)	3.1	2.3	Wakefield (n=8)	0	0

Note. n = total live + dead white pine stems for both 1/10th acre plots per town.

At the town scale, WPBR incidence >20% for all white pines (alive and dead) occurred in seven towns distributed throughout the state (Figure 2.11).

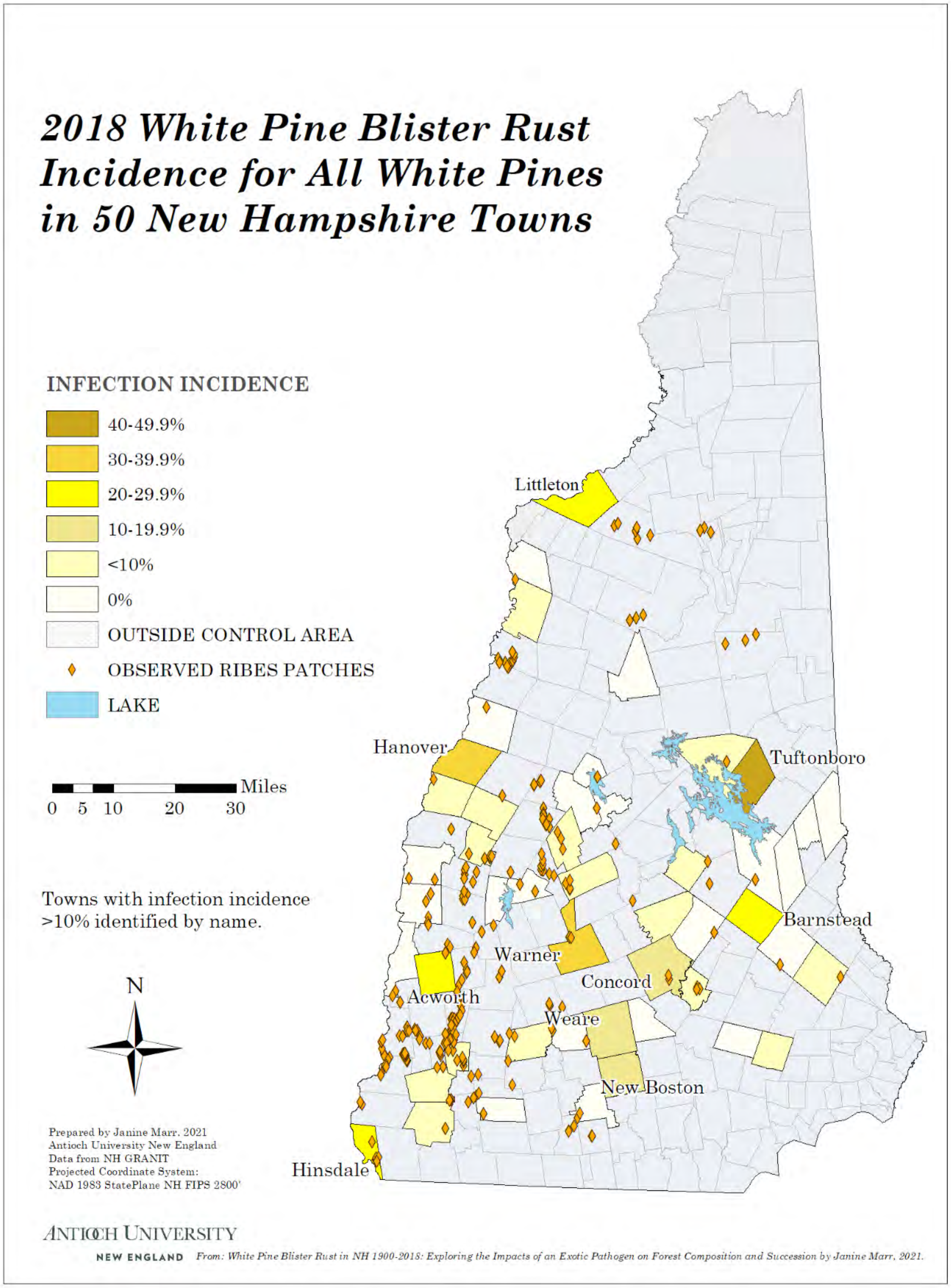


Figure 2.11. WPBR incidence and *Ribes* presence for New Hampshire towns in 2018.

Historical WPBR incidence data were available for living pines in 15 of the 50 towns surveyed in 2018, some as reports on the average incidence for the entire town, and others as incidence for one specific property (Table 2.6). Overall, town incidence levels reported by the NH Office of Blister Rust Control during the early years of the epidemic were much higher than in 2018. The only two towns with WPBR incidence similar to the early years of the epidemic were Hanover and Warner.

Table 2.6

WPBR Incidence for Living Pines in 15 NH Towns in the 1920s and 2018

Town	Year	Historical %	2018%	Reference
Acworth	1929	70	26.8	Richardson (1929)
Alexandria	1929	72-94	0	Richardson (1929)
Andover (1 lot)	1924 1928	50 76	2.1	King (1925); United States Department of Agriculture, Office of Blister Rust Control (1928)
Bath	1922	25	0	NH Forestry Commission (1922)
Canterbury	1924	74-80	8.3	King (1925); United States Department of Agriculture, Office of Blister Rust Control (1928)
Charlestown	1929	20	0	Richardson (1929)
Hanover	1929	73-96	85.7	Richardson (1929)
Haverhill	1922 1923	25 20-35	6.3	NH Forestry Commission (1922); United States Department of Agriculture, Office of Blister Rust Control (1928)
Littleton	1919 1921	66.6 60-94	37.2	United States Department of Agriculture, Office of Blister Rust Control (1928); NH Forestry Commission (1922)
Loudon (1 lot)	1924	50	0	King (1925)
Lyme	1922 1929	25 72	0	NH Forestry Commission (1922); Richardson (1929)
Moultonborough	1928	30	6.7	United States Department of Agriculture, Office of Blister Rust Control (1928)
New London	1928	78	0	United States Department of Agriculture, Office of Blister Rust Control (1928)
Pembroke (1 lot)	1924	70	5.8	King (1925)
Sunapee	1928	52.5	0	United States Department of Agriculture, Office of Blister Rust Control (1928)
Wakefield (1 lot)	1928	25	0	United States Department of Agriculture, Office of Blister Rust Control (1928)
Warner (1 lot)	1924	60	58.3	King (1925)

Note. Historical data from: Richardson, G. F. (1929). New Hampshire's Most Valuable Forest Crop, White Pine; King, T., J. (1925). Is blister rust increasing?; United States Department of Agriculture, Office of Blister Rust Control. (1928). *Blister Rust and White Pine Demonstration Areas: New Hampshire*; NH Forestry Commission. (1922). Control of the White Pine Blister Rust. In Biennial Report of the Forestry Commission for the Two Fiscal Years Ending June 30, 1922.

Disease presence and distribution in nine NH counties, 1922-2018. By 1922, WPBR was documented in every county in New Hampshire (NH Forestry Commission, 1922), occurring in 85.6% of all towns in the nine counties fully within the control area, and in 54.8% of the 50 towns sampled in 2018. In 1922, WPBR was present in every town in Belknap and Strafford counties (NH Forestry Commission, 1922); however, in 2018, the disease was observed in 66.7% of the towns surveyed in Belknap County, and 33.3% of the towns surveyed in Strafford County (Table 2.7). The counties with similar percentages of towns with WPBR in 1922 and 2018 were Cheshire (>80%) and Hillsborough (≥60%); Cheshire was the county with the highest percentage of surveyed towns with WPBR in 2018.

Table 2.7

Percentage of Towns per County with WPBR in 1922 and 2018

County (Total Towns)	1922	2018	Sampled 2018
Belknap (n=10)	100	66.7	3
Strafford (n=10)	100	33.3	3
Sullivan (n=14)	92.9	33.3	6
Cheshire (n=22)	87	83.3	6
Carroll (n=18)	83.3	50	4
Grafton (n=38)	82.1	50	12
Merrimack (n=25)	81.5	66.7	9
Rockingham (n=36)	75.7	50	2
Hillsborough (n=29)	67.7	60	5
Statewide Average	85.6	54.8	

Note. 1922 data from NH Forestry Commission (1922); 2018 data from 50 sampled towns.

A map comparing the percentage of towns for each county with WPBR showed that the counties with the highest percentage of infected towns were distributed throughout the state in 1922, and in the central and southern portions of the state in 2018 (Figure 2.12).

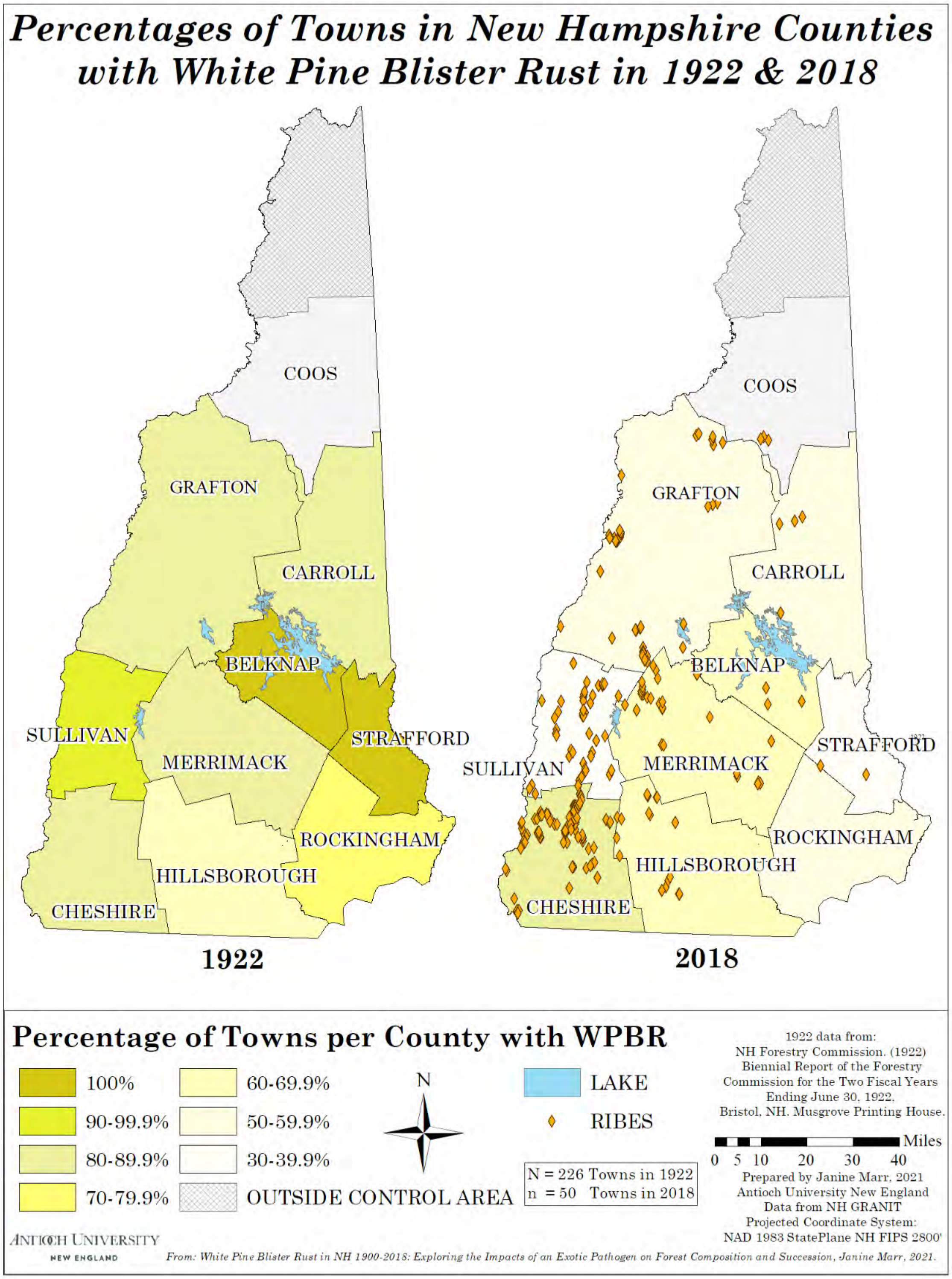


Figure 2.12. Towns per county with WPBR, 1922 and 2018, and 2018 *Ribes*.

Disease incidence in nine NH counties in 2018. In 2018, Carroll County had the highest WPBR incidence and Rockingham County had the lowest in both the live pine and combined live ad dead pine categories (Table 2.8). Hillsborough County had nearly equal incidence levels at 12.4% for live pines, and 12.3% for live and dead pines combined. Overall, WPBR incidence for live pines was higher than the incidence for combined live and dead pines.

Table 2.8

Incidence of WPBR in New Hampshire Counties in 2018

County	Live Pine %	Live + Dead Pine %	Total Towns
Carroll	33.2	21.9	4
Belknap	17.5	11.1	3
Merrimack	14.1	11.9	9
Hillsborough	12.4	12.3	5
Grafton	12.2	8.2	12
Sullivan	9.8	9.2	6
Cheshire	8.3	6.5	6
Strafford	5.3	4.2	3
Rockingham	3.1	1.4	2

Note. Nine of NH's 10 counties were surveyed; no stands were examined in Coos County in 2018.

Disease presence and distribution in six NH regions, 1998-2018. Results from a 1998 study on WPBR incidence in 50 New Hampshire towns reported that the western and northern regions of the state had a higher percentage of stands with WPBR; in 2018, WPBR was observed in more stands in the western and southern regions (Figure 2.13). In 2018, 85% of the stands surveyed in the North Country were infected with WPBR (Lombard & Bofinger, 1999), compared to 33.3% of the stands in 2018 (Table 2.9). The greatest increase occurred in the southwest region where incidence rose from 16.7% in 1998 to 42.3% in 2018.

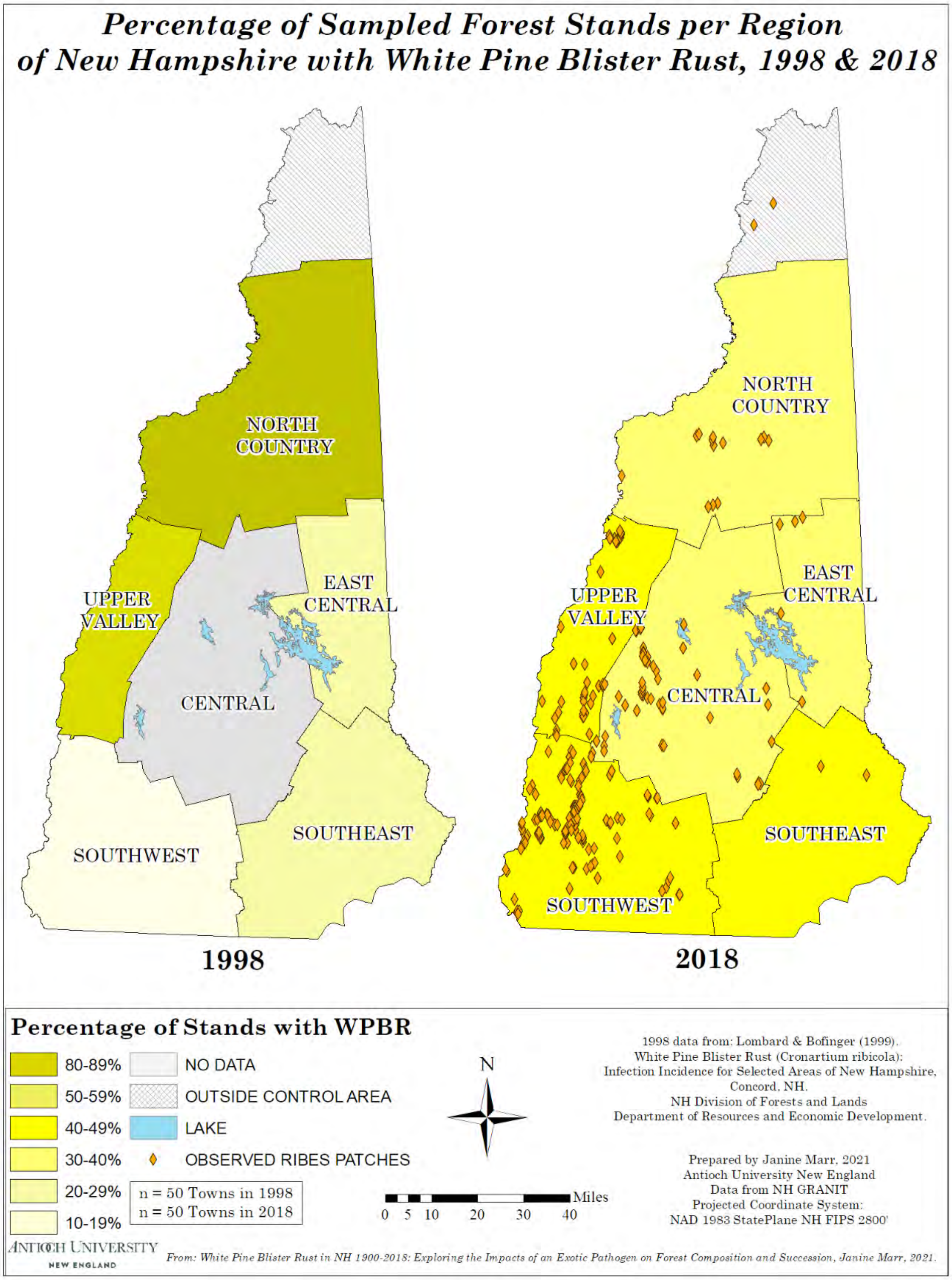


Figure 2.13. Stands with WPBR by region, 1998 and 2018, and 2018 *Ribes*.

Table 2.9

Percentage of New Hampshire Stands with WPBR by Region, 1998 and 2018

Region	1998	2018
North Country	85	33.3
Upper Valley	56	40
Southeast	28	44.4
East Central	20	33.3
Southwest	16.7	42.3
Central	n/a	30

Note. 1998 Data from Lombard & Bofinger (1999). No central region was designated in 1998 for comparison with 2018 survey data.

Disease incidence in NH regions, 1998-2018. White pine blister rust incidence was higher in 2018 than in 1998 for all regions of the state (Table 2.10). The greatest increase in incidence occurred in the East Central region. From 1998 to 2018, the Upper Valley was the only region that retained incidence levels below 5%.

Table 2.10

Regional Incidence of WPBR in New Hampshire 1998-2018

Region	1998 Live Pines	2018 Live Pines	2018 Live + Dead Pines
North Country	7.2	21.5	15.1
Upper Valley	2.7	5.7	5.4
Southeast	1.2	17.2	11.3
East Central	0.6	27.4	18.3
Southwest	0.3	12.4	11.5
Central	n/a	11.8	8.4
2018 Infected Pines		217	240
2018 Total Pines		1476	2154
2018 Statewide Incidence		14.7	11.1

Note. 1998 data for live pines from Lombard & Bofinger (1999). Statewide average for 1998 was 2.4%. No towns in the central region were surveyed in 1998.

Live pine incidence by size class. Statewide, the average WPBR incidence for live pines increased from 2.4% in 1998 (Lombard & Bofinger, 1999) to 14.7% in 2018. The sapling size class had the highest incidence for live pines in 2018 at 28%, followed by seedlings at 14.9% (Table 2.11). Incidence was related to size class: $X^2(3, N = 98) = 116.77, p < 0.001$.

Table 2.11

Size Class Comparison of Live and Dead Pines with WPBR in 2018

Total	Total Live	% Live Infected	Total Live + Dead	% All Pine Infected
Seedling	599	14.9	700	14.4
Sapling	422	28	835	15.2
Pole	165	4.2	316	2.8
Timber	290	1	303	1
Total	1476	14.7	2154	11.1

White pine blister rust incidence by *Ribes* presence. *Ribes* were found in 17 towns at distances from 0-5000’ from the center of a research plot. In seven stands, *Ribes* grew within 300 yards of infected pines. Two stands with *Ribes* had no pine. However, no relationship was detected between *Ribes* presence within 300 yards and WPBR infection $X^2(2, N = 98) = 0.1631$, $p = 0.92$.

Historically, *R. cynosbati* and *R. glandulosum* grew in every town where *Ribes* were observed in 2018 (Table 2.12). Additional *Ribes* species observed in 2018 included the native *R. americanum*, and the European *R. rubrum* and *R. uva-crispa*.

Table 2.12

Historical and 2018 Ribes Presence in Selected Study Towns

Town	Species	In Plot	<300 yards from Plot	>300 yards from Plot	Species Present Historically
Acworth	*R. americanum, R. rubrum*	✓	✓*	✓	*R. glandulosum, R. cynosbati*
Barrington	*R. glandulosum*		✓	✓*	*R. glandulosum, R. cynosbati, R. hirtellum*
Belmont	*R. uva-crispa*		✓*		*R. glandulosum, R. cynosbati, R. triste*
Canaan	*R. cynosbati*		✓*		*R. cynosbati. R. glandulosum*
Claremont	*R. glandulosum*		✓		*R. glandulosum, R. cynosbati*
Cornish	*R. cynosbati*		✓	✓	*R. glandulosum, R. cynosbati*
Deering	*R. glandulosum*		✓	✓	*R. glandulosum, R. cynosbati, R. rubrum*
Dublin	*R. cynosbati*		✓		*R. cynosbati, R. glandulosum, R. rubrum*
Hebron	*R. cynosbati*		✓	✓	*R. cynosbati. R. glandulosum*
Hinsdale	*R. cynosbati*		✓*		*R. triste, R. cynosbati, R. glandulosum*
Loudon	*R. glandulosum*			✓	*R. glandulosum, R. cynosbati*
Lyme	*R. cynosbati*		✓	✓	*R. cynosbati. R. glandulosum*
Moultonborough	*R. americanum*	✓*		✓	*R. cynosbati, R. glandulosum*
New London	*R. americanum*	✓			*R. glandulosum, R. cynosbati*
Pembroke	*R. glandulosum*			✓*	*R. glandulosum, R. cynosbati*
Strafford	*R. glandulosum*			✓	*R. glandulosum, R. cynosbati, R. hirtellum*
Warner	*R. americanum*		✓*	✓	*R. glandulosum, R. cynosbati*

Note. *Stand with WPBR infection in 2018. Historical data from United States Department of Agriculture, Office of Blister Rust Control (1928) unless otherwise noted. Belmont data, Keene (1923). Deering data, Connor (1950). Dublin data, Kline (1970a,1970b). Hinsdale data Van de Poll (1993) (*R. triste*), Hackett (1951).

Non-cultivated *Ribes* patches observed in 70 towns along stone walls, cellar holes, and roads were mapped to show the presence of native and non-native *Ribes* (Figure 2.14). The 76 towns in which permits have been issued by the NH Division of Forests and Lands to growers of cultivated *Ribes* were also mapped for informational purposes and to demonstrate the wide distribution of *Ribes* in New Hampshire.

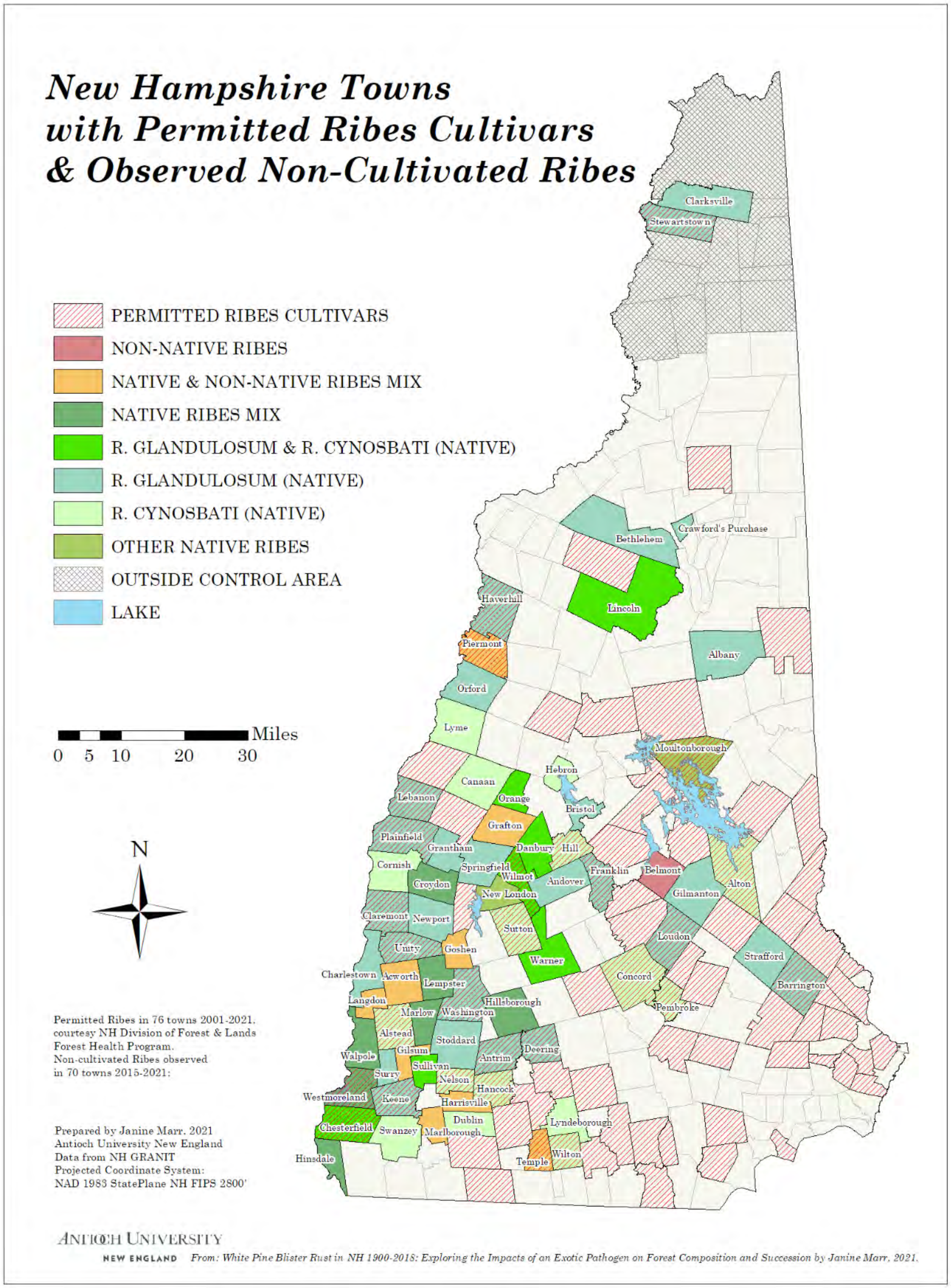


Figure 2.14. New Hampshire towns with permitted and/or non-cultivated *Ribes*.

White Pine Blister Rust Severity

White pine blister rust was observed on 217 living pines. Stem cankers were present in every town where WPBR occurred except Andover and Lebanon, where only branch cankers were observed.

White pine blister rust severity by size class. Of the 217 cankers examined, 83.9% were stem cankers. At least 50% of the infected live pines in each size class had stem cankers with a severity rating of 4 (<50% girdled) or 5 (>50% girdled) (Table 2.13). All severity classes were present in the saplings. Size class was related to the presence of stem or branch cankers: $X^2(3, N = 217) = 18.22, p < 0.001$. Stem cankers were observed more frequently than branch cankers in all size classes. No branch cankers were observed in the timber size class.

Table 2.13

Percentages of Size Class with WPBR Severity Ratings

Severity	Seedling	Sapling	Pole	Timber
#1 Low (n=2)	0	0.8	14.3	0
#2 Moderate (n=13)	0	11	0	0
#3 Serious (n=20)	4.5	11.9	28.6	0
#4 Severe (n=131)	84.3	44.9	14.3	66.7
#5 Lethal (n=51)	11.2	31.4	42.9	33.3
Total (n = 217)	100	100	100	100

Note. Low = branch canker > 24” from bole; Moderate = branch canker 6-24” from bole; Serious = branch canker <6” from bole; Severe = stem canker girdled <50% of bole; Lethal = stem canker girdled 50-100% of bole.

White pine blister rust severity by infection history. Lethal stem cankers (#5) that had girdled more than 50% of the bole were more likely to be found in stands with historical and repeat infection, while severe stem cankers (#4) were more likely to be found in stands with new WPBR infection only (Figure 2.15). The historical presence of WPBR was related to canker severity: $X^2(4, N = 217) = 19.67, p < 0.001$.

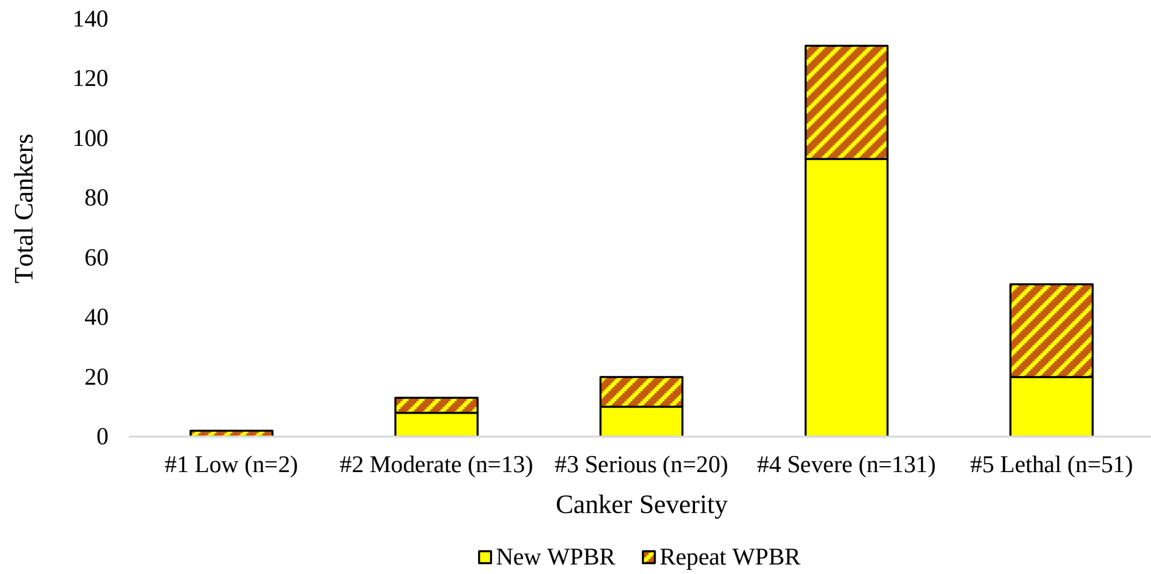


Figure 2.15. WPBR cankers (n=217) on living pine by severity and stand infection history.

Discussion and Conclusion

This study demonstrated changes in the presence and intensity of the disease in various locations of New Hampshire by comparing WPBR distribution and incidence in 2018 to historical records. The disease was more severe in the regeneration size classes. In addition. the presence of susceptible *Ribes* was not an indicator of WPBR infection.

Key Findings

Distribution. In 2018, WPBR was observed in each county and region in this study, although not in each town, supporting the results of research conducted during the historic WPBR epidemic (United States Department of Agriculture, Office of Blister Rust Control, 1928), and during recent years (Weimer, Munck, Cox, Villani, & Tanguay, 2013). Data from 1922 and 2018 suggested that Cheshire and Hillsborough counties along the state's southern border had both white pine populations and climatic conditions that continued to support WPBR infection. At the regional scale, the highest proportion of stands with WPBR shifted from the North Country in 1998 to the southern regions in 2018, suggesting a change in biotic or climatic conditions. However, sampling methods may contribute to the contrasting results. For example, the 1998 study assessed road-accessible pure white pine stands (>80% white pine) with no evidence of logging; where roads functioned as a wind tunnel, particularly within flat valleys, WPBR infection was less likely to occur (White, Brown, & Host, 2002). In contrast, the stands revisited in 2018 were historical white pine stands, often located near heavily-forested class VI roads, or away from public roadways altogether. Half of the stands had experienced historical WPBR infection, while some had been harvested decades ago for large white pine; both disturbances affected the presence and diversity of the size classes present in 2018. In addition, white pine, which represented 30% of the state's sawtimber, was more common in southern New

Hampshire in 2017 than in the northern region of the state (Morin et al., 2020). The difference in WPBR distribution from 1998 to 2018 is likely due to a combination of factors, including sampling differences and ecological factors.

This study found that WPBR had spread within the historic control area into stands that were previously disease-free. The advancement of WPBR into new, susceptible white pine populations, coupled with its low sustainability in previously-infected stands, suggests that New Hampshire’s white pine has not yet established a high rate of resistance to the disease, particularly in southern regions of the state.

Disease history. While historical disease presence at the stand scale was not a good predictor of WPBR presence in 2018, a pattern was evident at the regional scale. The regions with the highest proportion of infected towns in 2018 had documented WPBR infection prior to 1910: Littleton in the Upper Valley in 1900, attributed to infected nursery stock in Lyndonville, VT (Foster, 1930); and Marlow and Nashua in 1909 in the Southwest and Southeast regions, respectively (Newman, 1945; Spaulding, 1922). The state’s Southeast region also bordered the earliest documented infection in Maine, which occurred in 1897 at Kittery Point (Posey & Ford, 1924), across the Piscataqua River from Portsmouth and New Castle. Historical data, when combined with 2018 results at the regional scale, suggested that WPBR persisted in regions where it was first introduced more than a century ago.

Incidence and severity by size class. The seedling and sapling size classes had the highest proportion of WPBR infection, and the highest number of stem cankers in 2018. High incidence and severity in the seedling and sapling size classes were consistent with previous research in New Hampshire and Maine. Seedlings were five times more likely to be infected than the sawtimber size class in New Hampshire in 2014 (Munck et al., 2015). Saplings had the highest infection incidence in Maine in 1987, ranging from 9.2% in areas where *Ribes* eradication had occurred to 13.4% in areas without eradication, despite the observation of just two *Ribes* patches (Ostrofsky et al., 1988). The higher infection rates in the seedling and sapling size classes were also consistent with historical research that suggested WPBR was most likely to affect vigorous growth (Boyce, 1938), particularly, vigorous young growth, which was more susceptible to rapid decline and death by WPBR (Davis & Moss, 1940). Patton (1961) found younger trees were more likely to become infected with WPBR. In western studies, 40% of CO and WY limber pines (*Pinus flexilis* James) with stem cankers were less than two inches DBH (Kearns & Jacobi, 2007); in non-managed stands in AZ and NM, southwestern white pine (*Pinus strobiformis* Engelm.) saplings had the highest proportion of infected trees in all size classes (Goodrich, Waring, Auty, & Sanchez Meador, 2018).

In contrast, the 1998 New Hampshire study reported that large sawtimber over 14” DBH had the highest proportion of WPBR at 3.2% (Lombard & Bofinger, 1999). In 2018, the live sawtimber size class had an incidence rate of 1%, the lowest incidence in this study. Avery (1980) reported a low level of WPBR infection between 1975 and 1979 in New Hampshire, despite an increase in *Ribes* per acre from two to 46; the low level of infection was attributed to unfavorable weather for infection in August and September, and a lack of live branches within eight feet of the ground where most infections were known to occur. Infection in the 2018 seedling and sapling classes occurred within eight feet of the ground, supporting previous reports of young, vigorous growth, and live growth within eight feet of the ground as the most likely to become infected by WPBR. Despite the low incidence levels in the larger sawtimber size classes, this study supports previous research that found the smaller, regeneration size classes experienced more overall infection, more severe infection, and more mortality, affecting their advancement into the larger size classes.

***Ribes*.** In May of 2018, WPBR had infected *R. cynosbati*, *R. glandulosum*, *R. rubrum*, and *R. uva-crispa*; *R. americanum* was the only species free of WPBR when observed. In a study five years earlier, WPBR infection was confirmed on Cr *Ribes* cultivars in every county in New Hampshire (Weimer et al., 2013), indicating that the disease had overcome the cultivars' genetic resistance to WPBR. As a result, all Cr *Ribes* cultivars were removed from the list of permitted *Ribes* in New Hampshire (Munck et al., 2015). Together with 1920s field reports of WPBR on multiple *Ribes* species, including *R. cynosbati* and *R. glandulosum* (Newman, 1945; NH Forestry Commission, 1922; Spaulding, 1922; York, 1926), these findings suggest that both native and non-native *Ribes* are capable of serving as an alternate host to WPBR in New Hampshire and spreading the disease throughout the state's white pine region. The presence of *R. cynosbati* and *R. glandulosum* rooted in and on stone walls in the western and southern regions of the state, which made complete eradication difficult or impossible, suggests they were a contributing factor to the higher occurrence of WPBR observed in the southern and western counties of New Hampshire in 2018 (Figure 2.16).

Figure 2.16. *R. cynosbati* (left) and *R. glandulosum* (right) in stony habitats of NH. Photos by Janine Marr.

While this study did not specifically survey *Ribes* populations, *R. cynosbati* or *R. glandulosum* were found in all but five of the 70 towns where *Ribes* were observed. This finding suggests that: 1) native *Ribes*, and *R. cynosbati* and *R. glandulosum* in particular, may play a larger role in the spread of WPBR today than during the historic epidemic; and 2) managing *R. cynosbati* and *R. glandulosum* populations may help control WPBR spread in a future, changing climate. One observation worth noting was that *Ribes* were not found growing along roadsides where winter road salt was heavy; *R. glandulosum*, in particular, grew above the salt line or along Class VI roads that were not maintained during the winter (Figure 2.17). Salts were used historically to kill *Ribes*; prior to 1944, salt in the form of sodium chlorate was used in a foliar spray, or in combination with borax for treating cut *Ribes* crowns (Benedict, 1981; Offord, Moss, Benedict, Swanson, & London, 1952; Swain, 1931). In 1944, the chemical-based sprays 2,4-D and 2,4,5-T were introduced as more effective and easier to apply (Offord et al., 1952),

Figure 2.17. Ribes glandulosum above salt line, Kancamagus Highway, New Hampshire. Photo by Janine Marr.

A lack of *Ribes* was also observed where the understory was filled with dense honeysuckle (*Lonicera* spp.) or Japanese barberry (*Berberis thunbergii* DC) shrubs.

The presence of native *Ribes* in 69 of the 70 towns (29.6% of the towns in the historical control area) in 2018 may be the result of: 1) the re-establishment of eradicated populations from a seedbank; 2) the spread of existing plants or roots that escaped eradication or chemical spraying; or 3) the establishment of new populations. *Ribes* have germinated from seeds up to 70 years old (Fivaz, 1931) when cultivation, logging, uprooted trees, eradication, and weather events disturbed the soil and released the seeds (Zambino, 2010). *Ribes* seeds have been dispersed by birds, including the blue jay, catbird, cedar waxwing, robin, bluebird, crow, northern flicker, and ruffed grouse (Cooper, 1922). These three causes explain the presence of *Ribes* in a section of Gilsum, NH, in 2018. In Block 20, infected *R. cynosbati* and *R. rubrum* grew in areas where they had been re-worked (eradicated for a second time) in 1960 (Kline, 1960). In addition, *R. cynosbati* had spread to new areas beyond the roadsides and stone walls (Figure 2.18). Since 1951, the roads were widened, trees were cleared, and all of the afore-mentioned birds were observed on the property (J. Marr, personal observation, 2018). Today, no *Ribes* are found along the southernmost stonewall, which is shaded by dense hemlock, and the patch of *Ribes* on the northern portion of the map was mowed and restored to a hay field.

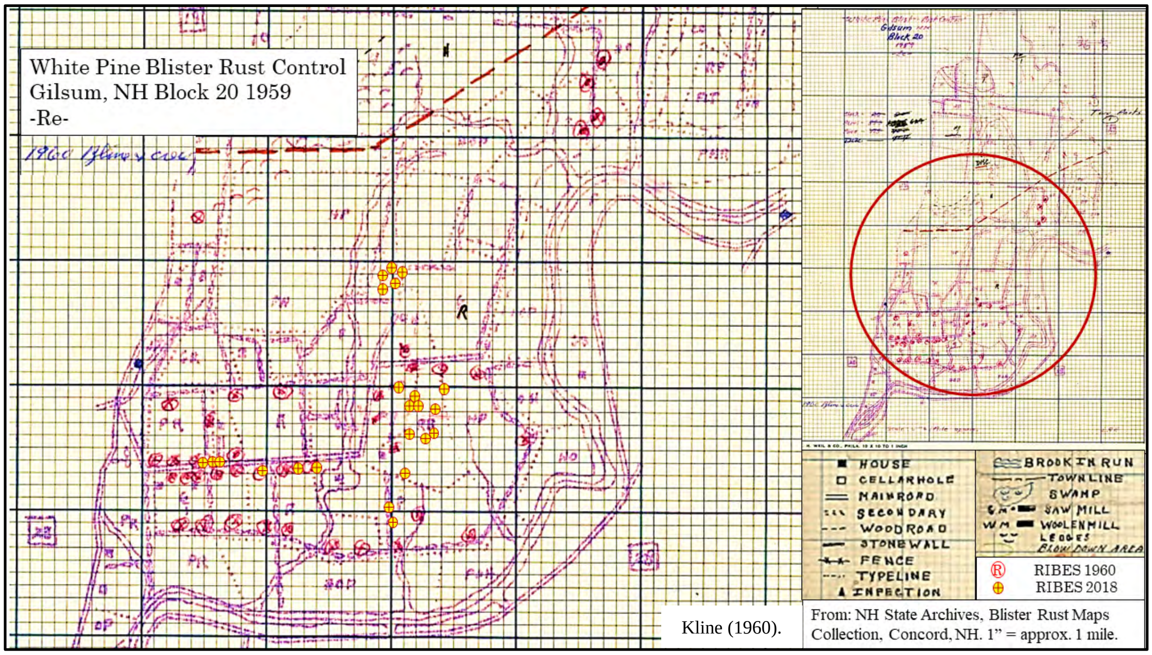


Figure 2.18. Ribes presence, 1960 and 2018, in a portion of Block 20, Gilsum, NH (Kline, 1960). Courtesy of NH Blister Rust Control Archives.

Comparing the presence of *Ribes* in 2018 to historical locations was beyond the scope of this study; however, the use of historical blister rust maps is recommended for landowners wishing to locate potential *Ribes* seed banks or populations, particularly in stands where white pine is desired as a commercial crop.

Incidence history and wild *Ribes*. Historical reports of WPBR incidence suggested that wild *Ribes* may have maintained WPBR in New Hampshire after the eradication of *R. nigrum*. During the epidemic, infection was attributed to the pasture gooseberry (*R. cynosbati*), particularly at Proctor Academy in Andover (United States Department of Agriculture, Office of Blister Rust Control, 1928), and throughout Grafton County. In 1928, New Hampshire Blister Rust Agent Thomas Kane stated:

> *Ribes cynosbati* grow in abundance in this locality [Grafton County] and are considerably larger than those found in the southern part of the State. As most of the pine

> lots in this district range in infection from 15% to 60%, it is to be assumed that the greater proportion of infection is caused by this kind of *Ribes* [*R. cynosbati*], since only a few other lots that I know of were damaged from other species. From my observation I have concluded that this [*R. cynosbati*] is the worst enemy of white pine in my district, as no *Ribes nigrum* are to be found (United States Department of Agriculture, Office of Blister Rust Control, 1928), (p.13a).

In 2018, *R. cynosbati* was the only species observed in Grafton County.

During the early years of the epidemic, the United States Department of Agriculture declared *Ribes nigrum*, the European black currant, to be the species most susceptible to WPBR in the East (Snell, 1941). By 1926, control efforts had almost completely eradicated *R. nigrum* from eastern white pine regions (Benedict, 1981; Maloy, 1997). A study on the susceptibility of cultivated red currants to WPBR documented wild *Ribes* growing as near or closer than cultivated red currants to infected pines, concluding that “red currants are not important in the spread of white pine blister rust” (Snell, 1941, p. 866). No direct comments were made on the role of wild *Ribes* in the spread of WPBR during that study; however, 70 years later, and despite reports from the blister rust control agents, wild *Ribes* were still considered unimportant: “In New England, early control was successful because *R. nigrum* was practically the only inoculum source; red currants (*R. rubrum*) and wild *Ribes* were not important” (Van Arsdel, 2011, p. 64).

Field observations in 2018, which located infected *R. rubrum* and wild *Ribes*, but no *R. nigrum*, were consistent with early studies in New Hampshire that suggested wild *Ribes* were capable of spreading WPBR (Boomer, 1932; Pennington, 1927; United States Department of Agriculture, Office of Blister Rust Control, 1928; York, 1926). Photos for the three years prior to the 2018 field research confirmed telia and basidia development on *R. cynosbati* and *R. glandulosum* in southern New Hampshire (Figure 2.19).

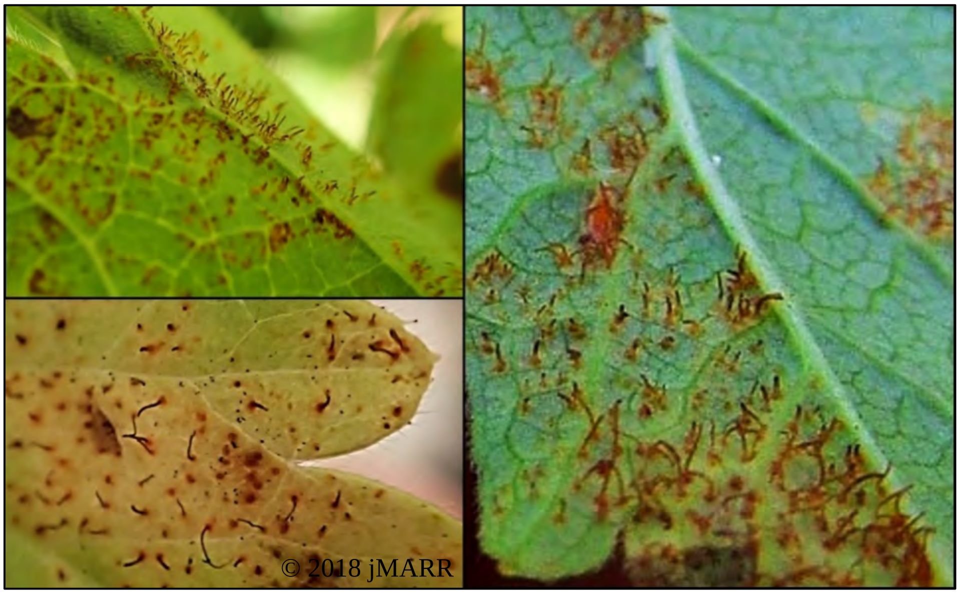


Figure 2.19. Telial columns and basidia on *R. cynosbati* (left) 7/15, 8/16; *R. glandulosum* (right) 10/17, Gilsum, NH. Photos by Janine Marr.

The viewpoint that wild *Ribes* are not important to the spread of WPBR, combined with a general lack of research on wild *Ribes* in the Northeast, and recent observations of *R. cynosbati* and *R. glandulosum* shrubs persisting in New Hampshire and becoming infected by WPBR where incidence levels have increased since 1998, highlight a need to determine the extent to which wild *Ribes* serve as hosts and transmitters of WPBR.

The presence of wild *Ribes* within the historical 300-yard buffer zone of a white pine stand was not a consistent predictor of WPBR infection in 2018 or historically (Detwiler, 1920; Spaulding, 1922). In 1922, a Deerfield, NH infection was attributed to *Ribes* spores that travelled more than 1000 yards to infect white pines (NH Forestry Commission, 1922). The likelihood of long-distance spore dispersal has been proposed in western studies where no relationship was found between *Ribes* presence and WPBR incidence and severity (Burns &

Howell, n.d.; Zambino, 2010). Muir & Hunt (2000) cautioned that, while long-distance spore dispersal most likely occurred on wild *Ribes*, commercial cultivation of susceptible *Ribes* species could enhance the spread of virulent races of *C. ribicola* throughout North America. This study found no commercial *Ribes* growing within 300 yards of the research plots. The lack of strong evidence for a relationship between wild *Ribes* within 300 yards of infected white pines, combined with the lack of commercial *Ribes* within 300 yards of the 2018 research plots, suggests that windborne *Ribes* spores can travel distances greater than 300 yards to infect white pines in New Hampshire.

Limitations

This study was the first in New Hampshire to use approximately 120 years of data to examine WPBR distribution, incidence, and severity. The use of historical maps, data, and research to connect the past with the present was limited due to records no longer archived in the defunct Office of Blister Rust Control. Missing blister rust maps reduced site selection to 25 towns with a high hazard rating in 1979. The purpose of this study was to compare historically-rated high and low hazard sites to determine if a pattern existed between their hazard ratings and WPBR incidence in 2018.

In addition to missing maps, the historical data available in the archives of the NH Office of Blister Rust Control and in the *Blister Rust News* were inconsistent in geographic scale, and years surveyed, limiting the time periods for comparison with 2018 data to 1922, and the 1929-1976 initial mappings. A comparison with the 1998 NH study was difficult in that its methodology focused on plot surveys from the center of current white pine stands, whereas this study focused on revisiting infected locations within historical white pine stands. It was unknown if the 1998 study sites supported *Ribes* or had a history of WPBR. Therefore, the data from 1998 was used as a general record of WPBR incidence, rather than to compare actual towns or research sites by WPBR history.

Future Research

This study demonstrated that WPBR has been able to persist in some historically-infected pine stands, and at levels that would have been considered high during the epidemic. To understand why WPBR reoccurs in some locations, research is needed that focuses on the unknowns: 1) the effects of New Hampshire's topography on WPBR and its hosts within the current and future climates to better predict the areas most likely to support WPBR (Van Arsdel, 2011); 2) which *Ribes* species are most likely to spread the disease, and how far their spores can travel to infect pines; 3) the best management practices for controlling susceptible *Ribes* near white pine stands; and 4) the potential existence of WPBR-resistant pines in New Hampshire's landscape that could become seed sources for future pine stock. Clarifying the relationships between climate, topography, and disease establishment is necessary to understand why the Upper Valley region, east of the Connecticut River, has maintained a high proportion of infected towns since 1998, and potentially, since WPBR was first introduced to New Hampshire. Identifying which *Ribes* species are more likely to spread WPBR will assist the pesticide industry in developing best management practices for landowners; the absence of a state-directed *Ribes* eradication program during the past 40 years has resulted in a lack of herbicide treatments that have been evaluated and approved for the foliar spraying of *Ribes* along stone walls and in wetlands, particularly during drought years when the *Ribes* shed their leaves prematurely (K. Lombard, personal communication, May 7, 2021; D. Cygan, personal communication, May 10, 2021; D. Rousseau, personal communication, May 12, 2021; D. Gladders, personal communication, May 13, 2021).

The goal of this research was to determine how the distribution of WPBR has changed since its introduction to New Hampshire more than a century ago. Despite observed infection throughout the state, 2018 incidence levels suggested that WPBR was most prevalent in the regions where it was first introduced. Researchers are encouraged to build upon the results of this baseline study and monitor WPBR distribution, incidence, and severity over time; doing so will: 1) advance the design and applicability of the rust severity index; 2) inform management practices to sustain New Hampshire's valuable white pine resources in a state where WPBR is both established and well-distributed; 3) clarify the role of native *Ribes* in sustaining WPBR in New Hampshire; and 4) answer the question, "Is WPBR spreading or intensifying in this changing climate, and should we be concerned about the resilience of our white pine?"

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Appendices

A-1. Documented White Pine Blister Rust Infection in New Hampshire 1900-1919

Town	Year	County	Reference
Andover	1914	Merrimack	United States Department of Agriculture, Office of Blister Rust Control (1928). *Blister Rust and White Pine Demonstration Areas: New Hampshire* (p. 31). United States Department of Agriculture, Office of Blister Rust Control.
Bartlett	1917	Carroll	Newman, L. E. (1945, June 25). Dates Pine and *Ribes* Infection First Found in New Hampshire Counties. Letter.
Brentwood	1916	Rockingham	Newman, L. E. (1944, October 14). Counties and Years Where Blister Rust Was First Observed on the Alternate Hosts. Map, Concord, N.H.: NH Blister Rust Control Program.
Canterbury	1917	Merrimack	United States Department of Agriculture, Office of Blister Rust Control (1928). *Blister Rust and White Pine Demonstration Areas: New Hampshire* (p. 31). United States Department of Agriculture, Office of Blister Rust Control.
Carroll	1917	Coos	Newman, L. E. (1944, October 14). Counties and Years Where Blister Rust Was First Observed on the Alternate Hosts. Map, Concord, N.H.: NH Blister Rust Control Program.
Dover	1917	Strafford	Newman, L. E. (1944, October 14). Counties and Years Where Blister Rust Was First Observed on the Alternate Hosts. Map, Concord, N.H.: NH Blister Rust Control Program.
Durham	1915	Strafford	Newman, L. E. (1944, October 14). Counties and Years Where Blister Rust Was First Observed on the Alternate Hosts. Map, Concord, N.H.: NH Blister Rust Control Program; Spaulding, P. (1922). Investigations of the White Pine Blister Rust (Bulletin No. 957). Washington, D.C.: United States Department of Agriculture.
Epping	1916	Rockingham	Newman, L. E. (1944, October 14). Counties and Years Where Blister Rust Was First Observed on the Alternate Hosts. Map, Concord, N.H.: NH Blister Rust Control Program.
Erroll	1918	Coos	Pennington, L. H. (1927). Epidemiology of white pine blister rust 1927 (pp. 66–70). Presented at the Thirteenth Annual Blister Rust Conference, Boston, Massachusetts.
Exeter	1916	Rockingham	Newman, L. E. (1944, October 14). Counties and Years Where Blister Rust Was First Observed on the Alternate Hosts. Map, Concord, N.H.: NH Blister Rust Control Program.
Gilford	1919	Belknap	Newman, L. E. (1945, June 25). Dates Pine and *Ribes* Infection First Found in New Hampshire Counties. Letter.

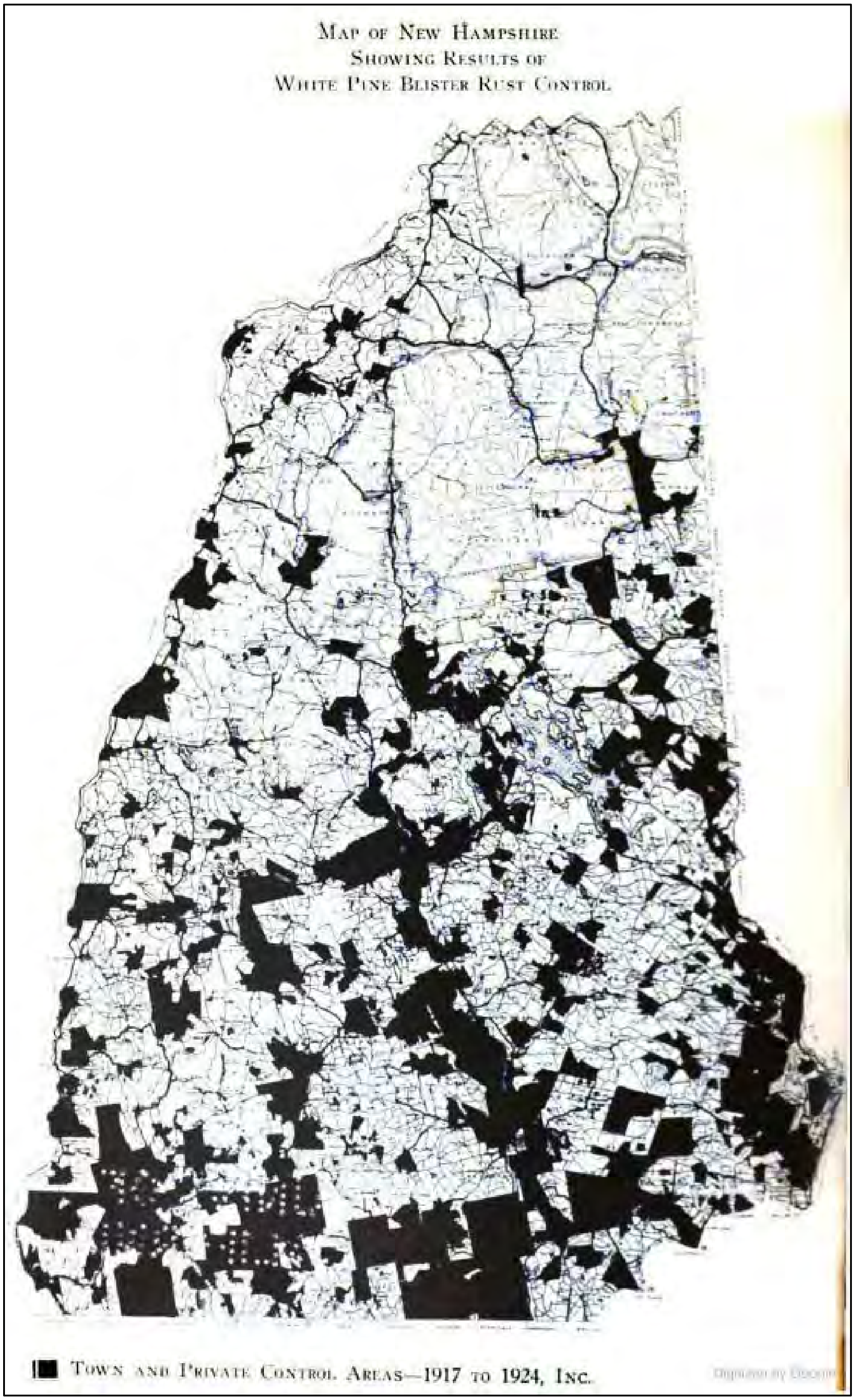
Table A-1 Continued

Town	Year	County	Reference
Hampstead	1916	Rockingham	Newman, L. E. (1944, October 14). Counties and Years Where Blister Rust Was First Observed on the Alternate Hosts. Map, Concord, N.H.: NH Blister Rust Control Program.
Hill	1912	Merrimack	Foster, J. H. (1930). October 16-morning session: Field trip under the direction of L.E. Newman and E.C. Filler-Littleton and St. Johnsbury. In *Report of the Proceedings of the Sixteenth Annual Blister Rust Control Conference Held in Littleton, New Hampshire October 15th to 17th, 1930* (pp. 4–6). Littleton, NH.
Hillsborough	1917	Hillsborough	Newman, L. E. (1944, October 14). Counties and Years Where Blister Rust Was First Observed on the Alternate Hosts. Map, Concord, N.H.: NH Blister Rust Control Program.
Intervale	1916	Carroll	Snell, W. H. (1941). The relation of cultivated red currants to the white pine blister rust in New York State. *Journal of Forestry*, *39*(10), 859–867.
Jackson	1917	Carroll	Boomer, S. H., & Newman, L. E. (1950). *The Hurlin Plantation: A Case Study* (p. 10). Concord, N.H.: Bureau of Entomology and Plant Quarantine, Division of Plant Disease Control.
Kensington	1916	Rockingham	Newman, L. E. (1944, October 14). Counties and Years Where Blister Rust Was First Observed on the Alternate Hosts. Map, Concord, N.H.: NH Blister Rust Control Program.
Landaff	1910	Grafton	Filler, E. C. (1925). Heavy infection at Landaff, New Hampshire. *Blister Rust News*, *9*(12), 17–18.
Littleton	1900	Grafton	Foster, J. H. (1930). Field trip under the direction of L.E. Newman and E.C. Filler--Littleton & St. Johnsbury. In *Report of the Proceedings of the 16th Annual Blister Rust Conference, Held in Littleton, New Hampshire, October 15th to 17th, 1930*. Littleton, NH: U.S. Department of Agriculture Bureau of Plant Industry, Office of Blister Rust Control; United States Department of Agriculture, Office of Blister Rust Control. (1928). *Blister Rust and White Pine Demonstration Areas: New Hampshire* (p. 31). United States Department of Agriculture, Office of Blister Rust Control.
Marlow	1909	Cheshire	Newman, L. E. (1923, March 20). Letter to Louis E. Hayes, Alton, NH, about WPBR; Spaulding, P. (1922). Investigations of the White Pine Blister Rust (Bulletin No. 957). Washington, D.C.: United States Department of Agriculture; State of NH Forestry Commission. (1920). *State of New Hampshire Biennial Report of the Forestry Commission for the Two Fiscal Years Ending August 31, 1920* (p. 89). Concord, N.H.: NH Forestry Commission.

Table A-1 Continued

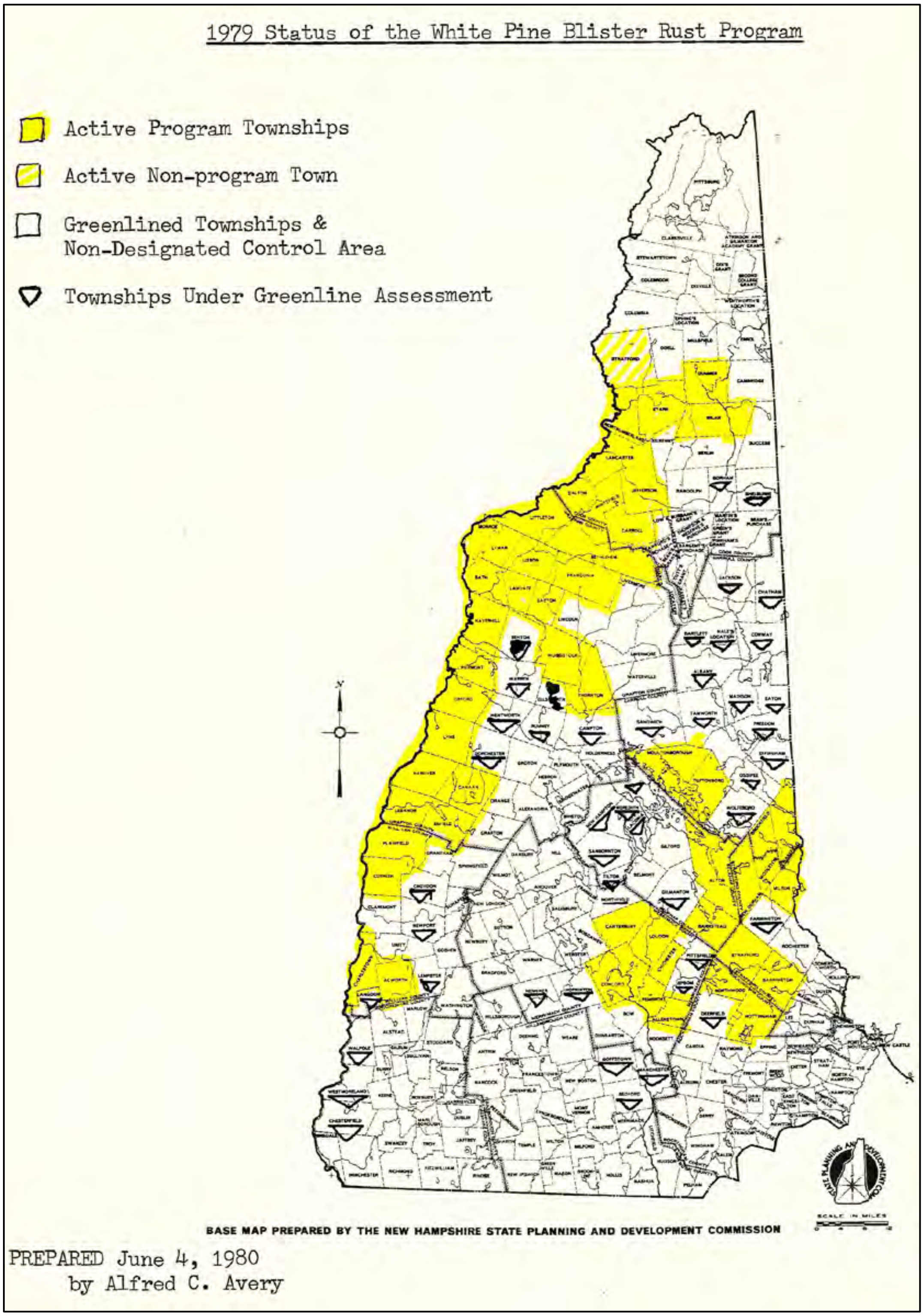
Town	Year	County	Reference
Meredith	1919	Belknap	Newman, L. E. (1945, June 25). Dates Pine and *Ribes* Infection First Found in New Hampshire Counties. Letter.
Milford	1917	Hillsborough	Newman, L. E. (1944, October 14). Counties and Years Where Blister Rust Was First Observed on the Alternate Hosts. Map, Concord, N.H.: NH Blister Rust Control Program.
Nashua	1909	Hillsborough	Newman, L. E. (1944, October 14). Counties and Years Where Blister Rust Was First Observed on the Alternate Hosts. Map, Concord, N.H.: NH Blister Rust Control Program.
New London	1917	Merrimack	United States Department of Agriculture, Office of Blister Rust Control (1928). *Blister Rust and White Pine Demonstration Areas: New Hampshire* (p. 31). United States Department of Agriculture, Office of Blister Rust Control.
North Conway	1916	Carroll	Newman, L. E. (1945, June 25). Dates Pine and *Ribes* Infection First Found in New Hampshire Counties. Letter.
Nottingham	1916	Rockingham	Newman, L. E. (1944, October 14). Counties and Years Where Blister Rust Was First Observed on the Alternate Hosts. Map, Concord, N.H.: NH Blister Rust Control Program.
Pittsfield	1918	Merrimack	VT Forest Service, & NH Forestry Department. (1925). Report of forestry meeting and blister rust demonstration at Waterford, VT. *Blister Rust News*, *9*(1), 22–24.
Stratham	1916	Rockingham	Newman, L. E. (1944, October 14). Counties and Years Where Blister Rust Was First Observed on the Alternate Hosts. Map, Concord, N.H.: NH Blister Rust Control Program.
Sunapee	1917	Sullivan	United States Department of Agriculture, Office of Blister Rust Control (1928). *Blister Rust and White Pine Demonstration Areas: New Hampshire* (p. 31). United States Department of Agriculture, Office of Blister Rust Control.
Weare	1914	Hillsborough	United States Department of Agriculture, Office of Blister Rust Control (1928). *Blister Rust and White Pine Demonstration Areas: New Hampshire* (p. 31). United States Department of Agriculture, Office of Blister Rust Control.

B-1. White Pine Blister Rust Control Area 1917-1924



State of New Hampshire Forestry Commission (1924). Courtesy of NH Blister Rust Control Archives.

B-2. 1979 Town Hazard Ratings for New Hampshire



Avery, A. C. (1980). Courtesy of NH Blister Rust Control Archives.

Chapter Three: White Pine Blister Rust Hazard Ratings for New Hampshire 1963-2018

Abstract

White pine blister rust (WPBR) is a non-native disease that has been killing New Hampshire's eastern white pine (*Pinus strobus*) for more than a century; however, the disease's current distribution is unknown, complicating management efforts for the commercial white pine industry. This study compared the 2018 distribution of WPBR in New Hampshire with locations designated at risk for infection by two historical hazard ratings tools. The 1963 map of WPBR infection zones for the Northeast (Charlton, 1963) defined the areas where the climate was most likely to support the development and dispersal of spores that would infect white pines. The 1979 map by the New Hampshire Blister Rust Control Program (Avery, 1980) assigned hazard ratings to towns based on the presence of biotic factors, including the alternate disease hosts, gooseberries and currants (*Ribes spp.*), and evidence of recent pine infection. This study assessed the accuracy of each ratings method in predicting the presence of WPBR in 2018. One hundred research sites in 50 New Hampshire towns were surveyed for WPBR during the spring of 2018. Disease presence was mapped onto each hazard map to determine if a relationship existed between hazard ratings and WPBR presence. The 1963 model was then evaluated using climate data from 1979-1998 and 1999-2018 to test the accuracy of the model with more recent climate data. Key findings included: the historical hazard ratings did not accurately reflect disease presence in 2018; *Ribes* infections occurred one month earlier than 90 years ago; and a significant relationship existed between WPBR, white pine regeneration, and other pine diseases. Additional research is needed on the adaptability of the WPBR pathosystem to climate changes over time to advance hazard rating tools for white pine management.

Keywords: white pine blister rust, *Cronartium ribicola*, NH Blister Rust Control Program, eastern white pine, *Pinus strobus*, *Ribes*, hazard ratings

White Pine Blister Rust Distribution in New Hampshire 1918-2018

White pine blister rust (WPBR), caused by the exotic fungal pathogen *Cronartium ribicola* Fisch., was introduced to the United States on imported five-needled white pines (*Pinus* spp.) before 1888 (Spaulding, 1914). The exotic disease spread to native white pines and the alternate disease host, native and non-native *Ribes*. By 1919, WPBR was widespread in the Northeast, the Lake States, Ontario, and Quebec (Benedict, 1981). White pine blister rust kills susceptible white pines of all ages and sizes (Burns et al., 2012; Hatala et al., 2011; Loehman et al., 2018; Worrall, 2019), endangering forest health and sustainability, and threatening the economic wellbeing of New Hampshire's timber industry, which depends upon white pine as a dominant source of timber and income. In 2009, sales of softwood saw logs, pulpwood, and chips were three times higher than hardwood sales, despite less than 20% of New Hampshire forests growing softwood timber (North East State Forester's Association, 2011). By 2016, pine led the biomass market at more than two billion cubic feet, more than double the biomass for red oak, hemlock, and red maple (Morin & Lombard, 2017). The risk for WPBR establishment is high where eastern white pine (*Pinus strobus* Fisch.), *Ribes*, a source of inoculum, and climatic conditions such as narrow fog valleys, dew pockets, and small forest openings that support the development of the disease co-exist (Charlton, 1963; Van Arsdel, Riker, Kouba, Suomi, & Bryson, 1961). Over time, however, the disease has adapted and established in warmer and drier western climates of the United States (Kinloch Jr., 2003). Unlike the western and Lake States, recent research on WPBR resistance of eastern white pine in the New England landscape is limited. The recent identification of a mutated strain of *C. ribicola* that infected resistant *Ribes* cultivars in New Hampshire (Munck, Tanguay, Weimer, Villani, & Cox, 2015), elevated the need for contemporary research on the use of hazard ratings for white pine management.

Hazard rating maps that predicted the potential for WPBR incidence in specific landscapes (Geils, Conklin, & Van Arsdel, 1999) were developed for the Northeast (Appendix C-1) in 1963 (Charlton), and for New Hampshire (Appendix C-2) in 1979 (Avery, 1980). The 1963 Northeast ratings were derived from a probability equation that incorporated climate and weather patterns for the Northeast at that time, including temperature, precipitation, and air movement during the spring-fall infection season (Charlton, 1963). Conditions favorable for the production of basidiospores and white pine infection were: 1) temperatures during the day not exceeding 90 degrees Fahrenheit and 60-68 degrees overnight; 2) 60-72 hours of high moisture from rain, humidity, fog, or dew; and 3) air movements that allowed for spore dispersal (Charlton, 1963). Infection probability was depicted on a map as low, medium, and high hazard zones. A high hazard rating indicated that the probability for infection was greater than 60% due to the presence of favorable conditions each year that could result in serious stand damage without protective measures; a medium hazard rating indicated an infection probability between 40% and 60% because favorable conditions might occasionally be present and some stand damage could occur if protective measures were not taken; and a low hazard rating indicated an infection probability of less than 40% because favorable climatic conditions were seldomly present, if at all, so no stand damage was expected (Charlton, 1963). The 1963 hazard zones were used in two studies with differing results: in 1987, a Maine study reported a higher total of diseased trees on low hazard sites (Ostrofsky, Rumpf, Struble, & Bradbury, 1988); in contrast, a 1998 NH study found the highest rates of infection in high hazard zones (Lombard & Bofinger, 1999).

The 1979 New Hampshire hazard rating map emerged from the new control standards that were established in 1975, which shifted the focus from evidence of *Ribes* presence to evidence of pine infection, and reduced the acreage that qualified for *Ribes* eradication control work (Avery, 1980). The ratings system used biotic factors and topographic features to identify forested pine stands that would require additional blister rust control work (Avery, 1980). The biotic factors included adequate pine stocking, live branches within eight feet of the ground, gooseberries and currants (referred to as *Ribes* in this study), and WPBR presence. The topographic features included fog valleys and dew pockets. The criteria were based on field observations in New Hampshire during the previous 15-20 years that indicated: 1) low levels of infection; 2) a lack of pine acreage in the seedling-sapling size classes; and 3) a lack of favorable late-summer weather conditions to support white pine infection (Avery, 1980). In 1979, 52 townships remained on the active periodic examination schedule as high hazard areas; 129 townships had been greenlined as low hazard sites no longer in need of monitoring unless pine infection was found (Avery, 1980); and the remaining 45 townships were scheduled for a determination of hazard status in 1980 (Avery, 1980). To date, I have located no documents that confirm the 45 townships were examined, or that demonstrate the use of the 1979 hazard ratings. There have been no studies that compare the accuracy of the 1963 climatic variables with the 1979 biotic variables for predicting favorable WPBR conditions. It is therefore unknown if either of these hazard rating tools can inform the management of white pine as a timber resource or to sustain the species in New Hampshire's current and changing climate.

Cronartium ribicola, the fungal pathogen that causes WPBR, requires a favorable climate for the establishment, development, and spread of the disease; it is therefore important to understand how New Hampshire's climate may affect the WPBR pathosystem, not just white pine. New Hampshire's climate may foster the development of basidiospores that infect pine trees if the temperatures are optimal (Hirt, 1935) and adequate moisture is present, such as when dew forms (Agrios, 2005). Where daytime temperatures are too hot and nighttime temperatures are too cold for *Ribes* infection, conditions are also unfavorable for spore germination and infection of white pines (Van Arsdel, 1972). Changes in the state's climate since the development of the 1963 and 1979 hazard ratings are reflected in the annual records of mean precipitation and temperature for Concord, located in central New Hampshire (Figure 3.1).

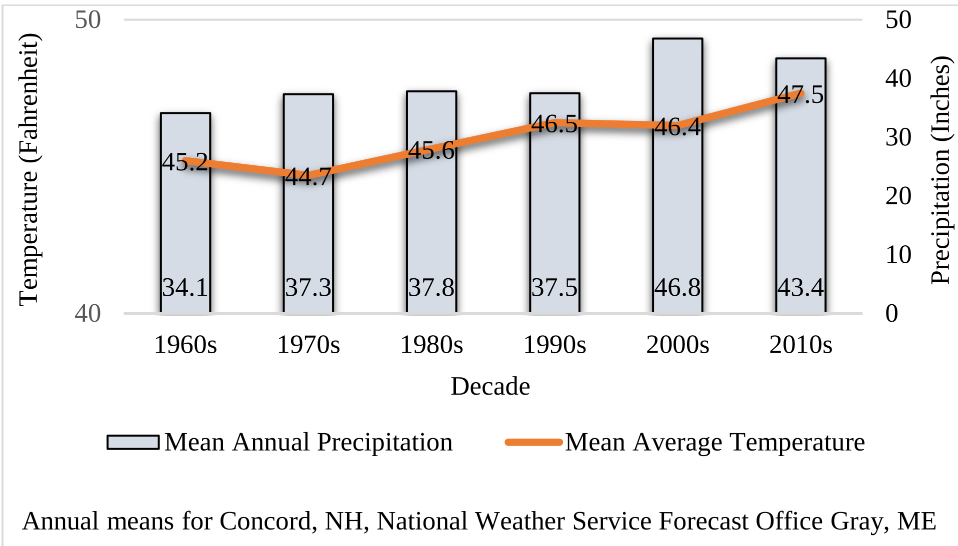


Figure 3.1. Mean annual precipitation and temperature, Concord, NH, 1960-2019.

The mean temperature for Concord increased 2.3 degrees Fahrenheit since the 1960s, while the mean precipitation increased by more than nine inches (Gray Weather Forecast Office, 2021). In general, the rising mean temperature over time is expected to lengthen the growing season and increase the abundance of pathogens (Janowiak et al., 2018). *Cronartium ribicola* is believed to have originated in a climate that is much cooler and drier than New Hampshire, east of the Ural Mountains in central Siberia (Hummer, 2000). Early research indicated that the pathogen required optimal temperatures 60-68°F and high humidity for spore production (Spaulding, 1929). It is unclear how the projected increase in temperature and change in precipitation patterns will affect the current WPBR pathosystem (Loehman et al., 2018); a warmer, wetter spring and earlier summer may allow for a longer period of spore production and increase WPBR infection and intensity (Loehman et al., 2018; Woods, Heppner, Kope, Burleigh, & Maclauchlan, 2010). New Hampshire’s changing climate may provide optimal conditions for WPBR infection throughout the state’s white pine region, regardless of *Ribes* presence and topographical features. Therefore, it is important to know the distribution of the disease and its hosts to understand which sites may be most favorable for WPBR establishment, and to inform white pine management practices.

The goal of this study was to determine if the hazard ratings from 1963 for the Northeast and 1979 for New Hampshire reflected the locations in the current landscape with the highest potential to support WPBR infection, based on the state’s current climate, topography, and biota. The objectives of this research were to: create a map depicting the current distribution of WPBR within the 1963 and 1979 hazard zones to determine their predictive ability in 2018; and analyze the 1963 and 1979 ratings criteria to determine which factors were more likely to be associated with WPBR presence in 2018.

Methods

Two WPBR hazard ratings management tools were compared in this study: the 1963 hazard ratings for the Northeast (Charlton, 1963) (Figure 3.2); and the 1979 hazard ratings for New Hampshire (Avery, 1980) (Figure 3.3). Each tool was created based on the knowledge of the climate and topographical features most likely to support WPBR infection, and the white pine timber type age classes present at that time. Hazard ratings projected the risk of infection, from low to high, and were depicted as zones on stationary maps.

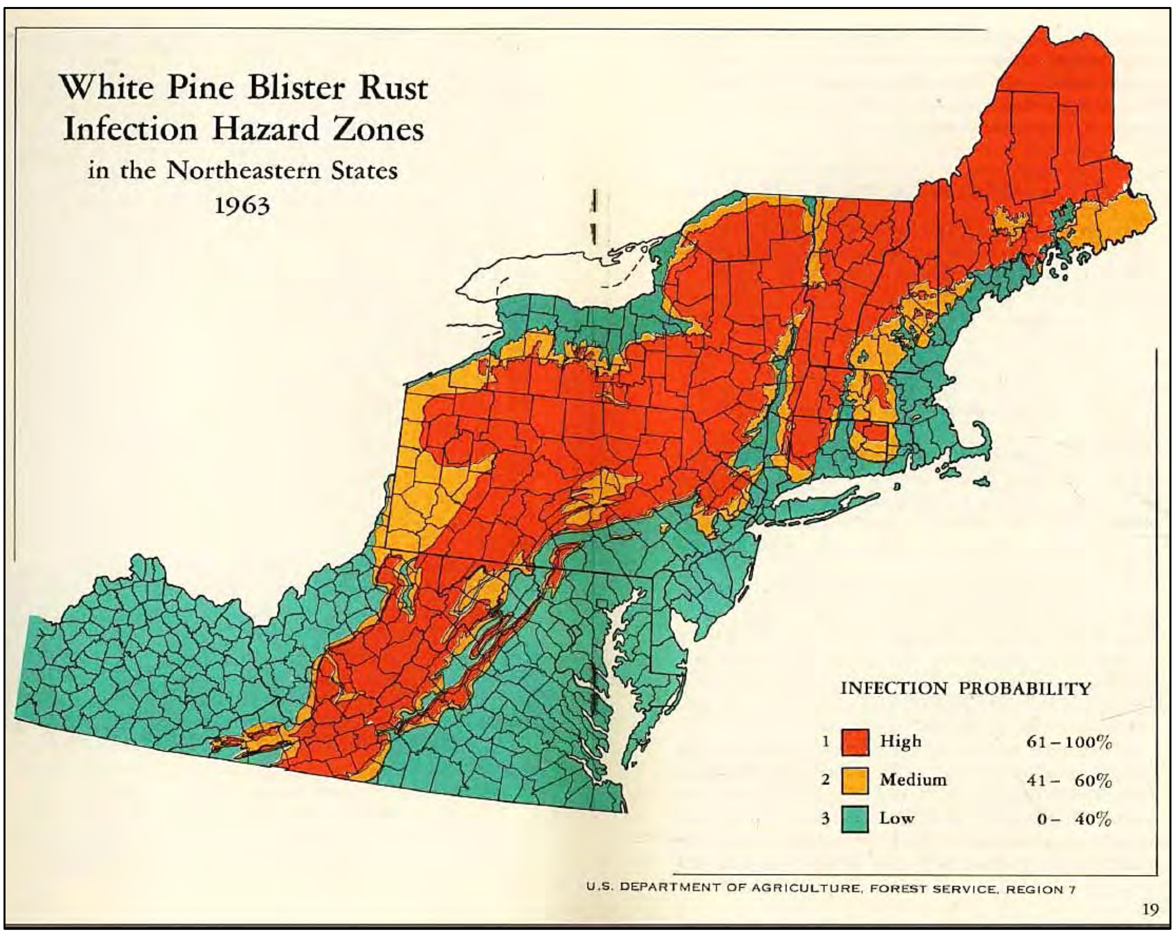


Figure 3.2. WPBR hazard map for the Northeast (Charlton, 1963). Courtesy U.S. Department of Agriculture.

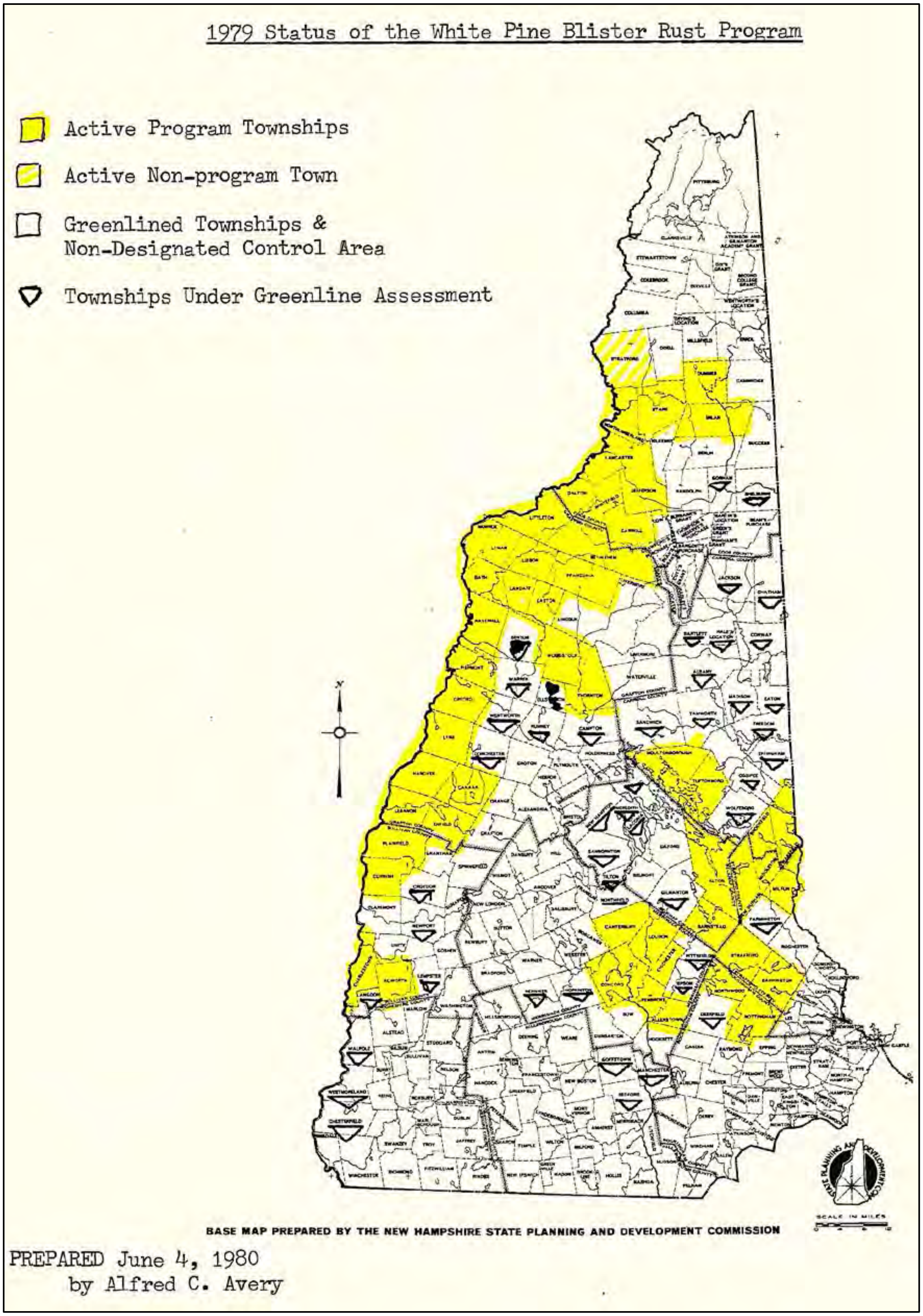


Figure 3.3. WPBR hazard map for New Hampshire (Avery, 1980). Courtesy NH Blister Rust Control Archives.

Each tool used a different method to measure the risk for infection. The 1963 Northeast climate method used climate data from July and August for New England and New York, and July through September for Pennsylvania and New Jersey (Charlton, 1963). Climate data included temperature, precipitation, and air movement. The 1979 hazard zones for New Hampshire used the presence of biotic criteria, including *Ribes*, and topographic features such as fog valleys and dew pockets that favored WPBR establishment (Avery, 1980).

Study Design

Two methods were used to test the accuracy of the 1963 and 1979 hazard ratings maps for predicting locations with the highest risk for WPBR in 2018: 1) the maps from 1963 and 1979 were compared with the 2018 field data on WPBR presence; and 2) the equation for the 1963 Northeast model was tested with current climate data from the National Weather Service and compared with 2018 field data.

Site selection. Research sites were selected throughout New Hampshire's historical WPBR control area that included all but the northernmost towns (Appendix C-1). Each research site was a white pine stand when mapped by the New Hampshire Blister Rust Control Program (NHBRCP) from 1929-1976. (See example Appendix C-2.) New Hampshire's two geographic provinces, based on climate, geology, hydrology, and potential natural vegetation (Cleland et al., 2007), were represented in this study: research sites in western and northern New Hampshire represented the Adirondack-New England Mixed Forest Province, characterized by mountains and glacial features; while research sites located in the Seacoast and Lakes Region represented the Northeastern Mixed Forest Province, with a varied topography, warmer climate, and longer growing season (Janowiak et al., 2018).

Fifty towns (Table 3.1; map Appendix C-3) were selected from the 226 towns in New Hampshire's historic control area (Appendix C-1). A computer-generated list of available towns on the 1979 hazard ratings map for New Hampshire was used to randomly select 25 towns with a high hazard rating and 25 towns with a low hazard rating (Figure 3.4). Towns met the following criteria to be eligible for selection in this study: 1) they were located within the historic 1926 control area; 2) they were given a high or low hazard rating by the NH Blister Rust Control Program in 1979; and 3) they had maps available in the archives of the NH Blister Rust Control Program to indicate the locations of pine infections.

Table 3.1

Towns Selected for 2018 New Hampshire White Pine Blister Rust Study

High Hazard		Low Hazard	
Acworth	Haverhill	Alexandria	Hinsdale
Alton	Lebanon	Andover	Keene
Barnstead	Littleton	Antrim	Lyndeborough
Barrington	Loudon	Belmont	New Boston
Bath	Lyme	Bristol	New London
Brookfield	Moultonborough	Candia	Raymond
Canaan	New Durham	Claremont	Sullivan
Canterbury	Pembroke	Danbury	Sunapee
Charlestown	Strafford	Deering	Swanzey
Concord	Thornton	Dublin	Troy
Cornish	Tuftonboro	Dunbarton	Warner
Enfield	Wakefield	Grantham	Weare
Hanover		Hebron	

Note. Hazard ratings were assigned to NH towns in 1979; from Avery (1980).

Two research sites were selected for each town from the archived blister rust maps. Each research site represented a historical pine stand as documented on the blister rust maps, and a high or low hazard rating from 1979 (Figure 3.4). One site was located where the blister rust maps documented a pine stand with infection; the second site represented a pine stand where no infection was mapped. The research sites were selected from the same map section and under the same ownership, when possible, to reduce differences in management, topography, and climate. Historical pine stands that were still forested in 2018, as confirmed by Google Earth Pro images (version 7.3.1.4507), were eligible for selection. Former pine stands that were reduced to less than five acres in size, or were eliminated completely due to highway construction, reservoirs, or housing developments, were not selected. In those instances, a replacement historical pine stand was selected from the same map.

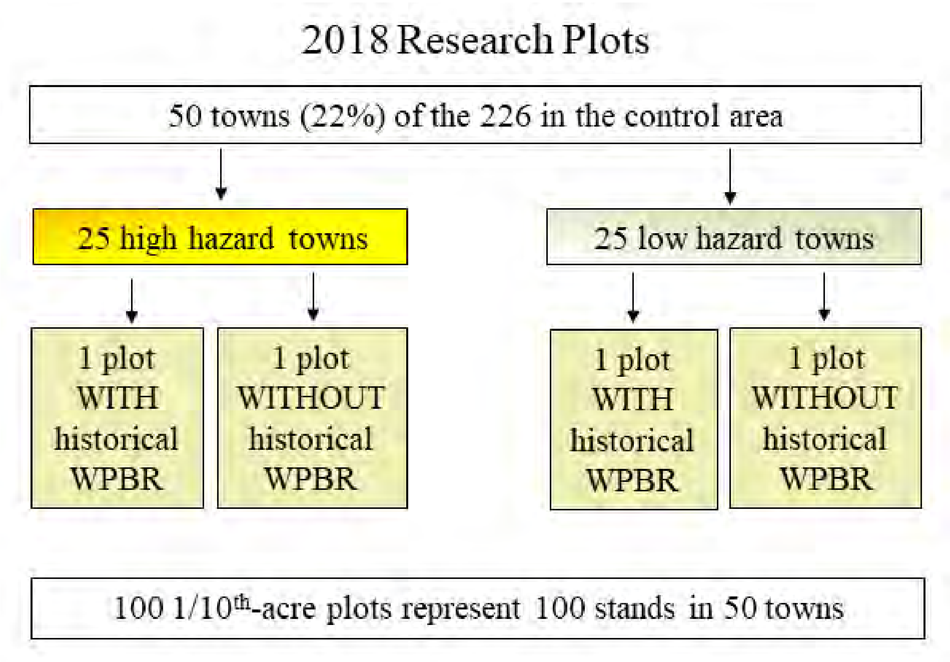


Figure 3.4. 2018 NH study design with plots stratified by hazard rating and infection history.

One 1/10th acre circular plot was situated within each research site. In the stand with WPBR history, the plot was placed where a black triangle on the blister rust map marked tree infection (see map Appendix C-2). The site with no infection was chosen by selecting the nearest pine stand at least 300 yards from any mapped pine infections. Plots were placed at least 300 yards from each other based on historic management practices that maintained a 200 to 300-

yard *Ribes*-free zone around white pine stands when WPBR was present (Detwiler, 1920; Spaulding, 1922), and for sampling independence for the *Ribes* criterion in the 1979 NH hazard ratings method.

Plots were located where no disturbances such as fire or hurricane blowdown had been historically mapped by the NH Blister Rust Control Program, and where no active or recent logging (<10 years) occurred (per Google map imagery and landowner confirmation). Each plot's center was mapped in ArcGIS (10.6) and the GPS coordinates were imported into a Garmin GPSMAP 60CSx for locating on the ground. Data were collected at each plot between May 1 and June 3, 2018 when cankers were actively releasing aeciospores.

Data Collection

Field data. Field data collected at each research site included: site characteristics (elevation and aspect as displayed by the Garmin GPS, and topographic position, such as valley, lower slope, mid-slope, upper slope, or ridge (Jenness, 2006)); stand characteristics, such as canopy opening size and type (large/small; open/closed), and the presence of the 1979 New Hampshire hazard ratings criteria. Topographic data were used to calculate the air movement factor in the 1963 Northeast model (Charlton, 1963). The size of the canopy opening was based on the definition provided by Van Arsdel (1972); an opening larger in diameter than the height of the surrounding trees was too hot during the day and too cold at night for infection to occur; however, openings smaller than the height of the surrounding trees created microclimates favorable to WPBR infection. An open canopy occurred where sunlight and moisture directly reached the forest floor; in a closed canopy, touching branches prevented moisture from reaching the floor, and kept the air too dry for WPBR infection of the lateral understory branches (Van Arsdel, 1961).

The 1979 New Hampshire criteria required evidence of: adequate stocking (at least 50 pine trees per acre (Benedict, 1981)); pine infection by WPBR within the past 10 years or the presence of at least one *Ribes* plant per acre; over 50% of pines bearing live branches within eight feet of the ground based on ocular estimates; and the presence of *Ribes* within 300 yards of the plot, using a Garmin GPS64Sc to measure distance. All white pines, alive or dead, with evidence of WPBR infection (aecial cankers and scars, including bark discoloration and swelling around the cankers), were included in the WPBR data (Ostrofsky et al., 1988). Observed WPBR cankers included active, inactive (non-sporulating), and dead cankers and scars (Phelps & Weber, 1969) (Figure 3.5).

Figure 3.5. White pine blister rust cankers on NH saplings in May, 2018: (left) active canker in Hinsdale plot (left); and non-sporulating (middle) and dead (right) cankers outside Lyme plot. Photos by Janine Marr.

Climate data. Climate data from the National Weather Service were used to test Charlton's 1963 hazard formula, which applied percentage factors to four variables supporting WPBR infection: 1) air movement; 2) averaged low nightly temperatures for July and August; 3) averaged high daytime temperatures for July and August; and 4) moisture, a combination of the cumulative average precipitation for July and August and the average number of days with at least .01 inches of rainfall (Charlton, 1963). Air movement, rated as poor, fair, or good in its relationship to supporting WPBR infection, was based on 2018 field data and included: elevation and aspect; topographic land form and relief, such as a narrow valley with uneven slopes; and vegetation and canopy cover that ranged from open land to a wooded stand with a closed canopy. For example, a site over 400 feet in elevation in a narrow valley with cool soils or several brooks and a northern exposure and open canopy would be rated good for air movement that fostered WPBR development.

National Weather Service summaries for the mean monthly temperatures and precipitation were compiled for July and August 1979-1998 and 1999-2018, and for August and September 1999-2018, from 44 New Hampshire cities available online (Gray Weather Forecast Office, 2021). September was added to the 1998-2018 analysis to determine if climate conditions were favorable for WPBR infection beyond July and August as included in the 1963 formula. Each town surveyed in 2018 was assigned a temperature or precipitation value from the nearest weather station if no report was available for that town specifically.

A town's combined mean precipitation for July and August was used to determine a moisture value from 0-1.0 based on the model's moisture factor chart (Charlton, 1963). A value was assigned to each increment where the average number of days with precipitation >0.01 inches on the Y axis met the total inches of precipitation for the two months on the X axis. For example, a location that received a combined average of eight inches of precipitation in July and August for an average of 31 days received a precipitation value of 0.6, while a location receiving a combined average of 11 inches of precipitation received a value of 0.4. In this study, the average number of days with precipitation > 0.01 inches for July and August was 31, and 30 for September.

The four factors of air movement, low and high temperatures, and moisture were multiplied together using Charlton's 1963 formula to produce a hazard rating that reflected the probability of favorable weather conditions in a given area capable of spore development, spore dispersal, and white pine infection. A high hazard rating was a value over 60%; medium hazard was 41-60%; and low hazard was ≤40%. The infection probabilities for each time period, 1979-1998 and 1999-2018, were compared with the 1963 ratings for each town to determine if a relationship existed between the WPBR hazard ratings for New Hampshire's climate during the three time periods and WPBR presence and incidence in 2018.

Data Analysis

The distribution and incidence of WPBR was analyzed in Chapter Two; the results were used for mapping the current WPBR distribution within both the 1963 hazard zones for the Northeast, and the 1979 hazard zones for New Hampshire towns, using ArcGIS 10.6. Mapped data were analyzed in R (version 3.44) and Excel using Chi-square tests to determine if historical hazard zones were associated with the 2018 distribution of WPBR. Site, stand, and climate factors from the 1963 and 1979 hazard ratings tools were analyzed using contingency tables to reveal relationships with WPBR presence. All tests used an alpha of 0.05.

Results

White pine blister rust was present, in high, medium, and low hazard zones using 1963, 1979-1998, and 1999-2018 climate data (Table 3.2). Seven towns were rated low hazard for 1963, 1979-1998, and 1999-2018; however, Candia was the only low-hazard town without WPBR infection in 2018. Hazard ratings, regardless of the climate data used, did not reflect WPBR presence in 2018: $X^2(4, N = 100) = 3.61, p = 0.46$.

Table 3.2

2018 Incidence and Hazard Ratings with 1963, 1979-1998, 1999-2018 Climate Data

Town, Stand & WPBR History	2018 Incidence	1963 Rating July + Aug	1979-1998 Risk % July + Aug	1979-1998 Rating July + Aug	1999-2018 Risk % July + Aug	1999-2018 Rating July + Aug
Acworth Hx	33.3	High	35.1	Low	0	Low
Acworth No	27.1	High	31.2	Low	0	Low
Alexandria Hx	0	High	32.6	Low	0	Low
Alexandria No	0	High	36.7	Low	0	Low
Alton Hx	0	Medium	24.9	Low	0	Low
Alton No	0	Medium	24.9	Low	0	Low
Andover Hx	0	High	29.9	Low	0	Low
Andover No	2.6	High	39.8	Low	0	Low
Antrim Hx	3.2	Medium	20.3	Low	0	Low
Antrim No	0	Medium	20.3	Low	0	Low
Barnstead Hx	23.8	Medium	20.3	Low	0	Low
Barnstead No	31.8	Medium	16.2	Low	0	Low
Barrington Hx	8.8	Low	11.6	Low	0	Low
Barrington No	0	Low	11.6	Low	0	Low
Bath Hx	0	High	49.7	Medium	<1	Low
Bath No	0	High	55.2	Medium	<1	Low
Belmont Hx	2.1	Medium	39.8	Low	0	Low
Belmont No	0	Medium	44.8	Medium	0	Low
Bristol Hx	0	High	20.4	Low	0	Low
Bristol No	0	High	24.5	Low	0	Low
Brookfield Hx	0	Medium	27.3	Low	0	Low
Brookfield No	0	Medium	32.8	Low	0	Low
Canaan Hx	6.3	High	31.3	Low	0	Low
Canaan No	0	High	31.3	Low	0	Low
Candia Hx	0	Low	34.7	Low	0	Low
Candia No	0	Low	27.0	Low	0	Low

Table 3.2 Continued

Town, Stand & WPBR History	2018 Incidence	1963 Rating July + Aug	1979-1998 Risk % July + Aug	1979-1998 Rating July + Aug	1999-2018 Risk % July + Aug	1999-2018 Rating July + Aug
Canterbury Hx	0	Medium	28.4	Low	0	Low
Canterbury No	15.4	Medium	36.5	Low	0	Low
Charlestown Hx	0	High	35.1	Low	0	Low
Charlestown No	0	High	35.1	Low	0	Low
Claremont Hx	0	High	44.2	Medium	0	Low
Claremont No	0	High	49.7	Medium	0	Low
Concord Hx	3.2	Low	12.2	Low	0	Low
Concord No	26.9	Low	12.2	Low	0	Low
Cornish Hx	0	High	49.7	Medium	0	Low
Cornish No	0	High	49.7	Medium	0	Low
Danbury Hx	7.7	High	28.6	Low	0	Low
Danbury No	0	High	12.2	Low	0	Low
Deering Hx	0	Medium	20.3	Low	0	Low
Deering No	0	Medium	28.4	Low	0	Low
Dublin Hx	0	Medium	28.4	Low	<1	Low
Dublin No	0	Medium	28.4	Low	<1	Low
Dunbarton Hx	0	Medium	24.3	Low	0	Low
Dunbarton No	0	Medium	24.3	Low	0	Low
Enfield Hx	10.5	High	33.1	Low	0	Low
Enfield No	3.4	High	38.6	Low	0	Low
Grantham Hx	1.2	High	44.2	Medium	0	Low
Grantham No	0	High	44.2	Medium	0	Low
Hanover Hx	62.5	High	32.6	Low	0	Low
Hanover No	18.8	High	36.7	Low	0	Low
Haverhill Hx	0	High	40.8	Medium	<1	Low
Haverhill No	14.3	High	40.8	Medium	<1	Low
Hebron Hx	0	High	32.6	Low	0	Low
Hebron No	0	High	36.7	Low	0	Low
Hinsdale Hx	26.9	Medium	19.5	Low	0	Low
Hinsdale No	14.3	Medium	31.2	Low	0	Low
Keene Hx	0	Low	15.6	Low	0	Low
Keene No	11.1	Low	15.6	Low	0	Low
Lebanon Hx	7.1	High	36.7	Low	0	Low
Lebanon No	0	High	36.7	Low	0	Low
Littleton Hx	40.5	High	33.1	Low	<1	Low
Littleton No	0	High	27.6	Low	<1	Low
Loudon Hx	0	Medium	16.2	Low	0	Low
Loudon No	0	Medium	32.4	Low	0	Low
Lyme Hx	0	High	28.6	Low	0	Low
Lyme No	0	High	28.6	Low	0	Low

Table 3.2 Continued

Town, Stand & WPBR History	2018 Incidence	1963 Rating July + Aug	1979-1998 Risk % July + Aug	1979-1998 Rating July + Aug	1999-2018 Risk % July + Aug	1999-2018 Rating July + Aug
Lyndeborough Hx	0	Medium	33.2	Low	0	Low
Lyndeborough No	0	Medium	37.9	Low	0	Low
Moultonborough Hx	1.8	Medium	54.6	Medium	0	Low
Moultonborough No	14.3	High	43.7	Medium	0	Low
New Boston Hx	0	Medium	12.2	Low	0	Low
New Boston No	20	Medium	16.2	Low	0	Low
New Durham Hx	0	Medium	34.9	Low	0	Low
New Durham No	0	Medium	39.8	Low	0	Low
New London Hx	0	High	49.8	Medium	0	Low
New London No	0	High	44.8	Medium	0	Low
Pembroke Hx	3.2	Low	36.5	Low	0	Low
Pembroke No	9.3	Low	32.4	Low	0	Low
Raymond Hx	0	Low	23.1	Low	0	Low
Raymond No	4.8	Low	19.3	Low	0	Low
Strafford Hx	0	Medium	28.4	Low	0	Low
Strafford No	0	Medium	32.4	Low	0	Low
Sullivan Hx	7.1	Medium	23.4	Low	0	Low
Sullivan No	0	Medium	27.3	Low	0	Low
Sunapee Hx	0	High	39.8	Low	0	Low
Sunapee No	0	High	34.9	Low	0	Low
Swanzey Hx	5.7	Medium	27.3	Low	0	Low
Swanzey No	0	Medium	27.3	Low	0	Low
Thornton Hx	0	High	32.8	Low	<1	Low
Thornton No	0	High	32.8	Low	<1	Low
Troy Hx	8	Medium	31.2	Low	0	Low
Troy No	0	Medium	31.2	Low	0	Low
Tuftonboro Hx	27.3	Medium	38.2	Low	0	Low
Tuftonboro No	43.1	Medium	38.2	Low	0	Low
Wakefield Hx	0	Medium	43.7	Medium	0	Low
Wakefield No	0	Medium	38.2	Low	0	Low
Warner Hx	50	Medium	28.4	Low	<1	Low
Warner No	0	Medium	20.3	Low	<1	Low
Weare Hx	0	Low	28.4	Low	0	Low
Weare No	16.7	Low	28.4	Low	0	Low

Note. Incidence for live and dead pines combined. Ratings based on Northeast hazard tool (Charlton, 1963). Risk percentage represented 0-100% probability for favorable WPBR conditions. Town infection history (Hx) or lack of (No) refers to WPBR presence in stands when mapped by the NH Office of Blister Rust Control 1929-1976).

1963 Hazard Ratings for New Hampshire

1963 Northeast hazard ratings with 1979-1998 climate data. When the 1979-1998 climate data were imported into the 1963 hazard model, the hazard ratings were reduced for all 43 high-hazard stands and 40 of the 43 medium-hazard stands.

1963 Northeast hazard ratings with 1999-2018 climate data. All stands in the 50 towns were rated low hazard when the equation for the 1963 Northeast model was applied to 1999-2018 climate data for July and August. Forty-four towns had average high temperatures above the model's 90-degree upper limit (Table 3.3) for WPBR spore survival and infection of white pines (Charlton, 1963). The 44 towns had a 0% probability for infection according to the model. Six towns with average high temperatures below 90 degrees received a probability rating of less than 1% for favorable WPBR infection conditions: Bath, Dublin, Haverhill, Littleton, Thornton, and Warner. Pines in Haverhill, Littleton, and Warner had WPBR in 2018.

Table 3.3

Average NH Temperature and Precipitation, July-August, 1979-1998, 1999-2018

Town	1979-1998 Low Temperature	1999-2018 Low Temperature	1979-1998 High Temperature	1999-2018 High Temperature	1979-1998 Precipitation	1999-2018 Precipitation
Acworth	56.2	44.6	82.2	90.6	8	9.6
Alexandria	55.7	48.7	82.1	91.5	7.9	9.1
Alton	54.5	51.2	81.4	92.1	7.9	8.2
Andover	54.5	46.1	81.4	90.2	7.3	8.2
Antrim	55.2	45.6	81.5	90.9	7.3	9.1
Barnstead	55.2	48.3	81.5	92.1	7	8.7
Barrington	55.7	48.3	81.7	92.1	8	7.9
Bath	53.6	46.4	79.2	88	7.9	8.4
Belmont	54.5	51.2	81.4	92.1	8	8.7
Bristol	55.7	48.7	82.1	91.5	8.9	9
Brookfield	54.6	48.3	80.9	92.1	8	7.8
Canaan	55.7	48.7	82.1	91.5	7	8
Candia	55.7	52.9	81.7	93.5	7.3	6.9
Canterbury	55.2	45.5	81.5	93.1	8.8	7.7
Charlestown	56.2	44.6	82.2	90.5	8	9.3

Table 3.3 Continued

Town	1979-1998 Low Temperature	1999-2018 Low Temperature	1979-1998 High Temperature	1999-2018 High Temperature	1979-1998 Precipitation	1999-2018 Precipitation
Claremont	53.6	43.2	79.2	90.9	7.3	8.4
Concord	55.2	45.5	81.5	93.1	8	7.7
Cornish	53.6	43.2	79.2	90.9	8	8.4
Danbury	55.7	48.7	82.1	91.5	7.3	8.4
Deering	55.2	45.9	81.5	92.3	7.3	8.6
Dublin	55.2	46.6	81.5	89.4	7.3	9.1
Dunbarton	55.2	45.9	81.5	92.3	8	8.6
Enfield	53.6	45.4	79.2	91.9	8	7.6
Grantham	53.6	45.4	79.2	91.9	8	7.6
Hanover	55.7	48.7	82.1	91.5	8	8.2
Haverhill	55.7	46.4	82.1	88	8	8.4
Hebron	55.7	48.7	82.1	91.5	8.8	8.7
Hinsdale	56.2	45.7	82.2	91.9	8.8	8.8
Keene	56.2	45.7	82.2	91.9	8	9.3
Lebanon	55.7	45.4	82.1	91.9	8	7.9
Littleton	53.6	38.6	79.2	88.7	7.3	9.2
Loudon	55.2	45.5	81.5	93.1	8	7.7
Lyme	55.7	48.7	82.1	91.5	7.5	8.2
Lyndeborough	56.8	47.7	81.6	94.2	8.9	8
Moultonborough	54.6	50.3	80.9	90.9	7.3	8.4
New Boston	55.2	50.1	81.5	92.8	7.9	8.5
New Durham	54.5	48.3	81.4	92.1	7.9	7.8
New London	54.5	43.2	81.4	90.9	7.3	8.5
Pembroke	55.2	45.5	81.5	93.1	7	7.6
Raymond	55.7	47.5	81.7	92.2	7.3	7.3
Strafford	55.2	48.3	81.5	92.1	8.8	7.9
Sullivan	56.2	45	82.2	90.4	7.9	9
Sunapee	54.5	43.2	81.4	90.9	8.8	8.5
Swanzey	56.2	45.7	82.2	91.9	8.9	9.4
Thornton	54.6	46.8	80.9	87.7	8.8	8.6
Troy	56.2	45.7	82.2	91.9	8.8	8.8
Tuftonboro	54.6	50.3	80.9	90.9	8.9	8.4
Wakefield	54.6	48.3	80.9	92.1	8.9	7.8
Warner	55.2	44.3	81.5	89.1	7.3	8.9
Weare	55.2	45.9	81.5	92.3	7.3	8.6
Average	55.2	46.8	81.4	91.4	7.9	8.4

Note. All temperatures in Fahrenheit. Precipitation represents average total for both months in inches.

The equation was repopulated with climate data from August and September, 1999-2018, to determine if conditions later in the growing season might better support white pine infection. Twelve towns exceeded the 90-degree limit and six towns averaged 90 degrees for the average high temperature (Table 3.4). The climate data for August and September also resulted in a low hazard rating for all 50 towns.

Thirty-eight towns had <1% probability for infection in August and September, compared to six towns in July and August. Twenty of the 38 towns with <1% of infection in August and September had WPBR in 2018. Favorable conditions for infection were more likely to occur in August and September than in July and August: $X^2(1, N = 100) = 83.12$, $p < 0.001$.

Table 3.4

2018 NH Hazard Ratings using August-September, 1999-2018 Climate Data in 1963 Model

Town	Low Temperature	High Temperature	Precipitation	1999-2018 Risk % Aug + Sept	1999-2018 Rating Aug + Sept
Acworth	38.7	88.7	8.2	<1	Low
Alexandria	42.8	89.4	7.4	<1	Low
Alton	45.1	89	8.3	<1	Low
Andover	39.7	89.7	7.2	<1	Low
Antrim	39.4	90.3	8.3	0	Low
Barnstead	41.4	90	7.1	<1	Low
Barrington	41.4	90	7.1	<1	Low
Bath	39.3	86.4	7.5	<1	Low
Belmont	44.2	89	8.3	<1	Low
Bristol	42.8	89.4	7.4	<1	Low
Brookfield	41.4	90	7.1	<1	Low
Canaan	42.8	89.4	7.4	<1	Low
Candia	45.7	91.2	7.4	0	Low
Canterbury	38.8	91.3	8.1	0	Low
Charlestown	38.7	88.7	8.2	<1	Low
Claremont	37	88.6	7.8	<1	Low
Concord	38.8	91.3	8.1	0	Low
Cornish	37	88.6	7.8	<1	Low
Danbury	42.8	89.4	7.4	<1	Low
Deering	39.4	90.3	8.3	0	Low

Table 3.4 Continued

Town	Low Temperature	High Temperature	Precipitation	1999-2018 Risk % Aug + Sept	1999-2018 Rating Aug + Sept
Dublin	40	87.1	8.7	<1	Low
Dunbarton	39.4	90.3	8.3	0	Low
Enfield	39.7	89.7	7.2	<1	Low
Grantham	39.7	89.7	7.2	<1	Low
Hanover	42.8	89.4	7.4	<1	Low
Haverhill	39.3	86.4	7.5	<1	Low
Hebron	42.8	89.4	7.4	<1	Low
Hinsdale	39.5	89.9	9.5	<1	Low
Keene	39.5	89.9	9.5	<1	Low
Lebanon	39.7	89.7	7.2	<1	Low
Littleton	32.9	86.9	7.4	0	Low
Loudon	38.8	91.3	8.1	0	Low
Lyme	42.8	89.4	7.4	<1	Low
Lyndeborough	42.1	88.7	8.6	<1	Low
Moultonborough	44.2	89	8.5	<1	Low
New Boston	39.4	90.3	8.3	0	Low
New Durham	41.4	90	7.1	<1	Low
New London	37	88.6	7.8	<1	Low
Pembroke	38.8	91.3	8.1	0	Low
Raymond	45.7	91.2	7.4	0	Low
Strafford	41.4	90	7.1	<1	Low
Sullivan	39.6	87.8	9.5	<1	Low
Sunapee	37	88.6	7.8	<1	Low
Swanzey	39.5	89.9	9.5	<1	Low
Thornton	40.3	85.8	7.6	<1	Low
Troy	39.5	89.9	9.5	<1	Low
Tuftonboro	44.2	89	8.5	<1	Low
Wakefield	41.4	90	7.1	<1	Low
Warner	37.9	86.6	8.7	<1	Low
Weare	39.4	90.3	8.3	0	Low
Total Average	40.5	89.3	7.9		

Note. Temperatures Fahrenheit. Precipitation (inches) represents average total for both months.

1963 hazard zones and 2018 infection. Nineteen of the 32 infected stands (59.4%) had a history of WPBR. Stands in the high and medium hazard zones were twice as likely as stands in the low hazard zones to have a history of the disease (Figure 3.6); however, the relationship was not significant: $X^2(4, N = 100) = 6.81, p = 0.15$.

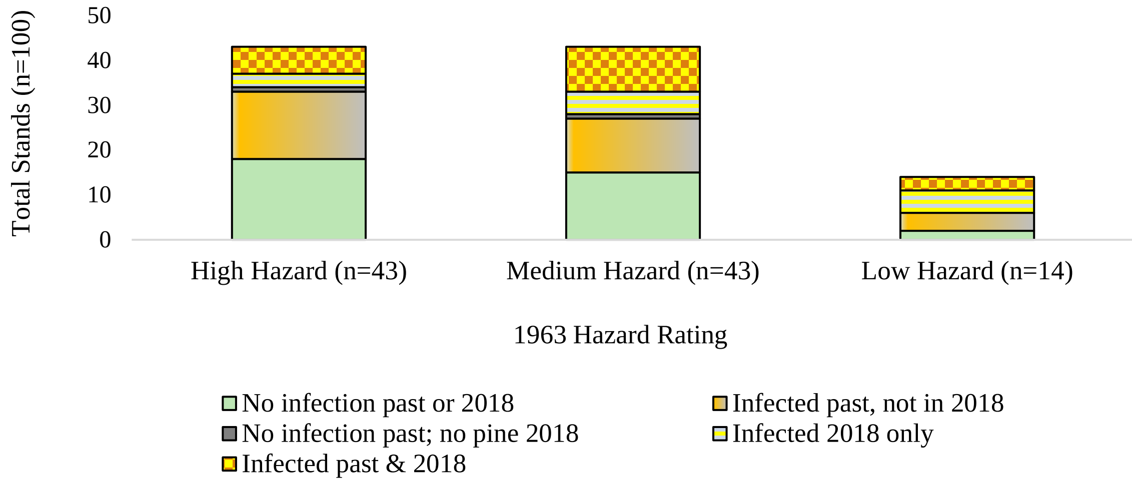


Figure 3.6. WPBR history for 100 stands in 2018 by 1963 hazard zones (Charlton, 1963).

When the 2018 stands were mapped, the stands with repeat infection (stars) and stands with new infection (circles) were distributed throughout the three 1963 zones (Figure 3.7).

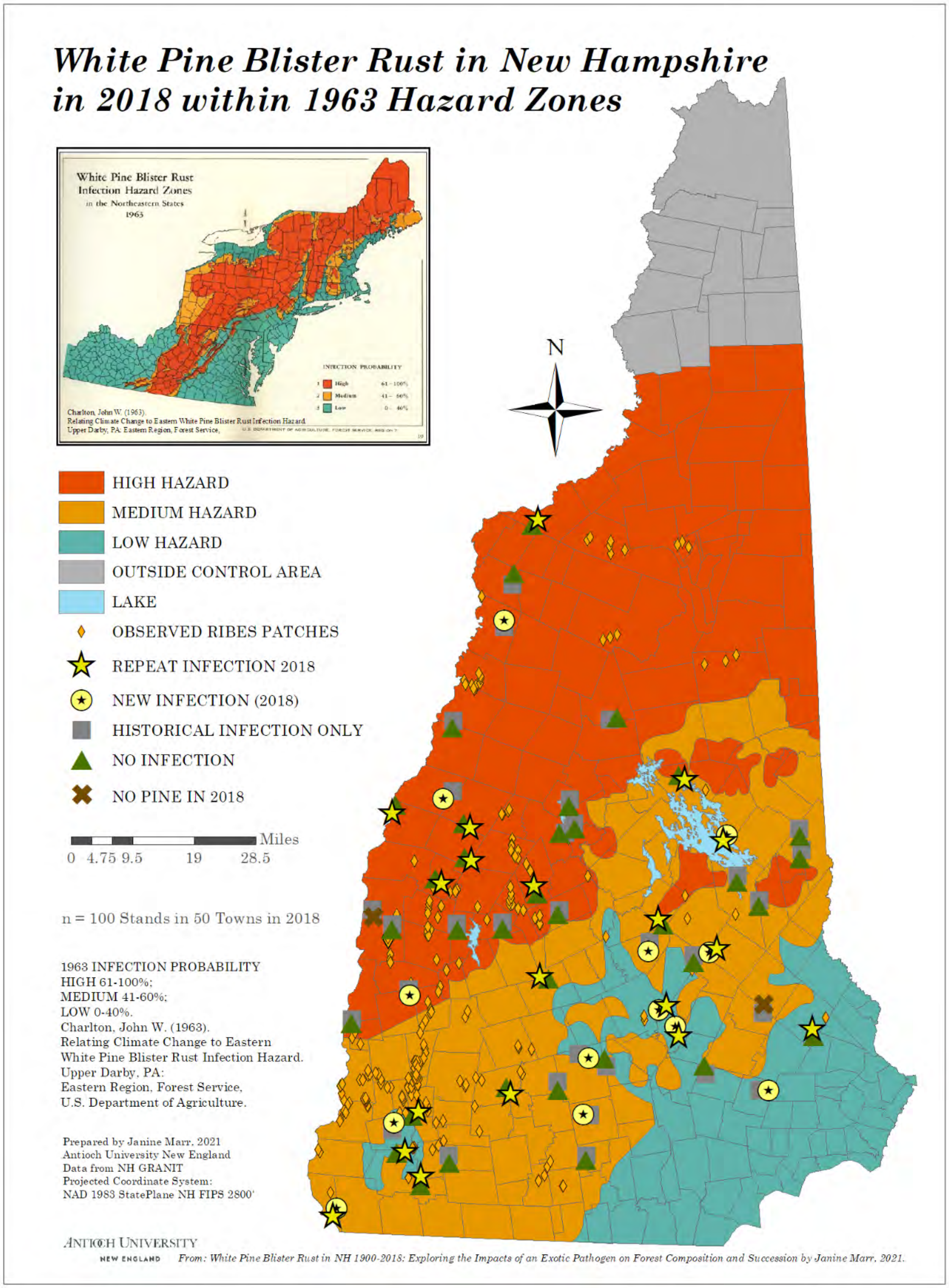


Figure 3.7. WPBR history for 100 NH stands in 2018 within the 1963 hazard zones.

Size class infection in 2018 by 1963 hazard zones. White pine blister rust infection was more likely to be found in low hazard zones for the sapling through timber size classes, and in the medium hazard zones for the seedling size class (Table 3.5). The high hazard zones contained the highest total stems for the pole size class, yet the highest incidence for pole-size pines occurred in the low hazard zones. Saplings were the only size class in which WPBR incidence was >10%, regardless of 1963 hazard rating.

Table 3.5

White Pine Blister Rust Incidence by Size Class and 1963 Hazard Zones

Size Class	1963 Hazard Zone	# WPBR	# No WPBR	# Stems	Relative % Infected
Seedling	High	18	196	214	8.4
Seedling	Medium	76	240	316	24.1
Seedling	Low	7	163	170	4.1
Seedling	Total	101	699	700	14.4
Sapling	High	32	197	229	14
Sapling	Medium	71	385	456	15.6
Sapling	Low	24	126	150	16
Sapling	Total	127	708	835	15.2
Pole	High	3	116	119	2.5
Pole	Medium	2	140	142	1.4
Pole	Low	4	51	55	7.3
Pole	Total	9	307	316	2.8
Timber	High	2	151	153	1.3
Timber	Medium	0	109	109	0
Timber	Low	1	40	41	2.4
Timber	Total	3	300	303	1
Combined	Total	240	1914	2154	11.1

Note. Incidence for live and dead pines combined. 1963 Hazard Zones (Charlton, 1963). *Relating Climate Change to Eastern White Pine Blister Rust Infection Hazard.*

Site and stand characteristics affecting the 1963 Northeast hazard ratings. Site and stand characteristics identified in the 1963 Northeast hazard model as influencing air movement and WPBR presence or severity included elevation (Appendix B-1), aspect (Appendix B-2, B-3), topographic position (valley; low, mid, and upper slopes; ridge), (Appendix B-4), and the presence (Appendix B-5) and age (Appendix B-6) of a canopy disturbance in the stand.

A Chi-square analysis of the 2018 data detected no relationships between the site and stand characteristics and WPBR presence or severity (Table 3.6).

Table 3.6

Site and Stand Characteristics in Relation to WPBR Presence and Severity in 2018

Characteristic	Relationship	Chi Square	P Value
Elevation	WPBR presence	1.87	0.6
Site Aspect	WPBR presence	0.44	0.93
Site Aspect	WPBR severity	1.37	0.71
Topographic Position	WPBR presence	2.66	0.62
Canopy Disturbance (Tree Removal)	WPBR presence	0.001	0.97
Canopy Disturbance Age	WPBR presence	4.39	0.36

1979 Hazard Ratings for New Hampshire

When the 2018 field data were incorporated into the 1979 hazard ratings formula, 46 of the 50 towns were assigned a low-hazard rating (Figure 3.8). In addition, all 25 towns rated high-hazard in 1979 were rated low-hazard in 2018, resulting in a significant reduction of towns with a high-hazard rating (Fisher's exact: $p < 0.001$).

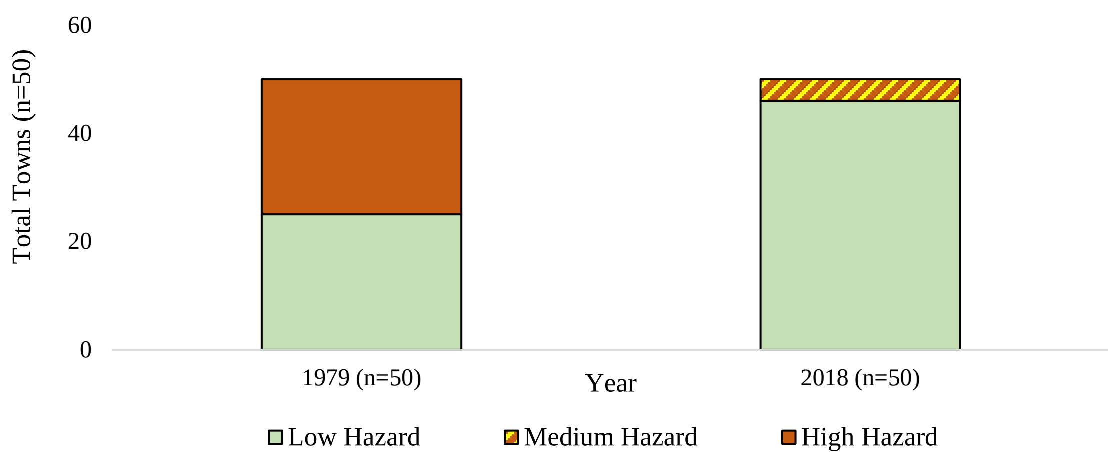


Figure 3.8. Hazard rating changes for 50 NH towns, using 1979 criteria and 2018 field data.

The four towns that did not receive a low-hazard rating in 2018, Acworth, Canaan, Hinsdale, and Warner, contained one stand with that met the criteria for high hazard, and one stand that met was rated low hazard. The ratings for each stand were combined for a medium-hazard rating for each town (Table 3.7).

Table 3.7

2018 WPBR Incidence and Hazard Ratings for NH with 1979 Ratings Model

Town	2018 Incidence	1979 Rating	2018 Rating	Town	2018 Incidence	1979 Rating	2018 Rating
Tuftonboro	40.9	High	Low	Belmont	1.8	Low	Low
Warner	38.3	Low	Medium	Andover	1.6	Low	Low
Hanover	33.3	High	Low	Grantham	1.2	Low	Low
Littleton	29.3	High	Low	Alton	0	High	Low
Acworth	27.4	High	Medium	Bath	0	High	Low
Barnstead	26.6	High	Low	Brookfield	0	High	Low
Hinsdale	24.2	Low	Medium	Charlestown	0	High	Low
New Boston	18.2	Low	Low	Cornish	0	High	Low
Concord	18.1	High	Low	Loudon	0	High	Low
Weare	11.9	Low	Low	Lyme	0	High	Low
Canterbury	7.1	High	Low	New Durham	0	High	Low
Keene	7.3	Low	Low	Strafford	0	High	Low
Enfield	6.3	High	Low	Thornton	0	High	Low
Barrington	5.9	High	Low	Wakefield	0	High	Low
Pembroke	5.7	High	Low	Alexandria	0	Low	Low
Sullivan	5.7	Low	Low	Bristol	0	Low	Low
Lebanon	5.3	High	Low	Candia	0	Low	Low
Haverhill	5	High	Low	Claremont	0	Low	Low
Danbury	4.8	Low	Low	Deering	0	Low	Low
Troy	4.5	Low	Low	Dublin	0	Low	Low
Raymond	3.2	Low	Low	Dunbarton	0	Low	Low
Antrim	2.9	Low	Low	Hebron	0	Low	Low
Moultonborough	2.5	High	Low	Lyndeborough	0	Low	Low
Canaan	2.3	High	Medium	New London	0	Low	Low
Swanzey	2	Low	Low	Sunapee	0	Low	Low

Note. Incidence for live and dead pines combined. Hazard ratings criteria: 1979 and 2018 (Avery, 1980). Towns with stands rated high and low were averaged for a medium hazard rating.

In 2018, WPBR presence was equally distributed between 14 towns that were rated high hazard in 1979 and 14 towns rated low hazard. The 1979 hazard rating was not related to WPBR presence in combined live and dead pines in 2018: (X^2(1, N = 50) = 0.04, p = 0.84); however, five of the seven towns with WPBR incidence over 20% were rated high hazard in 1979.

Infection history by 1979 hazard zones. Infection in 2018 was found in 10 high-hazard and nine low-hazard stands with a history of WPBR, and in eight high-hazard and five low-hazard stands that were infection-free when mapped 1929-1976 (Figure 3.9). In contrast, stands with no WPBR in 2018 included 15 high-hazard and 16 low-hazard stands with a history of WPBR infection. The 1979 hazard ratings were not related to WPBR infection history at the stand scale: (X^2(3, N = 98) = 1.45, p = 0.69).

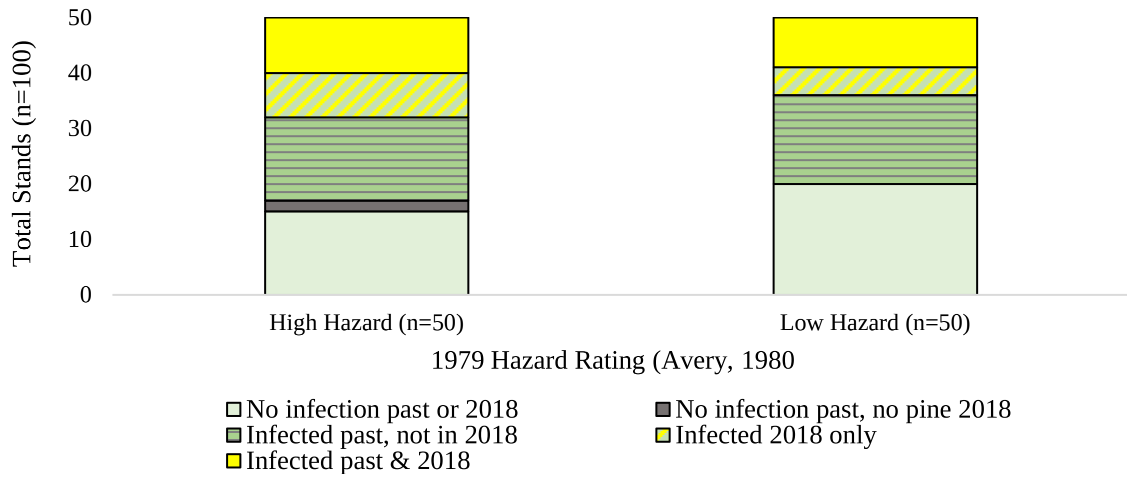


Figure 3.9. 1979 hazard ratings and infection history for 100 stands observed in 2018.

When mapped, the stands with WPBR in 2018 were well-distributed throughout both 1979 high and low hazard zones (Figure 3.10).

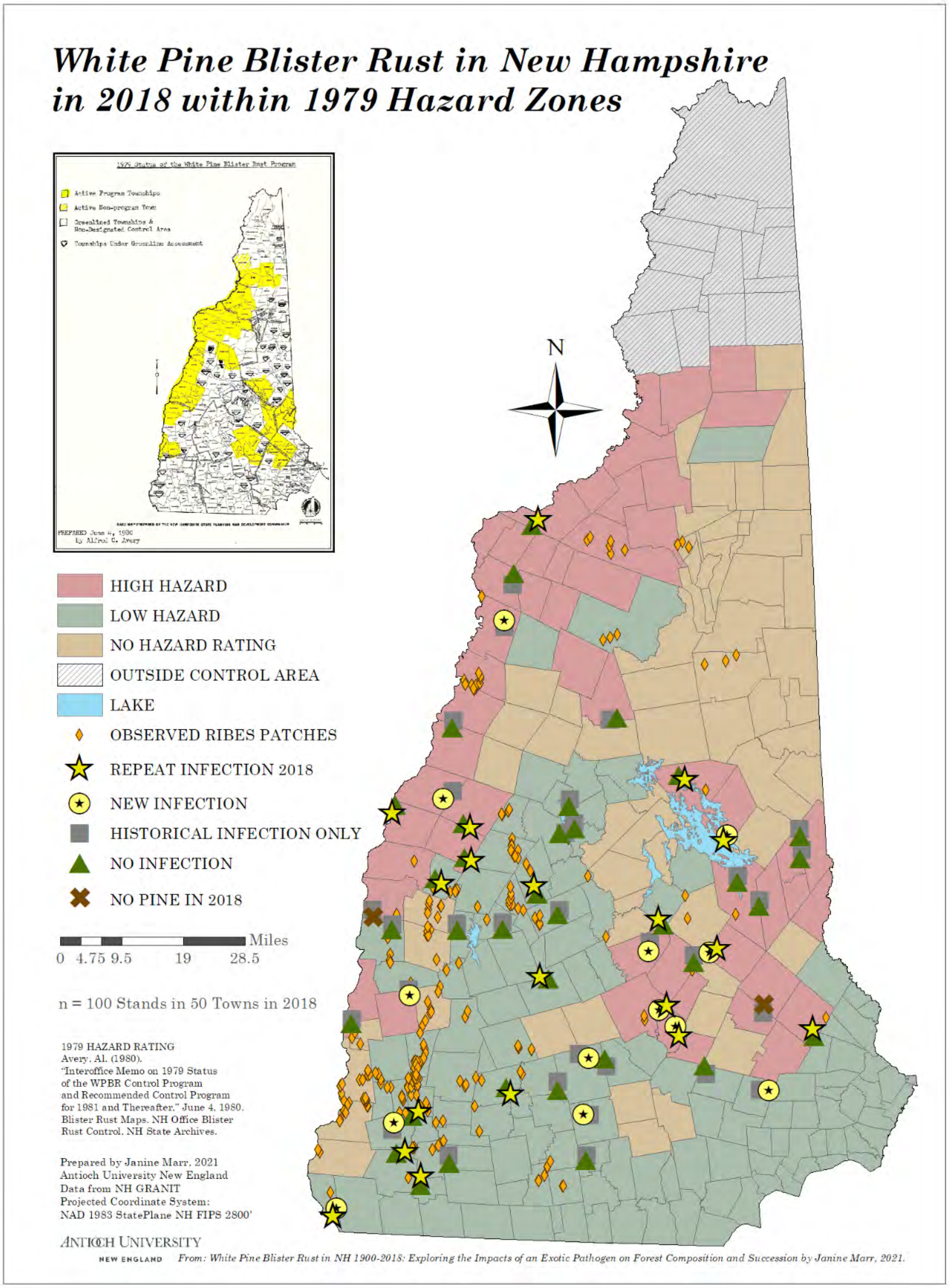


Figure 3.10. WPBR histories in 100 stands in 2018 within the 1979 hazard zones.

Size class infection by 1979 hazard zones. Towns in the 1979 high hazard zones supported more WPBR infection than low hazard zones, with the exception of the pole size class (Table 3.8). High-hazard towns also had a higher stem count in all but the sapling size class.

Table 3.8

2018 WPBR Incidence in Regeneration Size Classes by 1979 Hazard Zones

Size Class	1979 Hazard Zone	# WPBR	# No WPBR	# Stems	% Infected
Seedling	High	85	268	353	24.1
Seedling	Low	16	331	347	4.6
Seedling	Total	101	599	700	14.4
Sapling	High	67	350	417	16.1
Sapling	Low	60	358	418	14.4
Sapling	Total	127	708	835	15.2
Pole	High	8	160	168	4.8
Pole	Low	1	147	148	10.1
Pole	Total	9	307	316	2.8
Timber	High	2	187	189	1.1
Timber	Low	1	113	114	0.9
Timber	Total	3	300	303	1
Combined	Total	240	1914	2154	11.1

Note. 1979 hazard zones from (Avery, 1980). Totals for live and dead pines combined.

1979 hazard rating criteria. Of the four criteria a town needed for a high hazard rating using the 1979 method, the criterion most observed in 2018 was adequate stocking of at least 50 live pines per acre; 27 of the 50 towns surveyed in 2018 had adequate stocking of live white pine (Figure 3.11, Appendix A-1). The lack of adequate stocking prevented Hinsdale from receiving a high hazard rating in 2018. The criterion of WPBR presence within the past 10 years was met by 12 towns; eight of those 12 towns were rated high hazard in 1979.

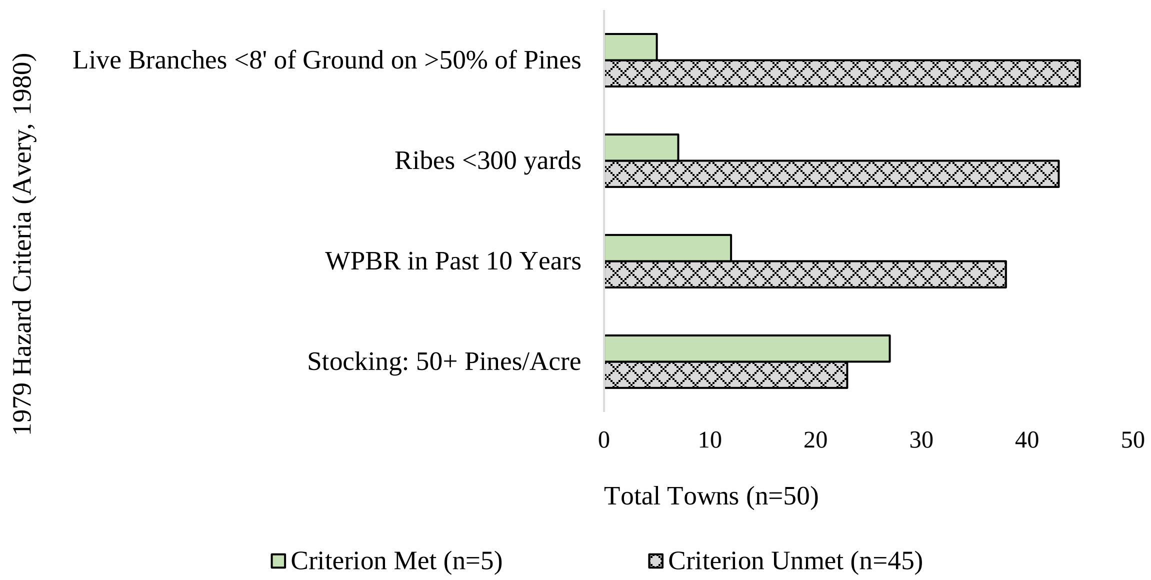


Figure 3.11. Total towns (n=50) in 2018 meeting the 1979 hazard rating criteria (Avery, 1980).

The two criteria least observed in 2018 were *Ribes* presence and live branches within eight feet of the ground for more than 50% of the live pines. Seven of the 50 towns met the requirement for *Ribes*; five towns met the requirement for live branches. A lack of live branches prevented Canaan from receiving a high hazard rating in 2018.

Stand and site characteristics. No clear relationships were detected between stand and site characteristics and the presence of WPBR or *Ribes* (Table 3.9). No association was found between WPBR and basal area, or stand stocking (Appendix B-7). No association was found between WPBR and the cardinal direction of *Ribes* <300 yards and <1000 yards from the center of a stand's research plot and the presence of WPBR (Appendix B-8), despite the observation that pine infection was more likely to occur in stands where *Ribes* grew to the north. No relationship was detected between canopy disturbance, such as tree removal due to harvesting, and the presence of *Ribes* in a stand (Appendix B-9).

Table 3.9

Stand and Site Characteristics Related to 2018 WPBR and Ribes Presence

Characteristic	Relationship	Chi Square	P Value
Basal Area (Stand Stocking)	WPBR presence	6.03	0.42
Cardinal Direction of *Ribes* <300 Yards from Plot Center	WPBR presence	3	0.55
Cardinal Direction of *Ribes* <1000 Yards from Plot Center	WPBR presence	4.6	0.33
Canopy Disturbance (Tree Removal)	*Ribes* presence	2.4	0.12

Pine diseases as a stand characteristic. A significant relationship was found between WPBR and other pine diseases. Many stands positive for WPBR also contained *Caliciopsis pinea* (Caliciopsis) and/or white pine needle damage (WPND), (Appendix B-10). The three diseases occurred together in 14.3% of the 98 stands with white pine, and 43.8% of the 32 stands with WPBR. Caliciopsis and WPND were more prevalent in stands infected by WPBR, X^2 (3, N = 98) = 38.70, $p < 0.001$ (Figure 3.12).

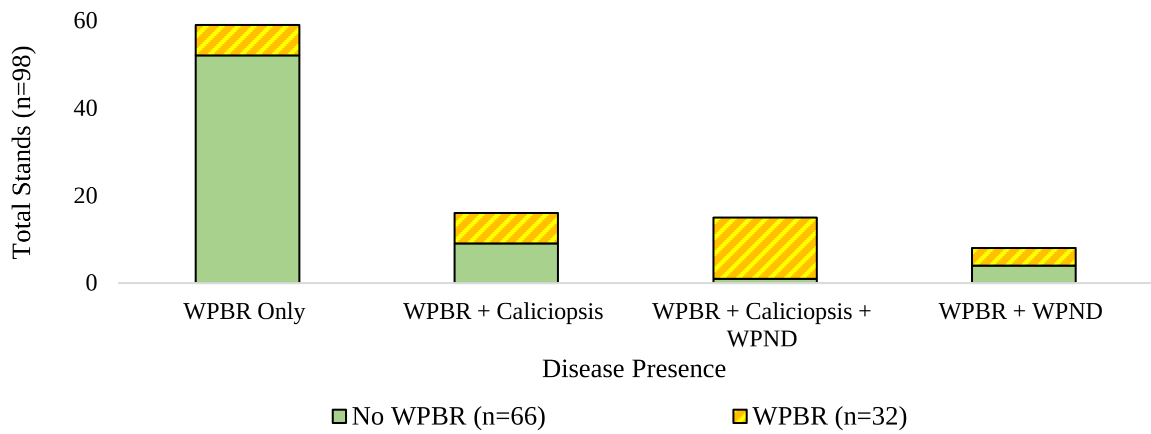


Figure 3.12. WPBR, WPND, and *Caliciopsis pinea* in 98 stands with white pine.

Combinations of two diseases were less prevalent in the stands: infection by WPBR with Caliciopsis was 7.1%; WPBR with WPND was 4.1%; and Caliciopsis with WPND was 1%.

Caliciopsis pinea was the only disease in 9.2% of the stands; WPBR was the only disease in 7.1% of the stands; and WPND was the sole disease in 4.1% of the stands.

Site and stand characteristics for towns with medium hazard ratings in 2018. Common characteristics for all four towns with a 2018 medium hazard rating included: 1) a small canopy opening; 2) a water body to the west of the stand; and 3) stony soils (Table 3.10).

Table 3.10

A Comparison of Four NH Stands with High Hazard Ratings in 2018

Stand	Acworth	Canaan	Hinsdale	Warner
Historical Infection	No	Yes	Yes	Yes
Ribes Distance	<300 Yards	<300 Yards	<300 Yards	<300 Yards
Ribes Direction from Stand	North	West	North	West
% Pine in Stand	35.5	21.6	10.6	55.4
% Pine Dead	20	62.5	14.3	38.7
% Pine in Regeneration Sizes	100	75	85.7	100
Missing Regeneration Sizes	None	Pole	Pole	Pole
Disturbances	WP Removal; WPBR; WPND	WP Removal; WPBR	WP Removal; Windthrow; WPBR	WPBR; WPND
Years Since Disturbances	<15 Years	>50 Years	<25 Years	<15 Years
Canopy Opening Size	Small	Small	Small	Small
Topographic Position	Ridge	Upper Slope	Mid Slope	Valley
Elevation in Feet	1547	1114	538	528
Aspect	East	West	South	South
Miles from Water Body	8	12	0.53	9.57
Direction to Water Body	West	West	West	West
Water Body Type	CT River	CT River	CT River	Lake Sunapee
Soil Type	Marlow Fine Sandy Loam; 0-8% Slopes; Very Stony	Pillsbury Fine Sandy Loam; 3-8% Slopes; Very Stony	Tunbridge-Berkshire; 15-25% Slopes; Very Stony	Tunbridge-Lyman-Becket; 15-25% Slopes; Very Stony
Forest Soil Group	IA	IIB	IA	IB
White Pine Site Index	66	60	75	75

Note. WP = white pine. CT = Connecticut River. Soil type, soil group, site index from Natural Resources Conservation Service, 2019.

An Overlay of White Pine Blister Rust Hazard Zones 1963-1979

No geographical patterns were detected between hazard ratings and WPBR presence when mapping each research site within the 1963 and 1979 hazard zones; WPBR was evenly-distributed throughout the state in 2018 (Figure 3.13).

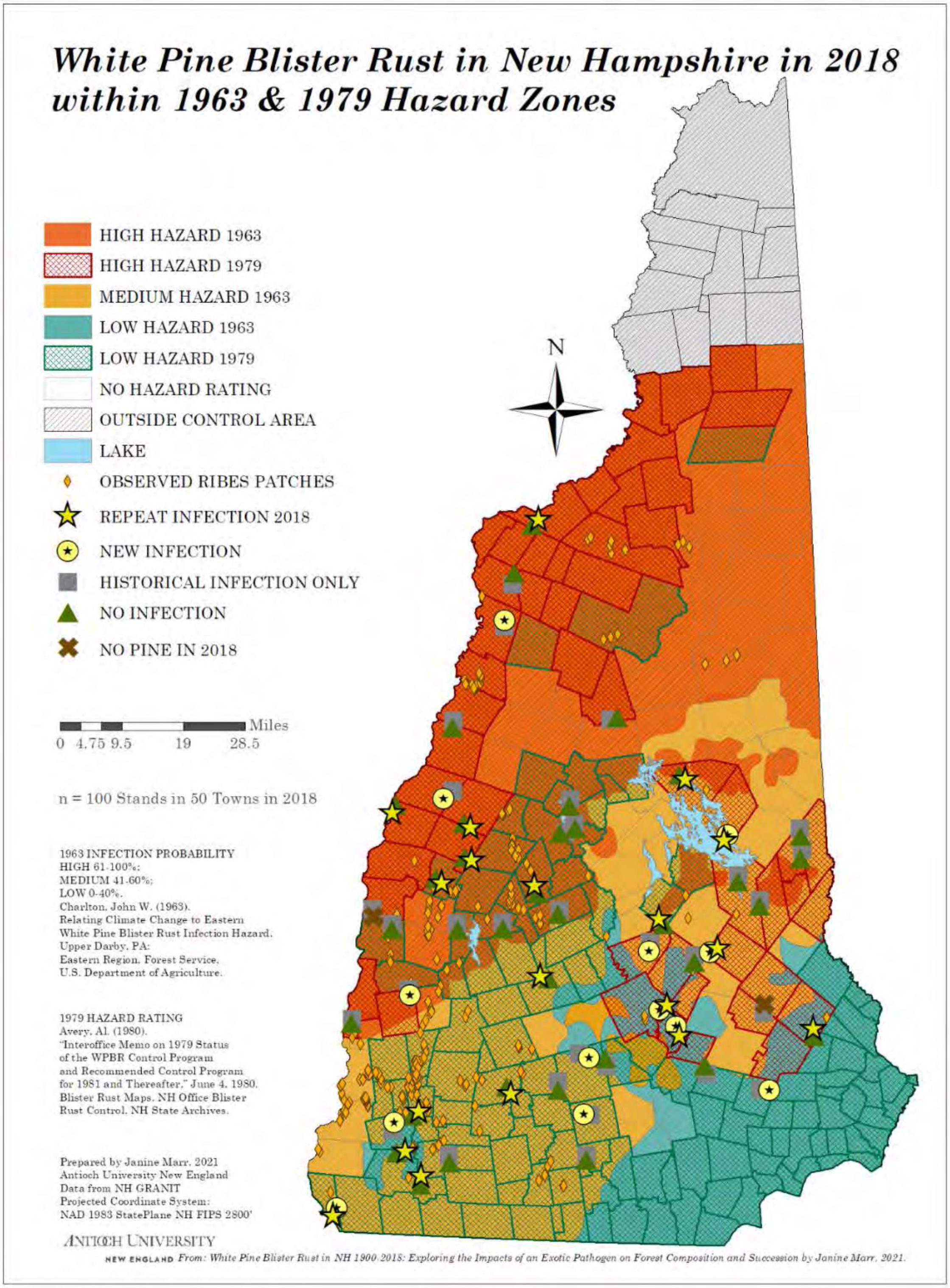


Figure 3.13. WPBR presence within 1963 and 1979 hazard zones for 100 stands.

Discussion and Conclusion

The goal of this research was to determine if either of the hazard rating tools were accurate and useful in guiding management practices for New Hampshire's white pine in the 21st century. The tools were not accurate and could not be used to predict locations in New Hampshire most likely to support WPBR in 2018. The concepts behind the tools, however, may prove useful. In this study, the hazard rating tools illustrated changes that occurred since their development in 1963 and 1979 in the presence and distribution of WPBR in New Hampshire. These changes and key findings are discussed below.

Key Findings

Hazard rating tools. In this study, neither hazard tool correctly predicted where WPBR would be most prevalent in 2018. The 1963 Northeast hazard tool failed using the 1963 map, and an updated formula that included climate data from 1979-1998 and 1999-2018. Sites positive for recurring WPBR infection, both historically and again in 2018, were more apt to exist in areas designated as medium hazard in 1963, where the model projected weather conditions favorable for infection were unlikely to occur every year (Charlton, 1963). In 2018, however, the medium hazard zones supported the highest incidence of WPBR in the seedling and sapling size classes. In contrast, new infections at sites without a history of WPBR were more likely to exist in the 1963 high hazard zones where favorable weather conditions occurred frequently enough to result in stand damage (Charlton, 1963). In 2018, the high hazard zones supported the highest WPBR incidence for sawtimber over 10" DBH.

These findings both contrast and support prior New England research that utilized the 1963 Northeast hazard map. In 1987, a Maine study reported the highest average incidence of WPBR where *Ribes* had not been eradicated: in high hazard zones for seedlings; and low hazard zones for saplings and pole size timber (Ostrofsky et al., 1988). A 1998 New Hampshire study found that the highest mean incidence for all size classes occurred in the high hazard zones on the 1963 Northeast hazard map (Lombard & Bofinger, 1999). The finding that the 1963 Northeast map reflected where climatic conditions were most favorable for WPBR infection in 1963 and 1998, but not in 2018, suggested that the climatic conditions in New Hampshire may have changed. Recent climate data demonstrated that the daytime high temperatures have been increasing over the past few decades, while the nighttime low temperatures have been decreasing, resulting in an expansion of the range of temperatures in a 24-hour period.

The use of recent climate data with the Northeast model also challenged the theory that 90 degrees Fahrenheit was a limiting factor for the development, spread, and germination of WPBR spores (Charlton, 1963). Twenty-four of the 27 towns with WPBR in 2018 exceeded the 90-degree upper limit for July and August, 1999-2018; 12 exceeded the 90-degree upper limit for August and September. The other factors in the formula, air movement, average low temperature, and moisture, were within the ranges provided by the model. In this study, high temperature was the factor that affected the hazard ratings for each stand in all three scenarios (time period and season). Despite temperatures exceeding the upper limit of the model, WPBR occurred, suggesting that perhaps the upper temperature limit for spore development and WPBR infection may be higher than 90 degrees for some towns, based on a combination of climate, microclimate, topography, and vegetation (Anderson, 1973). Prior research in the Lake States found temperatures over 95 degrees, such as daytime temperatures in large forest openings, were too hot, and prevented infection on *Ribes*, and spore germination and infection on pines (Van Arsdel, 1972); however, the results are outdated and need to be reevaluated in today's climate. Recent research in western states suggests that, as WPBR spreads farther south into the high-elevation forests of California (Maloney, 2011), Arizona (Fairweather & Geils, 2011), and New Mexico (Goodrich, Waring, Auty, & Sanchez Meador, 2018), *C. ribicola* continues to adapt to hotter and drier climates. New Hampshire does not have the elevational ranges of the western states; however, the ability of *C. ribicola* to adapt to new climates in new latitudes and elevations suggests that the 90-degree Fahrenheit upper limit in the 1963 Northeast model should be revisited as a limiting factor for infection in New Hampshire's changing climate.

Despite the inability of the 1963 Northeast model to predict the locations most favorable for WPBR establishment in 2018, it did yield significant results. Hazard ratings changed for more than 75% of the stands using updated climate data: no stands received a high hazard rating with the 1979-1998 data; and all stands were rated low hazard with the 1999-2018 data. Van Arsdel, Geils, Zambino, and Guyon (2006) cautioned that a hazard map should not be evaluated based on its accuracy in predicting WPBR incidence, but rather, on its ability to be used as a management tool; however, the 1963 map for the Northeast may mislead managers into focusing control work in areas identified as high-risk in 1963. This study documented that in 2018, repeat stand infections and the highest incidence for the seedling and sapling size classes occurred in zones rated medium risk in 1963, suggesting that these areas may be where conditions are most favorable for WPBR infection in New Hampshire's current climate. However, I have located no supporting research that used the 1963 Northeast model to test the formula's temperature limits with projections for increases in precipitation and windstorms, to determine the model's accuracy under current and future climate scenarios.

The 1979 New Hampshire hazard ratings model was also unable to predict the locations where WPBR would be most prevalent in 2018. The hazard ratings changed significantly when 2018 field data were applied to the model. No towns met the criteria for a high hazard rating;

four towns were assigned a medium hazard rating; and 46 towns were rated low hazard, including three of the five towns with WPBR incidence over 20%. Incidence for regeneration size classes was highest in towns rated high risk in 1979 where WPBR was observed eight times more often in the seedling class than the timber size class. This finding supported a recent New Hampshire study in which seedlings were up to five times more likely to be infected than pines over nine inches in diameter (Munck et al., 2015). Overall, towns rated high hazard in 1979 were more likely to support WPBR infection in all size classes in 2018 than towns given a low hazard rating in 1979.

The New Hampshire model was based on biotic criteria and a 1973 forest inventory that reported 356,000 acres of white pine in the seedling-sapling size class (Avery, 1980). During a 2015 inventory of forest land in New Hampshire, approximately 500,000 acres were recorded as the red/white pine forest type in all size classes; since 2007, a large increase occurred in white pine seedlings, while white pine saplings decreased (Morin & Widmann, 2016). Historically, seedlings and saplings were more likely to become infected by WPBR and die more quickly than larger trees due to vigorous growth and the shorter distances from infected branches to the main stems where girdling occurs (Benedict, 1981; Boyce, 1938). These regeneration size classes typically die rapidly when infected with WPBR, usually within two to four years (Cleaver et al., 2016; Lu, Sinclair, Boult, & Blake, 2005; Schoettle, Jacobi, Waring, & Burns, 2019; Schwandt, Kearns, & Byler, 2013), quickly disappearing from the stand and making an inventory difficult (Filler, 1933). Predicting how many acres of New Hampshire's white pine regeneration may succumb to WPBR, grow into a larger and potentially less-susceptible size class, or escape the disease due to a climate, microclimate, or sheltering overstory unfavorable to infection (Van Arsdel, 1972) is problematic. This study has shown that developing a risk map to reflect WPBR risk in a dynamic landscape is challenging. In order to be useful to forest managers today, the map would require regular and frequent updating to illustrate the loss of white pine stands from timber harvesting, land conversion or development, and disturbances such as WPBR. The premise for the model was simple: if pine stands were well-stocked with live branches within eight feet of the ground where WPBR infection was most likely to occur (Crump et al., 2011; Schwandt et al., 2013); and if the stand was located in a dew pocket or fog valley that fostered infection (Avery, 1980; Charlton, 1963; Spaulding, 1929); and if *Ribes* grew as a source of inoculum within 300 yards of the stand where historical research indicated risk of infection was high (Avery, 1980; Detwiler, 1920; Spaulding, 1922); and if the stand contained evidence of infection in the past decade (Avery, 1980); then the potential for WPBR was high. and the stand should be managed for WPBR. However, I have located no studies that tested this theory or model to determine their accuracy and applicability to forest health and management, or to identify towns that required regular control work. The 1979 NH hazard ratings map was unable to explain why WPBR was found where it was in 2018, and at the intensity or severity observed. The study has shown that the presence of biotic criteria, such as white pine regeneration or *Ribes*, was not sufficient for developing an accurate hazard ratings map for New Hampshire.

***Ribes* presence as a WPBR risk indicator.** In 2018, white pine infection was unrelated to *Ribes* presence. Research in 2013 indicated that pine infection in New Hampshire was significant if infected *Ribes* cultivars were found within the historical 300-yard buffer zone (Munck et al., 2015). In 2018, infected pines were found where native and non-native *Ribes* grew within the 300-yard buffer zone in Acworth, Hinsdale, and Warner; however, in Barrington, the closest observed *Ribes* were over 300 yards away from infected pines, and in Pembroke, over 500 yards from infected pines. (See Chapter Two for more information on the

Ribes species observed in 2018.) The Barrington and Pembroke infections suggested that spores may travel longer distances than the historical 300-yard zone, similar to infections in the Lake States where *Ribes* spores travelled more than 467 yards to infect white pines (Van Arsdel, 1961). The 2013 New Hampshire study also concluded that infected pines were more likely to be found east or west of infected *Ribes* (Munck et al., 2015), suggesting that geographic location in relation to prevailing winds may affect WPBR presence. In 2018, *Ribes* were more prevalent to the north and west of infected pine stands. The results of this study did not support *Ribes* presence, proximity, and cardinal direction within the historic 300-yard buffer zone as important factors in the infection of New Hampshire's white pines in 2018.

Ribes density, or the number of *Ribes* per acre, has been used to measure WPBR risk. One rust index, based on research in Idaho and Montana (Hagle, McDonald, & Norby, 1989), assigned a very low risk to sites with less than one *Ribes* per acre and a very high risk to sites with more than 1000 *Ribes* per acre. An example of its use with 2018 data suggests that the index may not be appropriate for New Hampshire. Stands in New London and Acworth, where *Ribes americanum* P. Mill. and *R. rubrum* L. grew as groundcovers, equivalent to more than 1000 *Ribes* per acre, would have received a very high rating, indicating that risk for WPBR was very high. However, the New London stand, which was disease-free in 1940 (Leafe, 1940), supported a large population of *Ribes* plants beneath disease-free white pines; and in Acworth, the stand that was disease-free in 1936 (Harrington, 1936) and eradicated in 1968 (NH Office of Blister Rust Control, 1968), supported dense *Ribes* growth beneath dead pines whose cause of death could not be determined (due to the absence of bark and a classic spindle-shaped trunk from girdling by the live canker). In contrast, a stand in Hinsdale with an infection incidence over 30% had no *Ribes* in the plot and would have been given a very low rating on the rust index scale. These examples suggest that a rust index, based on total *Ribes* per acre within the plot or stand, may not reflect WPBR risk in New Hampshire.

Disease presence as a WPBR risk indicator. In Oregon, a hazard rating method was proposed that used the percentage of live and dead trees with cankers to indicate WPBR risk (Koester, Savin, Buss, and Sniezko, 2018): high hazard sites exhibited cankers on 78% of the pines; while less than 28.5% of pines had cankers on low hazard sites. When the 2018 New Hampshire data were analyzed using the canker-based method for Oregon, the hazard ratings were similar to the 1963 climate-based method for the Northeast for four out of six selected sites. Stands in Acworth, Hinsdale, Littleton, New Boston, Tuftonboro, and Warner received a medium hazard rating by the canker percentages method. In 1963, four of the stands were rated medium-hazard, and two high-hazard. While the Northeast model used climatic data to determine WPBR risk, and the canker-based method documented cankers visible at the time of data collection, I have found no studies that: 1) compare the two methods for accuracy and applicability; and 2) indicate if a relationship exists between historical and current infection levels based on canker presence in New Hampshire.

An intriguing result of this study was the significant relationship between *Caliciopsis*, WPND, and WPBR presence in a stand. The three diseases co-occurred in 43.8% of all infected stands, suggesting that the fungal diseases may require similar environments for establishment, such as high humidity and moisture in the spring (Wyka, Munck, Brazee, & Broders, 2018); however, I have located no studies that have researched this combination of diseases on five-needled white pines. Further research is needed on the co-occurrence of these fungal diseases, their responses to a projected warmer and wetter climate in New England, and their effects on the health and sustainability of white pine as a forest resource (Broders, Munck, Wyka, Iriarte, &

Beaudoin, 2015; Costanza, Whitney, McIntire, Livingston, & Ghandi, 2018; Van Arsdel, 2011; Wyka et al., 2018).

Site and stand characteristics as WPBR risk indicators. In 2018, many of the site and stand characteristics often associated with WPBR risk were not related to disease presence in New Hampshire. Similar to research conducted in Wyoming and Colorado 15 years earlier (Kearns & Jacobi, 2006, 2007), no relationship was detected in 2018 between site aspect and WPBR presence. Unlike research in the Rocky Mountains, where elevation and slope position had a significant effect on the presence of WPBR (Kearns & Jacobi, 2006), no relationship was found in New Hampshire between elevation, which ranged from 198 feet to 1547 feet, slope position, and WPBR. Prior research in the Lakes States reported that the base of a north-facing slope should produce favorable conditions for pine infection due to the accumulation of cooler air and a shorter duration of solar radiation, in contrast to upper slopes facing south that were least likely to support WPBR because their maximum exposure to solar radiation prevented the accumulation of cool air required for infection (Anderson, 1973). In New Hampshire, no sites supported WPBR at the base of north-facing slopes or at a south-facing upper slope. Canopy openings smaller than the height of the surrounding trees may produce temperature and moisture conditions favorable for the development of WPBR infection (Anderson, 1973; Tsopelas, 1983; Van Arsdel, 1972); however, in 2018, no significant relationship was observed between canopy disturbance size and WPBR presence. It is interesting to note, however, that the four stands rated high hazard using the 1979 NH method had small canopy openings.

Climate Changes. New Hampshire’s climate has become warmer and wetter during the past century, with a noticeable change in the past four decades (Climate Solutions New England Sustainability Institute, 2014) that has increased the length of the season for WPBR spore dispersal and infection, particularly during the spring. Historical records documented observations of early urediniospores on native gooseberries June 8 and 9, 1926, in Epsom and Allenstown, NH, and June 7, 1932, in Carroll County (Boomer, 1932; Pierce, 1926). In 2018, urediniospores were present weeks earlier on native and non-native *Ribes* species (Figure 3.14): 1) on native *R. cynosbati* L. (May 3 in Hinsdale, May 29 in Canaan, and June 2 in Cornish) and *R. glandulosum* Grauer (May 17 in Loudon); and 2) on non-native *R. rubrum* L. (May 23 in Acworth), and non-native *R. uva-crispa* L. (May 24 in Belmont).

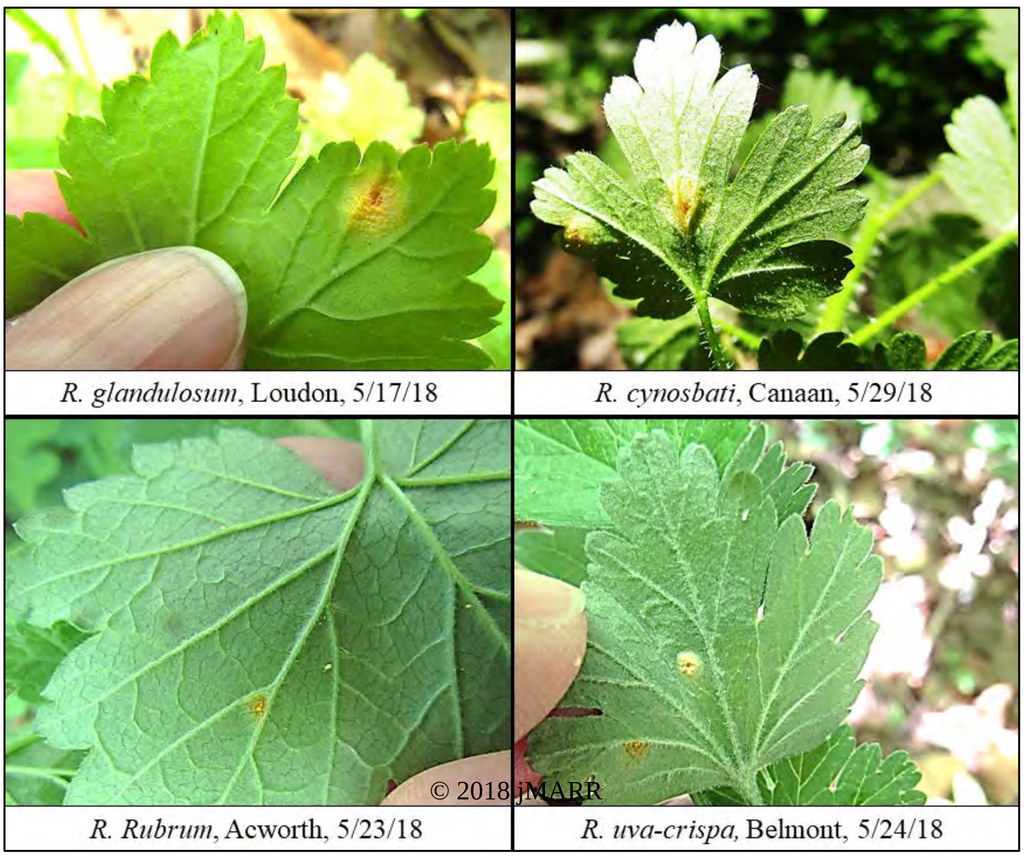


Figure 3.14. Infection on native (top) and non-native (bottom) *Ribes* in NH, May 2018. Photos by Janine Marr.

The 2018 field observations of urediniospores, one month earlier than reported in 1926 and 1932, suggest that New Hampshire's WPBR infection season may start earlier than during the years of the epidemic. Although I located no studies from New Hampshire or the Northeast that have compared *Ribes* infection dates over time, I previously photographed urediniospores in New Hampshire on: *R. glandulosum* 5/27/15 (Gilmanton), 5/29/16, and 5/13/17 (Gilsum); and on *R. cynosbati* 5/29/16, and 5/13/17 (Gilsum). The 2015-2017 observations supported the results of this study that suggested *Ribes* develop urediniospores in New Hampshire's current climate earlier than in 1926 and 1932.

Future Research

Early research in the United States and Canada concluded that WPBR infection was dependent upon the local climate and microclimate (Zsuffa, 1986). The two environmental factors considered most important for disease development are temperature and moisture (Agrios, 2005). This study demonstrated the 1963 Northeast model with 1999-2018 climate data and found that average high temperatures over 90 degrees Fahrenheit may not prevent the production of spores or infection of pines as expected in 1963. This study also found that *Ribes* infection is occurring one month earlier than nearly a century ago, suggesting that the WPBR season may be increasing over time, despite the 1979 NH model's finding that *Ribes* presence in a stand was not indicative of WPBR. These results question the relationship between climate and biotic responses in the WPBR pathosystem. Additional research on how our climate has changed, is changing, and is projected to change, may identify differences over time in phenology and dormancy as a result of the longer growing season.

In order to manage for healthy white pine and control the effects of WPBR, it is necessary to verify that the WPBR pathosystem has adapted to a warmer climate in New Hampshire. Adapting to the changing climate can result in an earlier infection season for *Ribes* and a longer season in which *Ribes* can infect white pines. During the droughty spring of 2018, WPBR infection was observed on *Ribes* in four research locations. Climate data showed that the average nighttime low temperatures had decreased in recent years, while the average daytime high temperatures had increased. Research that explores the relationship between temperature and infection on *Ribes* will advance our understanding in three critical areas: 1) if dew formation during early morning low temperatures fosters more infection than daytime high temperatures can limit; 2) if north-facing low slopes and depressions are more likely to support *Ribes* infection as they did in the Lakes States (Anderson, 1973); and 3) if WPBR has adapted to a wider range of temperatures in New Hampshire's current climate. Understanding how *Ribes* can become infected during a droughty spring season may increase our understanding of *Ribes* susceptibility and, in particular, the role of native *Ribes* in the spread of disease and infection of white pine.

During the epidemic, NH Blister Rust Control workers spent the summer months eradicating *Ribes* to reduce pine infection. In the current climate, however, basidiospores may infect pines earlier than August and September, requiring earlier eradication work (See Chapter Two for early infection dates of spore stages on *Ribes*).

Infected regeneration, especially seedlings, may be affected by climatic conditions at a finer scale than larger trees which may have established under a different climate (Landguth, Holden, Mahalovich, & Cushman, 2017) and level of WPBR susceptibility. Regeneration <5" DBH can identify where trees may establish within the current climate (Bell, Bradford, & Lauenroth, 2014). while infected regeneration may indicate where optimal climatic conditions exist for WPBR (Shepherd et al., 2018) and other pine diseases during earlier or longer seasons than in the past. As a species, New Hampshire's white pine must be resilient and sustainable (Schoettle. Jacobi, Waring, & Burns, 2019) to support a healthy timber industry and maintain ecosystem services. Foresters need silvicultural strategies based on current climate knowledge to manage for healthy, sustainable white pine in New Hampshire's changing climate. Researchers can assist foresters by clarifying how our current climate affects *C. ribicola*, white pine, *Ribes*, and the establishment and spread of WPBR (Loehman et al., 2018; Wyka et al., 2018).

This study used two different hazard ratings tools to determine their applicability as a management tool and to explore which factors may support WPBR establishment in New Hampshire. Neither tool explained why WPBR was found where it was, in the past or present, and at the incidence levels observed. The Northeast and New Hampshire hazard tools were static maps, based upon climate data from the 1950s and early 1960s, and biotic data from the 1970s. Additional research may identify a reliable management tool that includes the current climatic and biotic data to accurately assess the risk for WPBR at the stand or forest level, and fulfill a critical need for landowners managing white pine as a crop or forest product (Schwandt et al., 2013). Ideally, the tool would account for host density and age, as well as climate and topography. While this study did not advance our knowledge about which host, stand, site, or climatic factors have the most influence on WPBR establishment, it did highlight two research opportunities to advance WPBR control and white pine management: the effects of a changing climate on the WPBR pathosystem; and the development of a hazard ratings tool that reflects the dynamic nature of New Hampshire’s climate and white pine forests.

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Appendices

A-1. Presence of 1979 Hazard Criteria in 2018 Stands

Town	WPBR History	50+ Live Pines/ Acre?	50%+ Live Branches 8' Ground?	Pine Infection Last 10 Years or 1 *Ribes*/Acre?	*Ribes* < 300 Yards?	1979 Town Rating	2018 Stand Rating	2018 Town Rating
Acworth	✓	X	X	✓	✓	High	Low	
Acworth	X	✓	✓	✓	✓	High	High	Medium
Alexandria	✓	X	X	X	X	Low	Low	
Alexandria	X	X	X	X	X	Low	Low	Low
Alton	✓	✓	X	X	X	High	Low	
Alton	X	✓	X	X	X	High	Low	Low
Andover	✓	✓	X	✓	X	Low	Low	
Andover	X	✓	X	✓	X	Low	Low	Low
Antrim	✓	✓	✓	X	X	Low	Low	
Antrim	X	X	✓	X	X	Low	Low	Low
Barnstead	✓	✓	✓	✓	X	High	Low	
Barnstead	X	✓	✓	✓	X	High	Low	Low
Barrington	✓	✓	✓	✓	X	High	Low	
Barrington	X	✓	X	X	✓	High	Low	Low
Bath	✓	✓	X	X	X	High	Low	
Bath	X	✓	X	X	X	High	Low	Low
Belmont	✓	✓	X	✓	X	Low	Low	
Belmont	X	✓	X	✓	✓	Low	Low	Low
Bristol	✓	X	X	X	X	Low	Low	
Bristol	X	✓	✓	X	X	Low	Low	Low
Brookfield	✓	✓	X	X	X	High	Low	
Brookfield	X	✓	X	X	X	High	Low	Low
Canaan	✓	✓	✓	✓	✓	High	High	
Canaan	X	✓	X	✓	✓	High	Low	Medium
Candia	✓	✓	X	X	X	Low	Low	
Candia	X	✓	X	✓	X	Low	Low	Low
Canterbury	✓	X	X	X	X	High	Low	
Canterbury	X	✓	✓	✓	X	High	Low	Low
Charlestown	✓	X	X	X	X	High	Low	
Charlestown	X	X	X	X	X	High	Low	Low
Claremont	✓	X	X	✓	✓	Low	Low	
Claremont	X	✓	X	X	✓	Low	Low	Low
Concord	✓	✓	✓	✓	X	High	Low	
Concord	X	✓	✓	✓	X	High	Low	Low
Cornish	✓	X	X	X	✓	High	Low	
Cornish	X	No Pine	No Pine	X	✓	High	Low	Low

Table A-1 Continued

Town	WPBR History	50+ Live Pines/ Acre?	50%+ Live Branches 8' Ground?	Pine Infection Last 10 Years or 1 *Ribes*/Acre?	*Ribes* < 300 Yards?	1979 Town Rating	2018 Stand Rating	2018 Town Rating
Danbury	✓	✓	✓	✓	X	Low	Low	
Danbury	X	X	X	X	X	Low	Low	Low
Deering	✓	X	X	X	✓	Low	Low	
Deering	X	X	X	X	X	Low	Low	Low
Dublin	✓	X	X	X	✓	Low	Low	
Dublin	X	X	X	X	✓	Low	Low	Low
Dunbarton	✓	✓	X	X	X	Low	Low	
Dunbarton	X	✓	X	✓	X	Low	Low	Low
Enfield	✓	✓	X	✓	X	High	Low	
Enfield	X	✓	X	✓	X	High	Low	Low
Grantham	✓	✓	X	X	X	Low	Low	
Grantham	X	X	X	X	X	Low	Low	Low
Hanover	✓	✓	X	X	X	High	Low	
Hanover	X	X	✓	✓	X	High	Low	Low
Haverhill	✓	✓	X	X	X	High	Low	
Haverhill	X	✓	✓	✓	X	High	Low	Low
Hebron	✓	✓	X	X	X	Low	Low	
Hebron	X	X	X	X	✓	Low	Low	Low
Hinsdale	✓	✓	✓	✓	✓	Low	High	
Hinsdale	X	X	✓	✓	✓	Low	Low	Medium
Keene	✓	✓	X	X	X	Low	Low	
Keene	X	✓	✓	✓	X	Low	Low	Low
Lebanon	✓	✓	X	✓	X	High	Low	
Lebanon	X	X	X	X	X	High	Low	Low
Littleton	✓	✓	✓	✓	X	High	Low	
Littleton	X	✓	X	X	X	High	Low	Low
Loudon	✓	✓	X	X	X	High	Low	
Loudon	X	✓	X	X	X	High	Low	Low
Lyme	✓	✓	X	✓	X	High	Low	
Lyme	X	X	X	✓	✓	High	Low	Low
Lyndeborough	✓	X	X	X	X	Low	Low	
Lyndeborough	X	X	X	X	X	Low	Low	Low
Moultonborough	✓	✓	X	✓	✓	High	Low	
Moultonborough	X	✓	X	✓	X	High	Low	Low
New Boston	✓	✓	✓	X	X	Low	Low	
New Boston	X	✓	✓	✓	X	Low	Low	Low

Table A-1 Continued

Town	WPBR History	50+ Live Pines/ Acre?	50%+ Live Branches 8' Ground?	Pine Infection Last 10 Years or 1 *Ribes*/Acre?	*Ribes* < 300 Yards?	1979 Town Rating	2018 Stand Rating	2018 Town Rating
New Durham	✓	✓	X	X	X	High	Low	
New Durham	X	✓	X	X	X	High	Low	Low
New London	✓	✓	X	X	✓	Low	Low	
New London	X	✓	X	✓	✓	Low	Low	Low
Pembroke	✓	✓	X	X	X	High	Low	
Pembroke	X	✓	✓	✓	X	High	Low	Low
Raymond	✓	X	X	X	X	Low	Low	
Raymond	X	✓	X	✓	X	Low	Low	Low
Strafford	✓	X	X	X	X	High	Low	
Strafford	X	No Pine	No Pine	X	X	High	Low	Low
Sullivan	✓	✓	✓	X	X	Low	Low	
Sullivan	X	X	X	X	X	Low	Low	Low
Sunapee	✓	✓	X	✓	X	Low	Low	
Sunapee	X	✓	X	X	X	Low	Low	Low
Swanzey	✓	✓	X	✓	X	Low	Low	
Swanzey	X	✓	✓	X	X	Low	Low	Low
Thornton	✓	✓	X	X	X	High	Low	
Thornton	X	X	X	X	X	High	Low	Low
Troy	✓	✓	X	✓	X	Low	Low	
Troy	X	✓	X	X	X	Low	Low	Low
Tuftonboro	✓	✓	✓	✓	X	High	Low	
Tuftonboro	X	✓	X	✓	X	High	Low	Low
Wakefield	✓	X	X	X	X	High	Low	
Wakefield	X	✓	X	✓	X	High	Low	Low
Warner	✓	✓	✓	✓	✓	Low	High	
Warner	X	✓	X	✓	X	Low	Low	Medium
Weare	✓	✓	X	X	X	Low	Low	
Weare	X	✓	✓	X	X	Low	Low	Low

A-2. Stands with *Ribes* in 2018

Ribes in Stand	*Ribes* in Plot	*Ribes* < 300 yards	*Ribes* > 300 yards
Acworth (a, r)	Acworth	Acworth*	Acworth
Barrington (g)	Moultonborough*	Barrington	Barrington*
Belmont (u)	New London	Belmont*	Cornish
Canaan (c)		Canaan*	Deering
Claremont (g)		Claremont	Hebron
Cornish (c)		Cornish	Loudon
Deering (g)		Deering	Lyme
Dublin (c)		Dublin	Moultonborough
Hebron (c)		Hebron	Pembroke*
Hinsdale (c)		Hinsdale*	Strafford
Loudon (g)		Lyme	Warner
Lyme (c)		Warner*	
Moultonborough (a)			
New London (a)			
Pembroke (g)			
Strafford (g)			
Warner (a)			
34 Stands Total	4 Stands Total	18 Stands Total	14 Stands Total

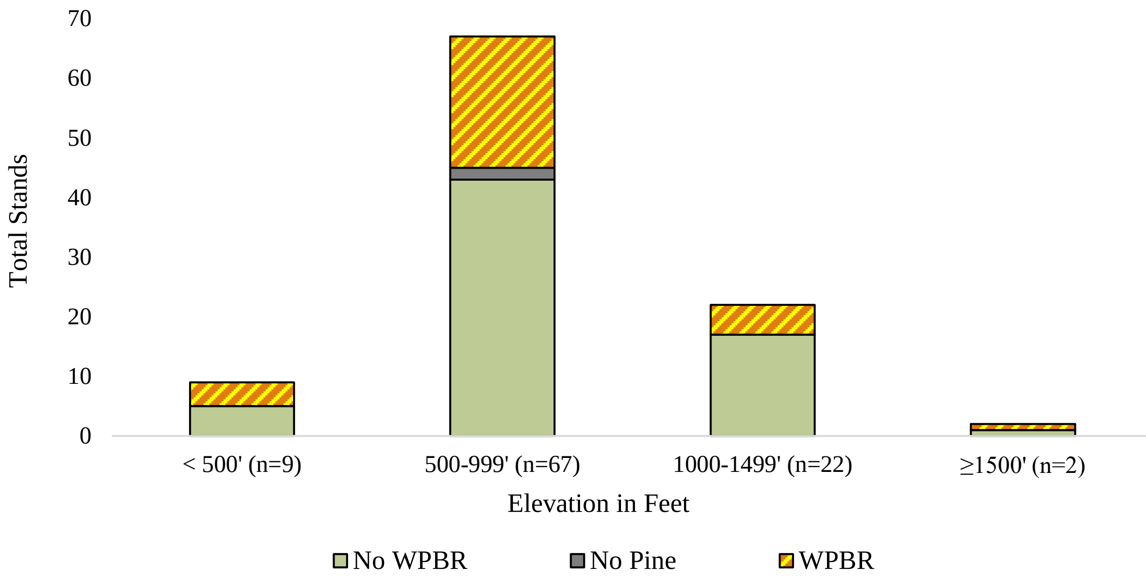
Note. * represents a stand with WPBR infection in 2018. Acworth and Deering had *Ribes* patches at two distances from same plot. *Ribes* species: a) *R. americanum*, c) *R. cynosbati*, g) *R. glandulosum*, r) *R. rubrum*, u) *R. uva-crispa*.

A-3. Comparison of WPBR, *Caliciopsis pinea*, and WPND on Pine in 98 Stands

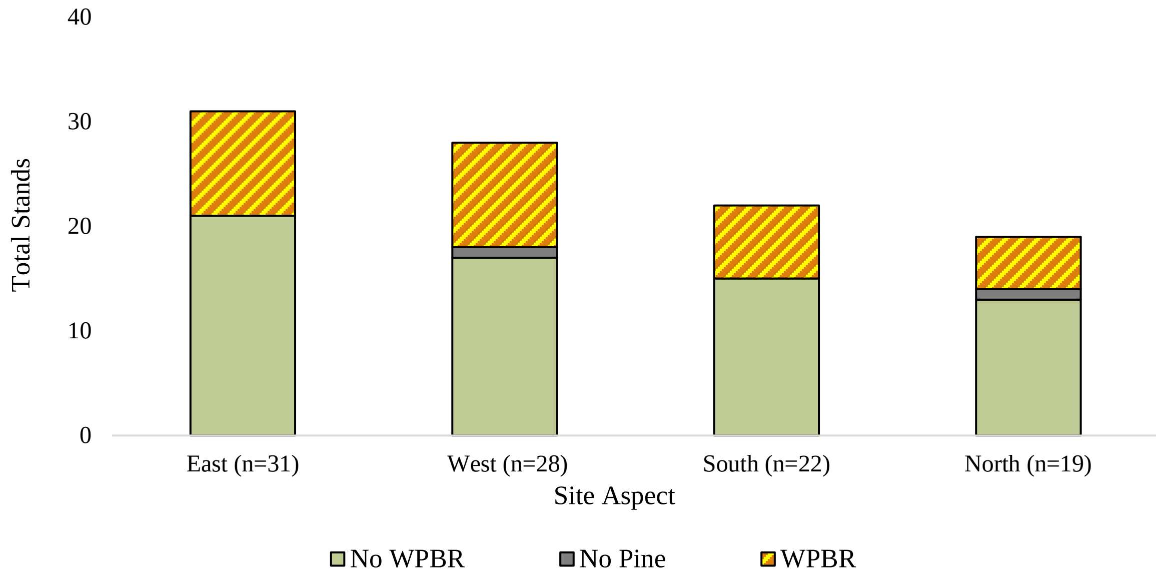
Disease Presence	# Stands No WPBR	% Stands No WPBR	# Stands WPBR	% Stands WPBR	Total
No other disease	52	53.1	7	7.1	59
Caliciopsis + WPND	1	1	14	14.3	15
Caliciopsis	9	9.2	7	7.1	16
WPND	4	4.1	4	4.1	8
TOTAL	66	67.3	32	32.7	98

Note. N = 98: two of the 100 stands observed in 2018 contained no white pine.

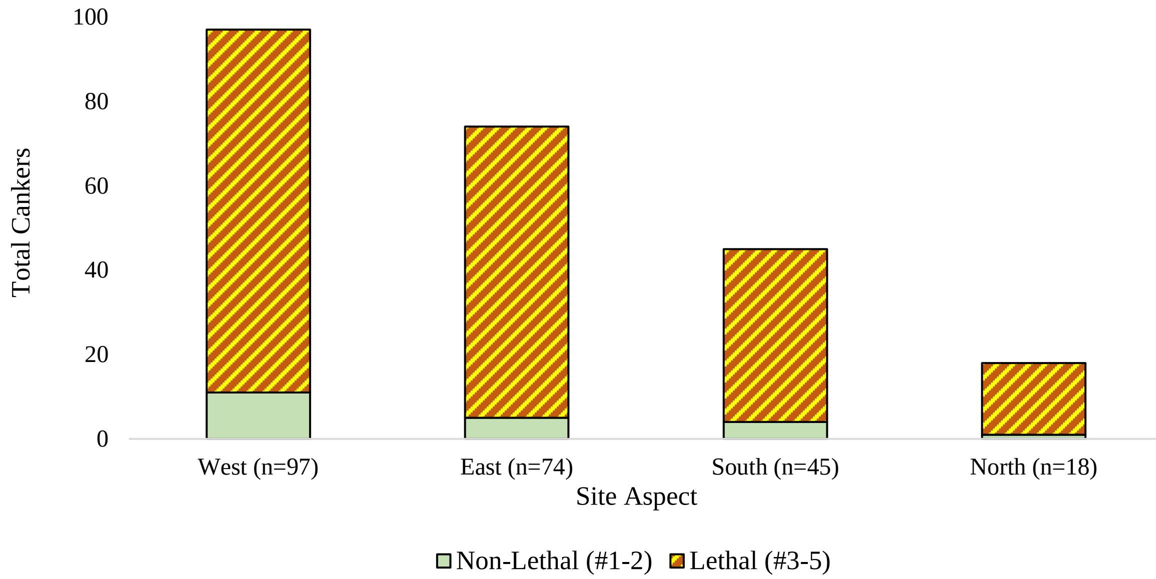
B-1. Elevation and WPBR Presence



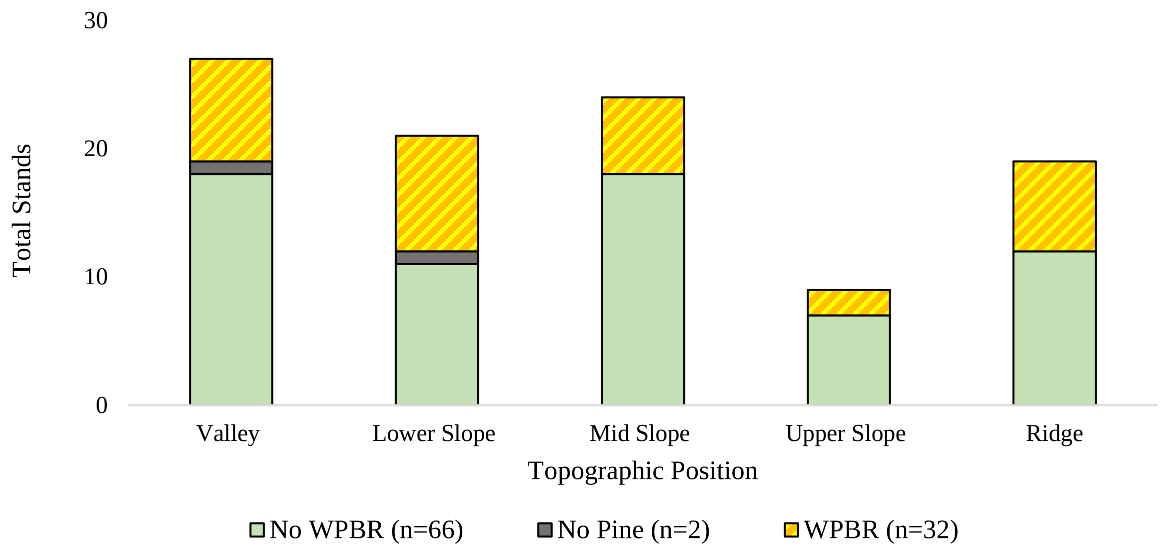
B-2. Site Aspect and WPBR Presence



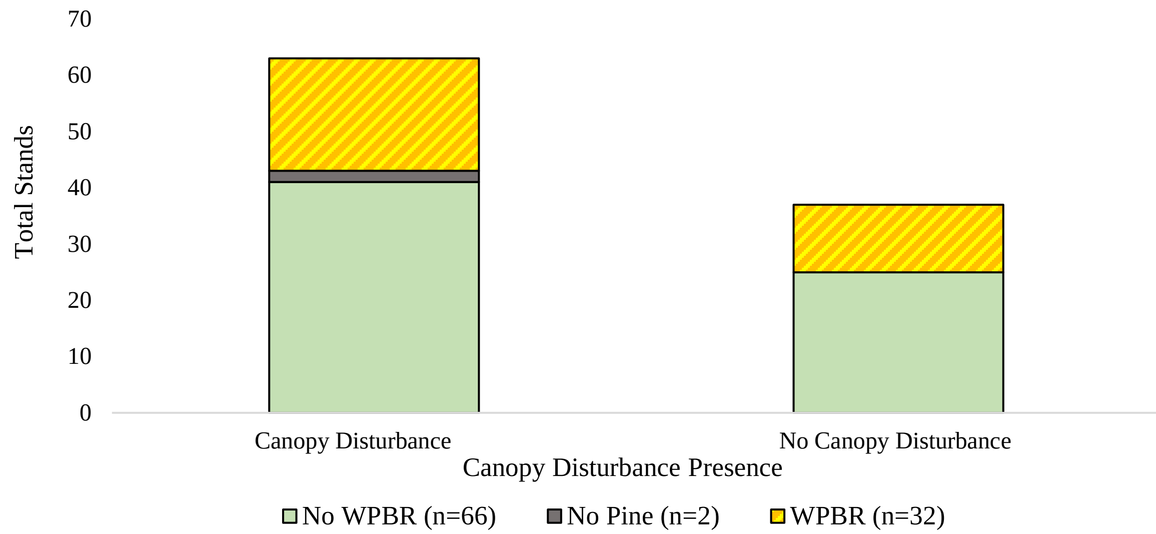
B-3. Site Aspect and WPBR Severity



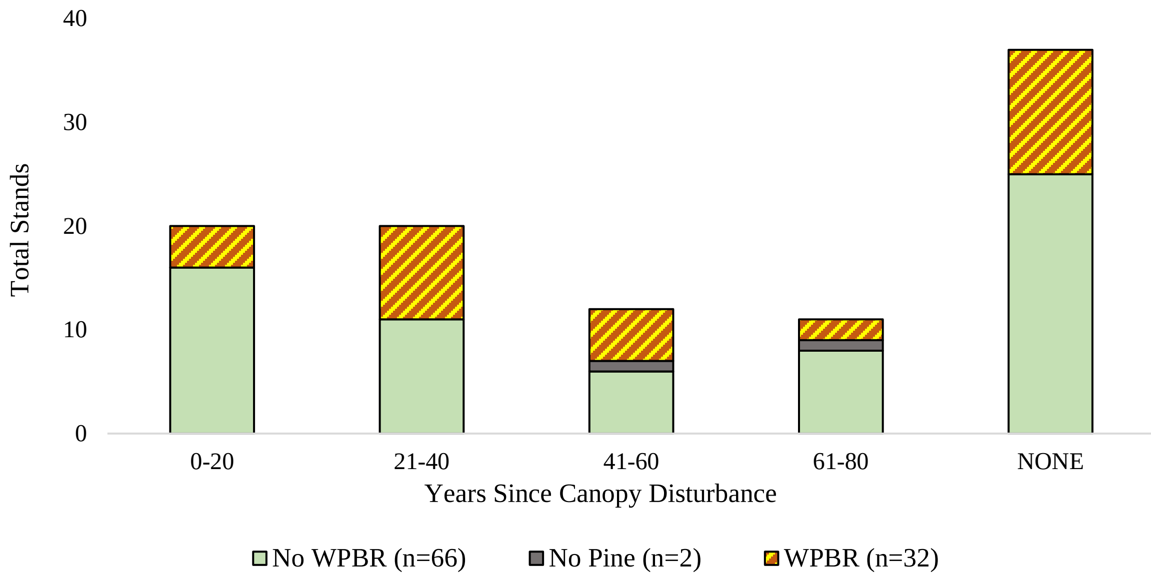
B-4. Topographic Position and WPBR Presence



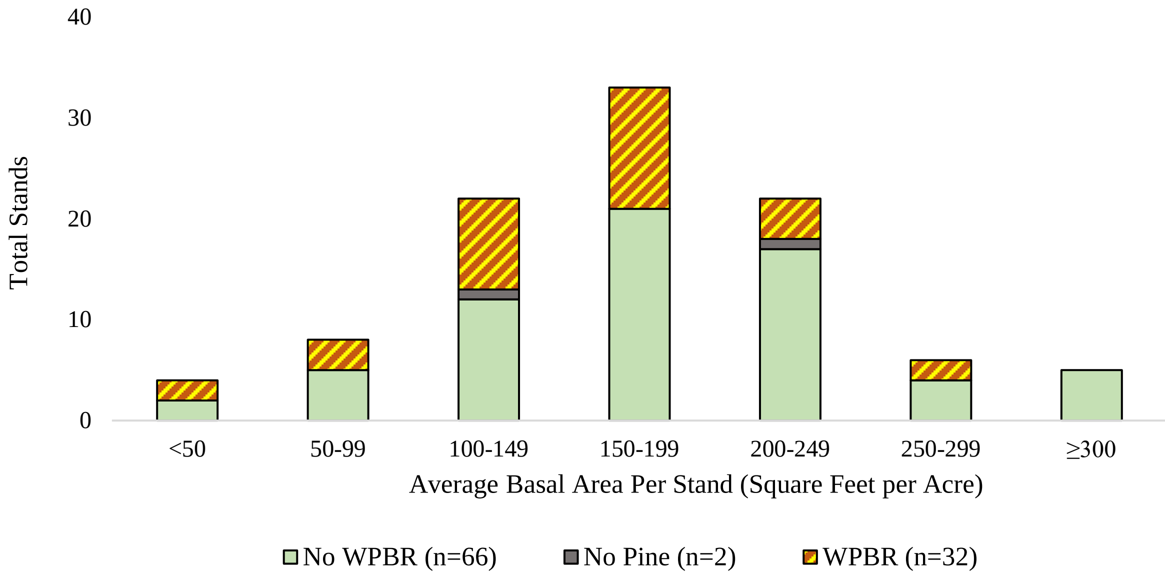
B-5. Canopy Disturbance (Tree Removal) and WPBR Presence



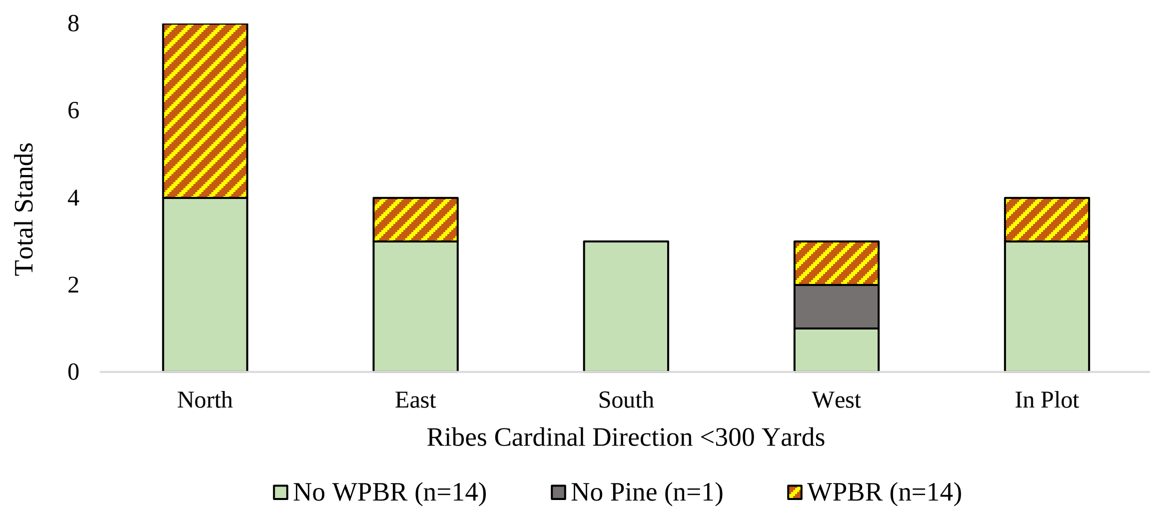
B-6. Canopy Disturbance Age and WPBR Presence

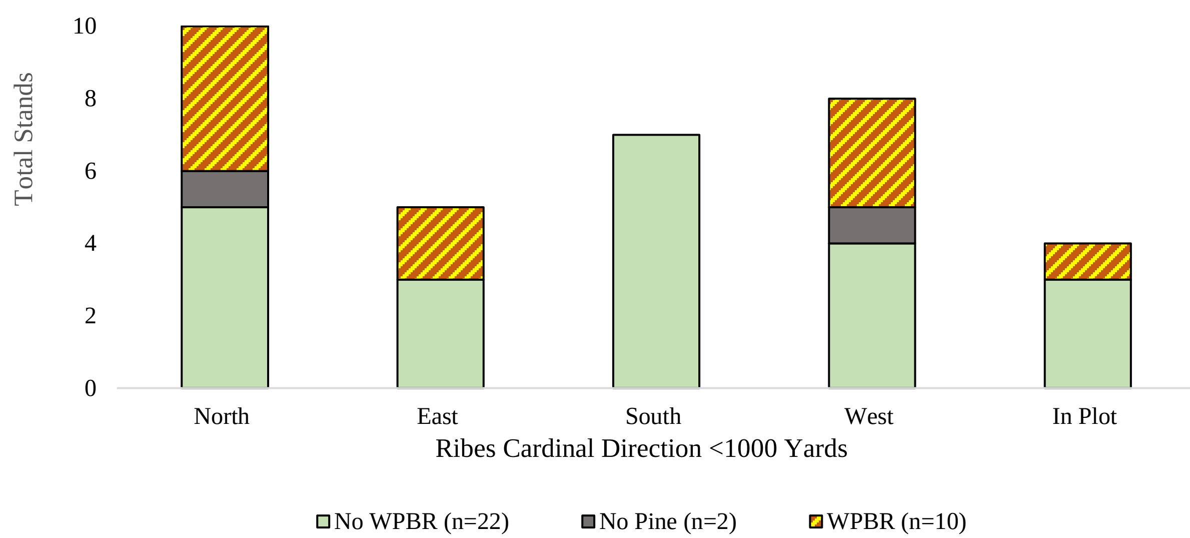


B-7. Basal Area (Stand Stocking) and WPBR Presence

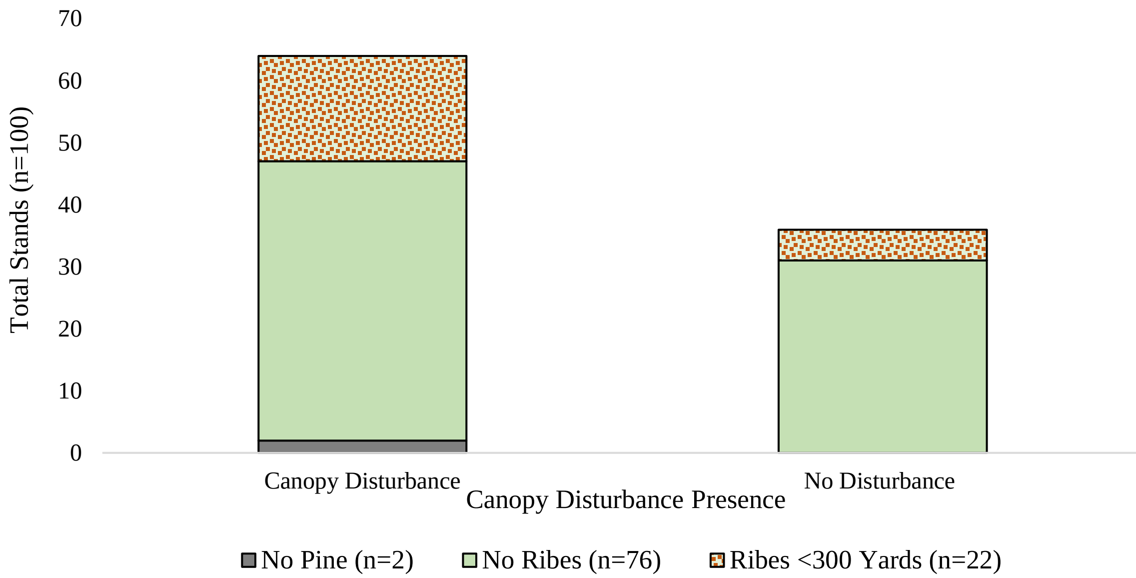


B-8. *Ribes* Cardinal Direction within 300 and 1000 Yards and WPBR Presence





B-9. Canopy Disturbance (Tree Removal) and *Ribes* Presence



B-10. Pine Canker, White Pine Blister Rust, and White Pine Needle Damage

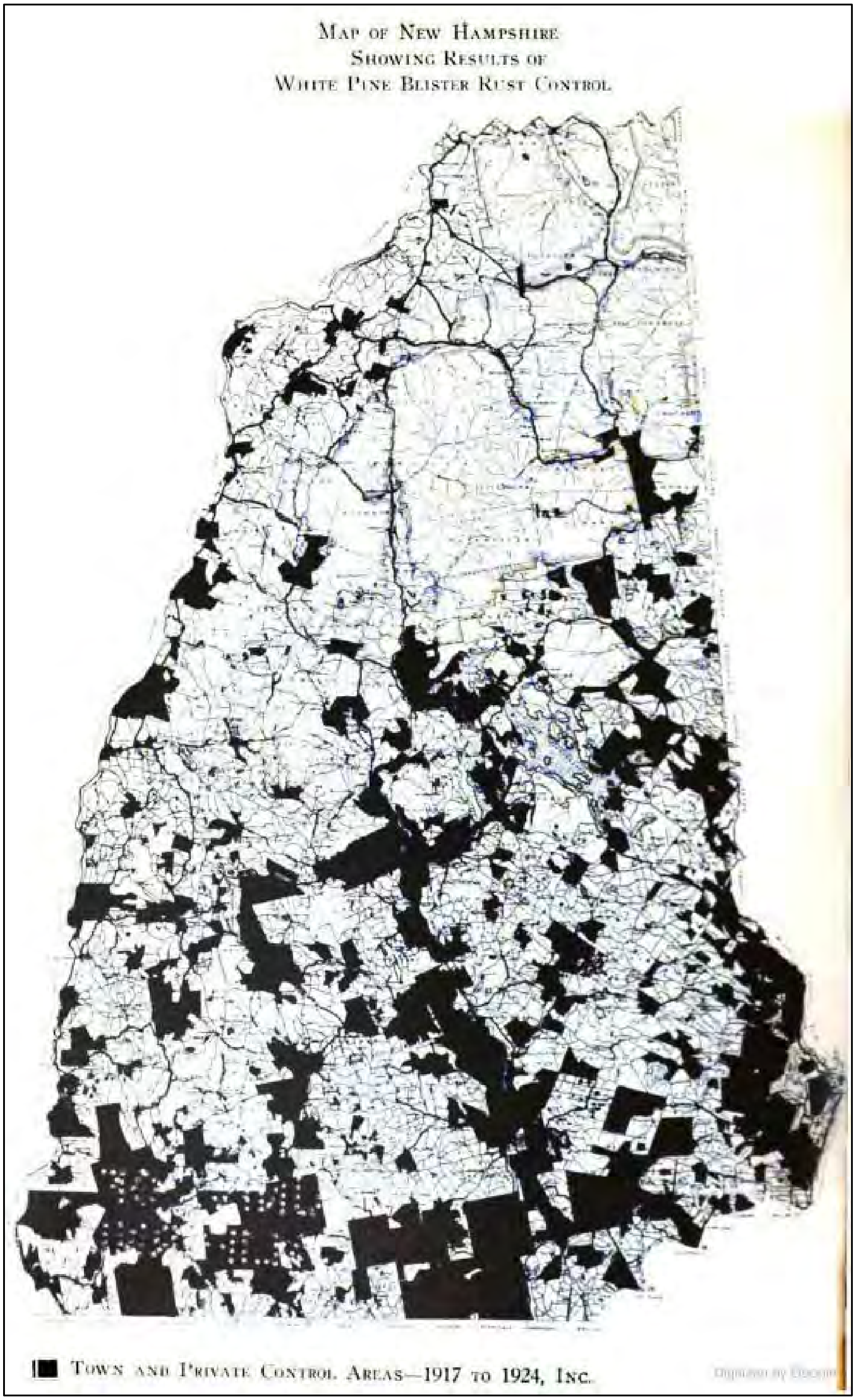
Left: Pine canker (*Caliciopsis pinea)* produces fruiting bodies that resemble tiny eyelashes.

Middle: WPBR fruiting bodies resemble golden-orange blisters.

Right: White pine needle damage (WPND) complex contains several pathogens including *Lecanostricta acicula*, *Bifuselia linearis*, *Lophophacidium dooksii*, and *Septorioides strobus.*

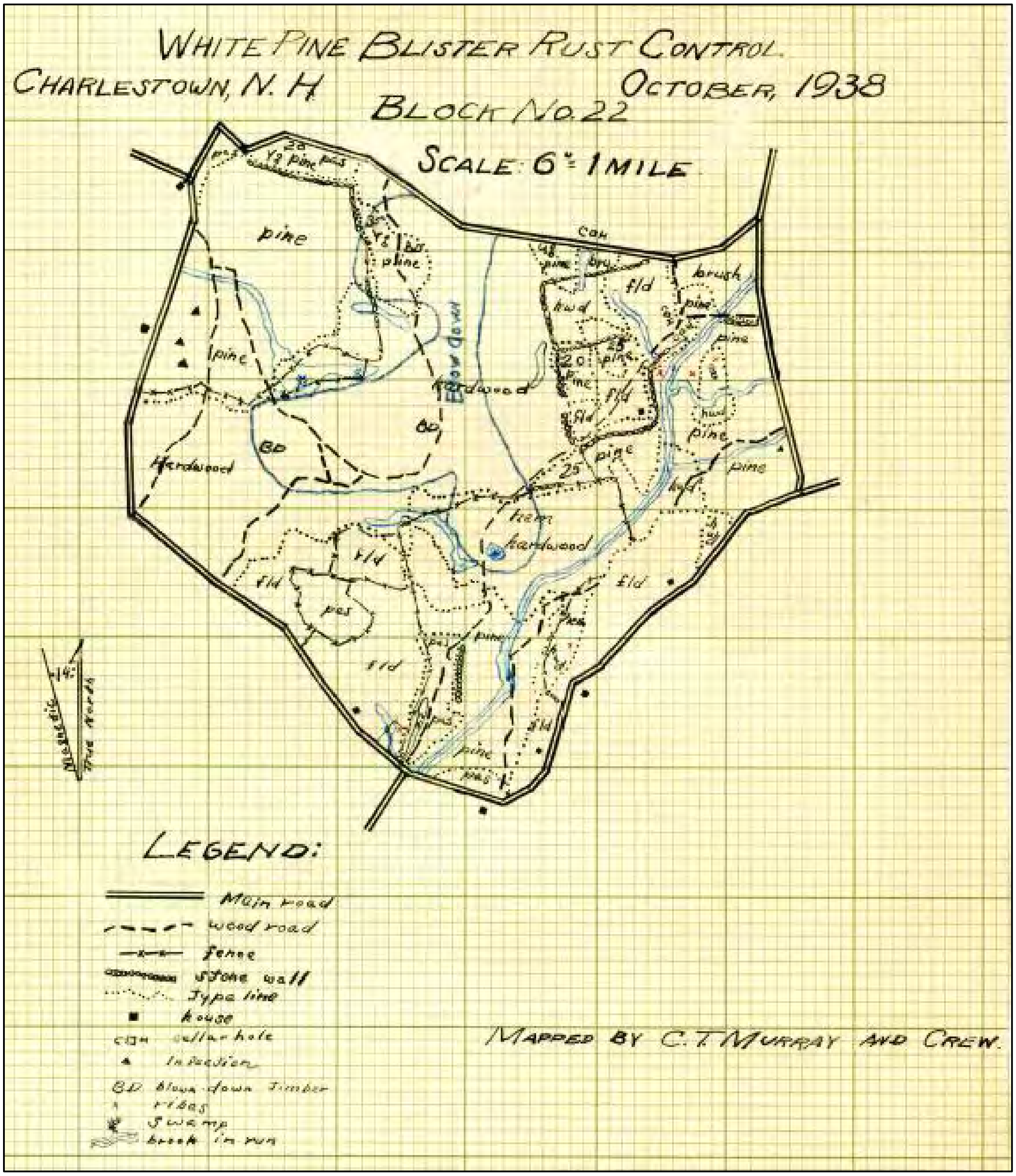
Photos by Janine Marr.

C-1. White Pine Blister Rust Control Area 1917-1924



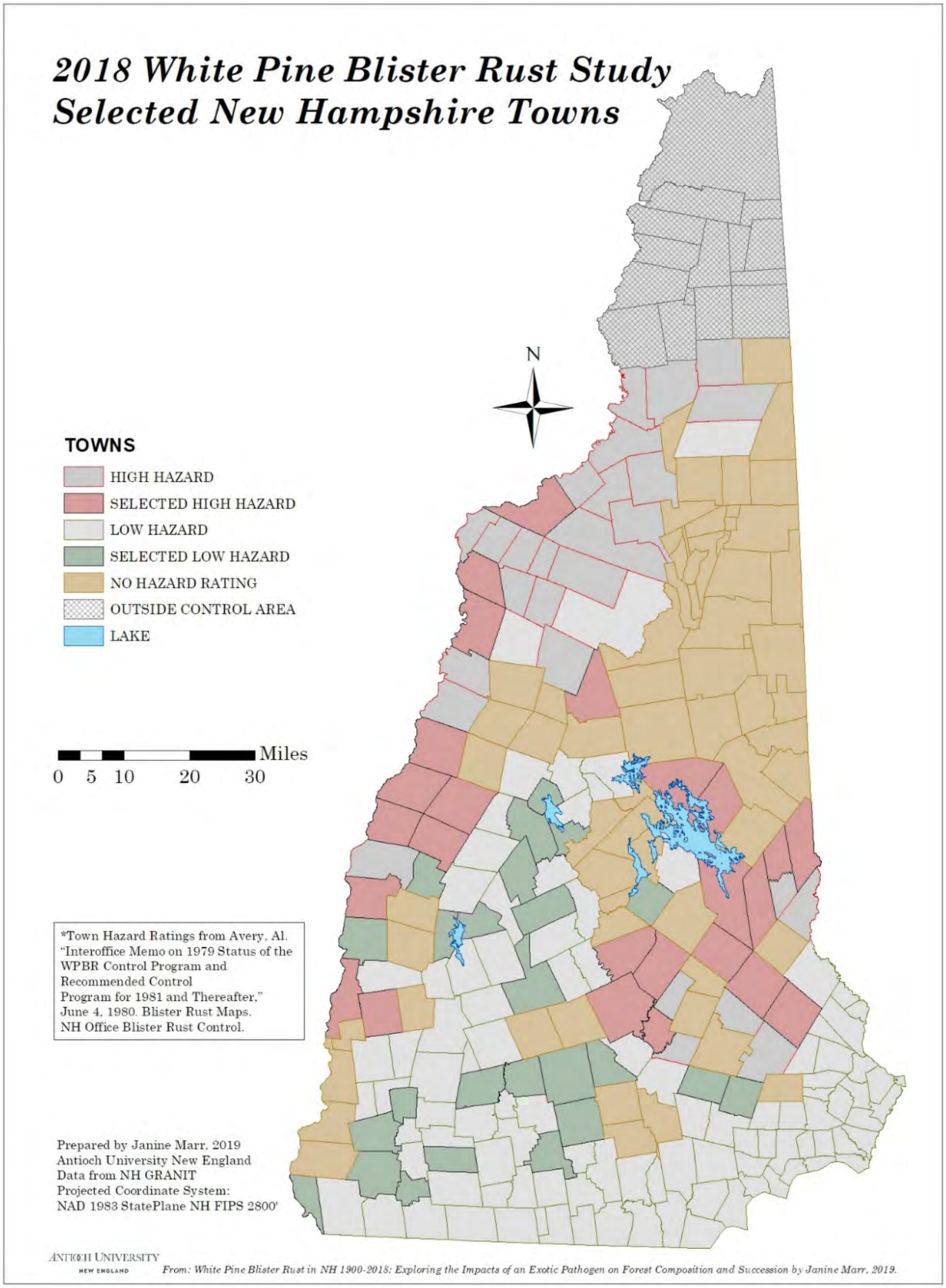
State of New Hampshire Forestry Commission. (1924). Courtesy of NH Blister Rust Control Archives.

C-2. White Pine Blister Rust Map for Block 22, Charlestown, NH, 1938



Murray, C. T. (1938). Courtesy of NH Blister Rust Control Archives.

C-3. 2018 New Hampshire White Pine Blister Rust Study Area



Chapter Four: The Impacts of the Exotic White Pine Blister Rust Disease on Forest Composition and Succession in New Hampshire's White Pine Forests

Abstract

This study examined the long-term impacts of an exotic disease, white pine blister rust (WPBR), on New Hampshire forests. Specifically, this study explored the relationships between WPBR and forest composition, species richness, structure, and succession by comparing historical data to data collected in 2018. The blister rust maps created by the NH Blister Rust Control Program from 1929-1976 provided a baseline for white pine dominance, size classes, and forest type for 100 selected pine stands throughout the state. The 2018 data from these stands included species, size classes, canopy cover, and presence of logging and WPBR disturbances. A model was introduced to conceptualize an exotic disease as a disturbance agent that affected, and was affected by, the environment over time. The primary question explored in this study was if the observed changes in forest type were a result of natural forest succession, or if WPBR was affecting the expected successional trajectory. Stand and white pine size class data were analyzed using Manion's imminent mortality concept and forest succession models. The results indicated that species composition was relatively similar throughout the state and that forest succession had occurred in the historical white pine stands as expected; however, stands with repeat WPBR infection retained the white pine regeneration size classes, while stands with no history of WPBR were dominated by species other than white pine, suggesting that WPBR may slow the advancement of forest succession. A model was created to demonstrate the successional trajectory of white pine over time with and without WPBR. Missing white pine size classes and high mortality rates suggested that the sustainability of white pine as a forest component was likely to be challenged by the presence of WPBR.

Keywords: white pine blister rust, *Cronartium ribicola*, eastern white pine, *Pinus strobus,* disturbance, forest composition, succession, sustainability, New Hampshire

The Impacts of an Exotic Pathogen on Forest Composition and Succession of White Pine Forests

White pine blister rust (WPBR), caused by the exotic fungal pathogen *Cronartium ribicola* Fisch., has been spreading throughout the five-needled white pine (*Pinus* sp.) regions of the United States since 1888 (Spaulding, 1914). The disease kills susceptible white pines of all ages and sizes (Burns et al., 2012; Hatala et al., 2011; Loehman et al., 2018; Worrall, 2019). White pine blister rust was first discovered in New Hampshire on a pine plantation in Marlow in 1909 (Spaulding, 1922). The age of the blister rust canker and the wood on which it grew (Martin, 1922) established early infection years as 1900 in Grafton County in western New Hampshire (Foster, 1930), and 1901 in Cheshire and Hillsborough counties in southern New Hampshire (Newman, 1945). By 1916, WPBR was present throughout the state's white pine region, which encompassed all but the northernmost portion of Coos County (Spaulding, 1922). New Hampshire's blister rust control program began eradicating gooseberries and currants (*Ribes* spp.), the alternate host of the disease, in 1917 (State of NH Forestry Commission, 1920). Records from the NH Office of Blister Rust Control indicated that the program was discontinued about 1980 and the last recorded eradication of *Ribes* occurred in the 1970s. Despite decades of control work and more than a century of research in the Northeast, WPBR and *Ribes* still persist in New Hampshire forests. The question addressed by this research is not why WPBR still persists, but rather, what has it done—how has WPBR impacted the natural succession of New Hampshire's white pine forests?

Research conducted in 2018 (Chapter Two) revealed that WPBR incidence levels in New Hampshire had increased since 1998; however, no published studies exist on the long-term effects of WPBR on the state's white pine forests. The disease kills regeneration size classes more quickly than larger size classes, affecting stand structure and species composition

(Loehman et al, 2018; Smith & Hoffman, 2000; Tainter & Baker, 1996). Forest managers must understand how WPBR, a non-native forest disease, which has been acclimating to New Hampshire's changing climate for more than a century, has impacted the growth, regeneration, and succession of white pine forests. To understand the long-term impacts of WPBR on New Hampshire's white pine forests, this study aimed to identify the role(s) of WPBR as a disease and disturbance agent.

The Role of Disease in the Forest

Disease is an integral component of an ecosystem and a primary agent responsible for maintaining species diversity in the forest (Copsey, 1985; van der Kamp, 1991; Winder & Shamoun, 2006). A forest with a diverse species composition and age structure is more resilient to other disturbances (Greenberg, Collins, McNab, Miller, & Wein, 2016; Pautasso, Schlegel, & Holdenrieder, 2015). Forest diseases may alter or enhance species diversity and density, community composition, and forest structure and succession (Loo, 2009; Lovett et al., 2006). Diseases may accelerate succession by removing early shade-intolerant colonizers and keystone species (Collinge, Ray, & Cully, 2008; van der Kamp, 1991), including the American chestnut (*Castanea dentata* (Marsh.) Borkh), balsam fir (*Abies balsamea* (L.) Mill.), and white pine (Baker, 1949; Kane, Varner, Stambaugh, & Saunders, 2020; Vermont Center for Ecostudies, 2021). Keystone species are adapted to disturbances that provide the space and substrate requirements needed for their establishment (Chapin, 2009). The removal of a keystone species from insect attacks or disease can result in a shift in the composition or structure of a plant community or forest (Collinge et al., 2008; Loo, 2009). White pine is a keystone species that provides important cultural, ecological, and economic services, including: indigenous medicine; breeding habitat, shelter, and nutrients for plants and animals associated with the species; and valuable timber for human use (Chapin, 2009; Collinge et al., 2008; Uprety, Asselin, & Bergeron, 2017; Zinck & Rajora, 2016).

Native forest diseases associated with keystone species such as white pine serve many functions in the forest, and in doing so, interact with and influence the forest's ecological processes. Diseases weaken and predispose trees to attacks by insects and pathogens, potentially hastening mortality (Greenberg et al., 2016); however, diseased and dying trees provide food, cover, and nesting sites for wildlife, including red squirrels which feed upon the living bark surrounding blister rust cankers (Pearce & Spaulding, 1942). Diseases that cause mortality at a large-scale may increase the impact of disturbance events such as fire or wind storms in a forest (Cobb & Metz, 2017). Such large-scale mortality may in turn predispose a tree to additional infection by increasing a site's temperature and humidity to levels that support disease, as with WPBR, or by creating entry wounds for pathogens (Cobb & Metz, 2017). Diseases can affect change at: 1) the individual, population, or larger community scales; 2) in both isolated populations and connected corridors; and 3) for short and long-term durations (Carlsson-Graner & Thrall, 2002).

Another role of disease in the forest is to shift forest structure. Some diseases, such as WPBR, can act as thinning agents (Boyce, 1938) that open the canopy, increase light, and contribute to species diversity (Atkins, Byler, Livingston, Rogers, & Bennett 1999; Crooks, 2002; Ostry & Laflamme, 2009). Other diseases, such as the root and butt rot fungi, create small gaps in the forest (Castello, Leopold, & Smallidge. 1995) where fast-growing or shade-tolerant species establish, often in place of species such as white pine (Lienard, Florescu, & Strigul, 2015). In the western United States and Canada, the canopy gaps initiated by root diseases are suitable for *Ribes* to establish and continue the spread of WPBR (Schwandt, Lockman, Kliejunas, & Muir, 2010). Large scale, long-term, and repeated disease infections may become epidemics or disturbance agents (Ostfeld, Keesing, & Eviner, 2008). Where WPBR and other diseases act as a major disturbance and create large canopy openings, disturbance-dependent, shade-intolerant species such as *Ribes* and white pine may establish (Zambino, 2010). When WPBR acts as a chronic and persistent disturbance that kills seedlings and prevents young trees from reaching a merchantable age, the white pine species may be reduced to a small or remnant component of the forest (Burdon, 1987; Tainter & Baker, 1996).

Few recent studies have examined the roles and long-term impacts of exotic diseases such as WPBR in North American forests. One study, based on data from the Forest Inventory Analysis National Program (FIA), reported that the density of exotic pests and diseases was highest in the Northeast (Lovett et al., 2016). The research built upon a conceptual framework for understanding the impacts of an exotic pest or pathogen on forest ecosystems in eastern North America. The framework included features of the pathogen (mode of action, host specificity, and virulence) and host tree (importance, uniqueness, and phytosociology) (Lovett et al., 2006). When analyzed by this framework, WPBR could be considered as virulent as the host-specific hemlock woolly adelgid (HWA) *Adelges tsugae* (Annand); both white pine and hemlock are dominant species in early and late successional forests respectively. Both species can occur in pure stands and maintain dominance in succeeding forests. WPBR causes tree mortality in 3-20 years depending upon size and susceptibility (Loehman et al., 2018), while HWA typically causes mortality to hemlock in 4-5 years (Lovett et al., 2006). Weighing these factors together, it is likely that the exotic pathogen (*C. ribicola*) and pest (HWA) will impact the structure and functioning of ecosystems where the tree species are a dominant component of the forest (Lovett, Canham, Arthur, Weathers, & Fitzhugh, 2006). Furthermore, exotic pests and diseases are the only disturbance agents that have nearly eliminated entire populations of susceptible species (Lovett et al., 2016); in western states, WPBR has been recognized as a major contributing factor in the severe decline of whitebark pine (*Pinus albicaulis* Engelm.) (Resler & Tomback, 2008; Retzlaff, Leirfallom, & Keane, 2016; Tomback & Achuff, 2010).

While diseases may act as disturbance agents at multiple scales within an ecosystem, the ecosystem may not react as one uniform plant community, due to variability in the susceptibility, resistance, and resilience of the overall community, the host, the alternate host(s), and the pathogen (Madden & Campbell, 1990). Misleading assumptions of a disease complex include: 1) that the host offers a constant area for infection; 2) that changes in disease presence are immediately visible; 3) that there is only one strain of the pathogen present in any location; and 4) that the spatial pattern of disease progression and spread is either random or uniform (Madden & Campbell, 1990).

WPBR is a perfect example of these misleading assumptions. *Ribes* plants shed their leaves when heavily infected, reducing the constant infection area (Miller et al., 1959). WPBR presence is often not visible until the flag or canker stages, 2-4 years after infection (Spaulding, 1911). Two strains of *C. ribicola* have been documented in New Hampshire (Munck, Tanguay, Weimer, Villani, & Cox, 2015). The spatial pattern and rate of disease progression upon an infected pine varies with the tree’s size, susceptibility, and vigor, but follows a relatively predictable pattern (Boyce, 1938; Phelps & Weber, 1969; Schwandt, Kearns, & Byler, 2013); however, in western states, host health and vigor were not determining factors in a tree’s ability to resist infection, particularly in relation to a changing climate (Loehman et al., 2018). The infection travels from an infected needle to the branch, and down the branch to the main stem, where it eventually grows completely around the tree, girdling and killing it (Hirt, 1964; Malloy, 2001; Schwandt et al., 2013). In some cases, however, western pines in the Rocky Mountains have died from multiple branch cankers before the disease could reach the main stem (Burns et al., 2008). Researching the role(s) and long-term impacts of WPBR as a disease and disturbance agent in white pine forests would clarify the interactions between pathogen, hosts, ecosystem, climate, disturbances, disease progression, and forest succession; it would also remove the misleading assumptions that challenge our management of WPBR as a disease and disturbance agent in New Hampshire's forests.

A Disease-Disturbance Model for White Pine Blister Rust

An ecological disturbance is a disruption to the physical or biological structure of an ecosystem by forces such as fire, wind, or falling trees (Bormann & Likens, 1979; Pickett, Wu, & Cadenasso, 1999). Disturbance events affect the changes in species composition and abundance, forest structure, and ecosystem resources and services associated with forest succession (Castello et al., 1995; Daubenmire, 1968; Drury & Nisbet, 1973; Grubb, 1977; Huston & Smith, 1987; Odum, 1969; Pickett, 1980; Walker, Fecko, Frederick, Johnson, & Miller, 2007).

White pine blister rust, an exotic disease with no known natural control agents in New Hampshire, can mimic disturbances that are large or small, and short or long in duration. The spatial and temporal variations of disturbance events add to the diversity of the forested landscape (Pulsford, Lindenmayer, & Driscoll, 2016). Historically, forest diseases were not conceptualized as disturbances (Cowles, 1911; Clements, 1916; Gleason, 1917; Tansley, 1935), even by the ecologists who investigated WPBR and *Ribes* for the blister rust control effort (Cooper, 1913; Hubert, 1931). In recent years, WPBR has been viewed as a disturbance agent in white pine forests (Clason, Macdonald, & Haeussler, 2014; Keane, 2017; Loehman et al., 2018; Sturrock et al., 2011).

In this chapter, I apply my disease-disturbance model to the long-term presence of WPBR in New Hampshire forests, specifically to look for patterns in forest stands where WPBR has repeatedly acted as a disturbance (Figure 4.1). The model depicts disease as a disturbance that affects the composition, structure, and overall functioning of an ecosystem. Changes at the ecosystem scale affect the presence and severity of the disease at the landscape scale, which, in turn, affects the forest and its successional trajectory.

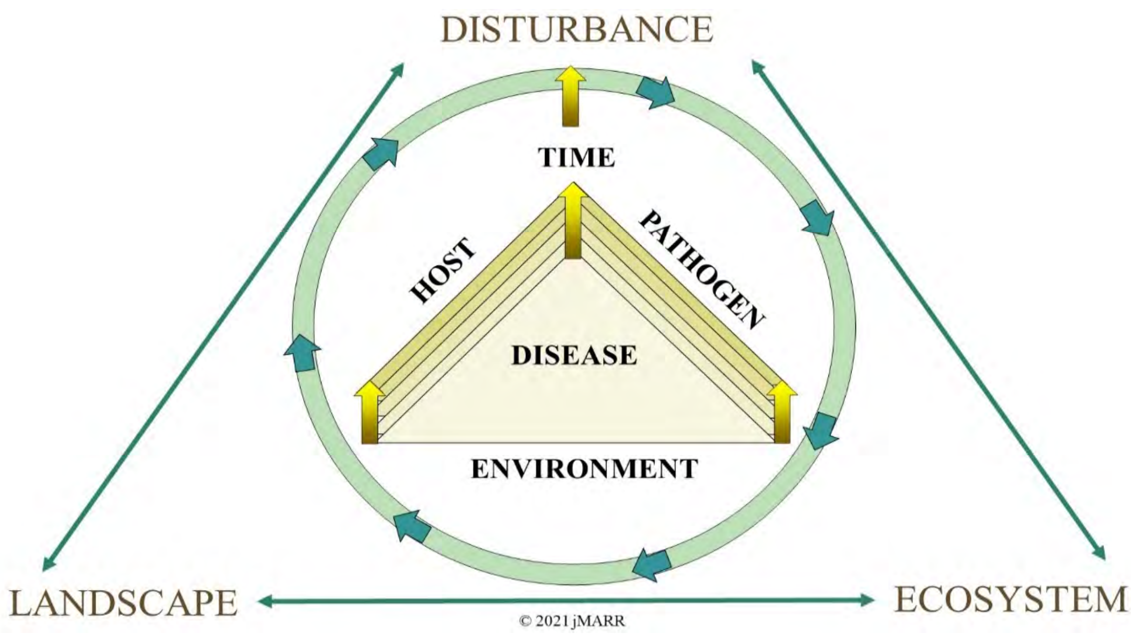


Figure 4.1. A conceptualization of the WPBR pathosystem as a landscape disturbance.

At the center of the model is the classic concept of the disease triangle (Stevens, 1960) which required three basic components to be present for disease to occur: a virulent pathogen capable of inciting disease (Winder & Shamoun, 2006); a susceptible host; and an environment favorable to disease development; the absence of any one component would prevent disease from occurring (Francl, 2001). The WPBR life cycle requires two hosts: the white pine, which is often killed by the disease, and *Ribes*, the host of the disease that produces the spores that infect the white pine. This disease-disturbance model includes a fourth element in the disease triangle: Time. Time is necessary for infection and disease spread to occur, although infection may vary from a few minutes to hours, and disease may not be noticeable for months or years (Francl, 2001). When time is added as the fourth component to the disease triangle on a three-dimensional z axis, the axis' depth or height represents the amount of time that has passed.

In Figure 1, each layer of the triangle may represent one year. If the pathogen or one of the hosts are not present during that year, no new infection can occur; however, the disease will continue to spread in trees already infected. If *Ribes* shed their leaves during a droughty summer, there may be a break in the disease cycle where no basidiospores reach and infect pine trees; those same pine trees may become infected the following year when moisture and temperature levels are optimal for spore production and pine infection.

Each component of the disease triangle affects and is affected by the biotic and abiotic disturbances inherent in the ecosystem (Castello et al., 1995). Biotic disturbances include plant invasions, herbivory, insect attacks, and diseases (Kautz, Meddens, Hall, & Arneth, 2017). Abiotic disturbances include pollution, wind events, fire, floods, and climate change (Keane, 2017). Additionally, disease may act as a biotic or abiotic disturbance. Examples of biotic disease disturbances include infections by fungi, bacteria, and viruses. Abiotic disturbances include decline diseases caused by drought and pollution. The ecosystem affects and is affected by these disturbances. The result is a disease that is involved in multiple feedback loops at varying scales with the ecosystem and larger landscape. The multiple scales address the impacts of disease as a disturbance on the health of one tree, on the diversity of a forest stand, and on the successional trajectory of a forest over time.

White Pine Blister Rust and Forest Succession

In this study, I explored the role of WPBR as an agent of change in forest succession. Forest succession is the replacement of one plant association or community by another, as a result of habitats and plant populations affecting each other (Clements, 1916; Daubenmire, 1968; Gleason, 1917). My focus is on secondary succession, which occurs when a disturbance agent alters the development of a sere, or stage, of natural forest succession (Clements, 1916). This study does not include primary succession, which begins with a barren substrate upon which plants establish (Clements, 1916).

Secondary succession in the northern deciduous forest was conceptualized as five stages: 1) weeds and grasses; 2) "pasture shrubs", including raspberry, blueberry, staghorn sumac, and *R. cynosbati*, *R. rotundifolium,* and *R. hirtellum*; 3) trees which established open woodland, including white pine, quaking aspen, gray birch, and paper birch; 4) trees which established under the pioneers, including sugar maple, beech, hemlock, red oak, and white ash; and 5) the final climax stage in which sugar maple, beech, and hemlock increased in dominance (Cooper, 1922). The climax stage lasted until a disturbance disrupted the process through increased light, nutrients, seed sources, and space for germination. *Ribes* and white pine are early-successional species that thrive on the mineral soil of disturbed landscapes (Zambino, 2010). Gooseberries (*Ribes* spp.), an alternate host of WPBR, commonly occurred in the grass and pasture stages where they produced more berries and had higher infection rates than in the mixed woodland or climax forest (Cooper, 1922). As a forest matures and the canopy closes, *Ribes* will gradually disappear until a disturbance, such as root disease, creates the light and space suitable for their growth (Cooper 1922; Stewart, 1953; Zambino, 2010).

White Pine Blister Rust Research

Available research on WPBR as a disturbance agent affecting forest succession is scarce. Much of the research on WPBR focuses on the life cycle, disease resistance, genetics, and management of white pine in regions where WPBR is known to occur. Most studies are based on a fine spatial scale, including the scale of an individual tree (Meentemeyer, Haas, & Vaclavik, 2012). The knowledge is then applied to the larger landscape level for management purposes. The purpose of this study was to understand the effects of WPBR on forests, rather than the effects of forests on WPBR. Therefore, disease presence was examined at both the tree and stand scales to determine how the long-term presence of WPBR has impacted white pine forests in New Hampshire. Of particular interest were any differences between stands with repeat infection (those infected historically and again in 2018), and stands with no WPBR (historically or in 2018). This study addressed five specific hypotheses:

1. If WPBR affects forest composition, then the live woody species will be different in stands with repeat infection than in stands with no history of WPBR;
2. If WPBR affects species richness, then the number of woody species will be different in stands with repeat infection than in stands with no history of WPBR;
3. If WPBR affects forest structure, then fewer vertical strata will be present in stands with repeat infection than in stands with no history of WPBR;
4. If WPBR affects forest succession, then a change in the sere or stage should be found in stands with repeat infection compared to similar stands with no history of the disease;

5. If WPBR affects white pine sustainability, then stands with repeat infection should have more missing white pine size classes than stands with no history of the disease (not attributable to logging).

The objectives of this research were to: 1) document forest composition and structure, species richness, and disturbance history observed at each research plot; 2) assign a forest type to each plot for comparison with historical maps created by the NH Office of Blister Rust Control; and 3) to analyze changes to each forest stand over time to determine if the changes were caused by natural succession or disturbances, including WPBR. The data were then used to: 1) examine the WPBR disease-disturbance model presented in this chapter; 2) to conceptualize the influence of WPBR on the successional trajectory of New Hampshire's forests; and 3) address the sustainability of white pine as a component of forests where WPBR has occurred.

Methods

This study combined field data from 2018 with historical data from the archives of the NH Blister Rust Control Program. See a full description of the methods in Chapter Three.

Study Design

Fifty towns (Table 4.1, Appendix C-1) were randomly selected from the 226 towns in New Hampshire's historic control area (see selection methods in Chapter Three); each town had been assigned a high or low hazard rating in 1979 (Avery, 1980) (Appendix C-2). Maps created by the NH Office of Blister Rust Control were available in the NH State Archives Blister Rust Collection for each selected town to: 1) indicate the locations of pine infections; and 2) depict stands without WPBR at the time of mapping (see example Appendix C-3). The same research plots were used as in chapters three and four. Data were collected at each plot between May 1 and June 3, 2018, when cankers were actively releasing aeciospores.

Table 4.1

Towns Selected for 2018 New Hampshire White Pine Blister Rust Study

High Hazard		Low Hazard	
Acworth	Haverhill	Alexandria	Hinsdale
Alton	Lebanon	Andover	Keene
Barnstead	Littleton	Antrim	Lyndeborough
Barrington	Loudon	Belmont	New Boston
Bath	Lyme	Bristol	New London
Brookfield	Moultonborough	Candia	Raymond
Canaan	New Durham	Claremont	Sullivan
Canterbury	Pembroke	Danbury	Sunapee
Charlestown	Strafford	Deering	Swanzey
Concord	Thornton	Dublin	Troy
Cornish	Tuftonboro	Dunbarton	Warner
Enfield	Wakefield	Grantham	Weare
Hanover		Hebron	

Note. High and low hazard ratings are from the NH Blister Rust Control Program (Avery, 1980).

Sampling Methods

Data were collected from multiple sources to answer the questions in this study and to determine if differences or patterns occurred when analyzing stands by WPBR history.

Field data. Data for an analysis of species composition and richness, forest structure, and succession were collected at each of the 100 plots. Field data included: 1) an inventory of each standing tree in the plot, alive or dead, by species, size class, and canopy position; 2) visible disturbances, including evidence of logging (tree stumps), windfall (pit and mound topography), invasive plant species, human activity (roads and trails), and disease. (See Chapter Three for the methods used to record disease disturbances.) Individual tree data also included diameter at breast height (DBH) (4.5 feet above the ground). Shrubs (native and non-native), and seedlings, >1' tall and <1" diameter, were recorded by species totals. Photographs were taken of the overhead canopy and the species present around the plot center. The canopy photos were used to assign the percentage of canopy cover.

NED-3 forest stand data. Field data were imported into the NED-3 (version 3.0.7.2) forest inventory program for the Northeast (Twery & Thomasma, 2019) for computation and analysis of species composition, species richness, forest structure (trees per acre, basal area), stand age, and forest type, based on species dominance. A descriptive classification of forest structure was created for each stand by combining data from NED-3, including the presence or absence of size classes (Table 4.2) and crown classes (strata) (Hibbs, 1983) (Table 4.3), with the USDA Forest Service classification system (Hall et al., 1995). In the USDA Forest Service model, structure consisted of tree canopy cover class (Table 4.4), tree strata class (Table 4.5), and size class.

Table 4.14

NED-3 Size Class Definitions

Size Class	Diameter at Breast Height (DBH) in Inches
Saplings	1-4.5
Poles	4.6-10.5
Small Sawtimber	10.6-16.5
Medium Sawtimber	16.6-23.5
Large Sawtimber	≥ 23.6

Note. From Twery & Thomasma (2019).

Table 4.3

Crown Classes (Strata) for New Hampshire Forests

Crown Class	Description
Dominant	Trees may extend above the canopy; light received throughout the day
Co-Dominant	Trees form the main canopy and receive light for most of the day
Intermediate	Trees shorter than co-dominants; receive direct overhead light only
Suppressed	Trees overtopped, growing below the canopy and above the shrub layer
Shrub	Trees and shrubs over 1' tall and ≥ 1" stem diameter
Ground	Seedlings and shrubs < 1' in height and < 1" in stem diameter

Note. From Hibbs (1983).

Table 4.4

Tree Canopy Cover Classes

Class	Percentage of Canopy Cover
None	< 10
Open	10-39
Moderate	40-69
Dense	≥ 70

***Note*.** Canopy cover classes per Hall et al. (1995).

Table 4.5

Tree Strata Classes

Tree Strata Class	Description
None	No strata present
Even	One stratum present; <30% difference in tree sizes
Uneven	Two or more strata present

Note. Tree strata classes per Hall et al. (1995).

Blister rust maps data. The blister rust maps provided information for determining each stand's historical structure and successional stage. Data retrieved from the blister rust maps included: 1) the year the block containing the stand was mapped; 2) the years *Ribes* were eradicated from the block; 3) the presence of WPBR on pine or *Ribes* within the stand; 4) the percentage of pine in the stand; 5) the pine size classes (reproduction under 6" DBH, poles 6-10" DBH, mature timber over 10" DBH); and 6) the stand's forest type based on dominant species.

Data Analysis

Stand analysis. The 100 stands were organized by WPBR history (repeat infection, historical infection only, new infection, or no infection) for comparative analysis of species richness, species composition, and forest structure. (Stands with repeat infection were infected at the time of mapping by the NH Blister Rust Control Program, and again in 2018. Stands with historical infection only were infected at the time of initial mapping, but not in 2018. Stands with new infection were infection-free at the time of mapping, but infected in 2018. Stands with no WPBR were infection-free when initially mapped and again in 2018.) The four WPBR stand categories were also divided into two by the presence or absence of logging disturbances to separate the impacts of logging and disease disturbances on forest structure, including missing strata and size classes (Table 4.6). Most of the analysis in this study included the eight stand categories.

To account for the differences in stand ages when analyzing forest structure, particularly in stands that were not old enough for trees to have matured into the larger sawtimber size classes, stands were divided into two age classes: under 80 years; and 80 years or older, the recommended rotation age for white pine in New England (Leak, Cullen, & Frieswyk, 1995).

Table 4.15

Organization of 100 Stands by WPBR and Logging Disturbances

WPBR History	Logged	Over Age 80
No WPBR (n=34)	10	5
Historical WPBR (n=30)	7	9
Repeat WPBR (n=20)	10	3
New WPBR (n=16)	6	3

An assumption of this study was that by age 80, the stand would have all size classes present, possibly with the exception of the large sawtimber size class, depending upon dominant species and disturbance history. Missing size classes for each stand were determined by first creating a size class and age comparison table for New Hampshire based upon size class presence in the 67 stands without logging disturbances. The table was based on the minimum age needed for the recruitment of each size class. The minimum age was then used to determine if a size class in each of the 100 stands was missing unrelated to stand age. For example, if a stand was older than age 39 (Table 4.7) and no pole-size trees were present, the pole-size class would be listed as missing. If a stand was older than 64 and no small sawtimber was present, the small sawtimber size class would be listed as missing. Size classes older than the stand were considered remnant. Missing size classes were analyzed for all species within a stand, and specifically, for white pine during the analysis of white pine sustainability.

Table 4.7

Size Class and Estimated Stand Age for Native Tree Species in NH Forests

Size Class	DBH"	Minimum Stand Age
Sapling	1-4.5	10
Pole	4.6-10.5	25
Small Sawtimber	10.6-16.5	64
Medium Sawtimber	16.6-23.5	80
Large Sawtimber	>23.5	110

Note. Size classes per NED-3, Twery & Thomasma (2019). Minimum stand age for pole size class per Leak et al. (1995).

The NED-3 program defined balanced size classes as the percentage of live stems in a forest stand for each size class that were necessary for sustaining timber production (Twery & Thomasma, 2019). Relative percentages of all live overstory stems were calculated in Excel for each size class in each stand for comparison with the NED-3 recommendations (Table 4.8). The same NED-3 recommendations were used to assess white pine sustainability for each stand.

Table 4.16

NED-3 Recommendations for Balanced Size Classes

Size Class	Stem Diameter	Stem Percentage
Regeneration	<1”	5-10%
Saplings & Poles	1-10.5” DBH	35-45%
Small Sawtimber	10.6-16.5” DBH	25-35%
Large Sawtimber	>16.5” DBH	10-15%

Note. From NED-3 Program, Twery & Thomasma (2019).

Canopy cover classes were determined by overlaying a grid onto the canopy photograph for each stand to determine if the percentage of canopy cover met the criteria for open, moderate, or dense (Hall et al., 1995). Each canopy was then assigned a rating based on the percentage of canopy cover.

Forest succession and seral stage ratings. Each stand was assigned a baseline forest succession stage using a northern deciduous forest succession classification system (Cooper, 1922) (Table 4.9). The northern system was based on species presence rather than an inventory count of stems and size classes in the stand, and therefore, was compatible with the historical forest types described on the blister rust maps. The 2018 succession stage was based upon the 2018 forest type assigned to each stand by NED-3.

Table 4.9

Forest Succession Stages for the Northern Deciduous Forest

Stage	Description	Plant Species
1 (Open Pioneer)	Non-woody pioneer species	Weeds and grasses
2 (Orchard-Pasture)	Pasture shrubs	Red raspberry, blueberry, *Ribes cynosbati*, juniper, staghorn sumac
3 (Pine)	Shade-intolerant tree species that established an open woodland	White pine (may develop pure stand), quaking aspen, gray and paper birches, red maple
4 (Mixed Forest)	Trees that established under pioneer species	Red oak, white ash, sugar maple, American beech, hemlock, yellow birch
5 (Climax Forest)	Shade-tolerant trees that develop stand dominance	Sugar maple, American beech, hemlock

Note. Forest succession stages from Cooper (1922).

Stands were assigned a combination rating when mixed stages were present. For example, a 1934 pine stand, equally dominated by white pine and a mix of red oak, white ash, and beech in 2018, was assigned a 3-4 rating for 2018. To determine differences in size classes within each successional stage, and to account for differences in classifications used by the NH blister rust agents and the NED-3 forest inventory program, historical stands on the blister rust maps were assigned to the following categories: “reproduction” stands were defined as saplings; “poles” were listed as poles; and “mature timber” stands were labelled small sawtimber.

To account for disturbances at the stand level that may affect the succession of various strata within a stand (Hall et al., 1995), each stand was given a seral stage rating, based on the presence of live potential natural community (PNC) indicator species in each of the six canopy classes (dominant, co-dominant, intermediate, suppressed, shrub, and ground). The shade-tolerant PNC indicator species for New Hampshire included: beech; hemlock; sugar maple; balsam fir; and red and white spruce (Cooper, 1922). All 100 stands were analyzed in Excel and coded using the percentages in Table 4.10. For comparison purposes, the classes were grouped into overstory (dominant and co-dominant), midstory (intermediate and suppressed), and understory (shrub and ground). Combined ratings were given to a story with mixed ratings; for example, an understory with 43% PNC species in the shrub canopy and 100% PNC species in the ground canopy would be assigned a combined mid-PNC seral stage for the understory.

Table 4.10

Seral Stage Criteria

Seral Stage	Description	Criteria
Early	Grasses, shrubs, shade-intolerant pioneer trees dominate	PNC species 0-10% of canopy class
Mid	Mix of early and late seral species	PNC species 10.1-50% of canopy class
Late	PNC species dominate	PNC species 50.1-75% of canopy class
PNC	Seral species absent or very scarce	PNC species 71.1-100% of canopy class

Note. Adapted from Hall et al., (1995). PNC: potential natural community, the shade-tolerant species most likely to perpetuate in a forest stand until a disturbance occurs.

Sustainability and baseline mortality. Baseline mortality (Manion, 2003) was assessed for all stands to determine if disease, in addition to forest succession, had an effect on forest composition, structure, and sustainability. Stands were grouped by WPBR history and the presence or absence of logging disturbances. The percentage of tree mortality for each size class was calculated in Excel. For the baseline mortality analysis, stems were grouped into one-inch diameter size classes ranging from .5 to 18 inches. Size classes over 18” DBH were remnant trees and removed from the analysis. Calculations were made for all species in each size class, and then for white pine only in each size class to address the question on white pine sustainability.

Data for each stand were compared by stand disturbance history using relative percentages for: species composition; missing strata and size classes; the presence of PNC indicator species; forest type and successional stages; and live white pine by strata and size class.

Means and ranges were used to compare trees per acre, basal area, species richness for each stand. In order to separate the effects of WPBR and logging as two disturbances of focus in this study, Chi-square tests were used to determine if relationships existed at the stand scale between WPBR history and logging disturbances, tree species presence, live white pine presence, missing white pine size classes, missing strata, basal area, forest types, successional stages, stand age in relation to the presence of PNC indicator species, baseline mortality percentages, and recommended size class distributions for sustainability. All tests used an alpha of .05.

Results

Forest Composition

The total number of live tree species ranged from 26 in stands with no history of WPBR to 21 in stands with repeat infection (Table 4.11).

Table 4.17

Comparison of Total Species for Live Trees in 100 Stands by WPBR History

Stand WPBR History	Species	Stands
No WPBR	26	34
Historical WPBR	22	30
New Infection	22	16
Repeat Infection	21	20
Total		100

Four species shared dominance in stands with repeat infection (Figure 4.2) and new WPBR infection (Figure 4.3): *Pinus strobus* L.; *Acer rubrum* L.; *Fagus grandifolia* Erhr; and *Betula lenta* L. Three species shared dominance in stands with historical infection (Figure 4.4) and no WPBR (Figure 4.5): *F. grandifolia*; *A. rubrum*; and *Tsuga canadensis* L. *Pinus strobus* was present in > 25% of stands with repeat and new infections, and < 10% of stands with historical infections or no WPBR.

All woody species, including native shrubs, were observed in a higher number of stands without WPBR than in stands that had repeat infection, with few exceptions: 1) *Populus grandidentata* Michx and *Pinus rigida* Mill. were only observed in stands with repeat infection; 2) *Carya ovata* (Mill.) K. Koch and *Populus tremuloides* Michx and invasive shrubs were observed in an equal number of stands with repeat and no WPBR infection; and 3) *Ribes* were observed in more stands with repeat infection. However, there was no significant relationship between WPBR history and species presence: $X^2(1, N=30) = 1.30$, $p = 0.25$.

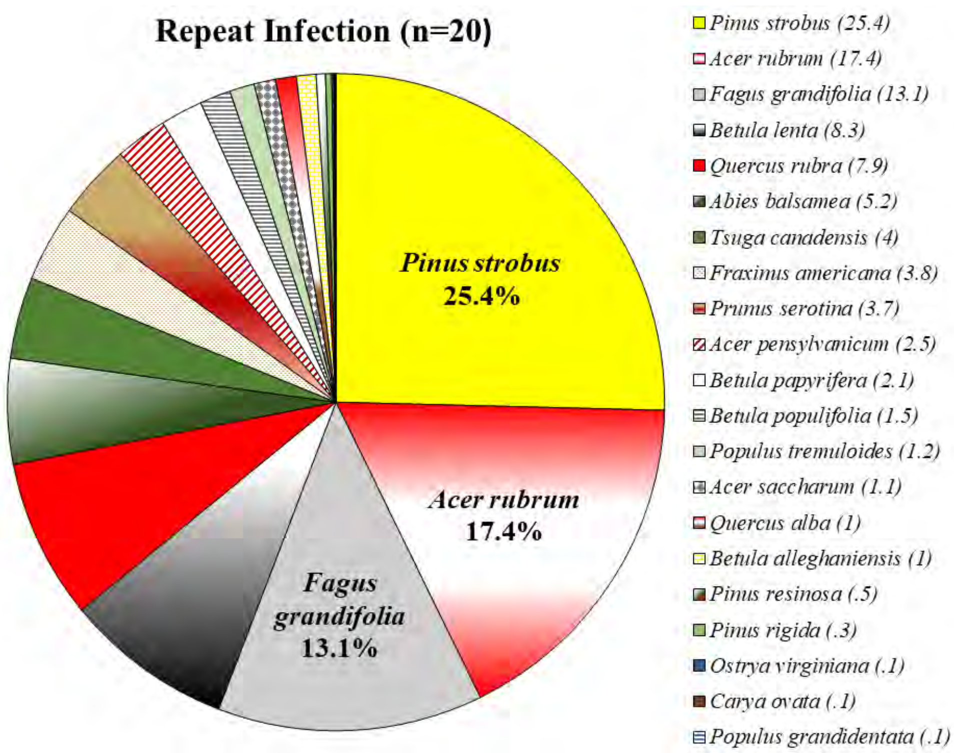


Figure 4.2. 2018 species composition for 20 stands with repeat WPBR infection.

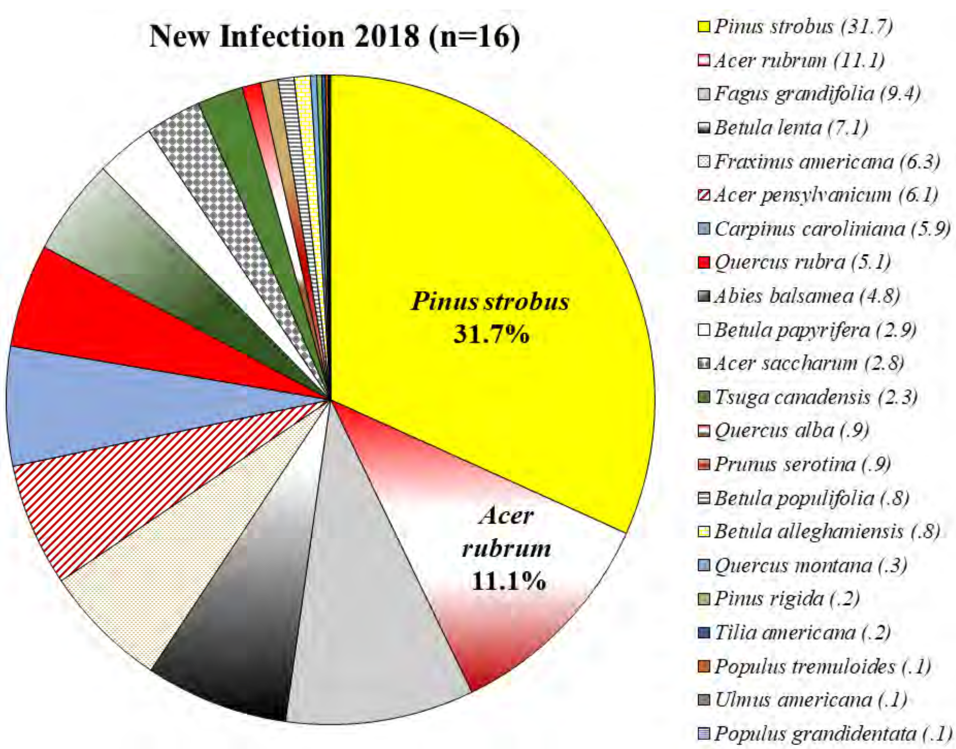


Figure 4.3. 2018 species composition for 16 stands with new WPBR infection.

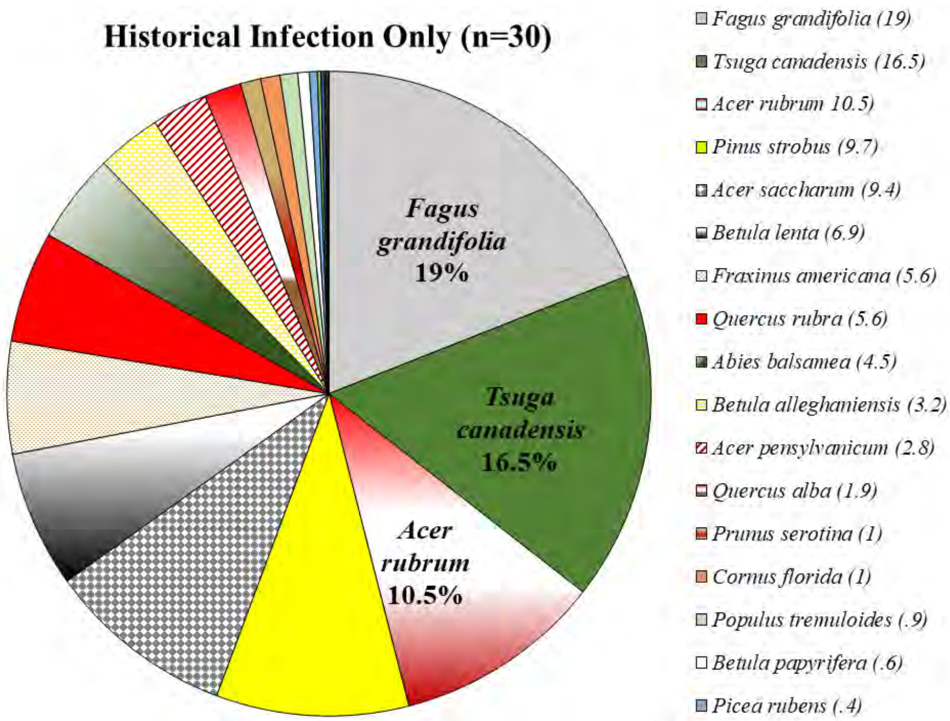


Figure 4.4. 2018 species composition for 30 stands with historical WPBR infection.

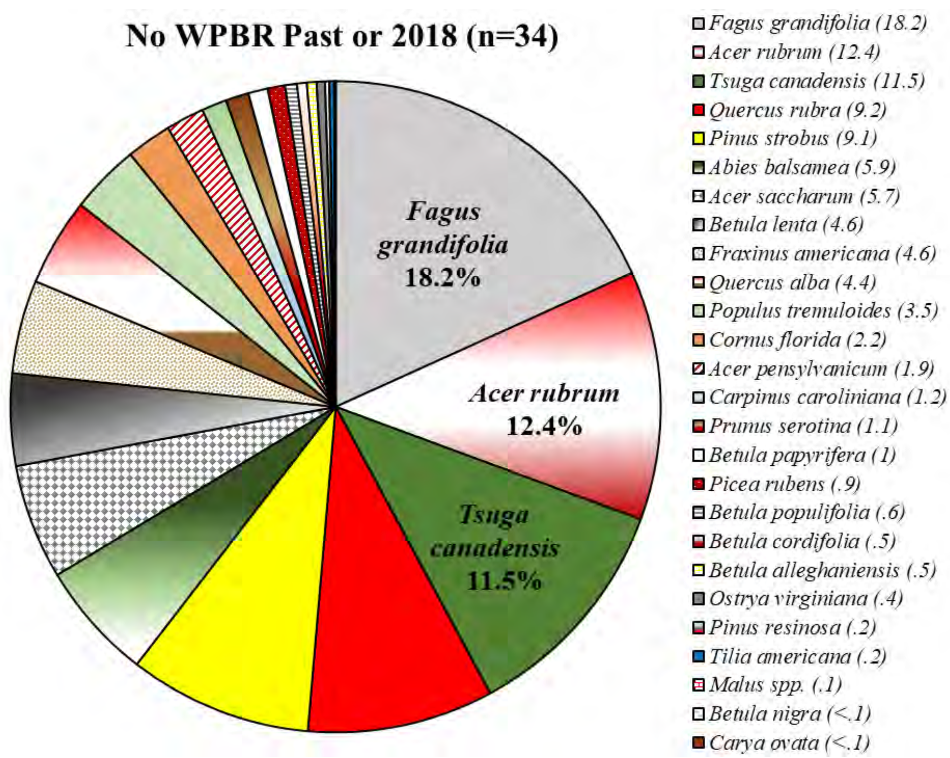


Figure 4.5. 2018 species composition for 34 stands with no WPBR infection.

A comparison of the early seral, white pine, and PNC species revealed that the early seral species and white pine were more likely to be found in stands with repeat or new infection, while PNC species were present in a higher percentage of stands without WPBR (Table 4.12). When viewed by the presence of logging disturbances, the three early seral species were more prevalent in stands without logging disturbances, particularly in stands with repeat and new WPBR infection. In contrast, white pine was observed in a higher percentage of stands with logging disturbances that had new infection or no WPBR. However, 20 stands had no living white pine stems in 2018 (Figure 4.6). Although a higher proportion of stands missing the live white pine component were in the historical infection or no WPBR categories compared to stands with repeat or new infection, no significant relationship was found: $X^2(3, N=20) = 1.03$, $p = 0.79$.

Table 4.12

Percentage of Stands with Early Seral, White Pine, and PNC Species

WPBR History	*Betula populifolia*	*Populus grandidentata*	*Populus tremuloides*	*Pinus strobus*	*Abies balsamea*	*Acer saccharum*	*Fagus grandifolia*	*Picea glauca*	*Picea rubens*	*Tsuga canadensis*
Repeat Unlogged (n=10)	3.9	0.1	1.4	25.8	0.4	1.4	11.1	0	0	4.0
Repeat Logged (n=10)	0	0	1.1	25.3	8.3	0.8	14.4	0	0	4.0
New Unlogged (n=10)	1.6	0.1	0.2	27.4	9.3	1.6	16.0	0	0	2.6
New Logged (n=6)	0	0	0	36.4	0	4.1	2.3	0	0	1.9
Historical Unlogged (n=23)	0	0.1	0.5	10.5	4.1	7.3	17.7	0.2	0.1	18.7
Historical Logged (n=7)	0	0	1.9	7.6	2.3	15.2	24.4	0	1.3	11.0
No WPBR Unlogged (n=23)	0	0	0	7.6	7.9	7.3	21.3	0	0.2	13.2
No WPBR Logged (n=10)	0.6	0	8.7	10.8	3.0	2.7	11.9	0	1.9	7.8

Note. Relative percentages are given for each disturbance category.

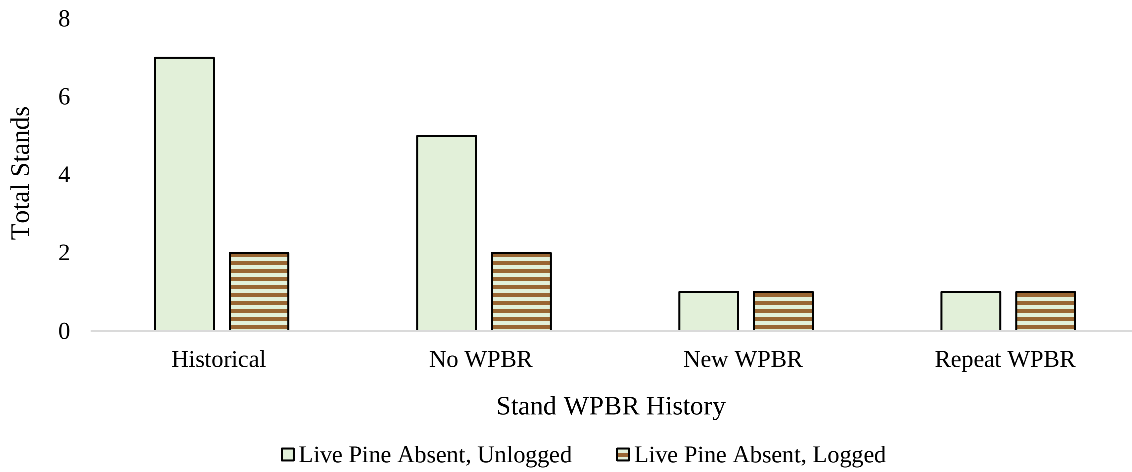


Figure 4.6. Distribution of 20 stands with no living white pine by disturbance history.

Among the PNC species, *A. saccharum*, *F. grandifolia*, and *T. canadensis* were observed in all stand categories; *T. canadensis* was the only species present in an equal or higher proportion of stands that were unlogged, compared to logged, regardless of WPBR history. *Abies balsamea* was present in < 10% of each stand type; with the exception of stands with repeat infection, it was more likely to occur in stands without logging disturbances. *Picea glauca* and *P. rubens* formed a very minor component of stands with historical infection or no WPBR where they occurred more often in stands with logging disturbances; neither species were observed in stands with repeat or new infection, regardless of logging history. Overall, no pattern was found between logging disturbances and PNC species presence.

Species richness. Average species richness was highest in logged stands without WPBR, and lowest in logged stands with repeat infection (Table 4.13). The highest average number of live tree species per stand, 13, was observed in stands with no WPBR, regardless of logging history. In contrast, the lowest average range of live species occurred in stands with repeat infection, regardless of logging history.

Table 4.13

Average Live Tree Species Richness for 100 Stands by Disturbance History

Stand History	Average Species	Species Range	Total Stands
No WPBR, Logged	9.7	6-13	10
No WPBR, Not Logged	8.1	4-13	24
New WPBR, Logged	8.8	8-11	6
New WPBR, Not Logged	7.9	6-11	10
Historical WPBR, Logged	8.4	7-12	7
Historical WPBR, Not Logged	7.3	4-12	23
Repeat WPBR, Logged	7.1	5-11	10
Repeat WPBR, Not Logged	7.2	4-10	10

Forest Structure

Ninety-five of the 100 stands observed in 2018 had canopy cover over 70%, defined by the USDA Forest Service (Hall et al., 1995) as dense (See photos in Appendix D-1). The five remaining stands had moderate canopy cover from 40-69%. The stands with moderate canopy cover included two stands with historical infection in Claremont and Wakefield, one stand in Concord with new infection, and two stands with repeat infection in Concord and Littleton. All stands with no history of WPBR had dense canopies. Each of the 100 stands also had two or more strata present and were categorized as uneven using the Forest Service criteria.

Vertical strata. All vertical strata were represented by a variety of live tree species; however, only the intermediate and suppressed layers were present in all 100 stands. The shrub stratum was the least-represented layer in all stands, particularly where WPBR was not observed historically or in 2018, regardless of logging history (Table 4.14). In the 67 unlogged stands, the shrub and ground strata were least-represented in stands infected historically.

Table 4.14

Percentage of Strata Present in 100 Stands by Disturbance History

Stand Logging History	Stand WPBR History	Dominant	Co-Dominant	Intermediate	Suppressed	Shrub	Ground
Logged (n=33)	Repeat (n=10)	100	90	100	100	90	100
	New (n=6)	100	100	100	100	100	100
	Historical (n=7)	85.7	85.7	100	100	100	100
	No WPBR (n=10)	100	90	100	100	80	100
Not Logged (n=67)	Repeat (n=10)	100	90	100	100	100	90
	New (n=10)	80	90	100	100	100	90
	Historical (n=23)	91.3	100	100	100	69.6	73.9
	No WPBR (n=24)	95.8	100	100	100	75	100

Trees per acre. Stands with repeat infection had the highest overall average trees per acre (TPA), regardless of logging history, while logged stands had higher TPA than unlogged stands, regardless of WPBR history. Stands with no WPBR history had the lowest average TPA, regardless of logging history (Figure 4.7).

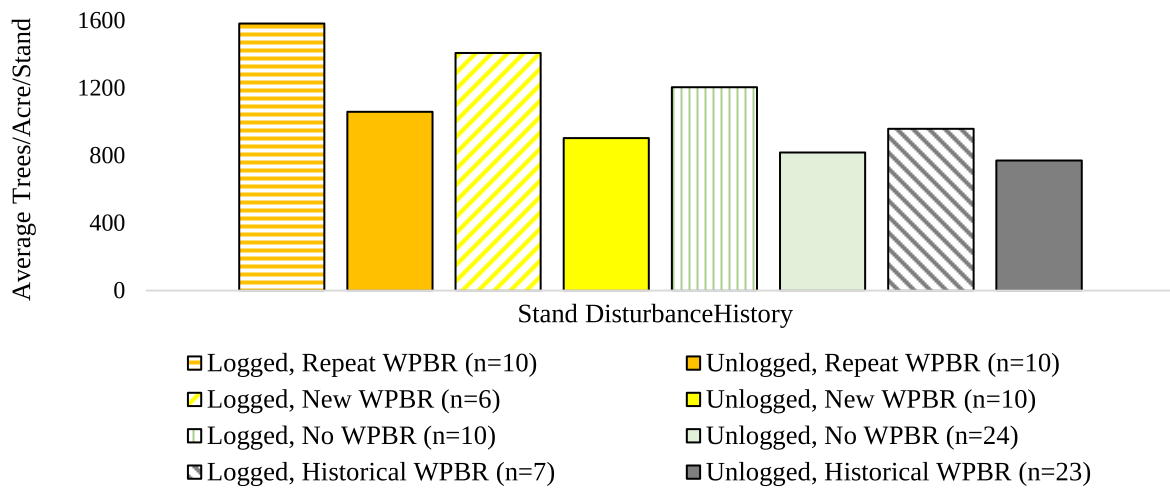


Figure 4.7. Average trees per acre for 100 NH stands by disturbance history.

Basal area. The total average basal area (BA) per acre was related to the disturbance history of a stand. The average basal area of a stand, when divided into three groups (300-499 ft^2/ac, 500-699 ft^2/ac, and 700-899 ft^2/ac), was affected by both WPBR history ($X^2(6, N=100) = 50.35$, $p < 0.001$), and logging history ($X^2(2, N=100) = 30,34$, $p < 0.001$). Eighty-seven percent of all 100 stands had an average BA of 500-699 ft^2/ac, regardless of WPBR or logging history; 34% of the stands had no WPBR infection; 20% were stands with repeat infection; and 67% had not been logged. Saplings accounted for <68% of the basal area in each disturbance history category (Figure 4.8). Stands with repeat WPBR infection had the highest average BA for pole size timber in logged stands and for large timber in unlogged stands; and the lowest average BA for medium timber, regardless of logging history.

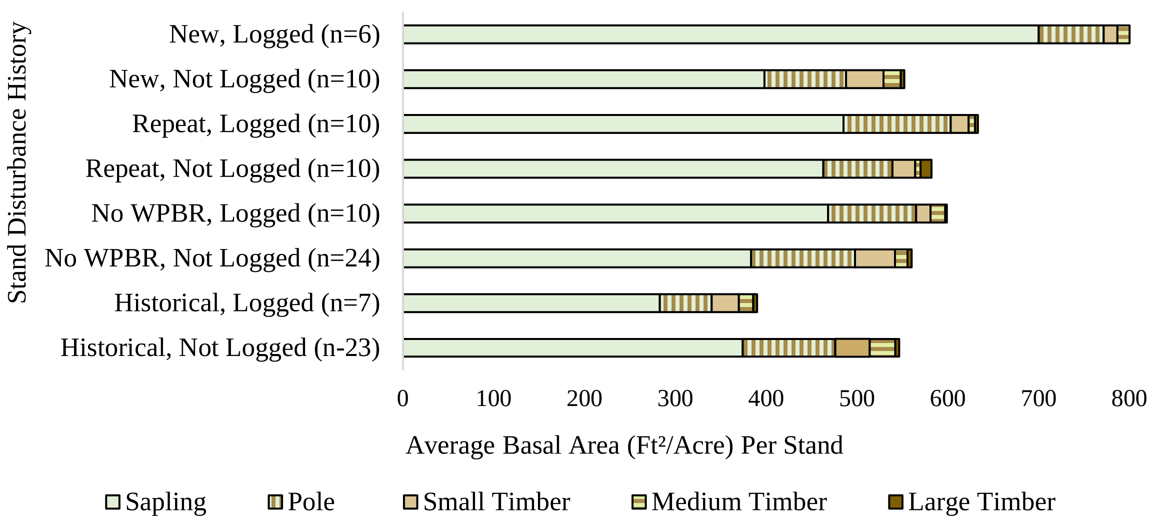


Figure 4.8. Average basal area for 100 stands by disturbance history and size class.

When basal area was analyzed by species, white pine had the highest BA for 34% of the 100 stands observed in 2018, followed by hemlock at 18%, beech at 11%, red maple at 10%, and sugar maple at 9% (Appendix B-1). Those five species represented the highest basal area per stand for 82% of the 100 stands. When disturbance histories were analyzed, white pine was the dominant basal area species for some stands in each category except stands with historical infection and logging disturbances (Figure 4.9). White pine dominance in basal area also occurred consistently in more stands without logging, regardless of WPBR history; however, the results were not significant: $X^2(3, N=34) = 3.80, p = 0.28$.

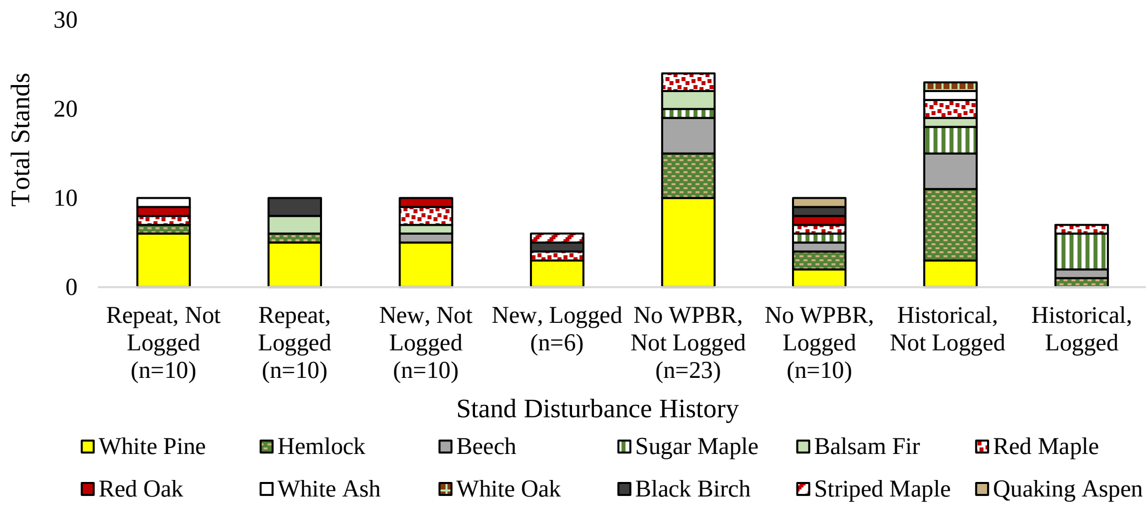


Figure 4.9. Dominant tree species per stand by basal area and disturbance history (n=100).

White pine size classes. Live white pine saplings were the only size class present in all 33 stands that had experienced logging (Table 4.15). In contrast, no size class was represented in all 67 stands that had experienced WPBR. The presence of live white pine size classes was related to stand disturbance history: $X^2(21, N=100) = 33.19, p = 0.04$. Stands with repeat infection had the highest relative percentage of saplings, poles, and small sawtimber in stands that experienced logging, and the highest percentage of seedlings, saplings, and poles in stands that had not been logged. In stands without WPBR, the seedling class had the highest relative percentage of live stems in logged stands and the lowest percentage in stands without logging.

Table 4.15

Live White Pine Percentage per Stand by Size Class and Disturbance History

Stand Logging History	Stand WPBR History	Seedling	Sapling	Pole	Small Sawtimber
Logged (n=33)	Repeat (n=10)	80	100	90	30
	New (n=6)	83.3	100	83.3	16.7
	Historical (n=7)	57.1	57.1	57.1	28.6
	No WPBR (n=10)	90	60	60	30
Not Logged (n=67)	Repeat (n=10)	30	90	80	60
	New (n=10)	20	10	60	40
	Historical (n=23)	17.4	60.9	69.6	56.5
	No WPBR (n=24)	4.2	83.3	79.2	66.7

Note. Relative percentage of stands for each size class by disturbance history.

Forest Succession

Forest succession stages. A comparison of the historical and 2018 successional stages for the 100 stands revealed that forest succession had advanced throughout the state in 82 of the 100 stands. No stands had reverted to an earlier sere. (A complete listing of stands by successional stages, Cooper's (1922) classifications, and NED-3's 2018 forest types are in Appendix A-1, A-2.) By 2018, 22 of the 29 Stage 3-4 stands had reached Stage 4 and Stage 5 (Figure 4.10).

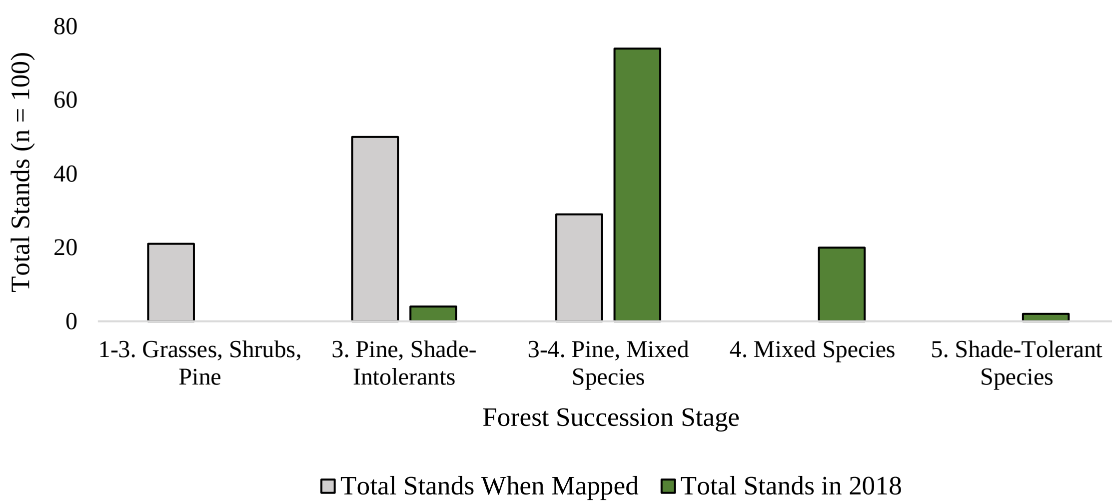


Figure 4.10. Total stands by succession stage (Cooper, 1922), historically and in 2018.

Two stands that were infected pine stands in 1940 advanced two successional stages, from Stage 3 to Stage 5; the New London stand succeeded to beech-maple, and the Wakefield stand succeeded to hemlock. In 2018, the only pine observed in each stand was in the seedling or sapling size classes.

By 2018, succession had occurred across all stand categories. Succession advanced in 90% of all 30 stands with historical infection, compared to 68.8% of the 16 stands with new infection (Figure 4.11). Fewer stands succeeded where logging and new or repeat WPBR occurred. Succession was not related to disturbance history: $X^2(7, N=100) = 7.57, p = 0.37$.

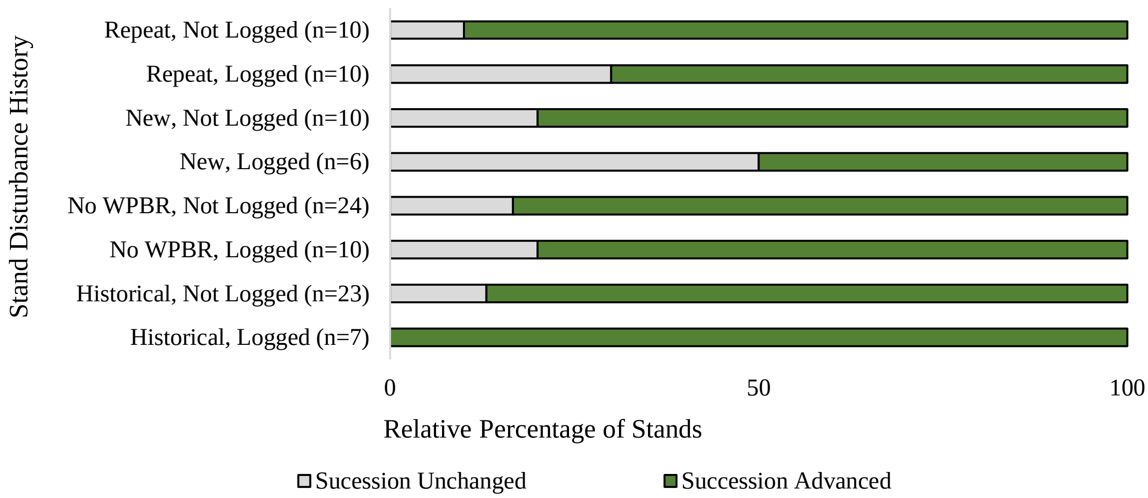


Figure 4.11. Succession status for 100 stands by disturbance history.

A map of forest succession stages (Cooper, 1922) showed that a high proportion of Stage 3 stands (pine and intolerant species) that were historically distributed throughout the state's white pine region had succeeded to Stage 3-4 pine and mixed species by 2018 (Appendix C-4).

Forest succession and forest types. The forest types assigned to each stand in 2018 by NED-3 also confirmed changes in forest succession (Figure 4.12). Eight stands throughout the state were assigned to the pure white pine category (>80% white pine); nearly one-third of all forest stands were classified as other hardwoods or mixed stands. (A photographic table of each stand and its forest type is in Appendix D-1). Three of the four stands that remained as white pine or succeeded to white pine were in central New Hampshire (Appendix C-5).

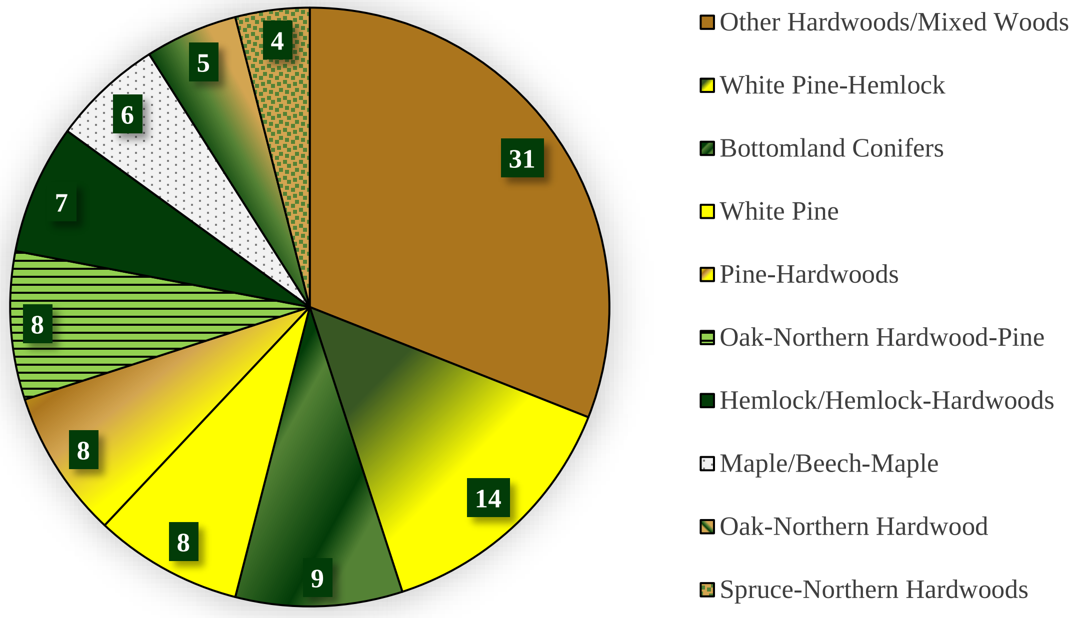


Figure 4.12. Total stands observed in each forest type in 2018 (n=100).

The NED-3 "other hardwoods/mixed woods" forest type was the only forest type with stands from all disturbance categories (Appendix B-2).

Thirty of the 100 stands were grouped into three forest types with white pine as a major component: white pine; pine-hardwoods; and white-pine-hemlock. Six of the 30 stands were logged (Figure 4.13). The pure white pine type was more likely to occur in stands with WPBR, while the succeeding white pine-hemlock type was more prevalent in stands with no logging or WPBR history; however, no statistically-significant relationship was found between disturbance and forest types with white pine as a major component: $X^2(12, N=30) = 19.31$, $p = 0.08$. In addition, the two logged stands that had no WPBR history did not support a forest type in which white pine was a major component.

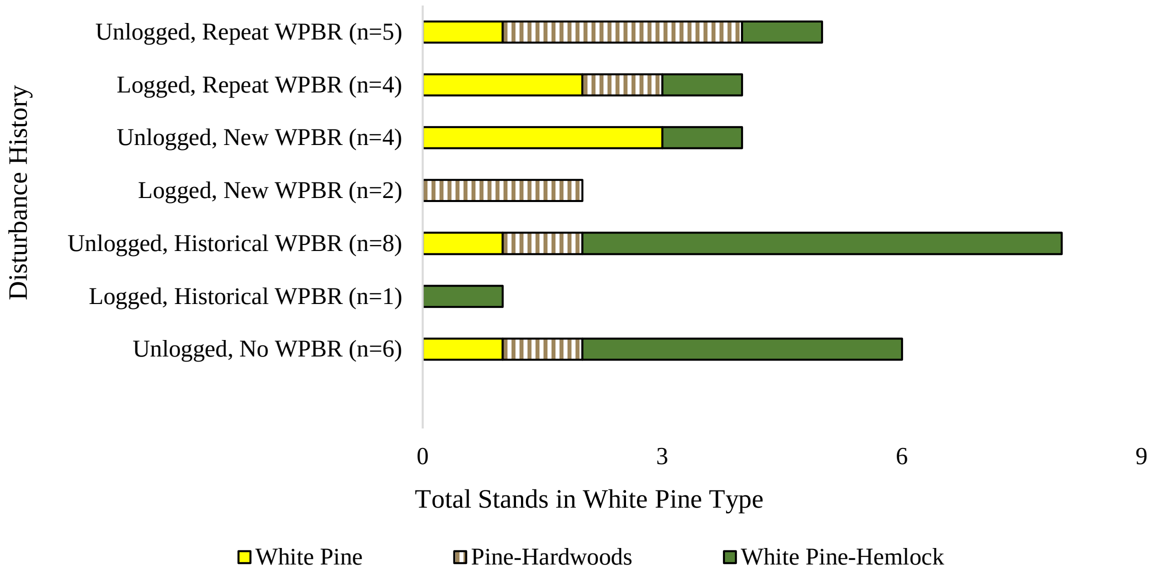


Figure 4.13. Thirty stands by white pine forest type and disturbance history.

Forest succession and canopy classes. An analysis of canopy class by seral stage (early, mid, late, potential natural community (PNC)) revealed that none of the 100 stands had completely succeeded to a PNC (Appendix A-3). Only one stand neared PNC status: the New London stand with historical infection and 100% PNC indicator species in all canopies except the ground layer that was in the mid-seral stage.

In the 67 stands without logging disturbances, the development of a PNC overstory, midstory, or understory was related to WPBR history. More than 60% of stands with either historical infection or no WPBR history had PNC midstories and understories, compared to stands with repeat infection that had no PNC midstories (Figure 4.14). The overstory was less likely to be dominated by PNC species for all stands; the PNC overstory was absent in all stands with no WPBR. The presence of WPBR and PNC layers were related: $X^2(6, N = 74) = 13.41$, $p = 0.04$.

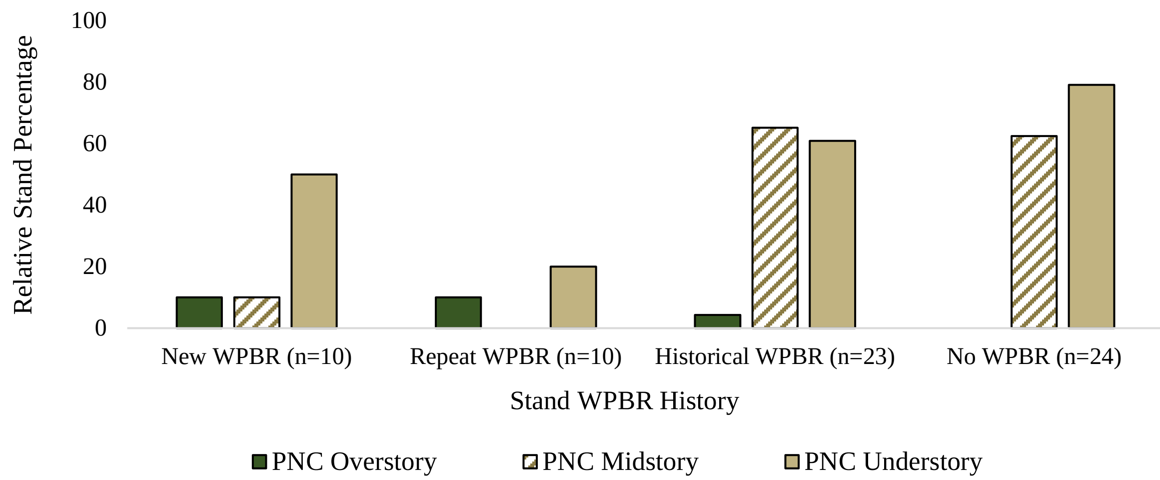


Figure 4.14. Presence of PNC layer in 67 unlogged stands by WPBR history.

A PNC seral stage was present in the overstory, midstory, or understory of 64.7% of the 17 stands over 80 years. A PNC overstory was present in 20% of the three logged stands with historical infection and 10% of the three unlogged stands with new infection (Figure 4.15). The highest percentage of stands with PNC midstories or understories occurred in unlogged stands with historical infection. No PNC overstories were observed in stands with repeat infection, or stands without WPBR. No relationship was detected between disturbance history and the presence of the three PNC overstories in this small sample size: $X^2(8, N = 27) = 6.46, p = 0.60$.

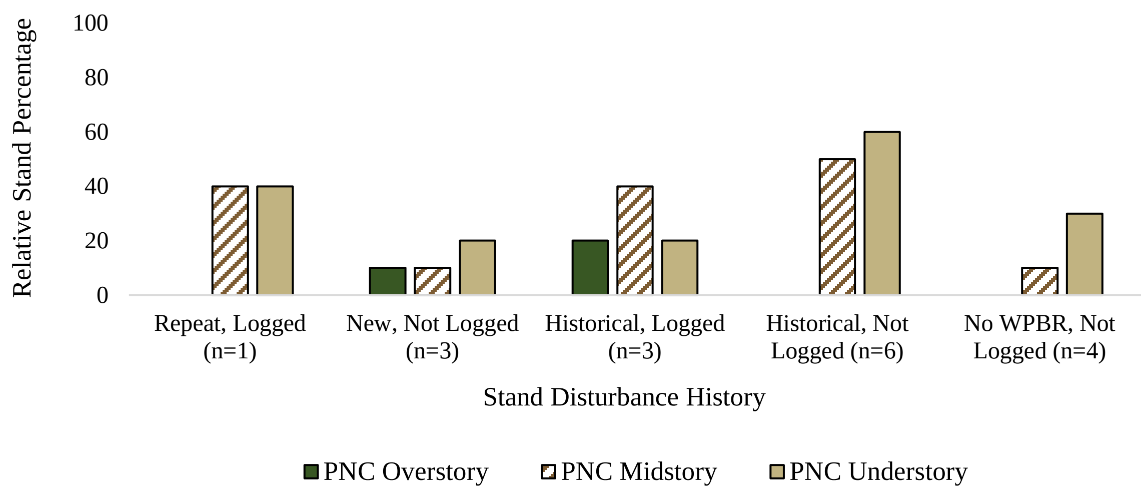


Figure 4.15. Presence of PNC layer in 17 stands > 80 years by disturbance history.

White Pine Sustainability

Baseline mortality. Ninety-two of the 100 stands contained white pine size classes with mortality over 20%, including all stands with repeat infection that had not been logged (Figure 4.16). In contrast, 57.1% of the seven stands with historical infection and logging disturbances had white pine size classes with mortality >20%, including Weare, where four of the 4-8" diameter size classes exceeded the 20% mortality level.

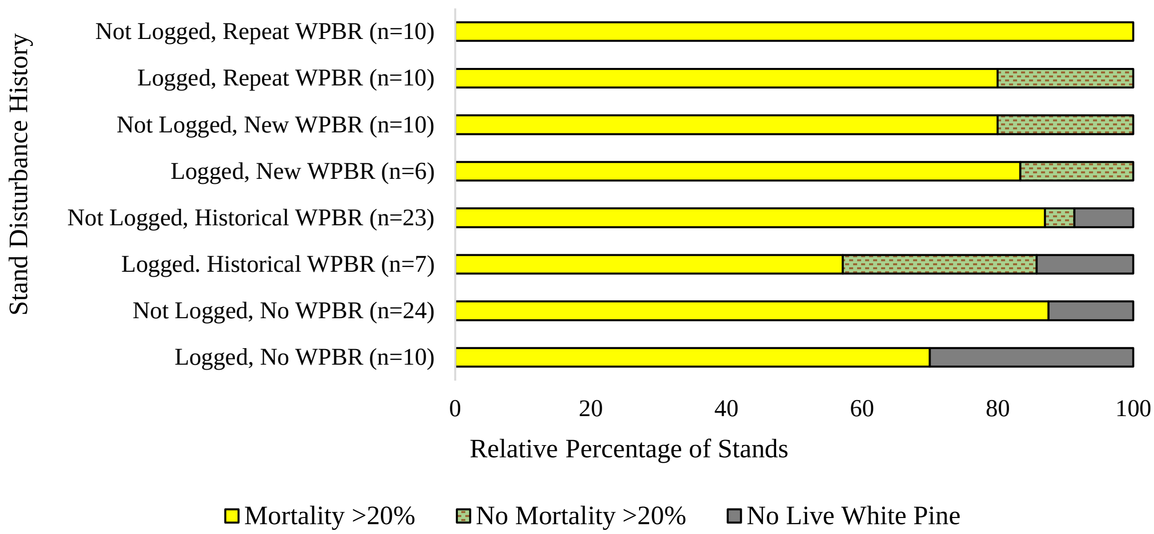


Figure 4.16. Relative percentage of 100 stands with mortality over 20% for at least one white pine size class 0.5-18" DBH.

Stands without logging disturbances had more size classes with mortality >20%, regardless of WPBR history. White pine mortality >20% was present in 16 of the 19 size classes (all but the 13, 15, and 17" diameter size classes) (Figure 16). Mortality >20% was related to disturbance history: $X^2(1, N = 243) = 19.82$, $p < 0.001$. Stands with repeat infection had the highest proportion of one and two-inch size classes with mortality >20%, at 50% and 70% of stands respectively. In addition, stands with repeat infection had mortality >20% in the 0.5-7" diameter size classes, regardless of logging disturbances (Figures 4.17, 4.18).

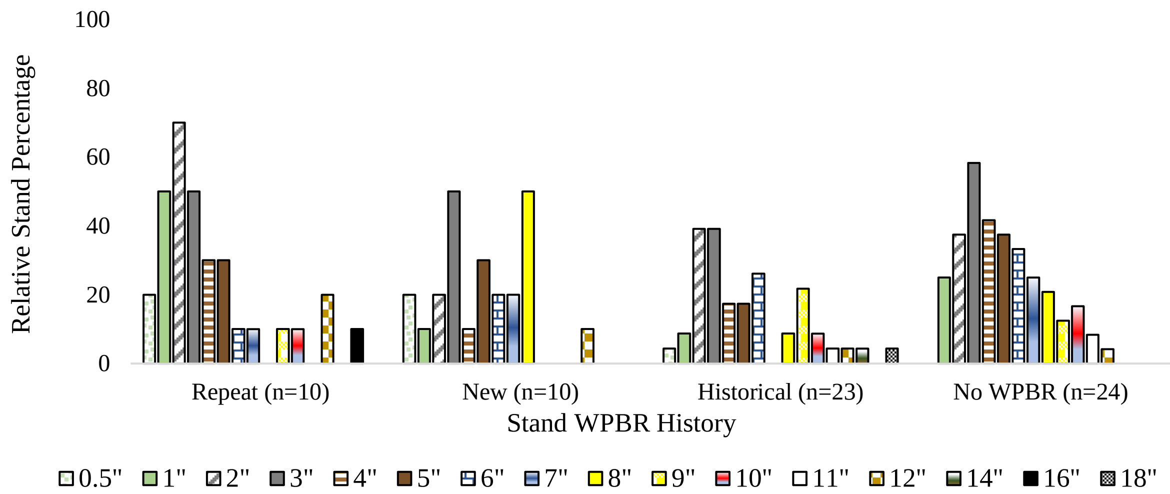


Figure 4.17. Relative percentage of stands with white pine mortality over 20% for each 0.5-18" DBH size class in 67 unlogged stands grouped by WPBR history.

White pine mortality >20% was present in 13 of the 19 classes (all but the 9, 12, 15, 16, 17, and 18" diameter size classes) in the 33 stands without logging disturbances, and in the 2" and 10" diameter size classes, regardless of WPBR history (Figure 17). Stands with repeat infection had the highest proportion of size classes with mortality >20%, particularly in the smaller diameters where 50% of the 2" to 4" diameter size classes had mortality >20%.

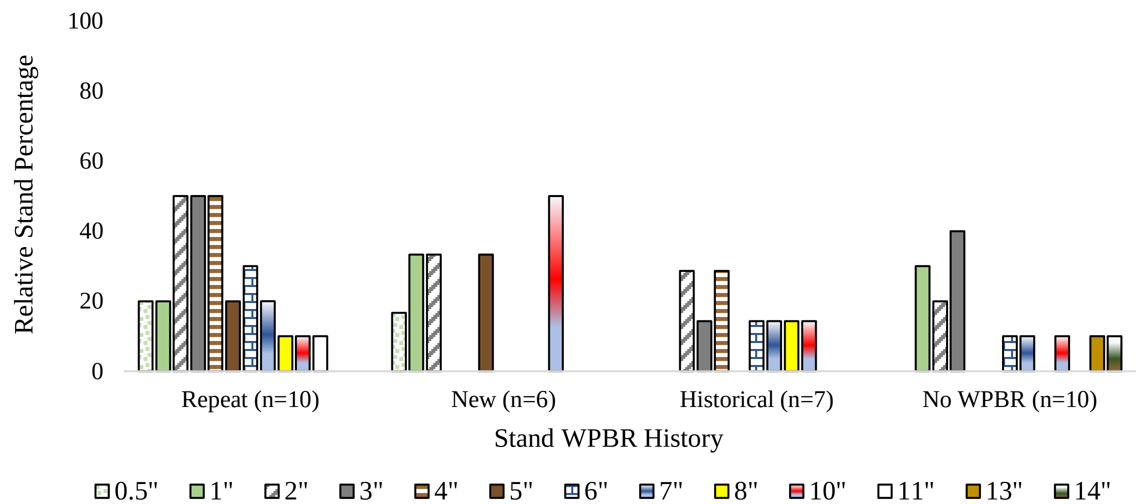


Figure 4.18. Relative percentage of stands with white pine mortality over 20% for each 0.5-18" DBH size class in 33 logged stands grouped by WPBR history.

Balanced live white pine size classes. Although no stand met the NED-3 recommendations for all four size classes, stands with repeat infection were more likely to meet or exceed the recommendations, regardless of logging history (Figure 4.19). In addition, large sawtimber was the only size class present in all disturbance categories. Overall, recommendations for each size class were more likely to be met in unlogged stands than logged stands with few exceptions: the seedling class in stands with new or no WPBR; saplings and poles in stands with repeat or no WPBR; and small sawtimber in stands with historical infection. The presence of balanced size classes for living white pine was related to disturbance history: $X^2(21, N = 138) = 50.01, p < 0.001$. A listing of balanced white pine size classes for 67 stands without logging disturbances is in Appendix A-4.

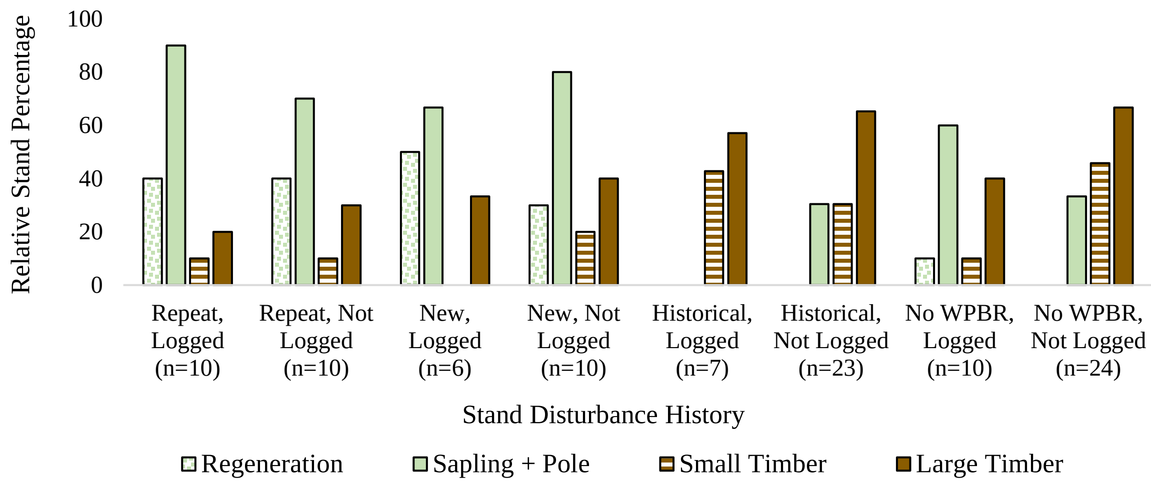


Figure 4.19. Relative percentage of 100 stands by disturbance history that met or exceeded the NED-3 size class distribution recommendations as applied to live white pine.

Discussion

Key Findings

Forest composition and structure. The 100 stands, which were white pine stands when mapped historically, were similar in tree species composition in 2018, regardless of WPBR history. Although white pine was a component in stands with and without WPBR, its dominance was limited to stands with repeat or new infection where it represented > 25% of the stems in a stand. In contrast, beech was the dominant species in stands with historical infection or no WPBR, comprising 18-19% of the stems per stand.

A contrast in species composition was notable in the shrub stratum. Live young pines were present in stands with repeat and new WPBR infection, but scarce or absent in stands with historical infection or no WPBR. In addition, stands with no WPBR supported native shrubs, while *Ribes* were more prevalent in stands with repeat infection. These findings together suggest that WPBR may have acted more as a disturbance than a thinning agent, particularly in stands with repeat WPBR infections, to promote the regeneration of disturbance-dependent white pine and *Ribes* (Zambino, 2010).

The smaller percentage of white pine stems in stands that experienced historical infection suggests that WPBR affected species composition by gradually reducing the white pine component through the infection and mortality of susceptible younger trees (Goheen et al., 2002; Smith & Hoffman, 2000; Keane, Loehman, Clark, Smithwick, & Miller, 2015). Twenty percent of the stands observed in this study had no living white pines; 45% of those stands experienced historical WPBR infection. The reduction of the white pine component supported statewide FIA data: the white/red pine type had declined from 750,000 acres in 1997 to 500,000 acres in 2018

(New Hampshire State Forest Action Plan Team, 2020); as a consequence, the cubic volume for white pine on New Hampshire's timberland was reduced to 21.5% (Leak et al., 2020).

While forest composition was similar throughout the 100 stands surveyed in New Hampshire in 2018, the dominance of some tree species has changed over time. The results of this study have shown that, despite the abundance of remnant, mature white pine and saplings in the 100 stands historically-dominated by white pine, only eight stands observed in 2018 remained in the pure white pine forest type. These results may not be indicative of the future composition of New Hampshire's white pine forests, however. Research that spanned four hundred years on the forests of the Northeast revealed their resilience; despite changes in forest structure and species dominance in some regions, the species that comprise today's forests were also present in pre-Colonial forests (Thompson, Carpenter, Cogbill, & Foster, 2013). Potential natural community species, such as beech and hemlock, have declined in abundance, mostly as a result of disease and insect pests; white pine, a keystone species, decreased in abundance in some regions and increased in others (Thompson et al., 2013). The variability in white pine composition was attributed to: 1) white pine's preference for disturbed sites and open fields which are variable due to human influences such as fire suppression and land conversion; 2) white pine's susceptibility to wind disturbances and disease, especially WPBR, that kills and removes white pine as a forest component; and 3) white pine's desirability as a valuable timber resource for construction purposes (Fahey, 2014; Loo, 2009; Thompson et al., 2013). All three factors have affected the current abundance and distribution of white pine in New Hampshire's forests. While the distribution of white pine in New Hampshire may also be attributed to site factors such as elevation, aspect, and soil type, identifying such factors was beyond the scope of this study. The U.S. Forest Service's 2017 forest inventory and analysis (FIA) data indicated that New Hampshire's forests were aging and that the white pine forests were concentrated in the southern portions of the state (Morin et al., 2020). In 2018, the white pine species was well-distributed throughout the historical white pine region, which was the focus area for this research.

The contributing factor to the infection of New Hampshire's white pine may be its susceptibility to WPBR, particularly in the younger size classes. The distribution of white pine, and its dominance in basal area, were not indicative of WPBR presence in 2018. In addition, no significant relationships were found between site characteristics and WPBR, including elevation, aspect, and topographic position (see Chapter Three). The state's eastern white pine population has not yet developed sufficient host resistance to the exotic pathogen *C. ribicola*. This lack of resistance has permitted WPBR to act with and in response to logging disturbances, forest diseases, climate change, and the natural forest processes of aging and succession to affect the abundance, dominance, and health of the white pine component observed in New Hampshire in 2018.

Forest succession. This study documented the advancement of forest succession seres in 82% of the stands in New Hampshire, including 90% of the stands with historical infection. No stands were categorized as PNC, although the New London stand with historical infection had 100% PNC species in all strata except the ground layer. A total of 268 *Ribes* were removed from the New London stand and its surrounding field edges by a blister rust work crew in 1925 ("Summary of *Ribes* Eradication," 1925), and the area was re-eradicated in 1940 when the infected young white pines were mapped (Leafe, 1940). Observations in 2018 confirmed that the remaining white pines were later removed and sugar maple was allowed to occupy the space. By 2018, sugar maple accounted for 37% of all stems in the dominant, co-dominant, intermediate, suppressed, and shrub layers, and 100% of all stems greater than 5” DBH. The ground layer was covered with *Ribes americanum* (over 400 per acre) and non-native Japanese barberry (*Berberis thunbergii* DC) shrubs. Tree seedlings included a mix of early, mid, and late successional species, including white pine and sugar maple. The New London stand exemplified a white pine forest affected by biotic and human disturbances that advanced natural forest succession towards PNC status through: 1) the presence of WPBR, which affected forest structure and succession by reducing the number of pines reaching cone-bearing size (Burns et al., 2012; Goodrich, Waring, Auty, & Sanchez Meador, 2018; Le Guerrier, Marceau, Bouchard, & Brisson, 2011; Maloney, Vogler, Jensen, & Delfino, 2012); 2) the removal of white pine by logging; 3) the regeneration of the alternate host of WPBR on the forest floor; and 4) the presence of a non-native, invasive shrub that competed with tree seedlings for space in the understory. The loss of white pine, the stand’s foundation species, allowed for changes to occur in forest dynamics, ecosystem services, species composition, and forest succession (Loo, 2009), which subsequently accelerated the natural successional trajectory of the 83-year-old stand. White pine blister rust does not spread from tree to tree; hence, infection removed individual trees throughout the stand, mimicking single tree selection, a silvicultural practice used by foresters to create small canopy openings that favor shade-tolerant species. As individual trees died from WPBR, or were removed by logging, the established mid and late-seral species grew into the overstory canopy, and, over time, the New London stand succeeded from white pine to a beech-maple forest type. A similar successional pattern was found during a study of the historical Great Lakes coastal pine forests, in which the white pine component had been reduced through two disturbance agents, WPBR, and the harvest of white pine (Fahey, 2014). In both examples, WPBR co-occurred with logging and the natural processes of forest succession to accelerate changes in species composition and forest succession.

Sustainability. White pine was the dominant timber species statewide; however, the species was not sustainable based upon the 2018 data applied to the baseline mortality concept (Manion, 2003), and the NED-3 recommendations for balanced size classes. Overall, mortality >20% for each one-inch size class was related to disturbance history, occurring in more unlogged stands than logged stands; however, the only category in which all unlogged stands had size class mortality >20% was the repeat infection category. The unlogged stands with repeat infection had the highest mortality for all stand categories in the one-inch and two-inch size classes, more than double the 20% baseline mortality rate. Similar to previous research conducted in New York, mortality >20% for the seedlings and saplings in the New Hampshire stands reduced the number of stems available to advance into the larger size classes and midstory, thereby affecting stand structure (Manion, 2003; Marks & Gardescu, 2005). Although logging impacted stand structure, WPBR may have had an even greater impact, particularly on the smaller size classes.

This study found that pine mortality due to WPBR was more likely to occur in the smaller size classes (0.5-6” diameter), consistent with recent research in New Hampshire (Munck, Tanguay, et al., 2015). In particular, the two and three-inch diameter saplings suffered more than 50% mortality by WPBR in stands without logging disturbances. Mortality over 50% can advance species replacement, and where WPBR kills more than 30% of the regeneration, white pine may be significantly reduced or lost as a component of the stand (Goodrich et al., 2018; Hagle, McDonald, & Norby, 1989; McMahon, Arellano, & Davies, 2019). Because of the high mortality rate observed in 2018, the white pine regeneration was at risk for replacement by other species, particularly in unlogged stands where WPBR occurred.

Mortality rates over 20% affected the balance of size classes recommended by the NED-3 program for sustainable stands. Stands with new or repeat infection met or exceeded the recommendations for the regeneration and sapling/pole size classes, including in logged stands. In contrast, the large sawtimber recommendations were met in unlogged stands that were infected historically or had no WPBR, suggesting that logging practices, which removed white pine sawtimber, reduced the size class distribution to below recommended levels. These contrasting differences in balanced size classes can be attributed to the disturbance history of each stand category; where WPBR and logging occurred, opened canopies regenerated white pine to meet the recommendations for the regeneration and sapling/pole size classes; where WPBR and logging were not observed, the natural stem exclusion phase of stand development removed young shade-intolerant stems as the canopy closed (Powell, 2012), and the most vigorous pines in the midstory advanced to the overstory as large sawtimber.

Overall, New Hampshire's forests are growing older, with large-diameter trees >12" DBH becoming more prevalent, while the number of smaller diameter trees is decreasing (New Hampshire State Forest Action Plan Team, 2020). The perpetuation of white pine in a stand is indicative of the amount and intensity of disturbances that occurred; multiple or intense disturbances that create large canopy openings result in more suitable growing conditions for white pine establishment (Abrams, 2001). Where WPBR occurred in New Hampshire, the disturbance created openings suitable for seedlings to establish and grow vigorously into the sapling and pole size classes, increasing the diversity of stem ages and stand strata (O'Hara, Latham, Hessberg, & Smith, 1996). The results of this study suggest that WPBR may be temporarily aiding the establishment of smaller-diameter trees to balance the smaller size classes in New Hampshire's aging forests.

The disease-disturbance model. The disease-disturbance model (Figure 4.1), applied to WPBR in this study, effectively depicted the effects of the exotic disease on the white pine forests of New Hampshire, in the individual stand, and larger landscape. White pine blister rust was observed where an adequate supply of susceptible hosts and inoculum occurred in an environment that fostered disease development. The disease continued to grow and kill individual trees. Over time, the disease became a disturbance that affected the stand's composition and structure. The disturbance altered the ecosystem by reducing or removing the white pine component. Succession advanced and further changed the composition and structure of the landscape-level forest. The landscape, once occupied by white pine, was now dominated by more shade-tolerant species. In the 20 stands with repeat infection, WPBR killed white pines, which were replaced by more shade-tolerant species until a subsequent disturbance opened the forest canopy; the plant hosts and pathogen then repopulated, and the cycle began again.

The disease-disturbance model, applied to a linear successional trajectory, demonstrates the compositional changes that can occur in stands with WPBR, compared to the natural trajectory for stands without WPBR (Figure 4.20). White pine regeneration dies and is replaced by shade-tolerant species; if no disturbances affect the forest canopy, structure, or composition, a potential natural community (PNC) develops that is comprised of shade-tolerant species.

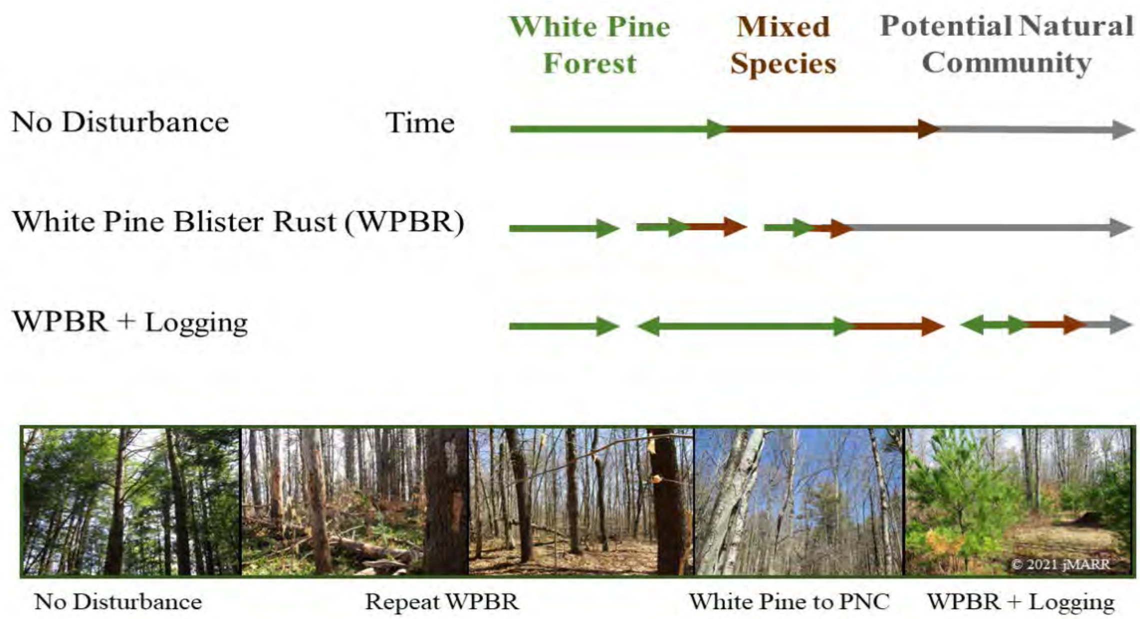


Figure 4.20. Conceptualization of disturbance impacts on the successional trajectory of NH's white pine forests. Photos by Janine Marr.

The results of this study were based upon surveys of 100 stands in 50 towns throughout New Hampshire during the spring of 2018. These results suggest that when, historically, WPBR infected a stand and removed the regenerating white pine component over time, succession was able to advance more rapidly into the PNC stage than if WPBR was not present. The death of a single pine that occupied a small growing space was more likely to be replaced with shade-tolerant hemlock or beech than another white pine. Where WPBR repeatedly infected a stand, or co-occurred with logging disturbances that created larger canopy openings and growing space, succession was delayed while the cone-bearing pines continued to repopulate the stand until the seed source was exhausted. Once the seed source was exhausted, established trees of other species, particularly those with more shade-tolerance, advanced into the growing space. The long-term impacts of WPBR on forest composition, structure, and succession affect the management of white pine, particularly as a timber resource.

White Pine Management in New Hampshire

Historical management for WPBR. New Hampshire's climate supports WPBR wherever white pine grows; therefore, an understanding of successful WPBR management practices will benefit landowners managing white pine today and into the future. Historically, WPBR management included: 1) removing *Ribes* within 300 yards from white pine timber; 2) pruning infected branches; and 3) maintaining a closed canopy to prevent *Ribes* establishment (Davis & Moss, 1940; Stewart, 1953; Van Arsdel, 1961). Stands were examined for *Ribes* regrowth at ten-year intervals after logging or natural events that disturbed the canopy and ground (Benedict, 1981); continued monitoring and eradication of *Ribes* were recommended to keep the disease under control in the future (Marty, 1966).

Current management for multiple white pine diseases. Today, managing for healthy white pine involves monitoring for multiple pine diseases. White pine needle damage complex (WPND) and pine canker (*Caliciopsis pinea* Peck) are projected to increase in incidence and intensity as the changing climate produces warmer, wetter springs (Weed, Ayres, & Hicke, 2013; Woods, Heppner, Kope, Burleigh, & Maclauchlan, 2010; Wyka, Munck, Brazee, & Broders, 2018). However, recommendations for reducing WPND and *Caliciopsis* incidence and severity contradict the recommendations for the management of white pine in areas where WPBR is also present. One silvicultural practice aimed at reducing *Caliciopsis* and WPND incidence is thinning a stand to increase sunlight and air flow; however, the increased sunlight, air flow, and temperature in the canopy can enhance WPBR establishment (Costanza, Whitney, McIntire, Livingston, & Gandhi, 2018; Munck, Livingston, et al., 2015), by: 1) stimulating *Ribes* germination and growth (Martin & Spaulding, 1949); and 2) by creating dew pockets in which the dew that forms on the needles permits infected *Ribes* spores to adhere and germinate if temperatures are favorable (Anderson, 1973; Charlton; 1963; Van Arsdel, 1972).

Where thinning treatments occur, the canopy openings should be monitored for *Ribes* establishment until the canopy closes and forest competition and shade prevent *Ribes* regrowth (Martin, 1944). In eastern Canada, pine growth and canopy cover occurred more rapidly when an herbicide was applied two seasons after the thinning treatment to reduce competition from other species (Santala, Aubin, Hoepting, Bachand, & Pitt, 2019). In Arizona and New Mexico, thinning treatments were recommended where WPBR had infected over 30% of southwestern white pine (*Pinus strobiformis* Engelm.) stands, followed by monitoring for seedling establishment and WPBR (Goodrich, et al., 2018). Where *Ribes* removal was an inefficient method for WPBR reduction, preventive pruning of the lower eight feet of live branches reduced microclimates favorable for the establishment of WPBR (Burns et al., 2008; Crump, Jacobi, Burns, & Howell, 2011; Hagle & Grasham, 1988; Stewart & Ritter, 1962). Pruning has also been recommended for eastern white pine in the Central States (Albers & Albers, 1998; Schwartz & Stanosz, 2004) and the Northeast (Bedker, O'Brien, & Mielke, 1995; Ostrofsky, Rumpf, Struble, & Bradbury, 1988); however, historical research demonstrated that pruning was not economically feasible for large forest stands unless ≤75 linear feet of trunks <4" DBH could be pruned per hour (Stewart, 1953).

The current recommendations for white pine management in New Hampshire are to: 1) use a shelterwood system to establish white pine regeneration under a white pine overstory and prevent moisture from forming on the young pines (Lombard & Bofinger, 1999; Wilkerson, Galbraith, Whitman, & Balch, 2011); and 2) maintain dense regeneration for 15-20 years to prevent excessive damage from WPBR and the white pine weevil, even though high pine densities may increase susceptibility to WPND and *Caliciopsis* (Leak et al., 2020). After 20 years, the overstory can be thinned while snow is on the ground to prevent damage to the newly-released pole-size pines. Other options for managing white pine include practices adopted in the western states: 1) reduce *C. ribicola* populations by removing alternate hosts and infected pines to reduce the percentage of non-resistant trees; 2) manage forest composition by increasing pine establishment to allow for natural selection of rust-resistant pines; 3) improve host vigor to withstand attacks by other insect pests and diseases; 4) plant rust-resistant pines; 5) promote regeneration in healthy stands to increase the diversity of age cohorts and potential resistance to WPBR (Schoettle & Sniezko, 2007).

Management challenges at the landscape scale. Two challenges for growing white pine throughout the white pine region include the introduction of *Ribes* cultivars, and the identification of disease-resistant white pines in the landscape. In the central United States, researchers advised that cultivation of commercial *Ribes* might form a bridge between the eastern and western strains of *C. ribicola* and increase the spread of WPBR (Muir & Hunt, 2000). In the Northeast, the results of a Vermont study cautioned that the introduction of WPBR-resistant *Ribes* cultivars could increase selection pressure on *C. ribicola* that could then adapt and produce new strains (Bergdahl & Teillon, 2000). In 2013, a New Hampshire survey of *Ribes* cultivars found that: 1) WPBR was present on both immune and resistant *Ribes* cultivars; 2) WPBR was more severe on immune cultivars than resistant cultivars; and 3) a vCr race of *C. ribicola* that had overcome the Cr gene for WPBR resistance in *Ribes* cultivars was present in New Hampshire (Munck, Tanguay, et al., 2015; Weimer, Munck, Cox, Villani, & Tanguay, 2013).

While research in the Northeast has contributed to our knowledge of commercial *Ribes* and WPBR resistance, studies in the central and western U. S. and Canada have begun to identify specific genes and traits that infer white pine resistance to the disease (Hunt, 2004; Jacobs, Burnes, David, & Blanchette, 2009; Kinloch & Dupper, 2002; Kinloch, Sniezko, Barnes, & Greathouse, 1999; Kinloch, Sniezko, & Dupper, 2003; Liu, Sniezko, & Ekramoddoullah, 2011; Pike et al., 2018; Schoettle, Sniezko, Kegley, & Burns, 2013; Smith, Burnes, Jurgens, David, & Blanchette, 2002; Sniezko et al., 2004; Sniezko and Kegley, 2014; Sniezko, Danchok, Savin, Liu, & Kegley, 2016). The possibility of WPBR resistance in native populations of the central and eastern states has been questioned, however. Trees that appear to be resistant to WPBR may have escaped infection because of factors other than genetics, such as the microclimate. Van Arsdel (1972) argued that climatic escape was much more common in North America than WPBR resistance. It is unknown if pine stands in New Hampshire free of WPBR have developed resistance to the disease during the past century or are an example of climatic escape. Identifying native white pine populations that are resistant to WPBR would offer landowners and timber managers a current and future tool for successfully growing healthy white pine in a climate and forested region that supports WPBR.

Management challenges within a changing climate. New Hampshire's changing climate affects white pine growth and health, particularly in the seedling size classes that are more vulnerable to changes in temperature and moisture during early establishment (Janowiak et al., 2018; Mohan, Cox, & Iverson, 2009; Rustad et al., 2012). White pine naturally establishes on dry, sandy sites where, if undisturbed, it succeeds to hemlock (Leak et al., 2020). New Hampshire's predicted increase in temperature will lengthen the white pine growing season (Chhin, Zalesny, Parker, & Brissette, 2018; Janowiak et al., 2018) and the WPBR infection season due to an earlier spring. The earlier spring season, combined with increased temperatures and moisture, is expected to increase the potential for higher WPBR incidence (Loehman et al., 2018; Wyka et al., 2018).

Under a variety of climate modelling scenarios (excepting large-scale disturbances and altered ecosystems), habitat suitable for white pine establishment and growth is expected to remain relatively stable during this century, with very little decrease in its range under high emissions scenarios (Janowiak et al., 2018). Although white pine is considered heat-tolerant, reports of its tolerance and resilience to drought are conflicting (Caspersen & Kobe, 2001; Fahey, Bialecki, & Carter, 2013; Boucher, Bernier, & Munson, 2001; Janowiak et al., 2018; Wilkerson, Galbraith, Whitman, & Balch, 2011). As a result, white pine biomass is projected to decrease from current climate levels approximately 10% under low emissions scenarios and 58% under high emissions scenarios due to: 1) increased temperatures, severe and damaging weather events, evapotranspiration, water stress from droughts, and non-native pathogen adaptability and infectivity (including *C. ribicola*); 2) decreased soil moisture affecting new growth of branches, needles, cones and overall reproduction potential; and 3) changes in below-ground carbon from soil respiration, and the presence of pollutants such as nitrogen, acid deposition, and sulfur that may affect nutrient cycling and intake (Janowiak et al., 2018; Mohan, Cox, & Iverson, 2009; Rustad et al., 2012). While white pine is expected to be more sensitive to changes in soil moisture availability, the *C. ribicola* pathogen will be more sensitive to changes in the timing and duration of precipitation events (Loehman et al., 2018; Sturrock et al., 2011). During an overstory thinning, the retention of some individual trees with a visible tolerance or adaptation to WPBR and changing temperatures and precipitation will: 1) provide a seed source with genetic diversity; and 2) increase the health and vigor of white pine as a species as it adapts to the future climate (Iverson & Prasad, 2001).

Although the effects of a changing climate on the incidence and severity of WPBR are unknown (Koester, Savin, Buss, & Sniezko, 2018), where WPBR removes white pine as a major component of the forest, pine-dependent ecosystems will become dominated by other species, changing their functional roles in the larger forest and landscape (Harvey, Byler, McDonald, Neuenschwander, & Tonn, 2008). The biggest challenge in managing an early-successional keystone species in the aging forests of New Hampshire is to understand how the changing climate affects the natural disturbance regime that promotes white pine establishment. The natural disturbance regime in the pre-settlement forests of the Northeast resulted in canopy gaps from wind, disease, insects, and mortality in patches less than 0.5 acres in size every 50-200 years (Seymour, White, & deMaynadier, 2002). As climate change increases the probability of severe weather events (Henry, Reiskind, Land, & Haddad, 2020), the changes in temperature and moisture may influence the frequency, duration, and intensity of natural disturbances, and alter disturbance regimes (Dale et al., 2001). However, a model that evaluated forest composition and succession in southern Quebec province found that, to date, anthropogenic disturbances were more directly linked to changes in forest composition than increased natural disturbances resulting from climate change (Danneyrolles et al., 2019). The findings suggested that disturbances may actually hinder a species or ecosystem’s ability to adapt to the projected increase in temperature (Danneyrolles et al., 2019). Disturbances such as increased flooding events, non-native species invasions, and insect pests and diseases are expected to impede the regeneration of native species such as white pine (Swanston et al., 2018). The future of white pine as a resilient species rests on its placement within larger forested landscapes and where it sustains a diversity of strata and size classes (Swanston et al., 2018; Wilkerson et al., 2011). Although managing for white pine in a changing climate is challenging, we can expect that the species will remain an integral component of our forests and timber industry into the future.

Limitations

This study compared forest composition in 2018 to historical pine stand data from blister rust maps created by New Hampshire's defunct Office of Blister Rust Control. The maps were not created for all towns during the same year, resulting in a range of data from 1929-1976. As a result, the forest composition in 2018 could not be compared to a specific year or decade for all 100 stands observed. In addition, the categories used by the blister rust agents to describe the composition of each stand differed from those favored today; this research combined multiple ratings systems to capture each stand's historical composition, and to serve as a baseline for future studies.

This study was unable to build upon WPBR research in the Northeast that spanned several decades because such studies do not exist. The lack of long-term studies on WPBR may be attributed to the belief that WPBR was no longer a threat due to: 1) the successful control of *Ribes nigrum* in the 1960s; and 2) the low incidence of the disease reported in New Hampshire in the 1990s (Benedict, 1981; Leak et al., 2020; Lombard & Bofinger, 1999; Van Arsdel, 2011). However, this study showed that changes occurred in New Hampshire's forests during the past century that cannot be attributed solely to natural forest succession. Rich opportunities exist for researchers wishing to understand the long-term effects of an exotic disease on a highly-valued timber resource in a changing climate.

Research Needs

Historical and current data advanced our knowledge of the long-term effects of WPBR in New Hampshire. A baseline was established for future studies on the occurrence of WPBR, the size class distribution of white pine, and the successional status of New Hampshire's forests. However, many questions arose from the results of this study. This research identified a need for the review of climatic and biotic variables and processes that support WPBR in the 21st century, including the roles of local climate and native *Ribes* in the spread of WPBR (Van Arsdel, 2011). Specific questions to address with future research include: 1) how do the biota, structure, nutrients, and climate of the forest, together, support WPBR over time; and 2) how do those supporting factors affect WPBR when they are altered by disturbances? Understanding how forest composition and succession may support WPBR establishment or persistence would aid in the control of the disease and the management of white pine.

The results of this study support a re-evaluation of white pine management strategies for New Hampshire; specifically, for the inclusion of climate science that addresses the potential for increased white pine disease incidence. We have no research on the effects of management practices such as clear cuts and shelterwoods in regenerating white pine on WPBR-invaded sites over time. Do the *Ribes* die out as the canopy closes, or have the hydrology and temperature changes forced *Ribes* to adapt to warmer, drier, and potentially shadier sites over time? Do silvicultural prunings prevent WPBR infection in young pine stands in New Hampshire? What roles do the soil types have in retaining white pine, *Ribes*, or microclimates favorable to WPBR establishment? What factors, including forest composition and structure, affect a site's ability to support or prevent repeat infections and white pine regeneration over several decades? Most importantly, how do we grow white pine for valuable timber resources in forests that are aging and succeeding, yet still supporting WPBR infections?

One question not addressed in this study was how climate change acted as a disturbance agent in tandem with WPBR and other disturbances to affect the composition and succession of New Hampshire's forests. Additional long-term research is needed to untangle the multi-layered impacts of: climate change; anthropogenic disturbances such as logging; and disturbances caused by non-native plants, insects, and diseases (Esser, 2020). Understanding these impacts could inform the development of a white pine climate vulnerability index (CVI) for New Hampshire and the Northeast. Building upon the work of Rogers, Jantz, and Goetz (2017), the CVI would assess white pine vulnerability to a changing climate by evaluating: 1) exposure to the changing climate (geography, topography, aspect, stratum, soil); 2) sensitivity to changing temperature, moisture, nutrient availability, and disturbance regimes (size and age classes); 3) susceptibility to increased WPBR presence and severity (resistance, tolerance, mortality) and potentially other co-occurring diseases; and 4) overall resilience and adaptive capacity as a species to respond to disturbances, including a changing climate.

Conclusion

New Hampshire's white pine forests continue to decline in size, challenged by many factors, including WPBR. This study combined both historical and current forest data and management strategies to assess the impacts of a non-native pathogen and a valuable timber species in a changing climate. Results suggested that the exotic disease WPBR, can assist with the advancement of late seral species into the forest overstory through the selective removal of single early-successional pines over time. By killing pines before they reach cone-bearing age, WPBR reduced the white pine component in a stand, impacting white pine sustainability, and potentially, forest succession.

By exploring the impacts of WPBR upon forests in New Hampshire, this study advanced our knowledge of: 1) the role of an exotic disease as a disturbance agent; 2) the ecological implications for white pine sustainability as a keystone species, forest type, and wildlife habitat; 3) the effects of WPBR interactions with other disturbance agents such as timber harvesting or climate change; and 4) management implications for our future forests. This study contributed to the literature by providing a disease-disturbance conceptual model and a WPBR succession impacts model for future research applications. In addition, this study resulted in baseline data for much-needed research on the impacts of an exotic pathogen on forest composition, succession, and sustainability in the white pine forests of New Hampshire and the Northeast.

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Appendices

A-1. Successional Stage Changes for 100 NH Stands from Initial Mapping to 2018

Succession Stage	1. Weeds, Grasses	1-3. Grasses, Shrubs, Pine	3. Pine, Shade-Intolerants	3-4. Pine, Mixed Species	4. Mixed Species	5. Shade-Tolerant Species	Total Stands
Total Stands When Mapped	0	21	50	29	0	0	100
Total Stands in 2018	0	0	4	74	20	2	100

Note. Successional stages (Cooper, 1922).

A-2. Historical and 2018 Forest Succession Stages for 100 Stands in New Hampshire

Stand/Location and WPBR History	Year Mapped	Succession Stage When Mapped (Cooper, 1922)	2018 Succession Stage (Cooper, 1922)	Successional Stage Change in 2018	NED-3 Forest Type in 2018	Stand Age in 2018 (NED-3)
Acworth WPBR	1936	1, 2, 3	3, 4	+	Other hardwoods	56
Acworth No WPBR	1936	3, 4	3, 4	=	Oak northern hardwoods	57
Alexandria WPBR	1929	1, 3	3, 4	+	Maple	62
Alexandria No WPBR	1930	3	4	+	Hemlock hardwoods	65
Alton WPBR	1935	3	3, 4	+	Other hardwoods	95
Alton No WPBR	1935	3	3, 4	+	Other mixed woods	98
Andover WPBR	1945	3	3	=	Pine	93
Andover No WPBR	1945	3	3, 4	+	Oak northern pine	95
Antrim WPBR	1942	3, 4	3, 4	=	White pine-hemlock	67
Antrim No WPBR	1942	2, 3, 4	4	+	Other hardwoods	61
Barnstead WPBR	1932	1, 3	3, 4	+	Other mixed woods	73
Barnstead No WPBR	1932	3, 4	3, 4	=	Other mixed woods	67
Barrington WPBR	1936	3	3, 4	+	Oak northern pine	73
Barrington No WPBR	1936	3	3, 4	+	Oak northern pine	80
Bath WPBR	1939	3	3, 4	+	Bottomland conifer	85
Bath No WPBR	1939	3	3, 4	+	Other mixed woods	61
Belmont WPBR	1941	3	3, 4	+	Pine hardwoods	60
Belmont No WPBR	1941	3, 4	3, 4	=	Spruce-northern hardwoods	52
Bristol WPBR	1949	3, 4	4	+	Other hardwoods	75
Bristol No WPBR	1949	3, 4	3, 4	=	Other hardwoods	72
Brookfield WPBR	1941	3	3, 4	+	White pine-hemlock	78
Brookfield No WPBR	1941	3	3, 4	+	Other hardwoods	55
Canaan WPBR	1932	3, 4	3, 4	=	Pine hardwoods	67
Canaan No WPBR	1932	3, 4	3, 4	=	Pine	99

Table A-2 Continued

Stand/Location and WPBR History	Year Mapped	Succession Stage When Mapped (Cooper, 1922)	2018 Succession Stage (Cooper, 1922)	Successional Stage Change in 2018	NED-3 Forest Type in 2018	Stand Age in 2018 (NED-3)
Candia WPBR	1936	2,3	3,4	+	Hemlock hardwoods	60
Candia No WPBR	1936	2, 3	3, 4	+	Other mixed woods	46
Canterbury WPBR	1933	3	3, 4	+	Oak northern hardwoods	61
Canterbury No WPBR	1933	3	3, 4	+	Other hardwoods	65
Charlestown WPBR	Oct. 1938	3	4	+	Hemlock	63
Charlestown No WPBR	Oct. 1938	1, 3	4	+	Oak northern hardwoods	52
Claremont WPBR	1931	3	3, 4	+	Other hardwoods	85
Claremont No WPBR	1947	3, 4	4	+	Other mixed woods	66
Concord WPBR	1975	2, 3, 4	3, 4	+	Oak northern pine	71
Concord No WPBR	1975	2, 3, 4	3, 4	+	Pine	49
Cornish WPBR	1946	3, 4	4	+	Maple	39
Cornish No WPBR	1946	3, 4	4	+	Maple	45
Danbury WPBR	1934	2, 3	3, 4	+	Spruce-northern hardwoods	65
Danbury No WPBR	1934	3	3, 4	+	Bottomland conifer	76
Deering WPBR	1955	3	3, 4	+	Bay-swamp pocosin	52
Deering No WPBR	1955	3	3, 4	+	Bay-swamp pocosin	43
Dublin WPBR	1941	3	4	+	Maple	68
Dublin No WPBR	1941	3	3, 4	+	Other hardwoods	62
Dunbarton WPBR	1933-1934	3	3, 4	+	Oak northern pine	74
Dunbarton No WPBR	1933-1934	2, 3	3, 4	+	Pine	123
Enfield WPBR	1935	3	3, 4	+	Bottomland conifer	71
Enfield No WPBR	1935	3	3, 4	+	Bottomland conifer	95

Table A-2 Continued

Stand/Location and WPBR History	Year Mapped	Succession Stage When Mapped (Cooper, 1922)	2018 Succession Stage (Cooper, 1922)	Successional Stage Change in 2018	NED-3 Forest Type in 2018	Stand Age in 2018 (NED-3)
Grantham WPBR	1936	3	4	+	Spruce-northern hardwoods	39
Grantham No WPBR	1958	3, 4	4	+	Other hardwoods	45
Hanover WPBR	1931	3	4	+	Spruce-northern hardwoods	58
Hanover No WPBR	1931	3	4	+	Other mixed woods	44
Haverhill WPBR	1944	3	3, 4	+	White pine-hemlock	83
Haverhill No WPBR	1944	3	4	+	Other hardwoods	91
Hebron WPBR	1948	3, 4	3, 4	=	Other hardwoods	88
Hebron No WPBR	1948	3, 4	3, 4	=	Other hardwoods	55
Hinsdale WPBR	1951	2, 3	3, 4	+	Other hardwoods	72
Hinsdale No WPBR	1951	3	4	+	Maple	75
Keene WPBR	1936	3	3	=	Pine	81
Keene No WPBR	1936	3, 4	4	+	Oak northern hardwoods	58
Lebanon WPBR	1937	3	3,4	+	Pine hardwoods	149
Lebanon No WPBR	1937	1, 3	3, 4	+	Other hardwoods	61
Littleton WPBR	1932	3	3, 4	+	Bottomland conifer	53
Littleton No WPBR	1932	3	3, 4	+	Bottomland conifer	79
Loudon WPBR	1936	3	3, 4	+	Other hardwoods	75
Loudon No WPBR	1936	2, 3	3, 4	+	White pine-hemlock	64
Lyme WPBR	1932	3	3, 4	+	White pine-hemlock	74
Lyme No WPBR	1932	3	3, 4	+	Other hardwoods	64
Lyndeborough WPBR	1932	3, 4	4	+	Hemlock hardwoods	72
Lyndeborough No WPBR	1932	3, 4	4	+	Hemlock	64

Table A-2 Continued

Stand/Location and WPBR History	Year Mapped	Succession Stage When Mapped (Cooper, 1922)	2018 Succession Stage (Cooper, 1922)	Successional Stage Change in 2018	NED-3 Forest Type in 2018	Stand Age in 2018 (NED-3)
Moultonborough WPBR	1936	2, 3	3	+	Eastern white pine (pure)	53
Moultonborough No WPBR	1936	2, 3, 4	3, 4	+	Bottomland conifer	71
New Boston WPBR +	1932	2, 3	3, 4	+	Pine hardwoods	50
New Boston No WPBR	1932	2, 3	3, 4	+	Pine	41
New Durham WPBR	1940	3, 4	3, 4	=	White pine-hemlock	68
New Durham No WPBR	1940	3	3, 4	+	Other mixed woods	87
New London WPBR	1940	3	5	+	Beech maple	83
New London No WPBR	1940	2, 3	3, 4	+	Pine hardwoods	75
Pembroke WPBR	1940	3	3, 4	+	Other hardwoods	59
Pembroke No WPBR	1940	3, 4	3, 4	=	Oak northern hardwoods	56
Raymond WPBR	1941	3, 4	4	+	White pine-hemlock	61
Raymond No WPBR	1941	3, 4	3, 4	=	White pine-hemlock	77
Strafford WPBR	1939	3	3, 4	+	Other hardwoods	56
Strafford No WPBR	1939	3, 4	4	+	Hemlock	75
Sullivan WPBR	1936	2, 3	3, 4	+	White pine-hemlock	82
Sullivan No WPBR	1936	3	3, 4	+	White pine-hemlock	89
Sunapee WPBR	1946	3	3, 4	+	White pine-hemlock	101
Sunapee No WPBR	1946	3	3, 4	+	Bottomland conifer	66
Swanzey WPBR	1934	3	3, 4	+	Oak northern pine	45
Swanzey no WPBR	1934	2, 3	3, 4	+	Oak northern pine	56
Thornton WPBR	1934	2, 3	3, 4	+	Bottomland conifer	95
Thornton No WPBR	1934	3, 4	3, 4	=	White pine-hemlock	62

Table A-2 Continued

Stand/Location and WPBR History	Year Mapped	Succession Stage When Mapped (Cooper, 1922)	2018 Succession Stage (Cooper, 1922)	Successional Stage Change in 2018	NED-3 Forest Type in 2018	Stand Age in 2018 (NED-3)
Troy WPBR	1937	3	3, 4	+	Oak northern pine	65
Troy No WPBR	1937	3	3, 4	+	Other hardwoods	50
Tuftonboro WPBR	1937	3	3	=	Eastern white pine (pure)	48
Tuftonboro No WPBR	1937	3	3, 4	+	Pine hardwoods	67
Wakefield WPBR	1940	3	5	+	Hemlock	68
Wakefield No WPBR	1940	3, 4	3, 4	=	Other hardwoods	72
Warner WPBR	1934	1, 2, 3	3, 4	+	Pine hardwoods	46
Warner No WPBR	1934	3, 4	3, 4	=	White pine-hemlock	46
Weare WPBR	1935	2, 3	3, 4	+	White pine-hemlock	96
Weare No WPBR	1935	2, 3	3, 4	+	Pine hardwoods	67

Note. Cooper (1922) succession stages for northern deciduous forests: 1) weeds and grasses; 2) “pasture shrubs”, including raspberry, blueberry, staghorn sumac, and *R. cynosbati*, *R. rotundifolium*, and *R. hirtellum*; 3) trees which established open woodland, including white pine, quaking aspen, gray birch, and paper birch; 4) trees that established under pioneers, including sugar maple, beech, hemlock, red oak, and white ash; and 5) the final climax stage in which sugar maple, beech, and hemlock increased in dominance.
+ denotes advance in succession; = denotes no change in successional stage

A-3. Percentage of PNC Indicator Species within Each Canopy Layer and Combined Seral Stage Classifications for 100 NH Stands

Location	WPBR History	Dominant	Co-Dominant	Intermediate	Suppressed	Shrub	Ground	Over-story	Mid-story	Under-story
Acworth	Repeat	0	100	7.7	37.5	75	7.3	E-PNC	E-M	L-E
Acworth	New	0	0	5	0	0	12.9	E	E	E-M
Alexandria	Historical	0	85.7	87.9	20	0	0	E-PNC	PNC-M	E
Alexandria	None	0	0	64.3	93.3	0	11.1	E	L-PNC	E-M
Alton	Historical	0	0	0	100	100	66.7	E	E-PNC	PNC-L
Alton	None	0	0	50	57.5	100	100	E	M-L	PNC
Andover	Repeat	0	0	83.3	50	79.2	12.5	E	PNC-M	PNC-M
Andover	None	0	0	0	33.3	2.3	11.1	E	E-M	E-M
Antrim	Repeat	50	53.8	36.4	0	0	59.3	M-L	M-E	E-L
Antrim	None	50	25	28.5	26.7	0	50	M	M	E-M
Barnstead	Repeat	0	0	12.5	56.2	0	3.3	E	M	E
Barnstead	New	0	0	40	6.8	0	0	E	M-E	E
Barrington	Repeat	0	0	38.1	33.3	83.3	42.9	E	M	PNC-M
Barrington	None	0	0	9.1	46.7	100	61.2	E	E-M	PNC-L
Bath	Historical	0	25	25	26.3	26.7	38.8	E-M	M	M
Bath	None	0	0	3.4	35.2	80	4.7	E	E-M	PNC-E
Belmont	Repeat	0	100	0	60	100	26.3	E-PNC	E-L	PNC-M
Belmont	None	0	0	11.2	44.4	100	73.7	E	M	PNC-L
Bristol	Historical	0	75	100	63.6	0	100	E-L	PNC-L	E-PNC
Bristol	None	0	0	12.5	20	0	83.3	E	M	E-PNC
Brookfield	Historical	0	0	36.9	92	100	94.2	E	M-PNC	PNC
Brookfield	None	0	0	34.7	41.5	25	27.9	E	M	M
Canaan	Repeat	0	0	0	18.8	40	66.67	E	E-M	M-L
Canaan	New	0	0	0	18.5	0	0	E	E-M	E
Candia	Historical	0	30	18.8	92.6	100	0	E-M	M-PNC	PNC-E
Candia	None	0	0	33.3	88.9	0	100	E	M-PNC	E-PNC
Canterbury	Historical	0	0	21.4	36.4	57.1	48	E	M	L-M
Canterbury	New	0	0	33.3	51.4	0	94.1	E	M-L	E-PNC
Charlestown	Historical	0	40	81.3	40.7	0	53.8	E-M	PNC-M	E-L
Charlestown	None	50	75	81	58.4	97.2	100	M-L	PNC-L	PNC
Claremont	Historical	0	0	33.3	19.4	53.7	41.7	E	M	L-M
Claremont	None	0	0	50	3.7	0	58.6	E	M-E	E-L
Concord	Repeat	0	0	0	0	0	0	E	E	E
Concord	New	0	0	0	0	0	0	E	E	E
Cornish	Historical	0	20	27.3	51.5	0	33.3	E-M	M-L	E-M
Cornish	None	0	33.3	16.7	20.9	100	25	E-M	M	PNC-M
Danbury	Repeat	16.7	80	50.1	50	25.7	22.2	M-PNC	L-M	M
Danbury	None	0	50	40	100	68.8	48.6	E-M	M-PNC	L-M
Deering	Historical	25	5.6	5.7	40	0	0	M-E	E-M	E
Deering	None	0	5.6	13.8	21.2	100	58.8	E	M	PNC-L

Table A-3 Continued

Location	WPBR History	Dominant	Co-Dominant	Intermediate	Suppressed	Shrub	Ground	Over-story	Mid-story	Under-story
Dublin	Historical	0	54.5	69.2	95	0	40	E-L	L-PNC	E-M
Dublin	None	0	57.2	63.2	100	96.7	96.4	E-L	L-PNC	PNC
Dunbarton	Historical	0	0	50	66.6	0	1.1	E	M-L	E
Dunbarton	None	0	25	25	60	0	26.5	E-M	M-L	E-M
Enfield	Historical	0	0	55.5	88.9	100	100	E	L-PNC	PNC
Enfield	New	0	0	16.7	100	77.8	91.7	E	M-PNC	PNC
Grantham	Repeat	0	0	70	100	26.3	6	E	L-PNC	M-E
Grantham	None	0	0	90.3	85	100	68.3	E	PNC	PNC-L
Hanover	Historical	50	0	63.7	85.7	33.3	37.5	M-E	L-PNC	M
Hanover	New	0	0	25	35.7	100	77.7	E	M	PNC
Haverhill	Historical	0	75	75	86.7	88.2	35.4	E-L	L-PNC	PNC-M
Haverhill	New	0	100	3.8	7.1	50	100	E-PNC	E	M-PNC
Hebron	Historical	0	0	45.5	69.2	100	14.3	E	M-L	PNC-M
Hebron	None	0	0	30.8	70	50	16.7	E	M-L	M
Hinsdale	Repeat	0	0	17.8	11.4	0	0	E	M	E
Hinsdale	New	50	0	0	0	100	0	M-E	E	PNC-E
Keene	Historical	0	28.6	0	90	91.7	100	E-M	E-PNC	PNC
Keene	New	0	9.1	16.7	28.5	37.9	7.1	E	M	M-E
Lebanon	Repeat	0	0	0	11.5	0	0	E	E-M	E
Lebanon	None	0	0	33.3	54.6	75	60	E	M-L	L
Littleton	Repeat	0	0	0	26.8	0	0	E	E-M	E
Littleton	None	0	0	65.3	100	88.8	80	E	L-PNC	PNC
Loudon	Historical	0	25	87.6	91.6	100	85	E-M	PNC	PNC
Loudon	None	0	33.3	58.4	81.3	100	77.3	E-M	L-PNC	PNC
Lyme	Historical	0	7.7	47.8	85.7	0	0	E	M-PNC	E
Lyme	None	0	0	22.2	11.2	42.9	24	E	M	M
Lyndeborough	Historical	33.3	0	0	76	100	75	M-E	E-PNC	PNC-L
Lyndeborough	None	0	50	75	100	0	48.2	E-M	L-PNC	E-M
Moultonborough	Repeat	0	0	0	0	0	0	E	E	E
Moultonborough	New	0	0	75	40	57.1	0	E	L-M	L-E
New Boston	Historical	0	0	0	0	100	25	E	E	PNC-M
New Boston	New	0	9.5	0	10.7	0	30	E	E-M	E-M
New Durham	Historical	0	25	28.6	70	0	8.7	E-M	M-L	E
New Durham	None	0	0	0	28.6	85.7	35.7	E	E-M	PNC-M
New London	Historical	100	100	100	100	100	16.1	PNC	PNC	PNC-M
New London	None	0	0	80	58.3	100	36	E	PNC-L	PNC-M
Pembroke	Repeat	0	0	13.3	5.9	0	5.4	E	M-E	E
Pembroke	New	0	0	3.6	6.8	0	0	E	E	E
Raymond	Historical	0	5.6	80	77.8	100	0	E	PNC	PNC-E
Raymond	New	0	0	10	48	100	0	E	E-M	PNC-E
Strafford	Historical	0	15.8	55	4.3	0	100	E-M	L-E	E-PNC
Strafford	None	100	40	75	100	100	96	PNC-M	L-PNC	PNC

Table A-3 Continued

Location	WPBR History	Dominant	Co-Dominant	Intermediate	Suppressed	Shrub	Ground	Over-story	Mid-story	Under-story
Sullivan	Repeat	0	0	55.6	57.1	71.5	63.7	E	L	L
Sullivan	None	0	50	61.5	83.3	0	88.2	E-M	L-PNC	E-PNC
Sunapee	Historical	0	33.3	100	94.1	100	0	E-M	PNC	PNC-E
Sunapee	None	50	36.4	63.2	95.5	100	100	M	L-PNC	PNC
Swanzey	Repeat	0	0	0	0	0	22.2	E	E	E-M
Swanzey	None	0	0	0	16	0	37.3	E	E-M	E-M
Thornton	Historical	0	0	43.5	92	100	0	E	M-PNC	PNC-E
Thornton	None	0	0	78.7	100	100	13.8	E	PNC	PNC-M
Troy	Repeat	0	0	11.1	7.7	100	0	E	M-E	PNC-E
Troy	None	0	0	0	34.7	0	88.2	E	E-M	E-PNC
Tuftonboro	Repeat	0	0	0	0	0	0	E	E	E
Tuftonboro	New	0	0	0	4.8	0	7.1	E	E	E
Wakefield	Historical	100	0	80	100	93.5	28	PNC-E	PNC	PNC-M
Wakefield	None	0	0	55.1	33.3	100	30	E	L-M	PNC-M
Warner	Repeat	0	0	20.7	12.2	0	31.4	E	M	E-M
Warner	None	0	0	56.7	100	100	100	E	L-PNC	PNC
Weare	Historical	0	33.3	67.4	86.3	0	40	E-M	L-PNC	E-M
Weare	New	0	37.5	81	45.8	0	20.6	E-M	PNC-M	E-M

Note. WPBR stand history: repeat denotes infection when mapped by the NH Blister Rust Control Program and when observed in 2018; new denotes no infection when mapped but WPBR present in 2018; historical denotes infection present when mapped by the NH Blister Rust Control Program but no WPBR observed in 2018; none denotes no historical or 2018 infection (Cornish and Strafford had no WPBR historically or in 2018 and no white pine in 2018).

Dominant and co-dominant canopies combined into overstory; Intermediate and suppressed canopies combined into mid-story; shrub and ground layers combined into understory.
E: early seral with 0-10% of canopy in indicator species (beech, hemlock, sugar maple, balsam fir, red/white spruce); M: mid seral with 10.1-50% of canopy in indicator species; L: late seral with 50.1-75% of canopy in indicator species; PNC: potential natural community with 75.1-100% of canopy in indicator species (adapted from Hall et al., 1995).

A-4. Live White Pine Overstory Percentages in 67 Stands Without Logging Disturbances

WPBR History	Town	Regeneration	Sapling + Pole	Small Timber	Large Timber
Repeat WPBR	Acworth	0	0	0	n/a
Not Logged	Barnstead	18.5	74.1	3.7	3.7
(n=10)	Barrington	0	72.7	18.2	9.1
	Canaan	0	50	**33.3**	n/a
	Concord	53.1	31.3	12.5	3.1
	Lebanon	0	22.2	0	77.8
	Moultonborough	0	90	10	n/a
	Sullivan	20	60	0	20
	Swanzey	16.7	83.3	n/a	n/a
	Troy	0	78.6	0	21.4
Repeat WPBR	Andover	0	**42.9**	42.9	**14.3**
Logged	Antrim	37.5	62.5	0	n/a
(n=10)	Belmont	0	80	20	n/a
	Danbury	27.3	63.6	0	9.1
	Grantham	0	0	n/a	n/a
	Hinsdale	0	86.7	0	**13.3**
	Littleton	0	97.9	2.1	n/a
	Pembroke	61.5	**38.5**	n/a	n/a
	Tuftonboro	0	100	n/a	n/a
	Warner	25	71.4	3.6	n/a
New WPBR	Canaan	18.5	**37.0**	22.2	22.2
Not Logged	Canterbury	0	72.7	9.1	18.2
(n=10)	Concord	**9.8**	90.2	0	n/a
	Enfield	0	33.3	**26.7**	40
	Hanover	0	100	0	n/a
	Haverhill	0	100	0	0
	Keene	66.7	33.3	0	n/a
	Moultonborough	0	**40**	0	60
	New Boston	3.1	96.9	0	n/a
-	Raymond	0	50	41.7	8.3
New WPBR	Acworth	52.6	47.4	n/a	n/a
Logged	Barnstead	0	100	0	n/a
(n=6)	Hinsdale	0	86.7	0	**13.3**
	Pembroke	58.8	**41.2**	n/a	n/a
	Tuftonboro	69.1	24.7	3.7	2.5
	Weare	0	33.3	0	66.7

Table A-4 Continued

WPBR History	Town	Regeneration	Sapling + Pole	Small Timber	Large Timber
No WPBR Not Logged (n=24)	Alexandria	0	0	0	n/a
	Alton	0	18.8	43.8	37.5
	Barrington	0	72.7	18.2	9.1
	Bath	0	20	**30**	n/a
	Bristol	0	80	0	20
	Candia	0	90	10	n/a
	Charlestown	0	0	0	n/a
	Cornish	0	0	0	n/a
	Danbury	0	0	0	100
	Dublin	0	50	n/a	n/a
	Dunbarton	0	50	0	50
	Grantham	0	0	100	n/a
	Lebanon	0	0	50	50
	Littleton	0	0	75	25
	Loudon	0	66.7	0	33.3
	Lyme	0	25	50	25
	Lyndeborough	0	0	0	100
	New Durham	0	0	71.4	28.6
	New London	0	30	60	**10**
	Sullivan	0	0	**25**	75
	Sunapee	0	20	60	20
	Thornton	0	33.3	**33.3**	33.3
	Wakefield	0	**40**	20	40
	Warner	0	71.4	0	28.6
No WPBR Logged (n=10)	Andover	0	**35.7**	21.4	42.9
	Antrim	0	0	0	n/a
	Belmont	0	83.3	n/a	16.7
	Brookfield	0	75	**25**	n/a
	Claremont	0	0	0	100
	Deering	0	0	n/a	n/a
	Hebron	0	100	n/a	n/a
	Swanzey	37.2	55.8	7.0	n/a
	Troy	0	88.9	n/a	**11.1**
	Strafford	0	0	0	n/a

Table A-4 Continued

WPBR History	Town	Regeneration	Sapling + Pole	Small Timber	Large Timber
Historical WPBR Not Logged (n=23)	Alexandria	0	0	0	100
	Alton	0	7.7	23.1	69.2
	Bath	0	20	**30**	50
	Bristol	0	100	0	0
	Brookfield	0	22.2	**33.3**	44.4
	Candia	0	62.5	**25**	**12.5**
	Charlestown	0	0	100	0
	Cornish	0	0	n/a	n/a
	Deering	0	0	0	0
	Dublin	0	0	0	100
	Dunbarton	0	3.3	6.7	n/a
	Enfield	0	20	20	60
	Haverhill	0	0	0	100
	Hebron	0	28.6	0	71.4
	Keene	0	33.3	**33.3**	33.3
	Lyme	0	**36.4**	36.4	27.3
	Lyndeborough	0	0	0	100
	New Boston	0	100	0	n/a
	New Durham	0	75	**25**	0
	Raymond	0	0	0	0
	Strafford	0	0	0	100
	Sunapee	0	0	16.7	83.3
	Thornton	0	26.7	13.3	60
Historical Logged (n=7)	Canterbury	0	33.3	**33.3**	33.3
	Claremont	0	25	0	75
	Hanover	0	0	100	n/a
	Loudon	0	0	60	40
	New London	0	0	0	0
	Wakefield	0	0	0	n/a
	Weare	0	33.3	0	66.7

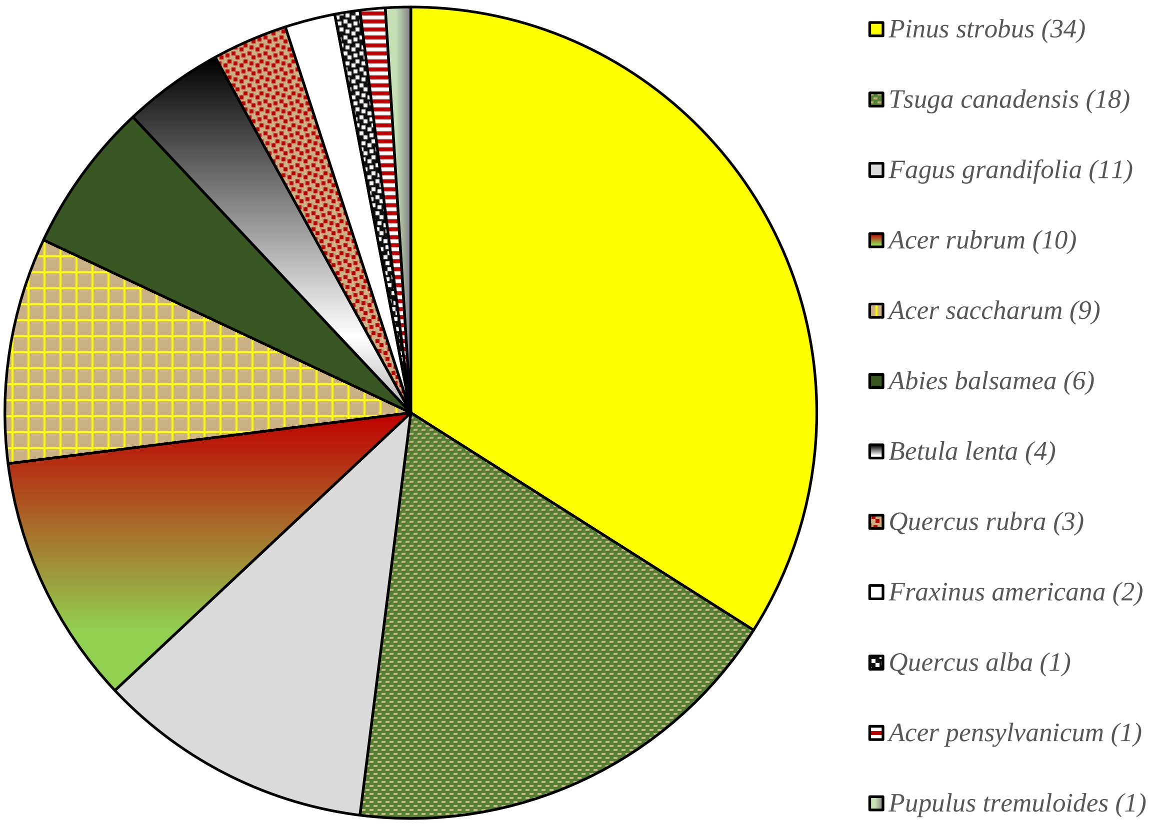
Note. White pine seedlings under .5” diameter excluded from overstory inventory.

N/A: stand not old enough to support size class.

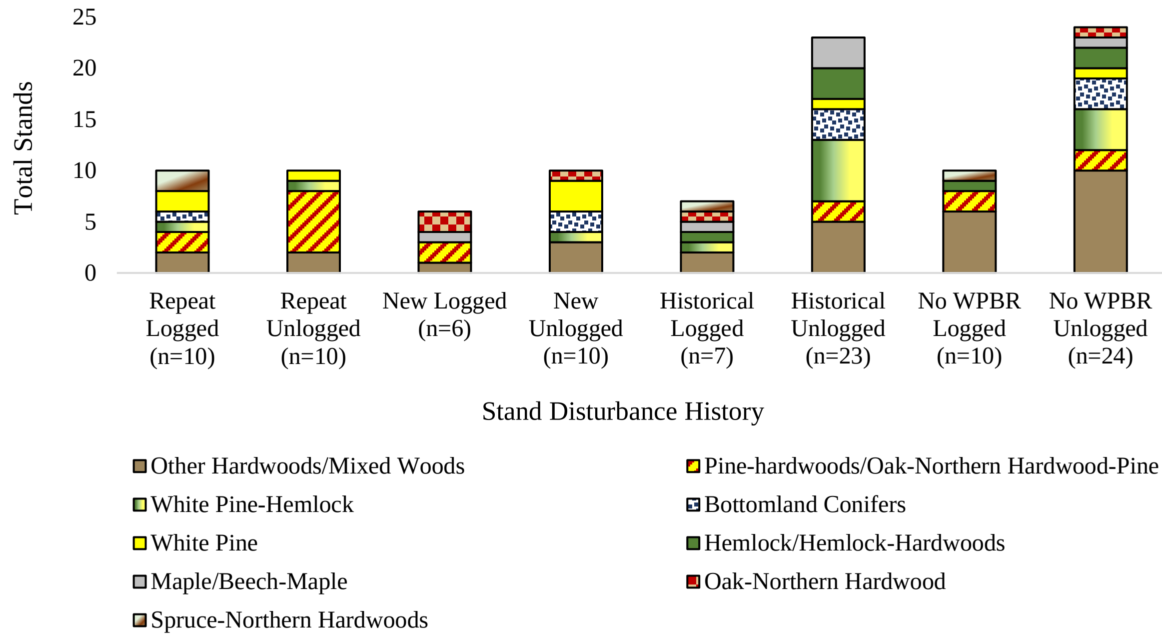
Bold percentages met NED-3 recommendations for the size class. Red percentages exceeded NED-3 recommendations.

For balanced size classes, NED-3 recommended:
5-10% of area in regeneration <1" diameter;
35-45% saplings + poles 1-10.5" DBH;
25-35% small sawtimber 10.6-16.5" DBH;
10-15% large sawtimber > 16.5" DBH.

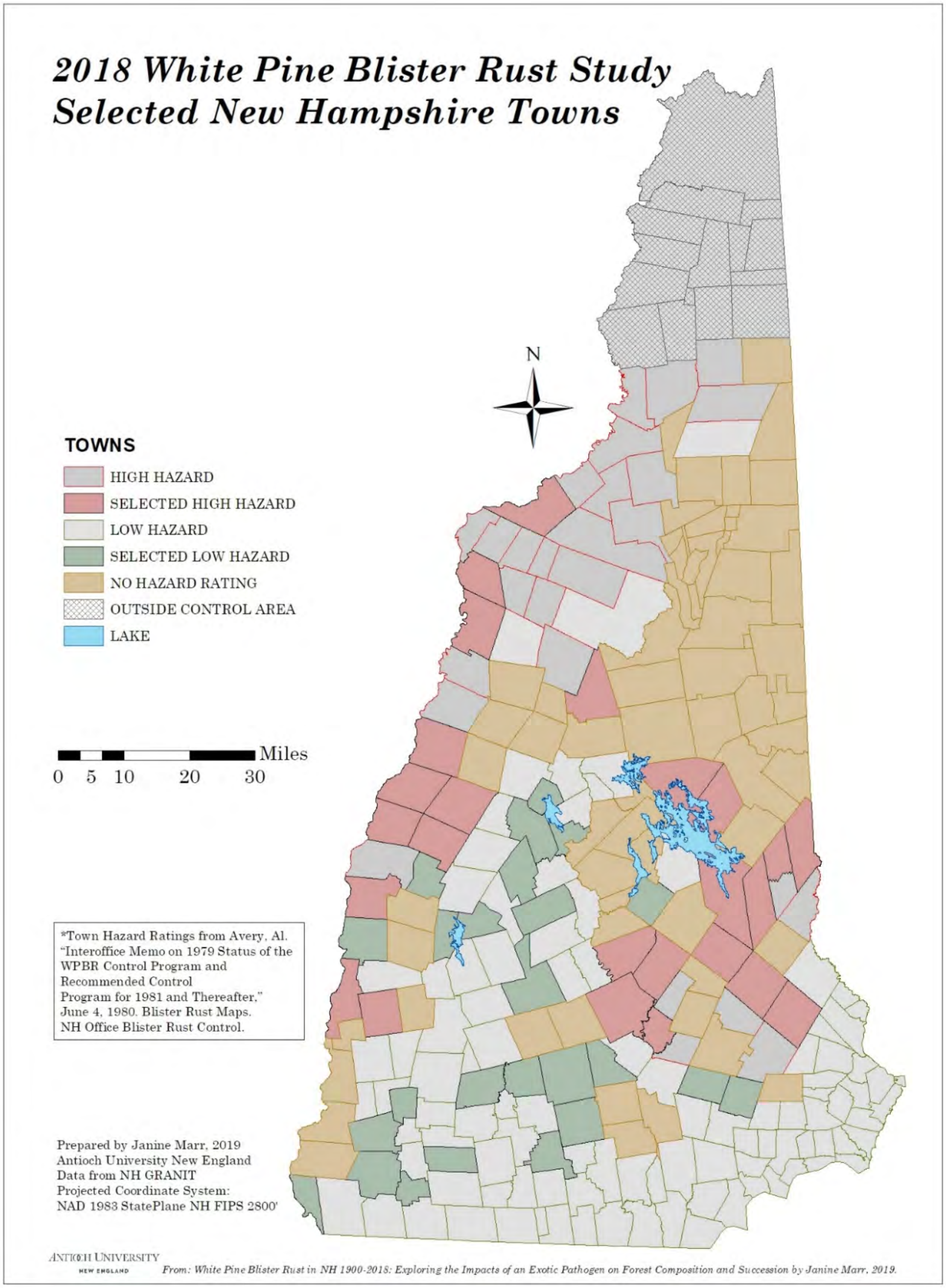
B-1. Dominant Tree Species by Basal Area For 100 New Hampshire Stands in 2018



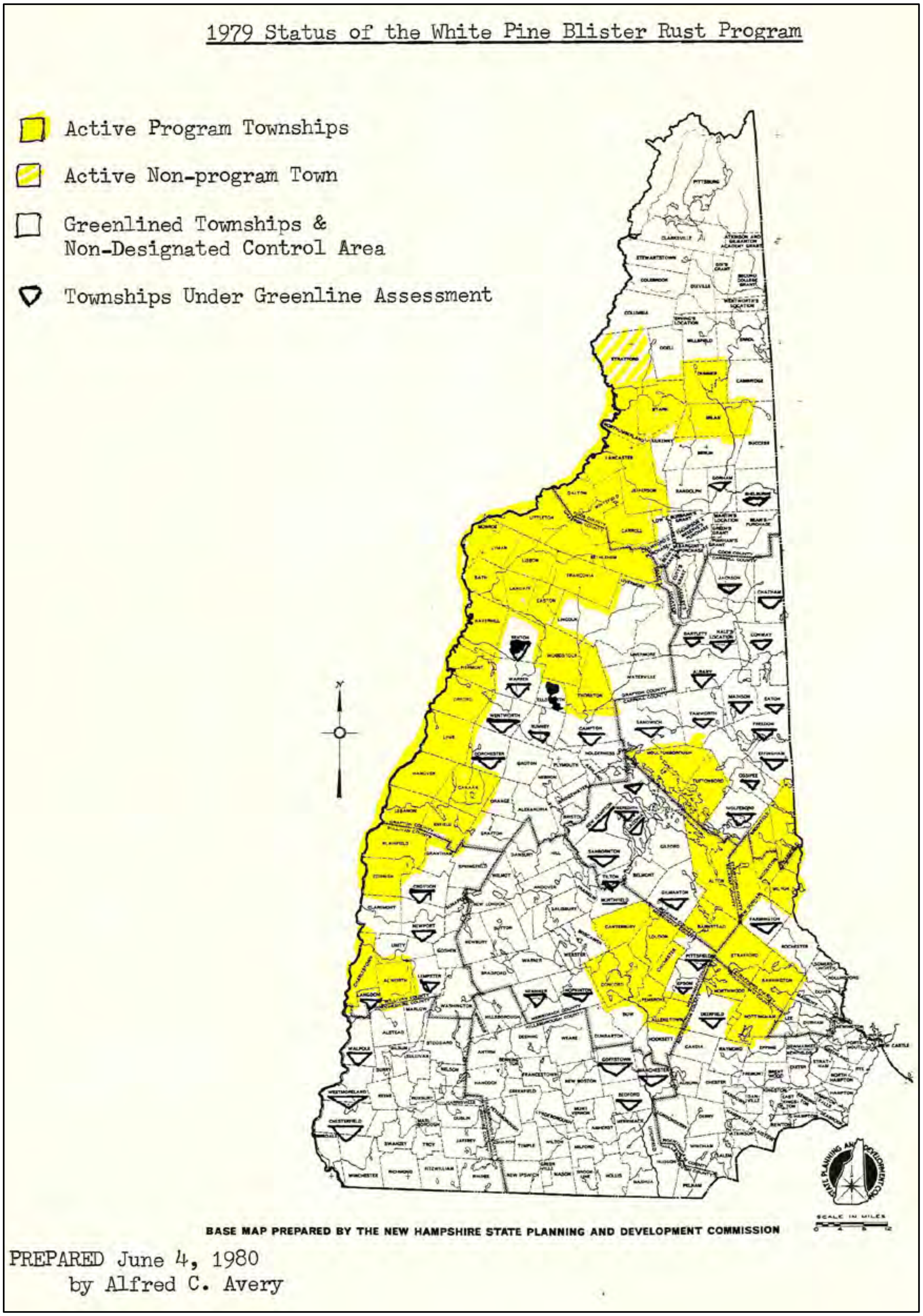
B-2. NED-3 Forest Types for 100 NH Stands in 2018 by Disturbance History



C-1. 2018 New Hampshire White Pine Blister Rust Study Area

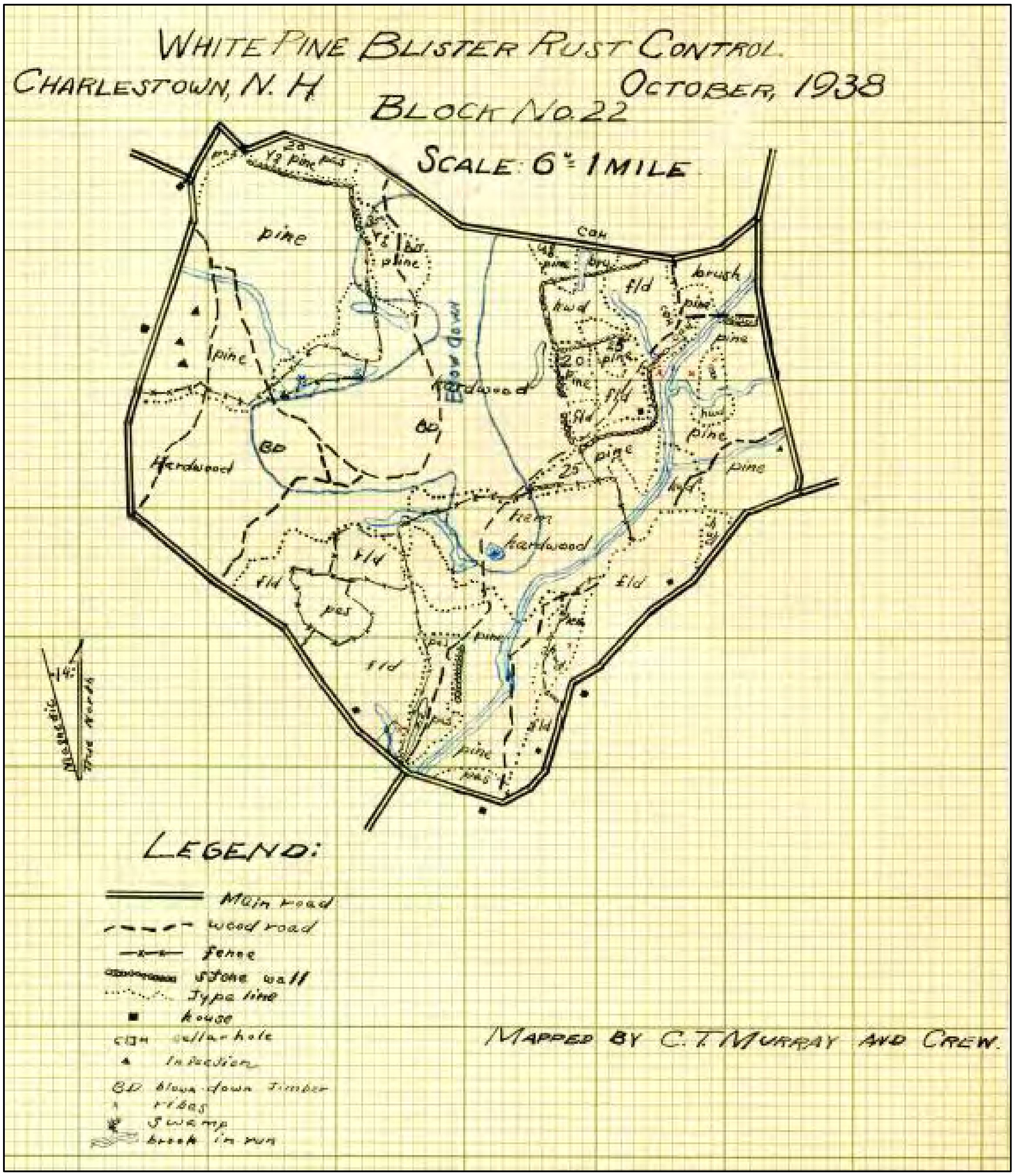


C-2. 1979 Town Hazard Ratings for New Hampshire



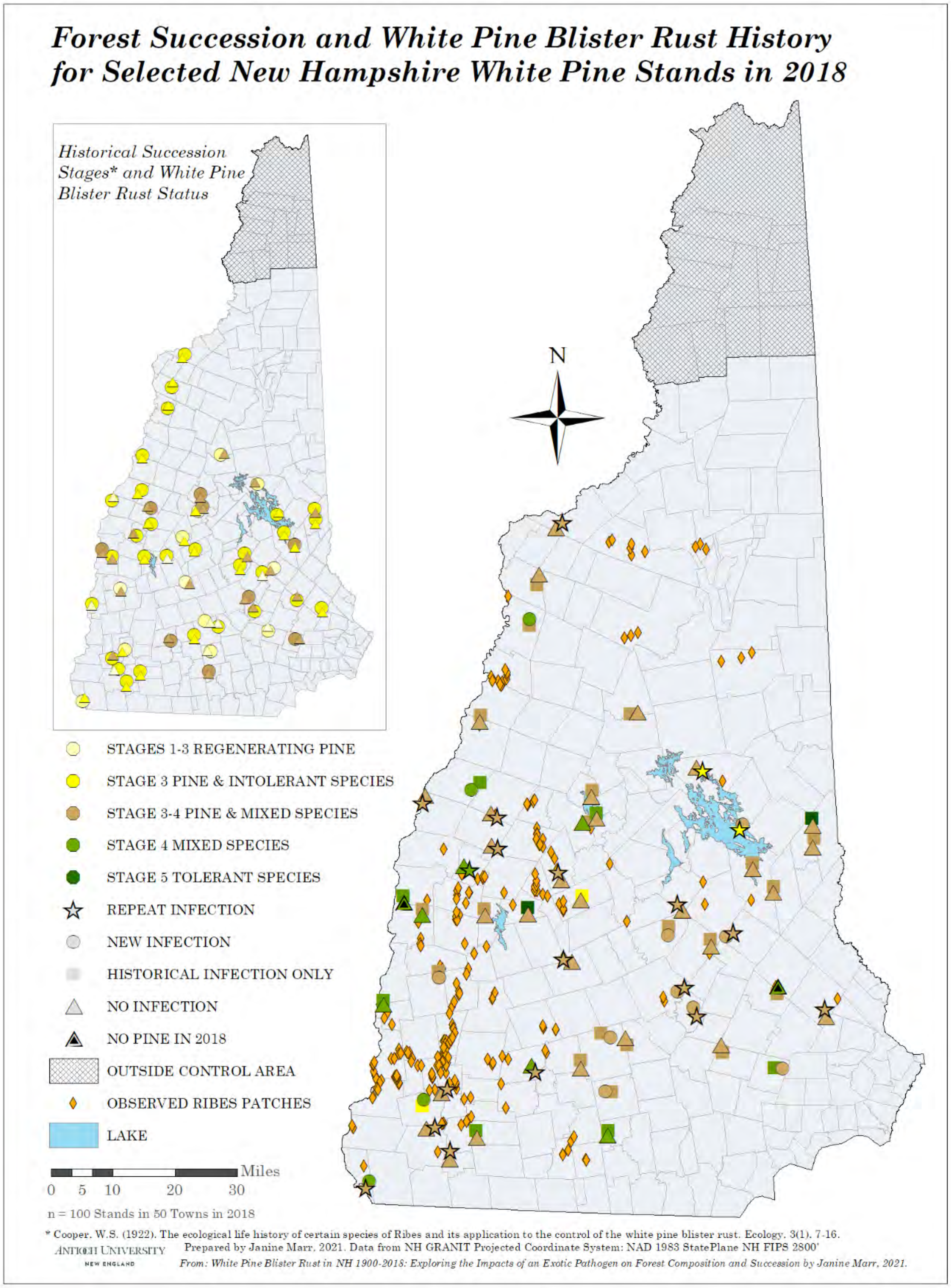
Avery, A. C. (1980). Courtesy of NH Blister Rust Control Archives.

C-3. White Pine Blister Rust Map for Block 22, Charlestown, NH, 1938

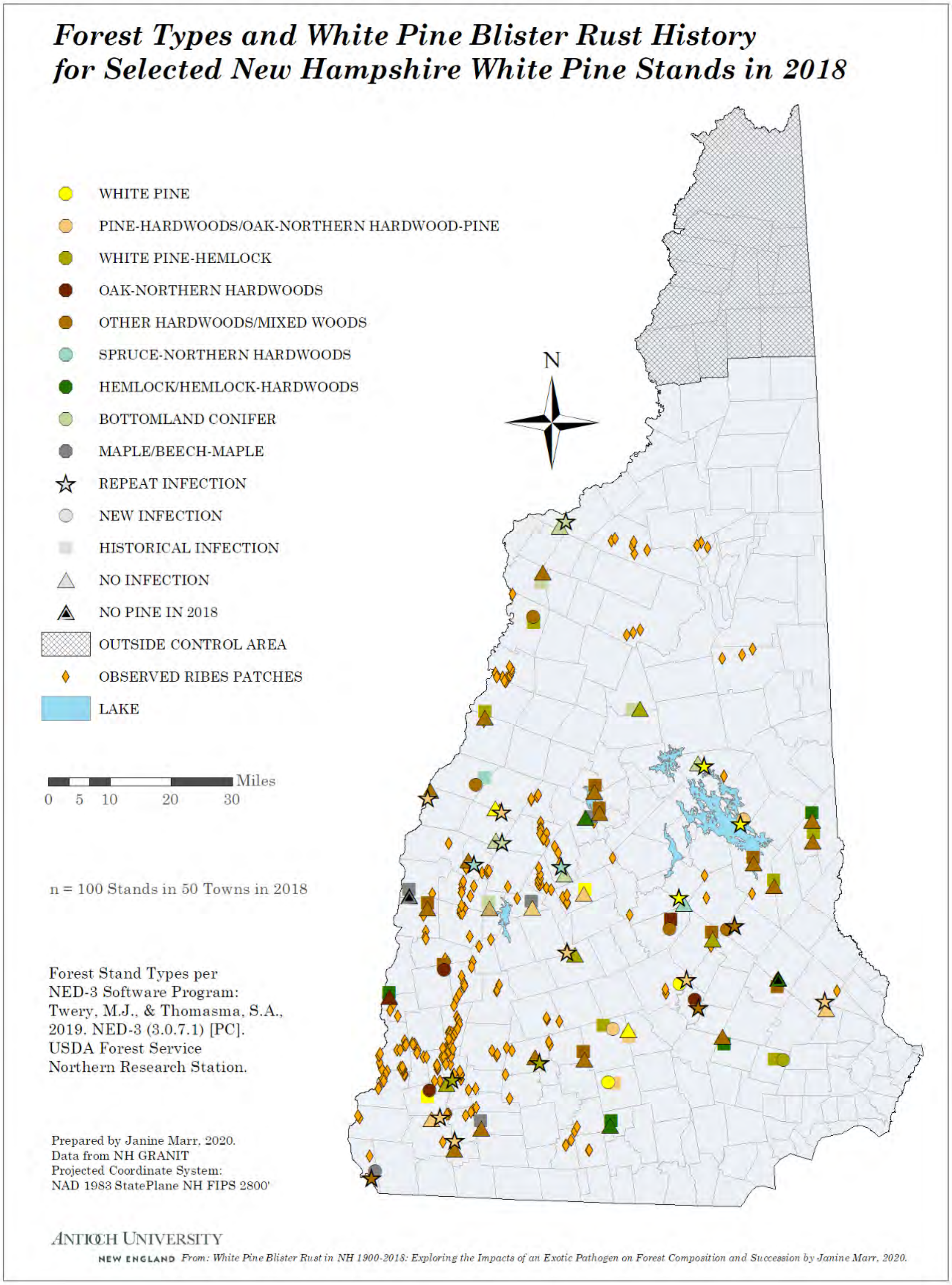


Murray, C. T. (1938). Courtesy of NH Blister Rust Control Archives.

C-4. Historical and 2018 Forest Succession Stages for 100 New Hampshire Stands



C-5. 2018 Forest Types for 100 New Hampshire Stands



D-1. Photographs of 100 Stands, Forest Types, and Canopies Observed in 2018

The following information identifies each of the two plots per town in this study, based on the presence or absence of WPBR documented at the time of mapping by NH Blister Rust Control agents. The control program divided each town into blocks, or regions, using roads, streams, and stone walls as natural dividers. The corresponding blister rust map block numbers listed below represent the section of town in which the research plot was located. For plots in which WPBR occurred historically, the coordinates represent where WPBR infection was documented on the blister rust maps. For plots that had no historical infection, the coordinates represent the location of the stand in 2018, at least 300 yards from the documented infection.

The canopy cover classifications (Hall et al., 1995) in 2018 included: open, <40% canopy cover; moderate, 40-69% canopy cover; dense, ≥70% canopy cover. The seral stages (Hall et al., 1995) included: early seral = intolerant seral species dominant; mid seral = PNC species and seral species approaching 50/50 mix; late seral = PNC species becoming dominant; PNC = potential natural community forms in which earlier seral species are scarce or absent.

Acworth: No Historical WPBR	**Acworth**: Historical WPBR
	
Location: 43°15'24.01"N; 72°14'58.11"W	Location: 43°15'34.44"N; 72°15'12.47"W
Blister Rust Map Block 19	Blister Rust Map Block 19
Canopy (Hall et al., 1995): Dense	Canopy (Hall et al., 1995): Dense
Seral Stage (Hall et al., 1995): Mid	Seral Stage (Hall et al., 1995): Mid

Note. Photos by Janine Marr. *Note*. Photos by Janine Marr.

Alexandria: No Historical WPBR	**Alexandria**: Historical WPBR
	
Location: 43°37'9.72"N; 71°47'33.32"W	Location: 43°37'13.02"N; 71°46'31.38"W
Blister Rust Map Block 26	Blister Rust Map Block 26
Canopy (Hall et al., 1995): Dense	Canopy (Hall et al., 1995): Dense
Seral Stage (Hall et al., 1995): Mid	Seral Stage (Hall et al., 1995): Mid

Note. Photos by Janine Marr. *Note*. Photos by Janine Marr.

D-1 Continued

Alton: No Historical WPBR	**Alton**: Historical WPBR
 	 
Location: 43°30'36.57"N; 71°14'49.60"W	Location: 43°30'45.57"N; 71°14'48.73"W
Blister Rust Map Block 30-1	Blister Rust Map Block 30-1
Canopy (Hall et al., 1995): Dense	Canopy (Hall et al., 1995): Dense
Seral Stage (Hall et al., 1995): Late	Seral Stage (Hall et al., 1995): Mid

Note. Photos by Janine Marr.

Note. Photos by Janine Marr.

Andover: No Historical WPBR	**Andove**r: Historical WPBR
 	 
Location: 43°26'18.16"N; 71°47'54.95"W	Location: 43°26'52.63"N; 71°47'31.78"W
Blister Rust Map Block 1	Blister Rust Map Block 1
Canopy (Hall et al., 1995): Moderate	Canopy (Hall et al., 1995): Dense
Seral Stage (Hall et al., 1995): Mid	Seral Stage (Hall et al., 1995): Late

Note. Photos by Janine Marr.

Note. Photos by Janine Marr.

Antrim: No Historical WPBR	**Antrim**: Historical WPBR
 	 
Location: 43° 3'4.03"N; 71°57'16.60"W	Location: 43° 2'55.55"N; 71°57'5.80"W
Blister Rust Map Block 8	Blister Rust Map Block 8
Canopy (Hall et al., 1995): Dense	Canopy (Hall et al., 1995): Dense
Seral Stage (Hall et al., 1995): Mid	Seral Stage (Hall et al., 1995): Mid

Note. Photos by Janine Marr.

Note. Photos by Janine Marr.

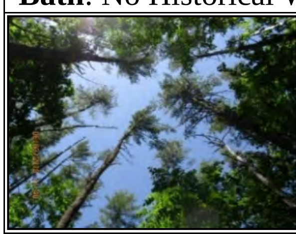
D-1 Continued

Barnstead: No Historical WPBR	**Barnstead**: Historical WPBR
 	 
Location: 43°21'24.25"N; 71°19'16.86"W	Location: 43°21'31.06"N; 71°19'8.69"W
Blister Rust Map Block 4	Blister Rust Map Block 4
Canopy (Hall et al., 1995): Dense	Canopy (Hall et al., 1995): Dense
Seral Stage (Hall et al., 1995): Mid	Seral Stage (Hall et al., 1995): Mid

Note. Photos by Janine Marr. *Note*. Photos by Janine Marr.

Barrington: No Historical WPBR	**Barrington**: Historical WPBR
 	 
Location: 43°10'29.98"N; 71° 0'37.80"W	Location: 43°12'18.81"N; 71° 0'42.75"W
Blister Rust Map Block 42	Blister Rust Map Block 42
Canopy (Hall et al., 1995): Dense	Canopy (Hall et al., 1995): Dense
Seral Stage (Hall et al., 1995): Mid	Seral Stage (Hall et al., 1995): Mid

Note. Photos by Janine Marr. *Note*. Photos by Janine Marr.

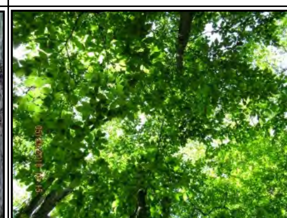
Bath: No Historical WPBR	**Bath**: Historical WPBR
 	 
Location: 44°10'10.01"N; 71°56'49.13"W	Location: 44°10'34.06"N; 71°55'44.49"W
Blister Rust Map Block 6	Blister Rust Map Block 6
Canopy (Hall et al., 1995): Dense	Canopy (Hall et al., 1995): Dense
Seral Stage (Hall et al., 1995): Mid	Seral Stage (Hall et al., 1995): Mid

Note. Photos by Janine Marr. *Note*. Photos by Janine Marr.

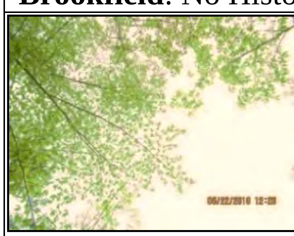
D-1 Continued

Belmont: No Historical WPBR	**Belmont**: Historical WPBR
 	 
Location: 43°28'51.91"N; 71°24'35.12"W	Location: 43°29'4.68"N; 71°24'38.10"W
Blister Rust Map Block 68	Blister Rust Map Block 68
Canopy (Hall et al., 1995): Dense	Canopy (Hall et al., 1995): Dense
Seral Stage (Hall et al., 1995): Mid	Seral Stage (Hall et al., 1995): Mid

Note. Photos by Janine Marr. *Note*. Photos by Janine Marr.

Bristol: No Historical WPBR	**Bristol**: Historical WPBR
 	 
Location: 43°37'47.34"N; 71°44'47.57"W	Location: 43°37'49.38"N; 71°44'59.42"W
Blister Rust Map Block 14	Blister Rust Map Block 14
Canopy (Hall et al., 1995): Dense	Canopy (Hall et al., 1995): Dense
Seral Stage (Hall et al., 1995): Mid	Seral Stage (Hall et al., 1995): Late

Note. Photos by Janine Marr. *Note*. Photos by Janine Marr.

Brookfield: No Historical WPBR	**Brookfield**: Historical WPBR
 	 
Location: 43°34'23.81"N; 71° 3'11.08"W	Location: 43°34'9.97"N; 71° 2'58.10"W
Blister Rust Map Block 22	Blister Rust Map Block 22
Canopy (Hall et al., 1995): Moderate	Canopy (Hall et al., 1995): Dense
Seral Stage (Hall et al., 1995): Mid	Seral Stage (Hall et al., 1995): Late

Note. Photos by Janine Marr. *Note*. Photos by Janine Marr.

D-1 Continued

Canaan: No Historical WPBR	**Canaan**: Historical WPBR
 	 
Location: 43°38'17.20"N; 72° 4'34.19"W	Location: 43°38'9.11"N; 72° 4'24.67"W
Blister Rust Map Block 12	Blister Rust Map Block 12
Canopy (Hall et al., 1995): Dense	Canopy (Hall et al., 1995): Moderate
Seral Stage (Hall et al., 1995): Mid	Seral Stage (Hall et al., 1995): Mid

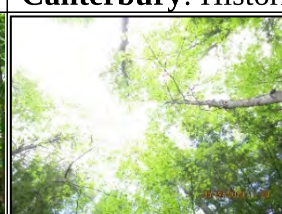
Note. Photos by Janine Marr.

Note. Photos by Janine Marr.

Candia: No Historical WPBR	**Candia**: Historical WPBR
 	 
Location: 43° 5'59.18"N; 71°20'59.48"W	Location: 43° 5'38.89"N; 71°20'48.19"W
Blister Rust Map Block 1	Blister Rust Map Block 1
Canopy (Hall et al., 1995): Dense	Canopy (Hall et al., 1995): Dense
Seral Stage (Hall et al., 1995): Mid	Seral Stage (Hall et al., 1995): Late

Note. Photos by Janine Marr.

Note. Photos by Janine Marr.

Canterbury: No Historical WPBR	**Canterbury**: Historical WPBR
 	 
Location: 43°21'43.33"N; 71°31'0.24"W	Location: 43°21'51.51"N; 71°30'55.18"W
Blister Rust Map Block 51	Blister Rust Map Block 51
Canopy (Hall et al., 1995): Dense	Canopy (Hall et al., 1995): Dense
Seral Stage (Hall et al., 1995): Mid	Seral Stage (Hall et al., 1995): Mid

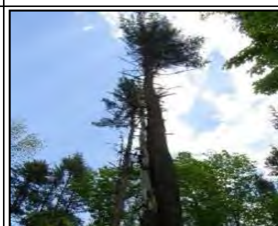
Note. Photos by Janine Marr.

Note. Photos by Janine Marr.

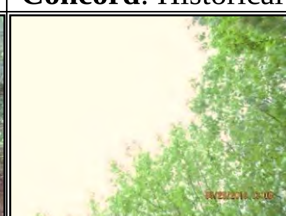
D-1 Continued

Charlestown: No Historical WPBR	**Charlestown**: Historical WPBR
 	 
Location: 43°11'31.26"N; 72°25'39.33"W	Location: 43°11'18.67"N; 72°25'48.99"W
Blister Rust Map Block 22	Blister Rust Map Block 22
Canopy (Hall et al., 1995): Dense	Canopy (Hall et al., 1995): Dense
Seral Stage (Hall et al., 1995): Late	Seral Stage (Hall et al., 1995): Mid

Note. Photos by Janine Marr. *Note*. Photos by Janine Marr.

Claremont: No Historical WPBR	**Claremont**: Historical WPBR
 	 
Location: 43°24'10.44"N; 72°18'41.73"W	Location: 43°24'5.57"N; 72°18'8.09"W
Blister Rust Map Block 50	Blister Rust Map Block 49
Canopy (Hall et al., 1995): Moderate	Canopy (Hall et al., 1995): Moderate
Seral Stage (Hall et al., 1995): Mid	Seral Stage (Hall et al., 1995): Mid

Note. Photos by Janine Marr. *Note*. Photos by Janine Marr.

Concord: No Historical WPBR	**Concord**: Historical WPBR
 	 
Location: 43°13'40.23"N; 71°28'38.51"W	Location: 43°13'48.97"N; 71°28'34.84"W
Blister Rust Map Block 66a	Blister Rust Map Block 66a
Canopy (Hall et al., 1995): Moderate	Canopy (Hall et al., 1995): Moderate
Seral Stage (Hall et al., 1995): Mid	Seral Stage (Hall et al., 1995): Mid

Note. Photos by Janine Marr. *Note*. Photos by Janine Marr.

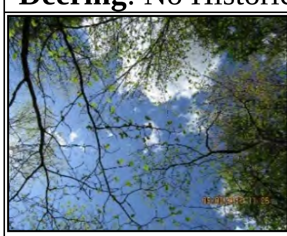
D-1 Continued

Cornish: No Historical WPBR		**Cornish**: Historical WPBR	
			
Location: 43°26'16.67"N; 72°22'18.50"W		Location: 43°26'25.77"N; 72°22'18.39"W	
Blister Rust Map Block 6		Blister Rust Map Block 6	
Canopy (Hall et al., 1995): Dense		Canopy (Hall et al., 1995): Dense	
Seral Stage (Hall et al., 1995): Mid		Seral Stage (Hall et al., 1995): Mid	

Note. Photos by Janine Marr. *Note*. Photos by Janine Marr.

Danbury: No Historical WPBR		**Danbury**: Historical WPBR	
			
Location: 43°29'52.54"N; 71°51'47.15"W		Location: 43°30'1.47"N; 71°51'54.47"W	
Blister Rust Map Block 25		Blister Rust Map Block 25	
Canopy (Hall et al., 1995): Moderate		Canopy (Hall et al., 1995): Dense	
Seral Stage (Hall et al., 1995): Late		Seral Stage (Hall et al., 1995): Mid	

Note. Photos by Janine Marr. *Note*. Photos by Janine Marr.

Deering: No Historical WPBR		**Deering**: Historical WPBR	
			
Location: 43° 2'44.94"N; 71°47'46.61"W		Location: 43° 3'12.61"N; 71°47'42.04"W	
Blister Rust Map Block 29		Blister Rust Map Block 29	
Canopy (Hall et al., 1995): Dense		Canopy (Hall et al., 1995): Dense	
Seral Stage (Hall et al., 1995): Mid		Seral Stage (Hall et al., 1995): Mid	

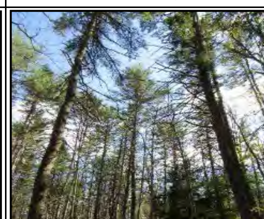
Note. Photos by Janine Marr. *Note*. Photos by Janine Marr.

D-1 Continued

Dublin: No Historical WPBR	**Dublin**: Historical WPBR
 	 
Location: 42°52'55.90"N; 72° 7'35.00"W	Location: 42°53'2.18"N; 72° 7'44.03"W
Blister Rust Map Block 4	Blister Rust Map Block 4
Canopy (Hall et al., 1995): Dense	Canopy (Hall et al., 1995): Dense
Seral Stage (Hall et al., 1995): Late	Seral Stage (Hall et al., 1995): Late

Note. Photos by Janine Marr.

Note. Photos by Janine Marr.

Dunbarton: No Historical WPBR	**Dunbarton**: Historical WPBR
 	 
Location: 43° 6'59.05"N; 71°39'16.67"W	Location: 43° 6'46.68"N; 71°39'19.23"W
Blister Rust Map Block 17	Blister Rust Map Block 17
Canopy (Hall et al., 1995): Dense	Canopy (Hall et al., 1995): Dense
Seral Stage (Hall et al., 1995): Mid	Seral Stage (Hall et al., 1995): Mid

Note. Photos by Janine Marr.

Note. Photos by Janine Marr.

Enfield: No Historical WPBR	**Enfield**: Historical WPBR
 	 
Location: 43°33'48.99"N; 72° 4'23.56"W	Location: 43°33'49.44"N; 72° 4'7.85"W
Blister Rust Map Block 71	Blister Rust Map Block 71
Canopy (Hall et al., 1995): Dense	Canopy (Hall et al., 1995): Dense
Seral Stage (Hall et al., 1995): Late	Seral Stage (Hall et al., 1995): Late

Note. Photos by Janine Marr.

Note. Photos by Janine Marr.

D-1 Continued

Grantham: No Historical WPBR		**Grantham**: Historical WPBR	
			
Location: 43°30'56.18"N; 72° 9'56.63"W		Location: 43°30'42.33"N; 72° 9'44.28"W	
Blister Rust Map Block 7		Blister Rust Map Block 7	
Canopy (Hall et al., 1995): Dense		Canopy (Hall et al., 1995): Moderate	
Seral Stage (Hall et al., 1995): Late		Seral Stage (Hall et al., 1995): Mid	

Note. Photos by Janine Marr.

Note. Photos by Janine Marr.

Hanover: No Historical WPBR		**Hanover**: Historical WPBR	
			
Location: 43°41'44.79"N; 72° 9'0.60"W		Location: 43°42'45.01"N; 72° 7'17.09"W	
Blister Rust Map Block 21		Blister Rust Map Block 19	
Canopy (Hall et al., 1995): Dense		Canopy (Hall et al., 1995): Moderate	
Seral Stage (Hall et al., 1995): Late		Seral Stage (Hall et al., 1995): Mid	

Note. Photos by Janine Marr.

Note. Photos by Janine Marr.

Haverhill: No Historical WPBR		**Haverhill**: Historical WPBR	
			
Location: 44° 4'57.98"N; 71°58'33.69"W		Location: 44° 4'36.40"N; 71°57'53.19"W	
Blister Rust Map Block 7		Blister Rust Map Block 7	
Canopy (Hall et al., 1995): Dense		Canopy (Hall et al., 1995): Dense	
Seral Stage (Hall et al., 1995): Mid		Seral Stage (Hall et al., 1995): Late	

Note. Photos by Janine Marr.

Note. Photos by Janine Marr.

D-1 Continued

Hebron: No Historical WPBR	**Hebron**: Historical WPBR
 	 
Location: 43°40'46.78"N; 71°45'51.44"W	Location: 43°40'57.63"N; 71°45'34.91"W
Blister Rust Map Block 6	Blister Rust Map Block 6
Canopy (Hall et al., 1995): Dense	Canopy (Hall et al., 1995): Dense
Seral Stage (Hall et al., 1995): Mid	Seral Stage (Hall et al., 1995): Mid

Note. Photos by Janine Marr. *Note*. Photos by Janine Marr.

Hinsdale: No Historical WPBR	**Hinsdale**: Historical WPBR
 	 
Location: 42°46'16.73"N; 72°28'9.60"W	Location: 42°46'23.43"N; 72°28'26.65"W
Blister Rust Map Block 3	Blister Rust Map Block 3
Canopy (Hall et al., 1995): Dense	Canopy (Hall et al., 1995): Moderate
Seral Stage (Hall et al., 1995): Mid	Seral Stage (Hall et al., 1995): Mid

Note. Photos by Janine Marr. *Note*. Photos by Janine Marr.

Keene: No Historical WPBR	**Keene**: Historical WPBR
 	 
Location: 42°58'16.88"N; 72°17'41.28"W	Location: 42°58'14.91"N; 72°17'53.14"W
Blister Rust Map Block 22	Blister Rust Map Block 22
Canopy (Hall et al., 1995): Dense	Canopy (Hall et al., 1995): Dense
Seral Stage (Hall et al., 1995): Mid	Seral Stage (Hall et al., 1995): Mid

Note. Photos by Janine Marr. *Note*. Photos by Janine Marr.

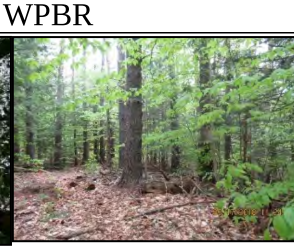
D-1 Continued

Lebanon: No Historical WPBR	**Lebanon**: Historical WPBR
 	 
Location: 43°36'16.19"N; 72°13'17.16"W	Location: 43°40'2.35"N; 72°18'4.36"W
Blister Rust Map Block 10	Blister Rust Map Block 10
Canopy (Hall et al., 1995): Dense	Canopy (Hall et al., 1995): Dense
Seral Stage (Hall et al., 1995): Mid	Seral Stage (Hall et al., 1995): Mid

Note. Photos by Janine Marr. *Note*. Photos by Janine Marr.

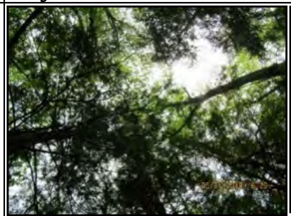
Littleton: No Historical WPBR	**Littleton**: Historical WPBR
 	 
Location: 44°18'25.49"N; 71°52'45.08"W	Location: 44°18'47.33"N; 71°52'2.26"W
Blister Rust Map Block 17	Blister Rust Map Block 17
Canopy (Hall et al., 1995): Dense	Canopy (Hall et al., 1995): Moderate
Seral Stage (Hall et al., 1995): Late	Seral Stage (Hall et al., 1995): Mid

Note. Photos by Janine Marr. *Note*. Photos by Janine Marr.

Loudon: No Historical WPBR	**Loudon**: Historical WPBR
 	 
Location: 43°19'49.85"N; 71°22'52.33"W	Location: 43°19'57.43"N; 71°22'59.18"W
Blister Rust Map Block 9	Blister Rust Map Block 9
Canopy (Hall et al., 1995): Dense	Canopy (Hall et al., 1995): Dense
Seral Stage (Hall et al., 1995): Late	Seral Stage (Hall et al., 1995): Late

Note. Photos by Janine Marr. *Note*. Photos by Janine Marr.

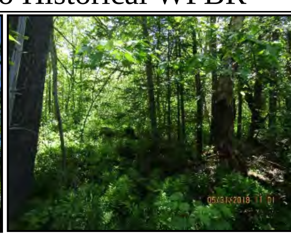
D-1 Continued

Lyme: No Historical WPBR	**Lyme**: Historical WPBR
 	 
Location: 43°51'16.81"N; 72° 7'25.79"W	Location: 43°51'15.05"N; 72° 7'13.31"W
Blister Rust Map Block 31	Blister Rust Map Block 31
Canopy (Hall et al., 1995): Dense	Canopy (Hall et al., 1995): Dense
Seral Stage (Hall et al., 1995): Mid	Seral Stage (Hall et al., 1995): Mid

Note. Photos by Janine Marr. *Note*. Photos by Janine Marr.

Lyndeborough: No Historical WPBR	**Lyndeborough** Historical WPBR
 	 
Location: 42°53'21.55"N; 71°42'42.53"W	Location: 42°53'16.87"N; 71°42'31.87"W
Blister Rust Map Block 23	Blister Rust Map Block 23
Canopy (Hall et al., 1995): Dense	Canopy (Hall et al., 1995): Dense
Seral Stage (Hall et al., 1995): Late	Seral Stage (Hall et al., 1995): Late

Note. Photos by Janine Marr. *Note*. Photos by Janine Marr.

Moultonborough: No Historical WPBR	**Moultonborough**: Historical WPBR
 	 
Location: 43°44'56.06"N; 71°24'54.47"W	Location: 43°44'39.21"N; 71°24'36.17"W
Blister Rust Map Block 17	Blister Rust Map Block 17
Canopy (Hall et al., 1995): Dense	Canopy (Hall et al., 1995): Dense
Seral Stage (Hall et al., 1995): Mid	Seral Stage (Hall et al., 1995): Early

Note. Photos by Janine Marr. *Note*. Photos by Janine Marr.

D-1 Continued

New Boston: No Historical WPBR	**New Boston**: Historical WPBR
 	 
Location: 42°59'30.82"N; 71°43'7.59"W	Location: 42°59'28.62"N; 71°42'55.79"W
Blister Rust Map Block 23	Blister Rust Map Block 23
Canopy (Hall et al., 1995): Dense	Canopy (Hall et al., 1995): Moderate
Seral Stage (Hall et al., 1995): Mid	Seral Stage (Hall et al., 1995): Mid

Note. Photos by Janine Marr. *Note*. Photos by Janine Marr.

New Durham: No Historical WPBR	**New Durham**: Historical WPBR
 	 
Location: 43°27'21.32"N; 71°10'51.45"W	Location: 43°27'25.23"N; 71°10'33.24"W
Blister Rust Map Block 37	Blister Rust Map Block 37
Canopy (Hall et al., 1995): Dense	Canopy (Hall et al., 1995): Dense
Seral Stage (Hall et al., 1995): Mid	Seral Stage (Hall et al., 1995): Mid

Note. Photos by Janine Marr. *Note*. Photos by Janine Marr.

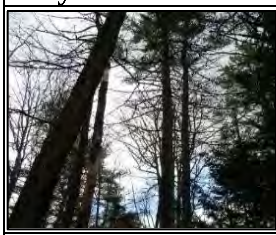
New London: No Historical WPBR	**New London**: Historical WPBR
 	 
Location: 43°24'17.53"N; 71°57'58.55"W	Location: 43°24'27.72"N; 71°58'3.91"W
Blister Rust Map Block 1	Blister Rust Map Block 1
Canopy (Hall et al., 1995): Dense	Canopy (Hall et al., 1995): Moderate
Seral Stage (Hall et al., 1995): Mid	Seral Stage (Hall et al., 1995): Late

Note. Photos by Janine Marr. *Note*. Photos by Janine Marr.

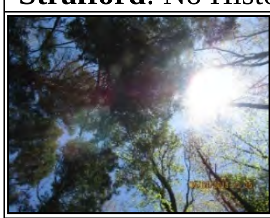
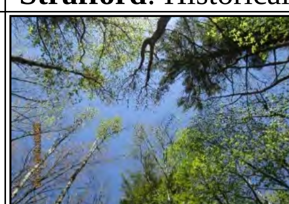
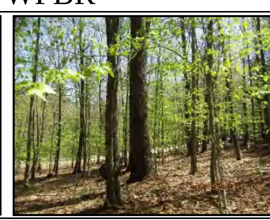
D-1 Continued

Pembroke: No Historical WPBR	**Pembroke**: Historical WPBR
 	 
Location: 43°10'50.80"N; 71°25'58.60"W	Location: 43°10'46.71"N; 71°25'46.34"W
Blister Rust Map Block 27	Blister Rust Map Block 27
Canopy (Hall et al., 1995): Dense	Canopy (Hall et al., 1995): Dense
Seral Stage (Hall et al., 1995): Mid	Seral Stage (Hall et al., 1995): Mid

Note. Photos by Janine Marr. *Note*. Photos by Janine Marr.

Raymond: No Historical WPBR	**Raymond**: Historical WPBR
 	 
Location: 43° 2'42.30"N; 71° 9'47.78"W	Location: 43° 2'43.87"N; 71° 9'59.84"W
Blister Rust Map Block 16	Blister Rust Map Block 16
Canopy (Hall et al., 1995): Dense	Canopy (Hall et al., 1995): Dense
Seral Stage (Hall et al., 1995): Mid	Seral Stage (Hall et al., 1995): Late

Note. Photos by Janine Marr. *Note*. Photos by Janine Marr.

Strafford: No Historical WPBR	**Strafford**: Historical WPBR
 	 
Location: 43°14'11.04"N; 71°10'6.29"W	Location: 43°13'58.32"N; 71°10'16.61"W
Blister Rust Map Block 26	Blister Rust Map Block 26
Canopy (Hall et al., 1995): Dense	Canopy (Hall et al., 1995): Dense
Seral Stage (Hall et al., 1995): Late	Seral Stage (Hall et al., 1995): Late

Note. Photos by Janine Marr. *Note*. Photos by Janine Marr.

D-1 Continued

Sullivan: No Historical WPBR	**Sullivan**: Historical WPBR
 	 
Location: 42°59'36.31"N; 72°13'50.24"W	Location: 42°59'35.90"N; 72°13'35.89"W
Blister Rust Map Block 15	Blister Rust Map Block 15
Canopy (Hall et al., 1995): Dense	Canopy (Hall et al., 1995): Dense
Seral Stage (Hall et al., 1995): Late	Seral Stage (Hall et al., 1995): Late

Note. Photos by Janine Marr. *Note*. Photos by Janine Marr.

Sunapee: No Historical WPBR	**Sunapee**: Historical WPBR
 	 
Location: 43°24'10.25"N; 72° 6'16.52"W	Location: 43°24'13.06"N; 72° 6'28.47"W
Blister Rust Map Block 30	Blister Rust Map Block 30
Canopy (Hall et al., 1995): Dense	Canopy (Hall et al., 1995): Dense
Seral Stage (Hall et al., 1995): Late	Seral Stage (Hall et al., 1995): Late

Note. Photos by Janine Marr. *Note*. Photos by Janine Marr.

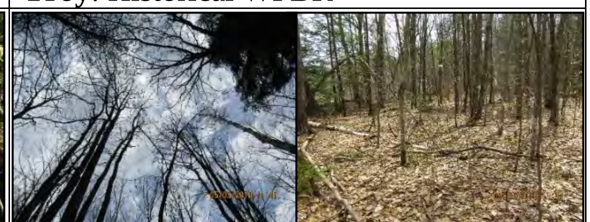
Swanzey: No Historical WPBR	**Swanzey**: Historical WPBR
 	 
Location: 42°54'27.10"N; 72°16'23.96"W	Location: 42°54'34.09"N; 72°16'6.46"W
Blister Rust Map Block 13	Blister Rust Map Block 13
Canopy (Hall et al., 1995): Dense	Canopy (Hall et al., 1995): Dense
Seral Stage (Hall et al., 1995): Mid	Seral Stage (Hall et al., 1995): Mid

Note. Photos by Janine Marr. *Note*. Photos by Janine Marr.

D-1 Continued

Thornton: No Historical WPBR	**Thornton**: Historical WPBR
	
Location: 43°53'57.93"N; 71°40'18.69"W	Location: 43°52'29.19"N; 71°37'18.42"W
Blister Rust Map Block 24	Blister Rust Map Block 24
Canopy (Hall et al., 1995): Dense	Canopy (Hall et al., 1995): Dense
Seral Stage (Hall et al., 1995): Mid	Seral Stage (Hall et al., 1995): Late

Note. Photos by Janine Marr. *Note*. Photos by Janine Marr.

Troy: No Historical WPBR	**Troy**: Historical WPBR
	
Location: 42°50'42.97"N; 72°12'38.25"W	Location: 42°50'35.80"N; 72°12'30.94"W
Blister Rust Map Block 13	Blister Rust Map Block 13
Canopy (Hall et al., 1995): Dense	Canopy (Hall et al., 1995): Dense
Seral Stage (Hall et al., 1995): Mid	Seral Stage (Hall et al., 1995): Mid

Note. Photos by Janine Marr. *Note*. Photos by Janine Marr.

Tuftonboro: No Historical WPBR	**Tuftonboro**: Historical WPBR
	
Location: 43°36'6.69"N; 71°16'57.09"W	Location: 43°36'15.59"N; 71°17'15.92"W
Blister Rust Map Block 56	Blister Rust Map Block 56
Canopy (Hall et al., 1995): Dense	Canopy (Hall et al., 1995): Moderate
Seral Stage (Hall et al., 1995): Mid	Seral Stage (Hall et al., 1995): Early

Note. Photos by Janine Marr. *Note*. Photos by Janine Marr.

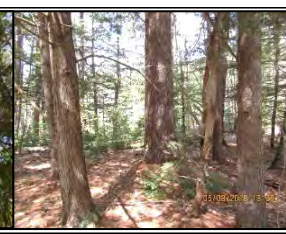
D-1 Continued

Wakefield: No Historical WPBR	**Wakefield**: Historical WPBR
 	 
Location: 43°36'39.27"N; 71° 3'14.23"W	Location: 43°36'46.63"N; 71° 3'21.66"W
Blister Rust Map Block 14	Blister Rust Map Block 14
Canopy (Hall et al., 1995): Dense	Canopy (Hall et al., 1995): Moderate
Seral Stage (Hall et al., 1995): Late	Seral Stage (Hall et al., 1995): Late

Note. Photos by Janine Marr. *Note*. Photos by Janine Marr.

Warner: No Historical WPBR	**Warner**: Historical WPBR
 	 
Location: 43°17'49.35"N; 71°50'28.91"W	Location: 43°17'57.26"N; 71°50'53.60"W
Blister Rust Map Block 4	Blister Rust Map Block 4
Canopy (Hall et al., 1995): Dense	Canopy (Hall et al., 1995): Dense
Seral Stage (Hall et al., 1995): Late	Seral Stage (Hall et al., 1995): Mid

Note. Photos by Janine Marr. *Note*. Photos by Janine Marr.

Weare: No Historical WPBR	**Weare**: Historical WPBR
 	 
Location: 43° 7'13.70"N; 71°42'48.28"W	Location: 43° 7'14.57"N'; 71°43'1.10"W
Blister Rust Map Block 9	Blister Rust Map Block 9
Canopy (Hall et al., 1995): Dense	Canopy (Hall et al., 1995): Dense
Seral Stage (Hall et al., 1995): Mid	Seral Stage (Hall et al., 1995): Mid

Note. Photos by Janine Marr. *Note*. Photos by Janine Marr.

Chapter Five: Seeing the Forest Beyond the Trees--Summarizing the Impacts of an Exotic Pathogen on Forest Composition and Succession

Seeing the Forest Beyond the Trees: Summarizing the Impacts of an Exotic Pathogen on Forest Composition and Succession

This dissertation aimed to answer the question of how an exotic forest pathogen, *Cronartium ribicola* Fisch., has impacted eastern white pine forests (*Pinus strobus* L.) after more than a century of existence in New Hampshire. The research combined historical ecological data and blister rust maps in a unique approach to understanding changes in the white pine forests over time. White pine stands mapped between 1929 and 1976 by the NH Office of Blister Rust Control were surveyed in 2018 to document species composition, stand structure, and disturbance history, including white pine blister rust (WPBR) presence. Specific research topics included: 1) WPBR distribution and incidence at multiple points in time; 2) the accuracy of existing hazard ratings maps in determining areas most favorable to the development of WPBR in New Hampshire in the 21st century; and 3) the long-term effects of WPBR on forest composition, succession, and white pine sustainability. The results of the research conducted in 2018 suggest that WPBR has impacted the forests of New Hampshire.

This chapter summarizes the key findings of the research conducted in 2018. It provides insight into the relevance of this research and highlights knowledge gaps for future research. Recommendations are suggested for landowners wishing to grown white pine in a changing climate where *Ribes*, WPBR, and other pine diseases may co-occur. This chapter concludes with lessons learned from the study and its process so that future researchers can better build upon the baseline created by this research.

Key Findings

White Pine Blister Rust Distribution and Incidence

In 2018, white pine blister rust (WPBR) was present throughout New Hampshire, and compared to research conducted in 1998 (Lombard & Bofinger, 1999), incidence levels were increasing. The 2018 findings supported recent research in New Hampshire that found WPBR was increasing in incidence, and that the disease was more likely to be found on the smaller white pine size classes (Munck, Tanguay, Weimer, Villani, & Cox, 2015).

During field research in 2018, native *Ribes* (*R. cynosbati* and *R. glandulosum*), alternate hosts of the disease, were observed with telial columns and evidence of basidiospores that infect white pines. *Ribes cynosbati*, the pasture gooseberry, was described in the 1920s as the most damaging *Ribes* species in Grafton County due to its heavy presence and disease susceptibility (United States Department of Agriculture, 1928). Field data from 2018 showed that *R. cynosbati*, typically found growing in and along stone walls, was more heavily-infected than other species. In 2018, roadside surveys documented *R. cynosbati* and *R. glandulosum*, the skunk currant, from the Massachusetts border as far north as the White Mountains of New Hampshire. The skunk currant, in particular, was well-established, including in: rock outcrops and roadside ledges; swamps and shady brooks; and old log landings. When the native and naturalized *Ribes* were mapped along with the towns where WPBR-resistant *Ribes* cultivars are grown by permit (Jen Weimer, personal communication), it became clear that *Ribes* were well-established and distributed throughout New Hampshire. The ability of both the native and cultivated *Ribes* cultivars to disseminate the disease, and their capacity to withstand changes in the climate that, as this study has shown, support rather than limit the disease, remain unclear.

The incidence of WPBR on *Ribes* and white pine in 2018 reinforced the historical warnings that *Ribes* eradication and control should not be abandoned (Martin, 1928), particularly if white pine is to be grown for profit. Historical eradication measures in the Northeast effectively reduced WPBR by 95% (Martin, 1944); however, the abandonment of the blister rust control program in the 1960s and 1970s has allowed *Ribes* to re-establish in New Hampshire's landscape, increasing the potential for white pine infection and mortality. The documentation of infected populations of native *Ribes* supported historical observations by blister rust agents and more recent concerns by researchers and pathologists; we still do not fully understand the role of wild, native *Ribes* in the WPBR pathosystem (Samman, Schwandt, & Wilson, 2003). Identifying the risk that native *Ribes* pose to the health of white pine forests in and beyond New Hampshire is important for the timber industry as well as our early-successional white pine-dominant landscapes.

Hazard Ratings Models

The process of comparing two hazard ratings models for the Northeast (Charlton, 1963) and New Hampshire (Avery, 1980) with WPBR distribution in 2018 resulted in three important findings related to New Hampshire's climate. Foremost was the conclusion that, as designed in 1963 and 1979, neither model was able to accurately predict the areas of New Hampshire at highest risk for WPBR in 2018. The 1963 Northeast model, when populated with current climate data, challenged the long-standing assumption in the scientific literature that temperatures above 90 degrees Fahrenheit would prevent spore development on *Ribes*, and germination on white pines. It remains unclear how temperatures can exceed the historical limit and yet, pines still become infected. As the climate of New Hampshire and the Northeast continues to warm, understanding the relationship between temperature and infection will become even more critical to WPBR control and white pine management.

A second significant finding related to climate was that WPBR co-occurred in stands with white pine needle damage complex (WPND) and pine canker (*Caliciopsis pinea* Peck), suggesting that a climate that favors WPBR may also support other white pine diseases. This finding is particularly important for forest managers wishing to control multiple diseases, especially when the recommendations may contradict each other. For example, WPBR is best managed with a closed canopy to prevent *Ribes* germination and dew pockets that favor infection (Davis & Moss, 1940; Goodrich, Waring, Auty, & Sanchez Meador, 2018; Stewart, 1953; Van Arsdel, Riker, Kouba, Suomi, & Bryson, 1961); while recommendations for managing WPND and pine canker suggest that thinning the canopy for increased airflow will help prevent disease development and spread (Munck, Livingston et al., 2015). Further examination is needed on the co-occurrence of these white pine diseases for the forest, the landscape, and the climatic region.

The third relevant finding that affects the accuracy of the hazard models, particularly the 1979 New Hampshire model, was the presence of WPBR urediniospores on *Ribes* leaves in May of 2018. The leaves had developed WPBR more than one month earlier than historically, according to first-hand accounts by blister rust agents published in the *Blister Rust News.* This data suggested that New Hampshire's climate has warmed during the past nine decades, and that spring is arriving earlier than during the years of the WPBR epidemic. An earlier or longer WPBR season may affects the severity and management of the disease. Management protocols, including *Ribes* eradication, may require changes in the timing and types of treatments used beyond the New England region as the climate continues to change.

Long-Term Impacts on Composition, Succession, and Sustainability

This study found that forest succession progressed over time as expected in New Hampshire; no stand had reverted to an earlier sere. Species composition was relatively similar across the state. However, stands affected by WPBR experienced an accelerated successional trajectory; shade-tolerant understory species, such as hemlock and beech, advanced into the overstory when WPBR killed the white pine understory. While WPBR may be viewed as a thinning agent of pine stands, this study showed that where incidence was above 20% for a size class, the size class was in danger of becoming replaced with other more shade-tolerant species. This finding is important, particularly for regions throughout the Northeast where shade-tolerant species such as beech or hemlock may dominate a stand at a young age.

White pine was the dominant timber species in New Hampshire in 2018. However, mortality >20% and unbalanced size classes occurred throughout the state. Evidence of dead and missing pole-size pines suggested that young pines were not advancing into the larger size classes. These findings support the results from the 2017 NH Forest Inventory and Analysis (FIA) which suggested, in the absence of management activities and disturbances to promote white pine establishment, white pine as a timber species will not be sustainable. The current species composition of New Hampshire forests favors a future forest with red maple, balsam fir, and red spruce in the overstory; white pine, red oak, hemlock, and sugar maple will become less prominent, affecting forest structure, resources, and succession (Morin et al., 2020). Without management to regenerate white pine, the species will be unable to retain its current stocking levels or position of dominance within the forest. White pine will be replaced by other species. White pine blister rust, through its ability to reduce white pine populations, may also be reducing the sustainability of the species.

Research Relevance, Implications, and Opportunities

This research addressed several gaps in the literature and advanced our knowledge of the WPBR pathosystem. First and foremost, it created a baseline for future research by documenting the current distribution and incidence of white pine and WPBR in stands that were historically dominated by white pine. This study, which utilized the historical blister rust maps to compare current and historical conditions of stands with and without the disease, was the first of its kind for New Hampshire and the Northeast. As a result, it has generated valuable information for long-term studies on white pine, WPBR, and the climate of New Hampshire and northern New England in relation to white pine growth and sustainability.

Another gap in the literature addressed by this study was the documentation of the presence of native *Ribes* throughout the state in the 21st century, more than 40 years after the demise of the blister rust control program, and their relationship to WPBR infection of white pine. While it is unknown if the *Ribes* observed in New Hampshire in 2018 were the result of a disturbed seedbank, or were established via wildlife dispersal, the observance of *Ribes* that: 1) exist on sites that were once eradicated; 2) were infected with WPBR; and 3) persisted despite dense cover, should be of concern to landowners and forest managers who want to retain healthy white pine as a component of the forest. This research reaffirmed the need to explore the relationship between native *Ribes* and the spread of WPBR in the Northeast region.

White pine forests have been succeeding into other forest types since the middle of the last century. In addition, the aging stands surveyed in 2018 showed stump evidence of mature white pines being removed by logging. However, this study also showed that forest succession and logging were not the only reasons that white pine has lost its dominance in some New Hampshire forests. The assumption that white pine, being disturbance-dependent, is resilient as a species and able to withstand some WPBR infection was challenged by the results of this study; WPBR: 1) occurred in stands with a dense canopy; 2) removed the white pine midstory; and 3) affected the natural processes of forest composition, stand structure, and succession. The disease's role in forest succession in the Northeast had not previously been addressed in the literature. Understanding the long-term impacts on forest succession will inform management practices that strive to maintain an early-successional white pine component for future generations. Studies that build upon this research will advance our knowledge of the relationship between forest succession and white pine sustainability in the absence of disturbances.

White pine sustainability in New Hampshire is challenged by the long-term presence of WPBR in a changing climate. While the focus of this research was not on climate change, the results serve as a baseline for additional research on the effects of increased temperatures and the presence of multiple diseases on individual trees or white pine forests. As landowners manage for resilience, resistance, and adaptive capacity of a species within a changing climate, they will require current information on the long-term relationships between keystone species and disturbance agents such as WPBR.

Rich opportunities exist to move the results of this research forward. Long-term studies on WPBR in the Northeast have never been initiated; developing such a study would advance our understanding of the factors that contributed to the persistence of the disease after 60 years of control efforts. The relationship between WPBR and other pine diseases offers opportunities to understand disease co-occurrences as compounding disturbance agents. We have yet to explore the possibility of white pine resistance to the *C. ribicola* strains present in New Hampshire. Identifying WPBR resistance in the Northeast, if it exists, may answer the question whether uninfected white pines are resistant to WPBR, or have escaped the disease due to climatic and site factors (Van Arsdel, 1972). Disease resistance in white pines would inform current state or federal regulations in the Northeast for propagating *Ribes* near white pine stands.

Management strategies for white pine and regulations for *Ribes* could be advanced through the development of predictive tools that build upon the historical models and findings from this research. These predictive tools could assist with proper white pine site selection that includes current and future climate projections and WPBR risk. One suggested tool is an updated hazard model that would include climate change factors such as earlier spring seasons and increased air movement due to more frequent and intense storms. Another useful tool would a white pine climate vulnerability index that could increase our understanding of the resilience of white pine in a changing climate.

Resilience and sustainability of white pine reach beyond New Hampshire to the entire Northeast region as challenges we face due to a changing climate. Studies that explore the potential for white pine as a species to thrive in New Hampshire (and beyond) as the forests mature, the climate warms, and the disturbances increase in frequency and intensity, would aid in the conservation of white pine as an important keystone species.

Recommendations

Based upon the results of this study, recommendations for the management of white pine and control of WPBR fall into two categories: research as discussed above; and silvicultural strategies. One of the oldest management techniques for controlling WPBR is still one of the most dependable: eradicating *Ribes* within white pine forests to reduce the potential for pine infection. A few historical practices are still recommended for managing white pine in areas where *Ribes* may occur. Where *Ribes* exist and white pine is not the regeneration goal, removing the mature white pine in winter when the ground is frozen will reduce disturbance to the soil where *Ribes* seeds may be stored. If white pine regeneration is a management goal, and a shelterwood method is practical, the stand should be monitored after each thinning treatment for three to five years to search for and remove *Ribes*, preferably in early spring when the plants are flowering and have not yet set fruit. Monitoring for *Ribes* during the month of May is recommended for New Hampshire, based on the results of this study, which documented plants fully-leaved and in flower at that time. When the overstory is thinned, as in a shelterwood cut, white pines that are disease-free should be retained to promote the genotypes that have the potential for the development of WPBR resistance. Stands in which the overstory is thinned to reduce white pine diseases (including WPND and pine canker) should be monitored for understory microclimates that may foster WPBR development. In those stands, pruning the lower eight feet of live branches from the pole-size trees is recommended where practical (Hagle & Grasham, 1988). When growing healthy white pine in a changing climate that may also support WPBR, maintaining a diversity of ages and size classes will create forest structure that supports and enhances the adaptive capacity of white pine as a species, thereby increasing its resilience.

Lessons Learned from the Forest Beyond the Trees

This study explored the question of how an exotic disease affected the forests of New Hampshire nearly 120 years after its introduction. Because white pine is a highly-valued timber resource, as well as a keystone forest species, it was important to understand the relationship between a tree species grown for timber and wildlife habitat, and an exotic disease that is capable of killing all five-needled white pine species in North America. In this study, the combination of historical and current data with a disturbance framework enhanced our understanding of how a white pine forest changes naturally from succession and unnaturally from a disease caused by an exotic pathogen. The use of historical data expanded the study from a single-point to one in which multiple time periods could be examined. The historical data allowed for a more complete description of a site, a town, or a county in relation to: 1) WPBR incidence, severity, and distribution; 2) host presence; and 3) control measures and successes. The historical data served as a baseline that connected the past to the present. The disturbance framework moved the focus of this research beyond the disease triangle and the death of an individual tree into larger spatial and temporal scales with multiple, interacting relationships. This unique study design addressed important research gaps and highlighted lessons about conducting research that spanned several decades.

Locating historical white pine stands was tedious and involved several steps and historical maps. The 1979 WPBR hazard ratings map for New Hampshire was used to select towns rated high or low hazard. The historical blister rust maps were used to locate sites with and without WPBR in each selected town. Throughout the selection process, I found that several historical pine stands had disappeared under town reservoirs, interstates, or housing developments, expanding the search for more potential research sites. The lack of early maps for some towns (1920s-1930s), suggests that some maps were thrown away when updates were made and blocks were discontinued from the eradication program. While the loss of early maps made less data available for the comparison of WPBR and *Ribes* over time, the lesson learned was that, for future studies, even early data may be relevant or useful as baselines and comparison studies.

Another source of lost information was related to the owners of the properties surveyed in 2018. I discovered, by driving by properties where landowners had not responded to my letters, that those properties were posted; they were therefore not included in my research. Most landowners responded to my research request in a positive manner, however. Connecting with them for permission to conduct research on their property became an outreach and education opportunity. I had conversations with landowners about WPBR and general forestry. I was invited to speak to conservation commissions about their properties selected for my research. And, to my enjoyment, I was told stories about the properties; the “pine rust” from the past; and making currant jelly. I learned that this research was an opportunity for landowners to learn alongside me, and for me to learn from them.

Although the pre-research phase was time-consuming, it generated a design unlike any other study conducted in New Hampshire. I observed and learned about white pine forests from long ago and the changes they experienced over time as a result of WPBR infection and forest succession. My observations were at the individual tree and year scales; however, I learned to see those trees at a forest scale over the course of a century. Seeing the succeeding white pine forest beyond the WPBR-killed trees was the most valuable lesson I learned from this research.

I learned through this research that WPBR had adapted to New Hampshire’s changing climate. Understanding how the changing climate has affected the WPBR pathosystem, and how changes to the hosts and the disease affect the forests, is important both for timber management and forest conservation. The results of this research have broader implications that extend beyond New Hampshire's climate. If other New England states also find that WPBR incidence and wild *Ribes* persist under dense canopies, then the issues highlighted by this study pertain to a much larger region than the state of New Hampshire. If other states in the region are also experiencing a decline in the white pine forest type that may be attributed to decades of WPBR infection, then the long-term effects of the disease are far-reaching, for landowners, conservationists, and timber managers. If other states experience warmer summers, yet WPBR survives, then the pathogen may have adapted to climates beyond New Hampshire's current climate, jeopardizing the future regeneration potential of several white pine species throughout the country. This research was not just about WPBR in the forests of New Hampshire; it provided an interdisciplinary methodology and baseline data for future research. It connected the scientific findings of the past with the advanced technology of the present to assist foresters, scientists, and landowners in managing for healthy and sustainable white pine for the future. It provided insight into the potential future implications of a biological invader that, with time, has adapted, transformed, and naturalized in a new climate on a new continent. Most importantly, this research helped me see the dynamic forest beyond the WPBR-infected pine trees.

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Map of 1979 Hazard Ratings for New Hampshire Towns

Avery, A. C. (1980). *1979 Status of the White Pine Blister Rust Program* [Map]. State of New Hampshire Forest Pest Program.

Janine Marr Fri, Apr 2, 2021 at 9:58 AM
To: "Lombard, Kyle"

I would appreciate it if you (as the person who would be the blister rust agent for the state, if that title were still used today), would grant me permission to use two maps for my dissertation.

One map is the unpublished one that Avery created in 1979 of the high and low hazard towns and is in your files (not yet in the state archives). 1979 Status of the White Pine Blister Rust Program

The second map was published in 1924 by the state of NH forestry commission: State of New Hampshire Forestry Commission. "State of New Hampshire Biennial Report of the Forestry Commission for the Two Fiscal Years Ending June 30, 1924." Concord, December 1924.

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Lombard, Kyle Fri, Apr 2, 2021 at 10:03 AM
To: Janine Marr

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Kyle Lombard

Forest Health Program Coordinator

NH Division of Forests and Lands

White Pine Blister Rust Control Area 1917-1924 New Hampshire

State of New Hampshire Forestry Commission. (1924). *State of New Hampshire Biennial Report of the Forestry Commission for the Two Fiscal Years Ending June 30, 1924* (pp. 39–47). State of New Hampshire Forestry Commission.

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permission

Lombard, Kyle Fri, Apr 2, 2021 at 10:03 AM
To: Janine Marr

Both of those are considered public. You're good to do as you wish with them. Maybe cite the source you pulled them out of but no permission to use them is needed.

Kyle Lombard

Forest Health Program Coordinator

NH Division of Forests and Lands

Map of 1963 Hazard Ratings for the Northeast

Charlton, J. W. (1963). *Relating Climate Change to Eastern White Pine Blister Rust Infection Hazard*. Eastern Region, Forest Service, U.S. Department of Agriculture.

Janine Marr Fri, Apr 2, 2021 at 10:04 AM
To: "Munck, Isabel -FS"

I need to contact someone within the forest service who has the authority to state that: 1) I have permission to reprint Charlton's hazard map in my dissertation; of that 2) the publication is considered public domain and no permission is necessary. Who should I contact?

Munck, Isabel -FS Fri, Apr 2, 2021 at 2:47 PM
To: Janine Marr

Hi Janine-

Here is the information. Thanks for asking,

Isabel Munck
Plant Pathologist

Forest Service

State and Private Forestry

From: Clark, Sandy- FS
Sent: Friday, April 2, 2021 2:18 PM
To: Munck, Isabel -FS
Subject: RE: [External Email]permission question

Hi Isabel,

Yes, this map is in the public domain, so no permission needed to use.

We're using the new Forest Service style guide that the WO just rolled out, which has guidance on bylines.

I'm not sure who "Charlton" is, but if you know the name of the person who created the map, you would cite it as:

USDA Forest Service map by [name].

If you don't have that info, it would be cited as USDA Forest Service map.

Hope this helps!

take care,

~ sandy

Sandra Clark
Supervisory Technology Transfer Specialist

Forest Service

Janine Marr Fri, Apr 2, 2021 at 10:04 AM
To: "Munck, Isabel -FS"

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NH Blister Rust Control Maps for New Hampshire

Kline. (1960). *White Pine Blister Rust Gilsum NH Block 20 1954 -Re- (Ribes re-eradication locations)*.

LaRock, J. H. (1941). *White Pine Blister Rust Control, Dublin N.H. Oct. 1941, Block # 4*.

LaRock, J. H. (1951). *White Pine Blister Rust Control, Gilsum, NH, 1936, Block No. 20* [Remapping of Allan D. Whitney's 1936 map].

Miles, M. C. (1938). *White Pine Blister Rust Control: Hanover, N.H. 1936, Block No. 15*.

Murray, C. T. (1938). *White Pine Blister Rust Control: Charlestown, N.H. October 1938, Block No. 22*.

The State of New Hampshire

DEPARTMENT OF STATE
DIVISION OF ARCHIVES & RECORDS MANAGEMENT

Janine Marr
Gilsum, NH

Dear Ms. Marr:

In response to your inquiry of April 2, 2021, the Blister Rust Maps at the New Hampshire State Archives are considered in the public domain, and do not need permission to reprint.

Sincerely,

Brian Nelson Burford
April 21, 2021