AN ABSTRACT OF THE THESIS OF

Zeynep Cicekli for the degree of Master of Science in Forest Ecosystems and Society presented on March 16, 2023.

Title: Projecting White Pine Blister Rust Hazard Ratings Under Climate Change in Southwestern Oregon.

Abstract approved:

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Glenn T. Howe

Sugar pine and western white pine are widely distributed, economically valuable, and ecologically important native tree species in North America. However, white pine blister rust (WPBR), caused by a non-native fungal pathogen, *Cronartium ribicola* J.C. Fisch. in Rabh., has substantially affected populations of these species. *Cronartium* is an obligate parasite, requiring two living hosts to complete its life cycle. White pines are the primary host, and *Ribes* species, *Castilleja*, and *Pedicularis* spp. are alternate hosts. Once *Cronartium* infects trees, it damages and kills branches, stems, or entire trees by causing branch and stem cankers. *Cronartium* requires cool temperatures and sufficient moisture to inoculate and spread among alternate and tree hosts. *Cronartium* infects white pines of all size, but it is more prevalent on younger and smaller trees.

Treatments to manage WPBR have included *Ribes* eradication, chemical spraying of *Ribes*, and thinning and pruning of tree hosts. However, these treatments are impractical and costly, and are not expected to eliminate WPBR. Another approach is to breed and deploy rust-resistant trees, and has been an ongoing effort

for over 50 years. Finally, another option for managing WPBR is to use rust hazard ratings (RHRs). RHRs are metrics reflecting current or potential rust infection levels of sites. Specific climatic conditions, site characteristics, and tree characteristics have been used to rate the rust hazard of sites in white pine regions.

For my research, I used data from Koester et al. (2018), who studied rust hazard at 265 sites in southwestern Oregon. The sites contained naturally regenerated sugar pine, naturally regenerated western white pine, rust-resistant sugar pine, and rust-resistant western white pine. I studied four rust traits, environmental variables, and tree characteristics. The rust traits consisted of percentage of trees with a stem canker (CANK%), average number of cankers per tree (NUM_CANK), average height of the highest canker (HT_CANK), and rust hazard index (RI). The environmental variables consisted of climate variables, aspect, slope, and elevation. The tree characteristics consisted of tree age, tree height, and average height growth (HT/AGE). In addition to the Koester et al data, I used the ClimateNA software program to obtain historical and future climate variables for the sites.

I developed rust and tree growth random forest regression models and used other analyses to identify (1) which rust traits were best for characterizing rust hazard, (2) which environmental variables were most closely associated with rust hazard, (3) how were rust traits affected by tree characteristics, (4) how was tree growth affected by environmental variables and rust traits, (5) how will rust traits change under future climates, and (6) how will tree growth change under future climates.

Based on random forest RSQ values, I concluded that CANK% and NUM_CANK were the best rust traits for characterizing rust hazard. My criteria for a good rust hazard index were that it is (1) closely associated with tree damage and death, (2) easy to measure precisely and accurately, (3) not confounded by non-rust tree variables, and (4) easy to predict from environmental variables. CANK% and NUM_CANK were relatively easy to measure precisely and accurately compared to HT_CANK and RI. Also, CANK% and NUM_CANK were more strongly associated with environmental variables, and were less confounded with non-rust tree variables. Thus, I used CANK% and NUM_CANK for further analyses.

Among the environmental variables, climate variables were the most important predictors of rust hazard (i.e., based on random forest variable importance statistics). Correlations indicated that rust hazard was greater at sites with milder temperatures, sufficient moisture, and longer growing seasons. Rust hazard was also higher at sites with northern, eastern, and northeasterly aspects. Rust hazard was positively associated with tree growth and negatively associated with tree age, but had little relationship to tree height. The possible explanation is that young susceptible trees were subjected to natural selection by WPBR. Thus, older stands probably have a higher proportion of rust resistant trees. I also observed that greater tree growth was associated with harsher climates and higher rust disease, but the reasons for this were unclear.

Next, I used my random forest regression models to project rust hazard and tree growth under climate change. In total, I analyzed 13 climate scenarios consisting of 12 future scenarios and one based on the 1931-1990 climate. The future climate variables were based on four Shared Socio-economic Pathways (SSPs), SSP1-26, SSP2-45, SSP3-70, and SSP5-85 and three 30-year time periods centered on 2025, 2055, and 2085.

I found projected increases in spring, summer, and winter temperatures, indicating longer growing seasons in the future. In addition, summer and autumn relative humidity were projected to decrease under all SSPs. According to the projections of rust hazard, WPBR will decline, but these changes will probably be small and uncertain. Declines in WPBR may occur because warmer and drier climates inhibit rust spore germination, infection, and dispersal. In contrast, I projected a small increase in the average growth rate of the pines, probably because the models projected a longer growing season with less rust disease.

The rust hazard models I developed should be particularly valuable for evaluating current rust hazards based on known climate conditions. However, many caveats make the future projections uncertain. To improve rust hazard prediction models, I recommend accounting for (1) the distributions of alternate hosts, (2) the occurrence of specific wave years, and (3) additional moisture-associated environmental variables.

Projecting White Pine Blister Rust Hazard Ratings Under Climate Change in Southwestern Oregon

by
Zeynep Cicekli

A THESIS

submitted to

Oregon State University

in partial fulfillment of
the requirements for the
degree of

Master of Science

Presented March 16, 2023
Commencement June 2023

Master of Science thesis of Zeynep Cicekli presented on March 16, 2023

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I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

Zeynep Cicekli, Author

ACKNOWLEDGEMENTS

I would like to thank my advisor, Dr. Glenn T. Howe, for his knowledge, guidelines, and support throughout this research; my committee, Dr. Richard A. Sniezko, Dr. Steven Strauss, and Dr. Kimberly Townsend, for their feedback and interest in this research; Harvey Koester, for his assistance; and the Ministry of National Education of Türkiye for funding this research.

Special thanks to my spouse, Mehmet Cicekli, for always being with me in this journey; and my daughter Asya and my son Yigit for their love; and my brother, Mehmet Gurdal, for his encouragement and support.

CONTRIBUTION OF AUTHORS

Glenn T. Howe assisted in developing models, interpreting results, clarifying text, and organizing chapters. His support and guidance were invaluable throughout the research process.

Richard A. Sniezko contributed his knowledge and expertise to this research project, which greatly enhanced the quality and relevance of the study.

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To my parents,

with love and gratitude.

1. Chapter 1

1.1 Background and Literature Review

1.1.1 Sugar pine and western white pine are ecologically and economically important species

Sugar pine (*Pinus lambertiana* Dougl.) and western white pine (*Pinus monticola* Dougl. ex D.Don) are five-needled white pine species (subgenus *strobus*). These species are native to the Pacific Northwest (PNW), which covers the western coast of North America from British Columbia to the Sierra Nevada Mountains of California, and to the interior side of the northern Rocky Mountains in eastern British Columbia, northern Idaho, and western Montana (Figure 1). In southwestern Oregon, western white pine and sugar pine are widely distributed (Goheen and Goheen 2014). The PNW is a mountainous region with cloudy and humid winters and hot summers, resulting in intense and frequent wildfires. Wet winters and dry summers also cause sharp changes in weather during the year. However, western white pine can tolerate these changes, resulting in being considered a generalist species. Compared to specialists, generalists survive across wide areas by being genetically adapted to a wide range of environmental conditions (Richmond et al. 2005). Sugar pine has the highest growth potential among pines (Kinloch 1984). This species ranges from sea level to 10,000 feet in elevation depending on temperature and precipitation, which limit its distribution (Larsen and Woodbury 1916; Kinloch 1984). Thus, they can be seen on northern slopes and at high elevations where the air holds abundant moisture (Larsen and Woodbury 1916).

Western white pine is adapted to the PNW, having become tolerant of fire and mostly resistant to native pests and diseases (e.g., root rots) (Byler et al. 2000). Because it is shade-intolerant, it requires sunlight to regenerate and grow (Hines 2013). Stand-replacing fires make canopy openings which allow seedlings to regenerate quickly and show excellent growth

(Loehman et al. 2011; Hines 2013). Western white pines dominate the region because of their regeneration ability (Loehman et al. 2011) and ability to live longer than other species (Byler et al. 2000). However, subsequent losses from wildfires, lack of regeneration opportunities, attacks from mountain pine beetle, and impacts of pathogens have dramatically reduced the planting of this species (Hines 2013). Thus, other climax species, such as western hemlock, Douglas-fir, and grand fir compete against western white pine (Schwandt et al. 2013). On the other hand, western white pine has a high capacity to sequester carbon, which can help mitigate global warming (Hines 2013). Thus, under changing climates, western white pine may become more desirable compared to other dominant species in the region (Hines 2013).

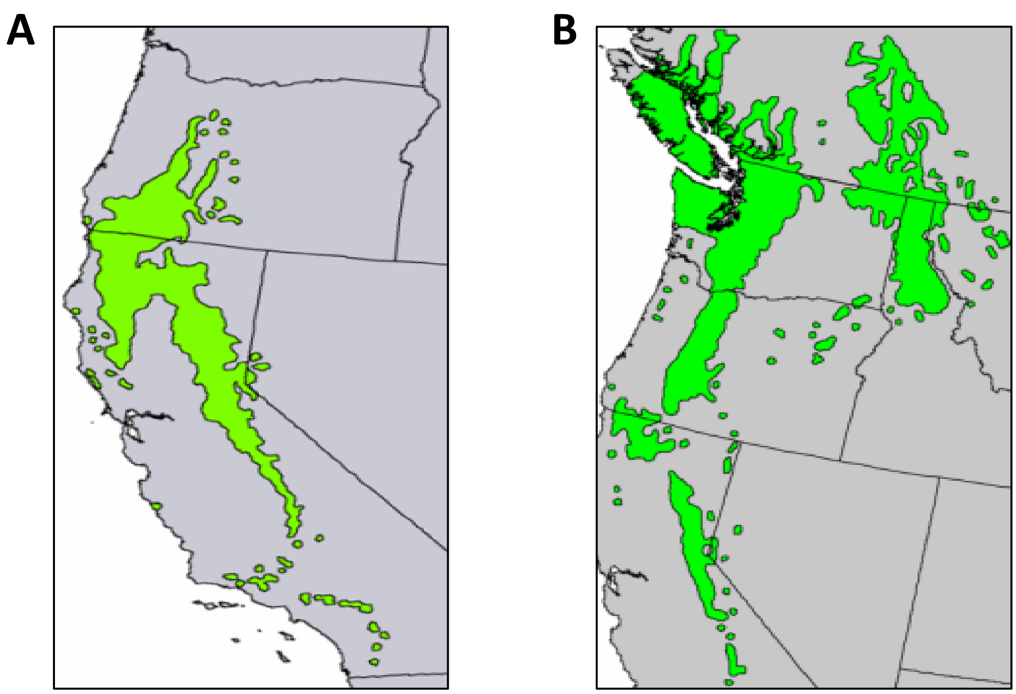

Figure 1. Range maps for sugar pine (A) and western white pine (B). Original maps are from Little (1971) and these figures are from the Data Basin web site (https://databasin.org/).

Sugar pine and western white pine have similar wood qualities and uses. Thus, they can be used almost interchangeably (Kinloch 1984). Sugar pine wood is whitish, scentless, lightweight, solid, easy to work with, and a good paint-holder. Thus, it has multifunctional uses such as for constructing boxes (e.g., used to transport sensitive products such as fruits and vegetables), windows, and panels that require robustness (Kinloch 1984). Western white pine is valuable for the timber industry because of its good wood quality, rapid growth (2 to 4 feet per year), and straight and long bole (e.g., over 150 feet) (Hines 2013). Its timber can be used in many applications, from construction lumber to furniture. This high demand led to increased harvesting pressure on these species between the early 1800s and late 1900s. However, failure to meet increasing demands for western white pine lumber led to the import of seedlings for reforestation (Muller 2002). Because of an introduced pathogen and other disturbances (e.g., mountain pine beetle), white pine nurseries and stands were damaged, and new plantations were difficult to establish. While it was one of the most preferred species, the area that contains substantial western white pine has been reduced by 90% since about 1900 (Hines 2013). Returning western white pine and sugar pine to the forests of the PNW will make a difference in terms of sustaining forest health and contributing to the economy.

1.1.2 White pine blister rust (WPBR) is a disease caused by a non-native fungal pathogen, *Cronartium ribicola*

The forest pathogen, *Cronartium ribicola* J.C. Fisch. in Rabh., is native to Asia, but was introduced into many regions, including Japan, Siberian Russia, Himalaya, and North America (Kim et al. 2010). The pathogen infects and damages white pine species (subgenus *strobus*) (Kim et al. 2010; Sniezko et al. 2011). Zhang et al. (2010) reviewed the history and behavior of *C. ribicola* in China, where all 12 taxa of white pine were infected by the pathogen. However, there may be two blister rust pathogens in China, one of which may be the same as the pathogen in the U.S. (Zhang et al. 2010; R. Sniezko pers. comm.). In any case, major damage was observed in China on *Pinus armandii* and *Pinus koraiensis* (Zhang et al. 2010). Although this damage may be caused by the rust pathogen, recent increases in infection may also result from changes in forest management or environmental conditions (Zhang et al. 2010; R. Sniezko pers. comm.). In Korea and Japan, imported *Pinus strobus* trees were susceptible, but native species were resistant to the pathogen. Furthermore, it has been possible to reduce blister rust disease in Korea by eradicating the alternate host (*Pedicularis resupinata*) and by removing infected Korean pine trees (La 2009). Thus, only minimal infection is now seen on *Pinus koraiensis* (La 2009; Kim et al. 2010). In the mid-1800s, the pathogen probably came to Europe from Russia on infected stone pine trees (*Pinus sibirica* Du Tor.), and then spread throughout the European countries on seedlings of eastern white pine (*Pinus strobus*) (Mielke 1943; Hummer 2000). The pathogen infects all nine native 5-needle white pines in the United States (Sniezko et al. 2011), which are eastern white pine (*Pinus strobus* L.), western white pine (*P. monticola*), sugar pine (*P. lambertiana*), whitebark pine (*P. albicaulis* Engelm.), limber pine (*P. flexilis* E. James), southwestern white pine (*P. strobiformis* Engelm.), foxtail pine (*P. balfouriana* Balf.), Rocky Mountain bristlecone pine (*P. aristata* Engelm.), and Great Basin bristlecone pine (*P. longaeva* D. K. Bailey) (The Plant List 2013). *Cronartium ribicola* first came to eastern North America on infected eastern white pine seedlings from Europe, specifically from France and Germany (Hummer 2000). Although the pathogen was seen on *Ribes* species, it was restricted to local regions in the 1880s, but spread throughout eastern North America by 1910 (Mielke 1943). In western North America, infected eastern white pine seedlings came from French nurseries on a single shipment in 1910 (Mielke 1943). However, Hunt (2009) stated multiple shipments might have been transported to multiple locations by 1930 in western North America. The disease developed and spread throughout British Columbia, and was recognized on white pines and alternate hosts by 1920 (Mielke 1943). The disease was first reported on natural sugar pine stands in Oregon in 1936 (Mielke 1938). Now, it can be seen in Quebec, New Mexico, Arizona to Idaho, Alberta, Oregon and California (Hummer 2000; Geils 2000; Fairweather and Geils 2011). The pathogen continues to spread throughout the distributions of these principal hosts, resulting in economic and ecological losses that concern foresters and pathologists (Hummer 2000).

There are 12 rust fungi in North America, most of which damage the stems and cones of “hard” pines (i.e., subgenus Pinus) (Peterson and Jewell 1968; R. Sniezko pers. comm.). One of these, *Cronartium ribicola,* is the causal agent of white pine blister rust that damages species in the white pine or “soft” pine group (subgenus *Strobus*) (Peterson and Jewell 1968). Some of the rust fungi have a microcyclic life cycle, which means that pine is infected by the spores from another infected pine (Geils et al. 2010). However, *Cronartium ribicola* is an obligate parasite, requiring two living hosts to complete its macrocyclic life cycle (Geils et al. 2010). *Ribes* species (e.g., currants and gooseberries) are the principal telial hosts, but the pathogen also alternates to species of *Pedicularis* and *Castilleja* in North America (McDonald et al. 2006).

The pathogen has five types of spores, spermatia, aeciospores, urediniospores, teliaspores, basidiospores. Spermatia are microscopic and non-infective hyphae that occurs in the initial phases of rust development on pines (Geils et al. 2010). Spermatia reside on pines over the winter and then produces blister rust-like aeciospores. The yellow, thick-walled, and homozygous aeciospores arise from infected tree bark to infect alternate hosts in the spring and early summer (Geils et al. 2010). Aeciospores can travel about ~700km via wind (Mielke 1938; Mielke 1943; Campbell and Antos 2000). On *Ribes*, urediniospores are repeatedly produced by pustules-like uredinia which intensify and spread WPBR among alternate hosts during the growing season (Geils et al. 2010). Teliospores are produced by brown, hair-like telia on *Ribes* leaves about 30 days after inoculation of aeciospores (McDonald and Andrews 1980). Teliospores produce basidiospores, which are brown, short-lived, wind-borne, thin-walled, and haploid. These basidiospores develop on the diseased alternate hosts, and then travel as far as ~2 km to infect the needles of white pines in late summer or early fall (Van Arsdel et al. 1956; Kinloch 2003; Geils et al. 2010). Because WPBR is perennial on pine hosts, aeciospores of previous years can be found on diseased tree stems (Geils and Vogler 2011). The optimum production of spores occurs below 20^{o}C, but the production was decreased in eastern U.S. when the temperatures were above 20^{o}C (Van Arsdel et al. 1956; Van Arsdel 1961). In cooler regions, moisture affects WPBR incidence and severity. For example, Hunt and Jensen (2000) observed higher rust infections through May to November when humidity was high, particularly during foggy days, but the infection was low during dry summers under cooler conditions of British Columbia. Thus, conditions in late summer and early fall are good predictors of infection (Thoma et al. 2019).

Although the pathogen does not cause mortality of *Ribes* species, it can reduce growth of white pines and even kill them within few years by damaging the cambium (Lombard and Bofinger 1999). The cambium is responsible for tree growth by producing the cells that transport photosynthate, water, and nutrients throughout the tree. The development of the disease appears to be similar on sugar pine and western white pine (Kimmey and Wagener 1961). Rust-related damage can be seen in the years following infection (Peterson and Jewell 1968; Hummer 2000). The signs of WPBR are very recognizable on tree and alternate hosts. The first signs of infected trees are yellowing needles and dead branches (Lombard and Bofinger 1999). The pathogen infects needles, shoots, and bark, and then grows within the living vascular tissues (Geils et al. 2010; Schwandt 2013). The resulting damage can be observed as diamond shaped cankers (i.e., deformations on bark) growing lethally and swelling on branches (Lombard and Bofinger 1999; Goheen and Goheen 2014). Cankers progress toward the bole about ~2 inches per year (McDonald et al. 1981; Schwandt 2013). Cankers that are at least 24 inches from the bole are less likely to reach the bole (Harvey 1967). Tree mortality may occur once a canker encircles the tree (McDonald et al. 1981). A high number of branch or stem cankers can also cause tree mortality (Mielke 1943; Burns et al. 2008). The growth rate of the tree host, growth rate of the pathogen, environmental conditions, and genetics affect canker expansion rate (McDonald et al. 1981; Schwandt 2013). WPBR progresses very slowly in trees and the damage may not be evident from outside the tree for a long time. Eventually, however, branch and top kills are seen and tree dies within 10 years (McDonald et al. 1981; Geils et al. 2010).

There may be more cankers on the lower part of the tree for a few reasons. First, because the lower part of the tree is oldest, it has had more time to become infected. Second, areas closer to the ground may be moister and more favorable for the pathogen (Koester et al. 2018). Finally, there may be more alternate hosts early in stand development because many more understory plants are present before crown closure occurs (R. Sniezko pers. comm. 2022).

Infected trees become more susceptible to other disturbances, and may die from attacks by beetles or other diseases (Geils et al. 2010). Sugar pines are more susceptible to the pathogen than are western white pines (Kimmey and Wagener 1961; Sniezko et al. 2020). Although western white pine is strong enough to withstand many disturbances (Hines 2013), it is susceptible to the disease at any age, but the disease is more prone to damage and kill younger trees (Geils et al. 2010). Widespread damage and death from blister rust disease has caused western white pine to disappear from many ecosystems (Hines 2013). The shift in PNW ecosystems has made the PNW forests more vulnerable to other disturbances (Schwandt 2001).

1.1.3 The activity of the disease is affected by climate and site conditions

According to Van Arsdel et al. (2006), it is important to understand the environmental factors that affect blister rust disease incidence and severity. Disease incidence refers to the percentage of diseased plants in the population. Disease severity refers to the quantity of disease on the plants. Humidity and temperature limit spore development, germination, inoculation, and spread (Van Arsdel et al. 2006; Geils et al. 2010). Particularly in cool and moist areas, the pathogen is common (Van Arsdel 1972). Smith-McKenna et al. (2013) studied the geographic and topographic factors that affect white pine blister rust in whitebark pine. In the areas with abundant water (e.g., near lakes and streams), they observed high occurrence of blister rust because the areas provided moisture for the development of disease and establishment of alternate hosts. Larson (2011) found a positive correlation between blister rust infection versus mean minimum temperatures in December and high temperatures in spring. On western white pine, for example, the disease is transmitted via spores in the autumn when humidity is high (Schwandt 2001). Thus, climate data can be used to infer where the pathogen can persist and develop WPBR disease (Frank et al. 2008).

Elevation is associated with changes in temperature and precipitation. At lower elevations, higher temperatures and lower humidity are typically observed. Although disease incidence tends to decline at lower elevations (Berg et al. 1975; Kearns and Jacobi 2007), blister rust disease is able to develop across a wide range of elevations, and continues to spread where adequate environmental and stand conditions exist (Smith et al. 2001). Landscape position affects the amount of solar radiation received, which is related to disease incidence and severity

(Smith-McKenna et al. 2013; Kearns et al. 2014). Kearns and Jacobi (2007) inspected white pine blister rust on *Pinus flexilis* in relation to stand-level geographic features and found that bottom slopes and northern and eastern aspects tended to have higher incidence of disease, presumably because wind patterns allow the pooling of cold and moist air. Larson (2011) also observed more blister rust infection at the bottoms of slopes, which are cooler and moister. However, according to a study conducted in British Columbia, more WPBR cankers were observed as the slope increased (Hunt 1983). Southern aspects may have lower infection levels because of exposure to sunlight, which decreases the duration of disease activity (Zambino 2010; Thoma et al. 2019). However, in areas that are higher and colder, and further from water sources, solar radiation has a positive effect (Larson 2011). In these areas, Larson (2011) found that more cankers were observed in areas with higher solar radiation. This is because the solar radiation provided milder temperatures required for disease development in these generally cold environments. Thus, disease incidence and severity are not uniform, but differ among locations. A wide range of topographic features can make favorable microenvironments for the pathogen.

1.1.4 There are no effective management techniques to prevent blister rust disease

Because of its complex lifecycle and invasiveness, *Cronartium* is difficult to eliminate from the ecosystem. Many techniques have been used to try to control the disease, including *Ribes* eradication, spraying chemicals on *Ribes* species, pruning of lower tree branches, thinning of damaged or dead trees, and breeding of rust-resistant white pines. The breeding efforts are valuable because they provide some level of resistance to the rust pathogen. However, other methods have not been fully successful, despite much time and money spent (Maloy 1997).

Ribes eradication aims to eliminate the disease by removing *Ribes* species and infected white pines from forests. The first eradication program began in 1909 and lasted until 1967

(Maloy 1997). Natural and cultivated *Ribes* species exist in North America. Although native *Ribes* species are moderately susceptible to the disease, cultivated *Ribes* species are highly susceptible. This is particularly true for European black currant (*Ribes nigrum*), which grows across wide areas of North America (Maloy 1997). Susceptible *Ribes* can be infected from long distances and develop many basidiospores, resulting in high hazard to white pine forests. Managers recognized that *Ribes* eradication may succeed in low to moderate hazard areas (Maloy 1997). For instance, *Ribes* eradication (i.e., removing the telial host, *Pedicularis resupinate*) and removing diseased trees was enough to control blister rust disease in Korea because blister rust has low infection capacity in the region (Kim et al. 2010). High susceptibility to blister rust of both alternate hosts and white pines in North America makes it necessary to eradicate *Ribes* repeatedly over very large areas. In addition, the extensive and rapid spread of the disease, and harsh topographic features, makes it essentially impossible to treat every site (Maloy 1997).

The failure to eradicate *Ribes* accelerated the use of chemicals on white pines starting in 1950 (Maloy 1997). Fungicides can be used under regulation by the US Department of Agriculture (EPA 2019). The antifungal chemicals, cycloheximide and phytoactin, were identified to control blister rust (Maloy 1997; Burns et al. 2008). Moss (1961) reviewed fungicide application on western white pines, noting that several methods have been developed. Some methods require one to identify infected white pines, remove infected bark, and prune off infected branches. This extra work demands skilled personnel and money. Some methods are more practical because they involve spraying the chemical solution directly on infected white pines from some level of height that depends on the tree height. For that, assistance was received from workers and aircraft such as helicopters. For all chemical treatments, the timing of application (i.e., during mid-summer or early fall before the trees are infected), environmental conditions, and the conditions of the application surface (e.g., leaves) are important (Burns et al. 2008). Although fungicides cannot be used across large landscapes, they can be used in some plantations and nurseries. However, Moss (1961) stated that roots and mycorrhizae of western white pine seedlings were harmed after testing fungicide applications aimed at protecting the seedlings from blister rust disease.

Pruning removes lower branches of pines. Because lower branches are more likely to become infected, pruning them may reduce infection and the spread of disease (Schwandt, et al. 2013). Especially in young trees, the foliage is close to the main stem, resulting in higher infection of tree boles (Schwandt, et al. 2013). The success of pruning is likely to be less where *Ribes* species and young trees are abundant (Hunt 1998). The timing of the pruning is also critical for white pines to escape from the pathogen. Trees can be pruned when they reach ~10 feet in height (Hunt 1998). However, at dense sites, pruning can be postponed until susceptible young trees are eliminated by WPBR (Weber 1964).

Pruning and thinning are effective when they are applied together. Thinning helps increase tree growth by reducing competition among trees. Therefore, fast-growing trees heal fast and have clear wood after being pruned (Weber 1964). However, thinning without pruning may increase the risk of rust infection. Because thinning provides more sunlight that reduces forest moisture, but also allows *Ribes* species to thrive. However, across the entire landscape, the application of thinning and pruning requires much time and money (Burns et al. 2008).

Overall, *Ribes* eradication, chemical treatments, thinning, and pruning may reduce the spread of the disease, but these practices must be repeated, and the disease may increase again in the area. The long-term solution may be to increase rust resistance by selecting appropriate populations or by breeding.

1.1.5 Genetic resistance and breeding

Genetic studies and tree breeding may help sustain sugar pine and western white pine. Whether a species has genetic diversity or resistance to disease influences its fate. Genetic studies were started in the 1950s after managers recognized that *Ribes* eradication was not adequate to eliminate and control the disease. Then, planting was initiated in the 1970s (Mahalovich 2010). With the introduction of the pathogen, managers studied the biology of the disease to understand the interactions among the elements of the pathosystem (Geils et al. 2010). Species develop defense mechanisms to resist pathogens (Millar et al. 2007). Thus, managers recognized that resistance to *Cronartium ribicola* naturally exists in white pine trees at varying levels (Hoff et al. 1980; Kinloch and Byler 1981; Sniezko et al. 2014; R. Sniezko pers. comm.). For instance, in Japan and Korea, blister rust disease does not cause serious problems in white pine forests presumably due to coevolution of the pine and rust (Kim et al. 2010). However, white pines in North American were severely impacted by the pathogen. This may be because the white pine populations in Japan and Korea have been exposed to the disease long enough to develop genetic resistance (Kim et al. 2010). In contrast, white pines in North America did not evolve with the pathogen, so did not develop resistance (Hummer 2000). Thus, managers established genetic resistance breeding programs to understand and improve resistance of white pine populations in North America. The USDA-Forest Service’s Dorena Genetic Resource Center (DGRC), Coeur d’Alene Nursery (CDA) in Idaho, Institute of Forest Genetics (IFG), and Placerville Nursery in California are running greenhouse tests and field trials to understand genetic resistance and improve resistance by breeding (McDonald et al. 2004; Sniezko 2004; Sniezko et al. 2011). They established many field trials for western white pine in the PNW (Sniezko et al. 2011; Sniezko et al. 2020). The aim was to achieve a long-term solution by having more genetically resistant trees in nature to restore this valuable species (Sniezko et al. 2012).

Western white pine and sugar pine are well studied in terms of genetic resistance to the pathogen (Bingham 1983; Sniezko et al. 2011; Sniezko et al. 2014; Sniezko and Liu 2021). Rust resistance mechanisms in white pines were categorized by King et al. (2010) as (1) ontogenetic resistance, (2) R-gene resistance, and (3) partial resistance. Ontogenetic resistance, also known as mature tree resistance, is positively correlated with tree age, which means seedlings and younger trees are more susceptible (King et al. 2010). R-gene resistance, also referred to as *Cr* gene resistance or major gene resistance (MGR), is controlled by a single gene (Kinloch and Dupper 1999; Kinloch and Dupper 2002). Heritable *Cr* gene resistance was discovered in sugar pine (*Cr1*), western white pine (*Cr2*), southwestern white pine (*Cr3*), and limber pine (*Cr4*) (Kinloch and Dupper 2002; Sniezko et al. 2014; Schoettle et al. 2014). The resistance patterns can be observed as hypersensitive-like reactions on tree needles, which is the initial point of infection (Sniezko et al. 2011). The hypersensitive response causes death of cells near the infected cells, and this inhibits the growth and spread of the disease (Kinloch et al. 1999; Kinloch and Dupper 2002; Sweeney et al. 2012). For MGR, this highly effective reaction is the main response of the tree to infection (Kinloch et al. 1999). Partial resistance, also known as slow rusting, is controlled by multiple genes, and allows hosts to tolerate the disease by slowing infection or canker growth (Kinloch and Byler 1981; Sniezko et al. 2014). This is thought to be the most effective resistance mechanism, but is affected by environmental conditions to varying degrees (King et al. 2010; Sniezko et al. 2014; Sniezko and Liu 2021).

The utility of genetic resistance also depends on the durability of resistance (Kinloch and Byler 1981; Sniezko et al. 2011; Weiss et al. 2020; Sniezko et al. 2020; Sniezko and Liu 2021; Liu et al. 2022). Kinloch and Byler (1981) identified one or more races of *Cronartium ribicola* that are virulent to R-gene resistance in sugar pine, and Kinloch et al. (2004) documented the geographic distribution of virulence to MGR in both sugar pine and western white pine. Rust resistance mechanisms in sugar pine were discussed by Kinloch et al. (2018), who concluded that partial resistance is effective against *Cronartium ribicola* races virulent to major gene resistance (MGR). Thus, selection of sugar pine seedlings with both MGR and partial resistance is probably the best strategy for enhancing disease resistance. It is important to improve resistance mechanisms to achieve durable resistance for future white pine and sugar pine populations (Kinloch and Byler 1981; Kinloch et al. 2018; Sniezko et al. 2020; Liu et al. 2022).

Whereas some resistance traits are inherited directly to the next generation, some vary depending on environmental conditions, such as stand conditions and climate (Park et al. 2013). Thus, populations tend to adapt locally and show genetic differences. Surprisingly, Kinloch and Byler (1981) observed dramatic increases in infection rates in sugar pine seedlings known to have major gene resistance. This may have resulted from changes in environmental conditions that allow the pathogen to produce higher spore loads and travel further distances in specific “wave years,” resulting in greater inoculation and spread of the disease. In addition, these conditions may have allowed rusts with low-frequency virulence mutations to reach and infect sugar pines, increasing the frequency of infection over time (R. Sniezko pers. comm.). These changes were associated with cooler and wetter late summers and early fall. Populations of western white pine from more northwestern sites and lower elevations show higher resistance (King et al. 2010). Hunt (2004) observed a decrease in rust resistance of western white pine seedlings that were moved from Idaho to coastal British Columbia, where the climate was "milder." Hunt (2004) observed more blister rust cankers on trees from western white pine seed orchards (i.e., consisting of genetically resistant F_2 progenies from Idaho) near the coastal range of British Columbia, compared to trees in interior British Columbia. Sniezko et al. (2020) found similar results that genetically resistant F_2 progenies of western white pine coming from Idaho seed sources show some concern on stability of white pine blister rust resistance.

1.1.6 Rust hazard ratings provide guidelines for managing WPBR

Rust hazard ratings (RHRs) reflect the existing or potential infection levels of white pine stands by considering environmental factors (Van Arsdel 1961). RHRs can be calculated at the scale of individual trees or stands. Individual tree ratings predict the differences in characteristics among individual trees (e.g., growth), whereas stand ratings reflect disease incidence and severity of the sites overall (Steele 1996).

This system was first developed for the Lake States in 1961 (Van Arsdel 1961), and have been widely used for other regions, such as New Mexico (Geils et al. 1999), British Columbia (Hunt 1983; McDonald 2000), and southern Oregon (Koester et al. 2018). RHRs provide useful information by creating an index associated with the incidence and severity of the disease, and the abundance of *Ribes* species (Geils et al. 1999). Van Arsdel (1961) delineated five hazard zones based on the suitability of the climate and observed infections. Then, control treatments were suggested for each hazard zone (Van Arsdel 1961; Van Arsdel et al. 2006). Maintaining a closed canopy and pruning lower branches were recommended to reduce blister rust infections (Van Arsdel 1961). Thus, the RHR system is useful for determining which management activities should be used by region, especially where the disease is common (Park et al. 2013).

RHR systems can be used to develop risk distribution maps that are important for making effective management decisions.

Managers have used the number of pine needles to estimate rust hazard because the pathogen enters through the stomata of the needles (Buchanan 1936; Van Arsdel 1961; Geils et al. 2010). Two methods were used to obtain the number of needles. First, for five-needled white pines, needle bundles were counted and multiplied by five (Buchanan 1936; Buchanan and Kimmey 1938). Second, tree crown height and width were used to estimate the number of needles (Buchanan 1936; Buchanan and Kimmey 1938). The number of cankers per 1000 needles per year was used as a rust index (Buchanan 1936; Buchanan and Kimmey 1938). McDonald et al. (1981) focused on the other key part of the rust life cycle, *Ribes*. They used the leaf (infection) surface area (cm^2) of *Ribes* as an input to a computer program that analyzed rust disease epidemics for western white pine. Tree characteristics associated with WPBR were considered by Hagle et al. (1989). They used the number of cankers per tree and tree characteristics associated with WPBR to develop a rust index (RI). The tree characteristics were tree age and tree height.

One of the broadest studies of RHRs was completed by Koester et al. (2018), who surveyed 265 sites of natural stands and plantations of genetically resistant trees in southern Oregon. According to this study, the hazard ratings of the sites were low to relatively high, and expected to increase. They concluded that using genetically resistant seedlots is critical to slow the decline of sugar pine and western white pine populations (Goheen and Goheen 2014; Koester et al. 2018).

1.1.7 Climate is changing

According to the latest IPCC report, global temperatures have continued to increase since pre-industrial times, and are predicted to rise more than 2°C during the 21st century (IPCC 2021). Climate change is altering forest ecosystems by impacting biotic and abiotic components. Climate change may reduce tree growth, change the distribution of populations, and lessen resistance to disturbances (Sturrock et al. 2011). For example, longer growing seasons enhance the development of insects and pathogens, increasing damage (Sturrock et al. 2011; Mitton and Ferrenberg 2012). Species may respond to these changes by migrating, adapting, or vanishing. Thus, to sustain biological diversity, it will be important for species migration rates to keep pace with changes in climate.

Currently, there is not enough information on the effects of climate change on WPBR (Koester et al. 2018). In the PNW, climate is expected to be warmer and wetter in the future (Mote and Salathé 2010), which might increase or decrease WPBR incidence and severity. It seems the relationship between white pines and white pine blister rust can be more complicated in the future. Thus, management techniques should be improved in light of genetic studies by considering shifts in the distributions of hosts and pathogen.

1.1.8 Climate can be modeled to project future changes in climate and ecosystems

Models help us to understand complex, dynamic systems in nature. General Circulation Models (GCMs) are climate models that use projected greenhouse gas concentrations in the atmosphere and other factors to infer future climates. However, GCMs are too coarse to project climatic conditions for specific locations, especially for mountainous areas (Wang et al. 2016). For instance, the resolution of GCMs may be about 100 to 300 km (about 186.41 mi), which is not fine scaled enough to predict climate variables over complex landscapes. Instead, the PRISM model (Parameter elevation Regression on Independent Slopes Model) is a climate interpolation model that uses weather station data to model spatial climate data at much finer scales (PRISM Climate Group 2021). Combined with ClimateNA (Wang et al. 2016), we can now obtain fine-scaled projections of future climates based on CMIP6 climate projections. CMIP6 is the Coupled Model Intercomparison Project phase 6 associated with the 6th IPCC Assessment Report (IPCC 2021).

Scientists develop climate change scenarios to project what the Earth`s climate might be like in the future. In IPCC AR5, Representative Concentration Pathways (RCPs) were used to project global warming by using greenhouse gas concentrations over the years based on CMIP5 projections (Van Vuuren et al. 2011). In 2021, AR5 was updated to AR6 using projections based on Shared Socio-economic Pathways (SSPs). These are the updated scenarios which use socioeconomic trends such as economic growth, population size, urbanization, and education to project future greenhouse gas concentrations (Riahi et al. 2017). SSPs are based on five different perspectives of how society will address climate change mitigation and adaptation, which are called SSP1-1.9, SSP1-2.6, SSP2-4.5, SSP3-7.0, and SSP5-8.5. The first number is the category of the SSP, and second number is the projected radiative forcing in 2100 (IPCC 2021). Radiative forcing increases with the increase in the concentration of atmospheric CO_2 (Shine et al. 1990). SSP1, the most optimistic scenario, predicts an increase in technological opportunities, economic growth and, thus, an increase in social well-being. Therefore, challenges in mitigating and adapting to climate change are expected to be low (Riahi et al. 2017). SSP2 and SSP3, the most pessimistic scenarios, project medium to high challenges for implementing climate change mitigation and adaptation. Both of these SSPs predict imbalances in society, such as differences in economic growth and education levels among countries, and disruptions to ecosystem services. SSP4 predicts low challenges to mitigation, but high challenges to adaptation. In contrast, SSP5 predicts high challenges to mitigation, but low challenges to climate change adaptation. Many studies used SSPs to understand the role of climate change in fungal diseases. For example, the potential suitable habitats of foliar and root pathogens were predicted and mapped using historical and future climates according to climate change scenarios of SSPs (Xu et al. 2020; Kim et al. 2021; de Carvalho Alves and Sanches 2022; Batista et al. 2023).

ClimateNA software provides climate data for North America at much higher resolutions (e.g., 1km) compared to global GCMs (Wang et al. 2016). ClimateNA can generate seamless climate data with elevation adjustment that is suitable for local climates, especially for mountainous areas (Wang et al. 2016). It uses PRISM data for current climate, and the CMIP6 climate projections associated with the 6th IPCC Assessment Report (Wang et al. 2016). ClimateNA estimates monthly, annual, seasonal climate variables using current and historical climate data between 1901-2014, and then projects future climates for the periods of 2020s (2011–2040), 2050s (2041–2070), and 2080s (2071–2100) under the SSPs SSP1-2.6, SSP2-4.5, SSP3-7.0 and SSP5-8.5. Future climate data can be obtain for three normal periods (2011-2040, 2041-2070, and 2071-2100) and five 20-year periods (2001-2020, 2021-2040, 2041-2060, 2061-2080, and 2081-2100) (Wang et al. 2016).

2. Chapter 2

2.1 Research Introduction

Sugar pine (*Pinus lambertiana* Dougl.) and western white pine (*Pinus monticola* Dougl. ex D.Don) are ecologically and economically important tree species. Sugar pine (SP) and western white pine (WWP) are five-needled white pines in the subgenus *strobus*. They grow naturally in the Pacific Northwest (PNW), from sea level to high-elevation forests, even beyond the tree line. They show optimum growth in moist habitats with fertile soils and sufficient sunlight (Hines 2013), but also survive in harsh environments where other less-tolerant conifers might not (Richmond et al. 2005; Tomback 2011). For example, western white pine and sugar pine are essential components of many higher-elevation forests.

These species have many desirable traits, including the ability to regenerate after fires and sequester large amounts of carbon. They are mostly resistant to native pests and diseases, and grow fast (Byler et al. 2000; Hines 2013). They provide many ecosystem services—they conserve soil and water, sustain other plants and wildlife (e.g., black bears and grizzly bears), and contribute to biodiversity (Kinloch et al. 1996; Mahalovich 2013). They are also valuable economically. Compared to other species in the region, they have high quality wood, which is valuable and profitable for the timber industry (Tomback 2011; Hines 2013). For example, western white pine was among the most widely planted and harvested tree species in the western United States until the beginning of the 20th century (Blodgett and Sullivan 2004; Hines 2013). However, white pines across North America have declined due to abiotic and biotic disturbances, particularly the non-native pathogen, *Cronartium ribicola*.

White pine blister rust (WPBR) threatens white pines. WPBR is a disease caused by a non-native fungal pathogen, *Cronartium ribicola* J.C. Fisch. in Rabh. *Cronartium ribicola* is an obligate parasite, requiring two living hosts to complete its macrocyclic life cycle (Geils et al. 2010). Five-needled white pines are the primary hosts. *Ribes* species (e.g., currants and gooseberries) are the principal alternate hosts, but the pathogen also alternates with species of *Pedicularis* and *Castilleja* in North America (McDonald et al. 2006). These alternate or telial hosts act as bridges to transfer the disease to white pines. The pathogen does not cause mortality of alternate hosts but damages and kills pine hosts (Geils et al. 2010). All nine native five-needled white pines in the United States are susceptible to WPBR (Sniezko et al. 2011).

In some ecosystems, the persistence of white pines is a concern because of WPBR.The blister rust pathogen enters through the stomata of pine needles, and then grows through the living tissue of branches and stems, resulting in swellings and cankers (Lombard and Bofinger 1999; Goheen and Goheen 2014). These branch and stem cankers cause the death of branches, top-kill, or even tree mortality. Consequently, WPBR reduces forest biomass and makes white pines vulnerable to other disturbances, such as bark beetles. Although sugar pine and western white pine can withstand many disturbances (Hines 2013), they are highly susceptible to WPBR at any age. Nonetheless, the disease is more prone to damage and kill younger trees (Geils et al. 2010). In addition, there is a concern that other climax species, such as western hemlock, Douglas-fir, and grand fir will outcompete western white pine in the PNW (Schwandt et al. 2013). The pathogen has continued to spread throughout the distributions of these principal hosts, resulting in economic and ecological losses that concern foresters and pathologists (Hummer 2000). Unfortunately, there are no effective management techniques to prevent blister rust disease. Thus, management of western white pine has been a battle for more than a century (Geils et al. 2010).

The severity of WPBR is associated with season, weather, and topography. In spring and early summer, thousands of yellow aeciospores arise from the bark of infected pine trees. These spores blow in the air up to a few hundred miles, and then land on alternate hosts. The alternate hosts produce urediniospores over summer, which spread infection on the plant itself, and also infect other alternate hosts. Brown basidiospores develop on the diseased alternate hosts, and then infect white pines in late summer or early fall. In particular, the fungal spores optimally germinate, inoculate, and disperse when humidity is high and temperatures are cool (Van Arsdel et al. 1957; Van Arsdel 1972; Geils et al. 2010).

'Wave years' occur when there are unusually favorable environmental conditions for the pathogen. Wave years are characterized by large increases in the production and spread of rust spores (Mielke 1943; Peterson 1971; Kinloch 2003; R. Sniezko pers. comm.). The intensity and frequency of rust infections are highly correlated with the frequency of wave years, but these relationships differ by region (Kinloch 2003). Wave years make it difficult to predict which sites will become most affected by WPBR because sites with low infection across many years may be indistinguishable from sites that suffer a major infection in a single wave year.

Site-to-site variation in WPBR is associated with topographic features that create favorable microenvironments for the pathogen. Favorable habitats include places such as lower slopes, narrower and wetter valleys and canyons, areas near cool water resources, and smaller canopy openings that supply a cooler, moister environment (Van Arsdel 1972; Frank et al. 2008; Smith-McKenna et al. 2013). Apart from environmental conditions, WPBR incidence and severity are impacted by the abundance and distribution of hosts, and the genetics of the host and pathogen (Geils et al. 1999; Geils et al. 2010; Kearns et al. 2012). Despite these known relationships, significant gaps in knowledge remain about the interaction between white pines and the blister rust pathogen (Geils et al. 2010).

Rust hazard ratings (RHRs) are used to manage WPBR. Rust hazard ratings are indicators or metrics designed to reflect the existing or potential rust infection levels of white pine stands (Van Arsdel 1961). Rust hazard ratings have been widely used to guide management of white pine stands, including in New Mexico (Geils et al. 1999), British Columbia (McDonald 2000), and southern Oregon (Koester et al. 2018). As described above, rust hazard has been associated with season, weather, and topography. The environmental conditions associated with WPBR incidence and severity have been used to develop RHRs and map rust hazard across the landscape (Van Arsdel 1961). Furthermore, the distribution and proximity of *Ribes* species and tree characteristics were also used (McDonald et al. 1981; Hagle et al. 1989; Geils et al. 1999; Koester et al. 2018).

A greater understanding of the relationships between climate and rust hazard would allow us to project changes in WPBR under climate change. Climate change has the potential to increase the incidence and severity of diseases caused by forest pathogens. Globally, today`s climate is already ~1.1 °C warmer than it was in 1850-1900, and is projected to rise more than 2 °C during the 21st century (IPCC 2021). However, changes in precipitation were projected to be inconsistent (IPCC 2021). In southwestern Oregon, there has been ~0.1 °C increase in temperature per decade since 1895 (Halofsky et al. 2022). However, no change was observed in annual precipitation (Halofsky et al. 2022). Climate change impacts biotic and abiotic components of forest ecosystems and their interactions, in positive and negative ways. For example, increases in temperature promote tree growth in areas with available water. In contrast, climate change is one of the major reasons for the decline in forest health in the western U.S.

(van Mantgem et al. 2009). It is difficult to project future changes in precipitation because of topographic variation, especially in mountainous regions. However, increases in temperatures alone can increase water stress in regions with limited water availability (Halofsky et al. 2022). The effects of climate change may be compounded because stressed trees are likely to be susceptible to other disturbances, including those caused by forest pathogens.

Because *Cronartium ribicola* requires mild temperatures and sufficient moisture to inoculate and spread (Geils et al. 2010), climate change may alter the pathogen's lifecycle. Consequently, the pathogen may abandon or expand its current distribution into new regions. Climate change may also increase epidemics in forests where it already occurs (Sniezko et al. 2011). Based on analyses of blister rust disease and climate change, Dudney et al. (2021) concluded the pathogen would probably move up in elevation and decrease its range at lower elevations in the future. Thus, warming temperatures could reduce WPBR incidence and severity in drier regions, and increase WPBR in moist regions (Sturrock et al. 2011).

Using knowledge about the historic relationships between climate and WPBR, future changes in rust hazard can be projected under climate change. Using ClimateNA (Wang et al. 2016), we can now obtain fine-scaled projections of future climates for future years and Shared Socio-economic Pathways (SSPs). SSPs, which the IPCC developed, are climate change scenarios that are commonly used to drive climate models and make future climate projections. These alternative scenarios are based on five sets of assumptions describing alternative pathways under different climate change adaptation and mitigation efforts. The assumptions are about future sustainable development, continued trends based on historical patterns, regional rivalry, inequality, and fossil-fuel development (Riahi et al. 2017).

Koester et al. (2018) studied rust hazard at 265 sites in southwestern Oregon. However, the results were not analyzed in relation to climate variables. They aimed to help design seed deployment zones for the blister rust resistance program by mapping the current rust hazard of these sites. The sites contained naturally regenerated sugar pine, naturally regenerated western white pine, rust-resistant sugar pine, and rust-resistant western white pine. In addition to assessing WPBR, they also recorded tree age, tree height, elevation, township, range, and section of the sites. I used the Koester et al. (2018) data to develop models for predicting rust hazard based on environmental variables. My research focused on predicting rust hazard and assessing potential changes in WPBR due to climate change. Specifically, I addressed five main questions: (1) Which rust traits were best for characterizing rust hazard? (2) Which environmental variables were most closely associated with rust hazard? (3) How were rust traits affected by tree characteristics? (4) How was tree growth affected by environmental variables and rust traits? (5) How will rust traits change under future climates? (6) How will tree growth change under future climates?

3. Chapter 3

3.1 Materials and Methods

3.1.1 Study Area

The study sites were located in southwestern Oregon. These sites were near the California border and in the Rogue River Basin near Cave Junction, Ashland, and Glendale, Oregon (Figure 2B). The region has various topographic structures, and is one of the most rugged areas in the state of Oregon. The complex geological structure of the region creates a unique diversity of local climate, vegetation, landscape features, and soil structure (Halofsky et al. 2016). The area has a Mediterranean climate with hot summers and cool and rainy winters (Halofsky et al. 2016). Elevation is the main factor causing differences in precipitation across this region. While abundant precipitation is observed at higher elevations, lower lands experience drought. Within the total forested area, sugar pine and western white pine have the greatest distributions among forest tree species (Goheen and Goheen 2014).

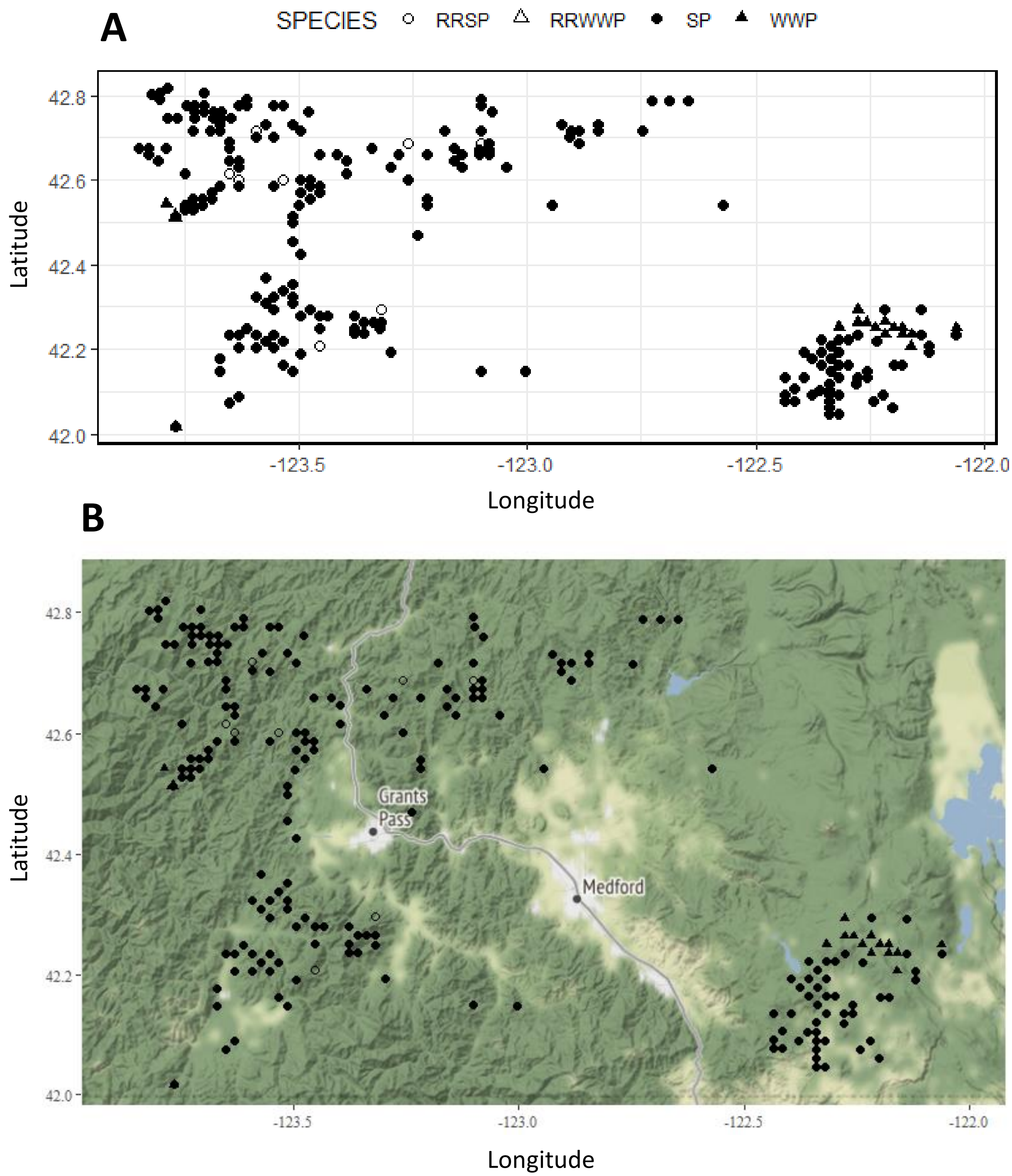

Figure 2. Locations of 265 study sites containing sugar pine (SP, ●), western white pine (WWP, ▲), rust-resistant sugar pine (RRSP, O), and rust-resistant western white pine (RRWWP, △) (Panel A). The view of the same sites on a topographic map (Panel B).

3.1.2 Plant Materials

I used 265 sites chosen from the lands of the Bureau of Land Management (BLM), USDA Forest Service, and private timber companies that were surveyed to assess rust hazard during the 1980s (Koester et al. 2018). Among the 265 sites ranging from about 7.4 to 98.8 acres (3 to 40 ha), 244 had more sugar pine (SP) and 21 had more western white pine (WWP) (Koester et al. 2018). One site, Hawk Creek, was a plantation of WWP progeny from rust-resistant parent trees (RRWWP). Nine sites were plantations of SP progeny from rust-resistant parent trees (RRSP). These RRSP sites were Mule Creek, Sand Creek, Stratton Creek, West Fork, Rum Creek, Mt. Peavine, King Mt., Lower Kirby Peak, and Grays Creek. The plantations were established in the mid-to-late 1960s (Koester et al. 2018). The RRWWP and RRSP trees were the open-pollinated and control-pollinated progeny of phenotypically "good standing" parent trees in wild stands (R. Sniezko pers. comm. 2022). Control crosses were made among some of the parent trees, and open-pollinated seeds were collected. The resulting seedling families were tested by artificially inoculating them with spores of *Cronartium ribicola* found on *Ribes* leaves. Later, the parent trees were rated for major gene resistance (MGR) to WPBR at the Dorena Genetic Resource Center (R. Sniezko pers. comm. 2022). Using this rust-resistance screening process, some parents were identified as being rust-resistant. Finally, the ten sites described above were planted with the open-pollinated and control-pollinated progeny of the disease-resistant parent trees (67 to 2780 trees per site).

At each of the 265 sites, sample trees were selected using the random path method, which is the standard for measuring rust hazard index (RI). The random path method involved walking 50 paces, looking left, and then selecting the nearest tree (Koester et al. 2018). At least 50 trees that were at least 10 years old and generally less than 20 feet (6 m) tall were sampled from each site (Koester et al. 2018). Trees that appeared to have died recently and had symptoms of canker were also measured (Koester et al. 2018). Measurements at each site consisted of rust variables, tree variables, and topographic variables (see below).

3.2 Measurements and Derived Variables

3.2.1 Rust Variables

At each site, the rust variables consisted of the percentage of trees with a stem canker (CANK%), average number of cankers per tree (NUM_CANK), average height of the highest canker (HT_CANK), and rust hazard index (RI) (Table 1). RIs of the sites were calculated using the rust hazard index computing program described by Hagle et al. (1989). Samples were collected using a protocol designed for measuring WPBR rust hazard index. This protocol aims to select trees when they are old enough to have been exposed to the disease for years (i.e., > 10 years old) but are short enough that cankers can be counted accurately (i.e., < 35 feet (11 m) tall) (Koester et al. 2018). Trees that appeared to have died recently and had symptoms of canker were also included in the sample and calculation of RI (Koester et al. 2018). The inputs to the program were tree ID, tree age (AGE), tree height (HT), and NUM_CANK. Based on these inputs, the program calculated rust hazard index (RI) as formulated below.

$$\text{Rust Hazard Index (RI)} = \text{number of cankers per 1000 needles per year} \qquad [1]$$

In general, the index varies between 0 and 1, and the disease becomes more intense as it approaches 1 (Hagle et al. 1989). The rust hazard index of the sites ranged from low (< 0.001) to relatively high (≥ 0.009) (Koester et al. 2018).

3.2.2 Tree Variables

Koester et al. (2018) measured tree age (AGE) and height (HT) at each site (Table 1). AGE was estimated by counting whorls. Using these measurements, I calculated average height growth (HT/AGE, feet/years) for each site.

Table 1. Tree variables used to study white pine blister rust at 265 sites in southwestern Oregon. These variables were measured by Koester et al. (2018).

Abbreviation	Description
Rust variables	
CANK%	Percentage of trees with a stem canker
NUM_CANK	Average number of cankers per tree
HT_CANK	Average height of the highest canker
RI	Rust hazard index
Tree size and age variables	
AGE	Average age (years)
HT	Average height (feet)
Tree growth variables	
HT/AGE	Average height growth (feet/year) calculated as HT/AGE
Tree species variables	
SPECIES	Sugar pine, western white pine, rust-resistant sugar pine, rust-resistant western white pine

3.2.3 Topographic Variables

The topographic variables consisted of aspect (ASPECT), elevation (ELEV), and slope (SLOPE). ELEV was recorded by (Koester et al. 2018). Then, I used USGS digital elevation models (DEMs) to derive ASPECT and SLOPE for each site. These DEMs consisted of longitude, latitude, and elevation information. Each DEM covered an area of 1x1 degree at a resolution of 1 arc-second, which is about 30 m (USGS). First, I downloaded GeoTIFF files covering the study area, namely, USGS_1_n43w123 and USGS_1_n43w124 from the U.S. Geological Survey. Then, I merged two DEMs to allow analysis of the full study area. According to the USGS web site, “ground spacing is approximately 30 meters north/south, but variable east/west depending on latitude.”

To obtain topographic variables of the sites, longitude and latitude information were needed. Thus, I converted township, range, and section information from the Koester et al. (2018) dataset to longitude and latitude using *sharpshootR* R package. I used code that calculates longitude and latitude of the section centroids, and then I used the *distGeo* R function to create raster extents corresponding to the sections that contained each test site. The potential location of each site was determined by finding at least four pixels that had elevation and aspect values that matched the elevation and aspect recorded by Koester et al. (2018). Koester et al. (2018) recorded aspect, the orientation of the slope, as a categorical variable (e.g., north (N) or south (S)). Thus, I first converted the categorical aspect variable to a range of azimuths in degrees (Table 2). Initially, a pixel was considered a match if it was within 15 meters of elevation and 11.25 degrees of azimuth for aspect (Table 2). However, these limits were progressively relaxed until at least four pixels were found. Ultimately, the average number of pixels associated with each site was 10.65, which equals about 296.1 ac (119.8 ha). Once I found the potential pixels for each test site, I obtained the mean slope (SLOPE, ^{o}) and aspect (ASPECT, ^{o}) for each test site using the *terrain* function from the *raster* R package (Table 2).

3.2.4 Climate Variables

I used ClimateNA v.7.01 to obtain climate variables for each of the 265 sites (Wang et al. 2016) (Table 3). First, I converted the merged GeoTIFF files from GeoTIFF to ASCII grid format to be used as input to ClimateNA. Second, I generated seasonal and annual climate variables for the years 1931-1960 and 1961-1990 for each raster point. I used climate data for these two time periods because the sites were surveyed in the mid-1980s (Koester et al. 2018), but the average

age of the trees on the oldest sites were 65 years. Third, I calculated the final climate variables for each raster point by taking the mean of the 1931-1960 and 1961-1990 values. Finally, I calculated mean climate values for the pixels associated with each site (see Topographic Variables).

Table 2. Aspect categories and azimuths used to study white pine blister rust at 265 sites in southwestern Oregon. Aspect was recorded by Koester et al. (2018).

Direction*	Azimuth mid-point (◦)	Azimuth range (◦)
North	0.0	348.75 – 11.25
North-northeast	22.5	11.25 – 33.75
Northeast	45.0	33.75 – 56.25
East-northeast	67.5	56.25 – 78.75
East	90.0	78.75 – 101.25
East-southeast	112.5	101.25 – 123.75
Southeast	135.0	123.75 – 112.5
South-southeast	157.5	112.5 – 146.25
South	180.0	146.25 – 191.25
Southeast-southwest†	180.0	146.25 – 191.25
South-southwest	202.5	191.25 – 213.75
Southwest	225.0	213.75 – 236.25
West-southwest	247.5	236.25 – 258.75
West	270.0	258.75 – 281.25
West-northwest	292.5	281.25 – 303.75
Northwest	315.0	303.75 – 326.25
North-northwest	337.5	326.25 – 348.75
FLAT	NA	NA
FLAT-northeast	NA	NA
Northwest-southeast	NA	NA

*Recorded aspect for each site (Koester et al. (2018). For analyses, aspect categories were converted to azimuths (°) (https://en.wikipedia.org/wiki/Azimuth, accessed on 08/20/2021).

†Sites recorded as having a Southeast-southwest aspect were analyzed as if they were recorded as having a South aspect.

Table 3. Environmental variables used to study white pine blister rust at 265 sites in southwestern Oregon.

Environmental variables (units)*	**Abbreviation**
Topographic variables (USGS)	
Aspect (degrees)	ASPECT
Elevation (feet)	ELEV
Slope (degrees)	SLOPE
Climate variables (ClimateNA)†	
Annual heat-moisture index (MAT+10)/(MAP/1000)) (°C/mm)	AHM
The day of the year on which FFP begins (Julian date)	bFFP
Hargreaves climatic moisture deficit (mm)	CMD
Hogg's climate moisture index (mm)	CMI
Degree-days below 0°C, chilling degree-days (dd)	DD_0 (DD<0)
Degree-days below 18°C, heating degree-days (dd)	DD_18 (DD<18)
Degree-days above 18°C, cooling degree-days (dd)	DD18 (DD>18)
Degree-days above 5°C, growing degree-days (dd)	DD5 (DD>5)
The day of the year on which FFP ends (Julian date)	eFFP
Extreme minimum temperature over 30 years (°C)	EMT
Hargreaves reference evaporation (mm)	Eref
Extreme maximum temperature over 30 years (°C)	EXT
Frost-free period (days)	FFP
Mean annual precipitation (mm)	MAP
Mean annual temperature (°C)	MAT
Mean coldest month temperature (°C)	MCMT
May to September precipitation (mm)	MSP
Mean warmest month temperature (°C)	MWMT
The number of frost-free days (day)	NFFD
Precipitation as snow (mm)	PAS
Mean annual relative humidity (%)	RH
Summer heat-moisture index ((MWMT)/(MSP/1000)) (°C/mm)	SHM
Temperature difference between MWMT and MCMT, or continentality (°C)	TD
Autumn Hargreaves climatic moisture deficit (mm)	CMD_at
Summer Hargreaves climatic moisture deficit (mm)	CMD_sm
Spring Hargreaves climatic moisture deficit (mm)	CMD_sp

Table 3 (cont.). Environmental variables used to study white pine blister rust at 265 sites in southwestern Oregon.

Winter Hargreaves climatic moisture deficit (mm)	CMD_wt
Autumn Hogg's climate moisture index (mm)	CMI_at
Summer Hogg's climate moisture index (mm)	CMI_sm
Spring Hogg's climate moisture index (mm)	CMI_sp
Winter Hogg's climate moisture index (mm)	CMI_wt
Autumn degree-days below 0°C (dd)	DD_0_at
Summer degree-days below 0°C (dd)	DD_0_sm
Spring degree-days below 0°C (dd)	DD_0_sp
Winter degree-days below 0°C (dd	DD_0_wt
Autumn degree-days below 18°C (dd)	DD_18_at
Summer degree-days below 18°C (dd)	DD_18_sm
Spring degree-days below 18°C (dd)	DD_18_sp
Winter degree-days below 18°C (dd)	DD_18_wt
Autumn degree-days above 18°C (dd)	DD18_at
Summer degree-days above 18°C (dd)	DD18_sm
Spring degree-days above 18°C (dd)	DD18_sp
Winter degree-days above 18°C (dd)	DD18_wt
Autumn degree-days above 5°C (dd)	DD5_at
Summer degree-days above 5°C (dd)	DD5_sm
Spring degree-days above 5°C (dd)	DD5_sp
Winter degree-days above 5°C (dd)	DD5_wt
Autumn Hargreaves reference evaporation (mm)	Eref_at
Summer Hargreaves reference evaporation (mm)	Eref_sm
Spring Hargreaves reference evaporation (mm)	Eref_sp
Winter Hargreaves reference evaporation (mm)	Eref_wt
Autumn number of frost-free days (days)	NFFD_at
Summer number of frost-free days (days)	NFFD_sm
Spring number of frost-free days (days)	NFFD_sp
Winter number of frost-free days (days)	NFFD_wt
Autumn precipitation as snow (mm)	PAS_at
Summer precipitation as snow (mm)	PAS_sm
Spring precipitation as snow (mm)	PAS_sp
Winter precipitation as snow (mm)	PAS_wt

Table 3 (cont.). Environmental variables used to study white pine blister rust at 265 sites in southwestern Oregon.

Autumn relative humidity (%)	RH_at
Summer relative humidity (%)	RH_sm
Spring relative humidity (%)	RH_sp
Winter relative humidity (%)	RH_wt
Autumn precipitation (mm)	PPT_at
Summer precipitation (mm)	PPT_sm
Spring precipitation (mm)	PPT_sp
Winter precipitation (mm)	PPT_wt
Autumn mean temperature (°C)	Tave_at
Summer mean temperature (°C)	Tave_sm
Spring mean temperature (°C)	Tave_sp
Winter mean temperature (°C)	Tave_wt
Autumn mean maximum temperature (°C)	Tmax_at
Summer mean maximum temperature (°C)	Tmax_sm
Spring mean maximum temperature (°C)	Tmax_sp
Winter mean maximum temperature (°C)	Tmax_wt
Autumn mean minimum temperature (°C)	Tmin_at
Summer mean minimum temperature (°C)	Tmin_sm
Spring mean minimum temperature (°C)	Tmin_sp
Winter mean minimum temperature (°C)	Tmin_wt

*Topographic variables were obtained from Digital Elevation Models (DEMs) downloaded from the U.S. Geological Survey (USGS) (https://apps.nationalmap.gov/downloader/#/, accessed on 01/05/2021).

†Climate variables were obtained from ClimateNA v.7.01 (Wang, et al. 2016). For the seasonal variable, autumn denotes September, October, and November; spring denotes March, April, and May; summer denotes June, July, and August; and winter denotes December, January, and February.

3.3 Statistical Analyses

3.3.1 Correlations

I calculated correlation coefficients among rust, tree, and environmental variables using *the cor* function from *the stats* R package. Correlations among selected dependent and independent variables were then displayed as heatmaps using *the pheatmap* function from *the pheatmap* R package.

3.3.2 Random Forest Models

I developed “Random Forest” (RF) regression models (Breiman 2001) to predict rust and tree growth variables from various independent variables. The dependent variables consisted of CANK%, NUM_CANK, HT_CANK, RI, and HT/AGE. According to the dependent variable analyzed, the independent variables consisted of subsets of 89 independent variables representing climate, tree growth, rust disease, and topography (Table 3).

First, I developed full models that included all independent variables that were selected *a priori*. This was done using the *randomForest* R package (ntree = 1000). Second, I pruned each full model by removing one variable at a time until I obtained a reduced model with nearly the same RSQ (≥ 98%) as the full model. To do that, I used the *cforest* function in the *party* R package to calculate the “variable importance” (VI) of each independent variable. Then, I re-ordered the variables based on their VI scores and effect on RSQ (i.e., amount of RSQ improvement). At each step, I calculated RSQ using the *randomForest* R package (ntree = 2000) and the reduced set of independent variables. This approach aimed to retain only the most important independent variables in the final reduced model. The relative importance of each variable in the final reduced model was evaluated using the VI score, %IncMSE. The performance of the reduced models versus the full models was judged by comparing the RSQ and root mean square error

(RMSE) values. RSQ is more informative and reliable than SMAPE, MAE, MAPE, MSE and RMSE to evaluate regression analyses (Chicco et al. 2021). Among the reduced models, I selected the tree growth model and the two rust models with the highest RSQ values for detailed evaluation and for making future projections of tree growth and rust disease. The dependent variables for these models were HT/AGE, CANK%, and NUM_CANK (see Results).

3.3.3 Climate Projections

I used ClimateNA v.7.10 to obtain seasonal and annual future climate variables for four Shared Socioeconomic Pathways (SSPs) and three time periods, 2011-2040, 2041-2070, and 2071-2100 based on the climate projections from CMIP6 (Wang et al. 2016). In total, I analyzed 13 climate scenarios consisting of 12 future scenarios and one based on the 1931-1990 climate. The procedure to generate future climate variables for the rust hazard sites was similar to the other ClimateNA procedures described above. Of the models described above, I used the rust and tree growth models with the highest RSQs to make future projections based on changes in climate. The dependent variables for these prediction models were CANK%, NUM_CANK, and HT/AGE. The independent variables consisted of SLOPE, ASPECT, ELEV, and future climate variables.

Summary statistics for the 13 climate scenarios described above included mean, median, minimum value, maximum value, quantiles, and standard deviation for the predicted rust and tree growth variables. I conducted one-way analyses of variance (ANOVA) using *the aov* function in *the stats* R package to compare predicted means of CANK%, NUM_CANK, and HT/AGE at the site-level for current climate versus future projected climates. For each SSP analysis (i.e., SSP1-26, SSP2-45, SSP3-70, and SSP5-85), I had four time period treatments (i.e., 1931-1990, 2011-2040, 2041-2070, and 2071-2100). For each SSP analysis, I tested whether differences existed among the four treatments ($P < 0.05$), and then used Tukey's HSD to identify which treatments differed from one another.

4. Chapter 4

4.1 Results

4.1.1 Approach

I used an observational approach to identify the relationships between rust traits versus environmental variables and tree characteristics at 265 sites in southwestern Oregon. I developed Random Forest (RF) regression models to predict rust traits and tree growth from climate, topographic, and tree growth independent variables. I developed the models using (1) only environmental variables as predictors, and (2) both environmental variables and tree characteristics to reveal the effects of the different independent variables. Once climate-based models were developed, I used future climate variables to project blister rust disease and tree growth for 12 climate scenarios.

4.1.2 Which rust traits were best for characterizing rust hazard?

I used RF regression models to identify which rust traits were best for characterizing rust hazard. For these analyses, rust traits were the dependent variables and environmental variables were the independent variables. I compared the rust traits based on the model RSQ values. The full models included all independent variables described in Tables 1 and 3. The reduced models included a subset of these variables selected using the *randomForest* R package.

All full and reduced models described in Tables 4-7 were significant at a p-value of < 0.001. Compared to the full models, the reduced models had higher RSQ values and fewer independent variables (Tables 4-7). Thus, only results from the reduced models are presented below. First, I analyzed the rust traits using only the environmental independent variables. Among the four rust traits, CANK% had the highest RSQ value (Table 4).

Next, I analyzed rust traits by adding tree growth, tree size, and tree age variables to the environmental variables. Compared to the other rust traits, CANK% had the highest RSQ values for all RF models, ranging from 45% to 49% (Tables 4-7). Based on RSQ, the overall rankings of the rust traits were CANK% > NUM_CANK > HT_CANK > RI. These results suggest that the CANK% models are better than the other traits for predicting rust hazard. NUM_CANK had the second-highest RSQ values overall (~34%; Tables 4-7). In contrast to CANK% and NUM_CANK, the RSQ values for HT_CANK and RI were low. RSQ values ranged between ~9-41% for HT_CANK, and the lowest RSQ values were consistently found for RI (Tables 4-7). The rust traits with the highest RSQ values (CANK% and NUM_CANK) were used for future projections of rust hazard (see below).

I found no strong evidence that sites with rust-resistant trees (SPECIES = RRSP and RRWWP) had less blister rust disease than did the naturally regenerated sites (SPECIES = SP and WWP). First, I included SPECIES as an independent variable in the RF models, but it did not appear in any of the reduced models (Tables 4-7). Second, based on ANOVA, the SPECIES means were not significantly different for CANK%, NUM_CANK, or RI (F-value = 0.265-0.369; p-value = 0.78-0.85). In contrast, HT_CANK was greater for the naturally regenerated SP sites (F-value = 9.46; p-value = $5.95e^{-06}$). Finally, the scatterplots and partial dependence plots of CANK% and NUM_CANK showed that there were no obvious differences between the naturally regenerated sites and rust-resistant sites (Figures 3-6). These results suggest that combined analyses of the rust-resistant and naturally regenerated sites are appropriate.

Table 4. Random Forest models used to predict rust traits from environmental independent variables.

Dependent variable	Reduced model* RSQ (%)	Reduced model* MSE	Full model† RSQ (%)	Full model† MSE	Variable importance score ranking of independent variables‡
Environmental independent variables					
CANK%	45.32	259.5	40.06	286.4	EMT, RH_at, NFFD_wt, Tmin_sm, RH_sm, CMD_sp, CMD, ASPECT
NUM_CANK	33.71	3.230	26.67	3.583	CMI_sm, Tmin_sm, bFFP, ASPECT
HT_CANK	9.05	3.374	-2.340	3.786	PAS, NFFD_sp, ELEV, NFFD_sm
RI	18.46	< 0.001	13.15	< 0.001	CMI_sm, Tmin_sm, RH_at, Tmin_sp, CMD, Eref_wt, NFFD_sp, DD18, PPT_sm, MWMT, SLOPE, ASPECT, RH_sp

* The reduced models included the rust variables and independent variables listed in the variable importance score column. RSQ is R-squared and MSE is mean square error.

† The full models included rust variables described in Table 1 and environmental variables described in Tables 2-3.

‡ Independent variables are listed in order of variable importance from highest to lowest based on %IncMSE.

Table 5. Random Forest models used to predict rust traits from environmental and tree growth independent variables.

	Reduced model*		Full model†		
Dependent variable	**RSQ (%)**	**MSE**	**RSQ (%)**	**MSE**	**Variable importance score ranking of independent variables‡**
Environmental and tree growth independent variables					
CANK%	49.08	242.5	44.03	264.7	HT/AGE, RH_sm, RH_at, Tmin_sm, Tmin_wt, CMD, TD, EMT, DD_18_sm, Tmin_sp, NFFD, DD_18, CMI_sm, MSP, PPT_wt, bFFP, SHM, ASPECT
NUM_CANK	34.83	3.190	28.40	3.498	CMI_sm, Tmin_sm, NFFD_sp, bFFP, ASPECT, HT/AGE
HT_CANK	18.38	2.987	1.890	3.629	bFFP, PAS, NFFD_sm, HT/AGE
RI	20.48	< 0.001	15.08	< 0.001	Tmin_sm, CMI_sm, RH_at, CMD, Tmin_sp, PPT_sm, DD18, NFFD_sp, MWMT, SLOPE, ASPECT, HT/AGE

* The reduced models included rust variables and independent variables listed in the variable importance score column. RSQ is R-squared and MSE is mean square error.

† The full models included rust and tree growth variables described in Table 1 and environmental variables described in Tables 2-3.

‡ Independent variables are listed in order of variable importance from highest to lowest based on %IncMSE.

Table 6. Random Forest models used to predict rust traits from environmental and tree size independent variables.

Dependent variable	Reduced model* RSQ (%)	Reduced model* MSE	Full model† RSQ (%)	Full model† MSE	Variable importance score ranking of independent variables‡
Environmental and tree size independent variables					
CANK%	46.46	253.7	40.32	282.3	Tmin_sm, NFFD_wt, RH_at, RH_sm, CMD, NFFD, bFFP, SHM, Tmin_sp, RH, ASPECT
NUM_CANK	33.47	3.249	26.03	3.614	CMI_sm, Tmin_sm, bFFP, ASPECT
HT_CANK	35.39	2.382	26.70	2.711	HT, bFFP
RI	26.58	< 0.001	20.00	< 0.001	CMI_sm, Tmin_sm, CMD, bFFP, Eref_wt, RH_at, MWMT, HT, ASPECT

* The reduced models included rust variables and independent variables listed in the variable importance score column. RSQ is R-squared and MSE is mean square error.

† The full models included rust and tree size variables described in Table 1 and environmental variables described in Tables 2-3.

‡ Independent variables are listed in order of variable importance from highest to lowest based on %IncMSE.

Table 7. Random Forest models used to predict rust traits from environmental and tree age independent variables.

	Reduced model*		Full model†		
Dependent variable	**RSQ (%)**	**MSE**	**RSQ (%)**	**MSE**	**Variable importance score ranking of independent variables‡**
Environmental and tree age independent variables					
CANK%	49.01	242.0	43.30	268.2	RH_at, RH_sm, EMT, Tmin_sp, AGE, Tmin_sm, Tmin_wt, DD_18_sm, CMD, CMI_sm, MSP, ASPECT
NUM_CANK	32.64	3.296	27.06	3.564	Tmin_sm, Tmin_sp, CMI_sm, NFFD_sp, ASPECT
HT_CANK	41.32	2.200	32.15	2.510	AGE, CMI, RH_at, bFFP
RI	24.23	< 0.001	16.94	< 0.001	RH_at, CMI_sm, Eref_wt, bFFP, MWMT, SLOPE, Eref_sm, CMD, AGE, ASPECT

* The reduced models included rust variables and independent variables listed in the variable importance score column. RSQ is R-squared and MSE is mean square error.

† The full models included rust and tree age variables described in Table 1 and environmental variables described in Tables 2-3.

‡ Independent variables are listed in order of variable importance from highest to lowest based on %IncMSE.

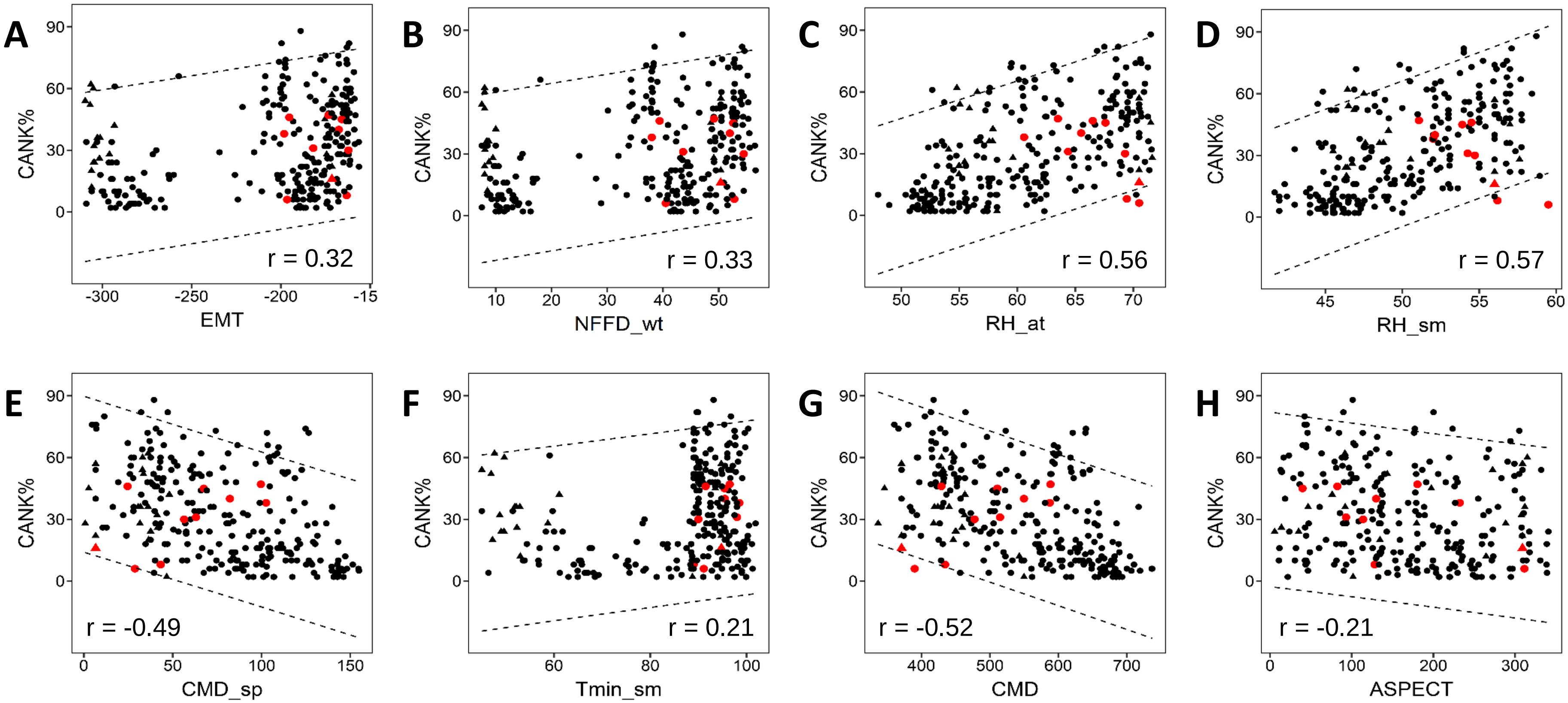

Figure 3: Scatterplots showing the relationships between CANK% versus the environmental variables listed in Table 4. Relationships between the percentage of trees with a stem canker (CANK%) versus (A) extreme minimum temperature over 30 years (EMT, °C), (B) number of frost-free days in the winter (NFFD_wt, days), (C) autumn relative humidity (RH_at, %), (D) summer relative humidity (RH_sm, %), (E) Hargreaves climatic moisture deficit (CMD_sp, mm), (F) summer mean minimum temperature (Tmin_sm, °C), (G) Hargreaves climatic moisture deficit (CMD, mm), (H) aspect (ASPECT, degrees). Black points are the values for the naturally-regenerated sites of sugar pine (SP, ●) and western white pine (WWP, ▲). Red points are the values for the rust-resistant sites of sugar pine (RRSP, ●) and western white pine (RRWWP, ▲). The dashed lines represent 95% prediction intervals.

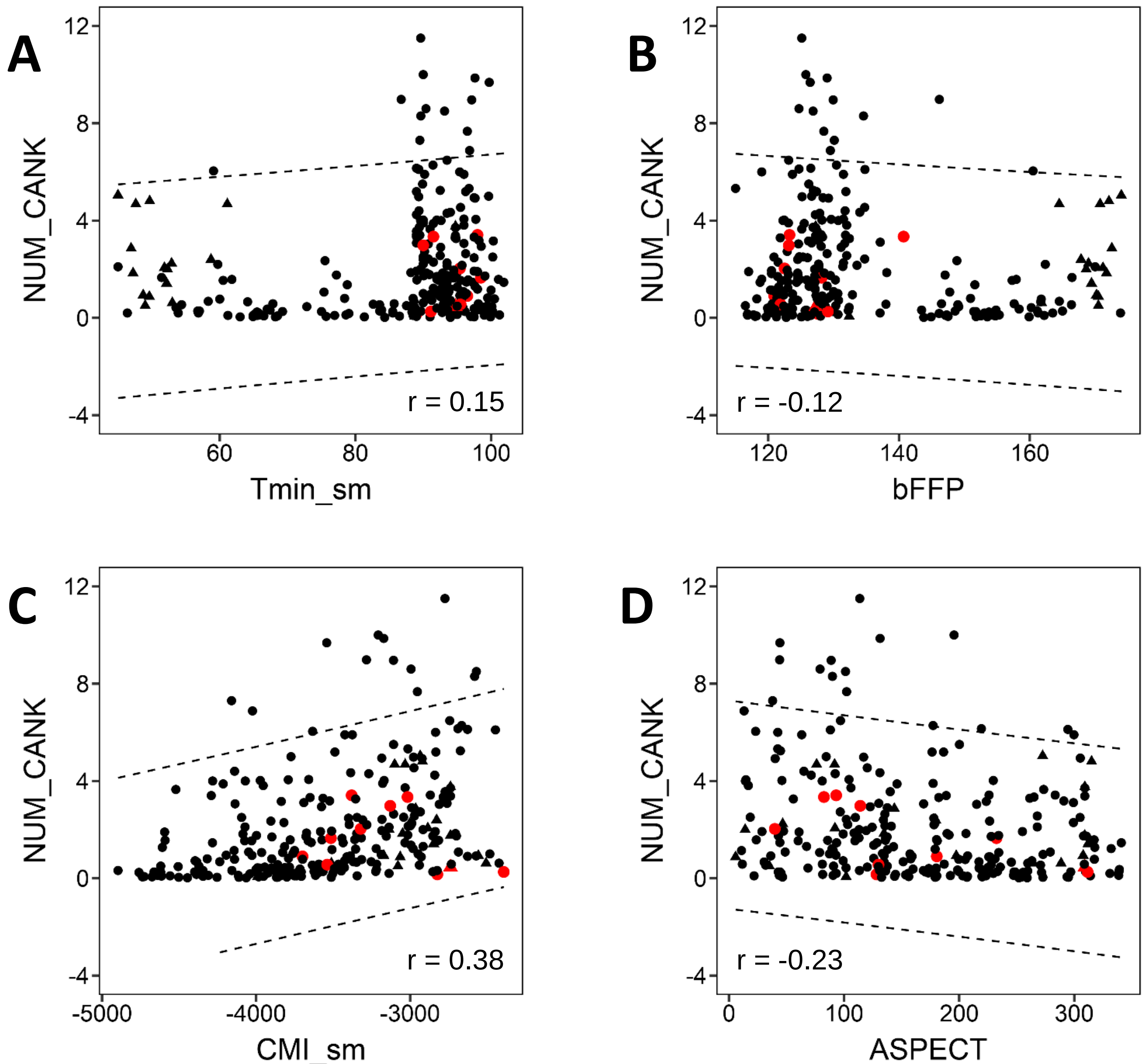

Figure 4: Scatterplots showing the relationships between NUM_CANK versus the environmental variables listed in Table 4. Relationships between the number of cankers per tree (NUM_CANK) versus (A) summer mean minimum temperature (Tmin_sm, °C), (B) day of the year on which the frost-free period begins (bFFP, Julian date), (C) summer Hogg's climate moisture index (CMI_sm, mm), and (D) aspect (ASPECT, degrees). Black points are the values for the naturally-regenerated sites of sugar pine (SP, ●) and western white pine (WWP, ▲). Red points are the values for the rust-resistant sites of sugar pine (RRSP, ●) and western white pine (RRWWP, ▲). The dashed lines represent 95% prediction intervals.

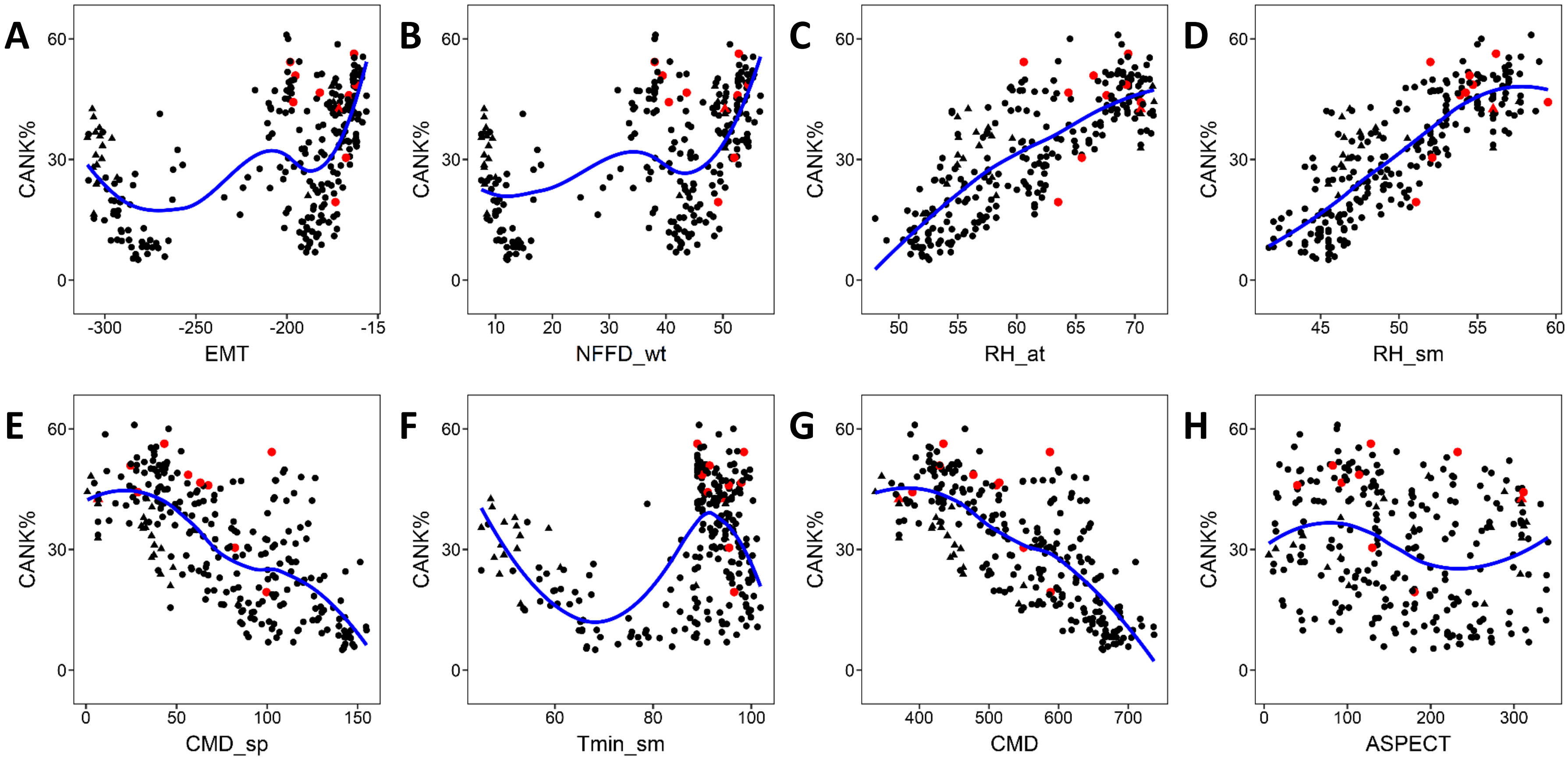

Figure 5: Partial dependency plots showing the relationships between CANK% versus the environmental variables listed in Table 4. Relationships between the percentage of trees with a stem canker (CANK%) versus (A) extreme minimum temperature over 30 years (EMT, °C), (B) number of frost-free days in the winter (NFFD_wt, days), (C) autumn relative humidity (RH_at, %), (D) summer relative humidity (RH_sm, %), (E) Hargreaves climatic moisture deficit (CMD_sp, mm), (F) summer mean minimum temperature (Tmin_sm, °C), (G) Hargreaves climatic moisture deficit (CMD, mm), (H) aspect (ASPECT, degrees). Black points are the values for the naturally-regenerated sites of sugar pine (SP, ●) and western white pine (WWP, ▲). Red points are the values for the rust-resistant sites of sugar pine (RRSP, ●) and western white pine (RRWWP, ▲).

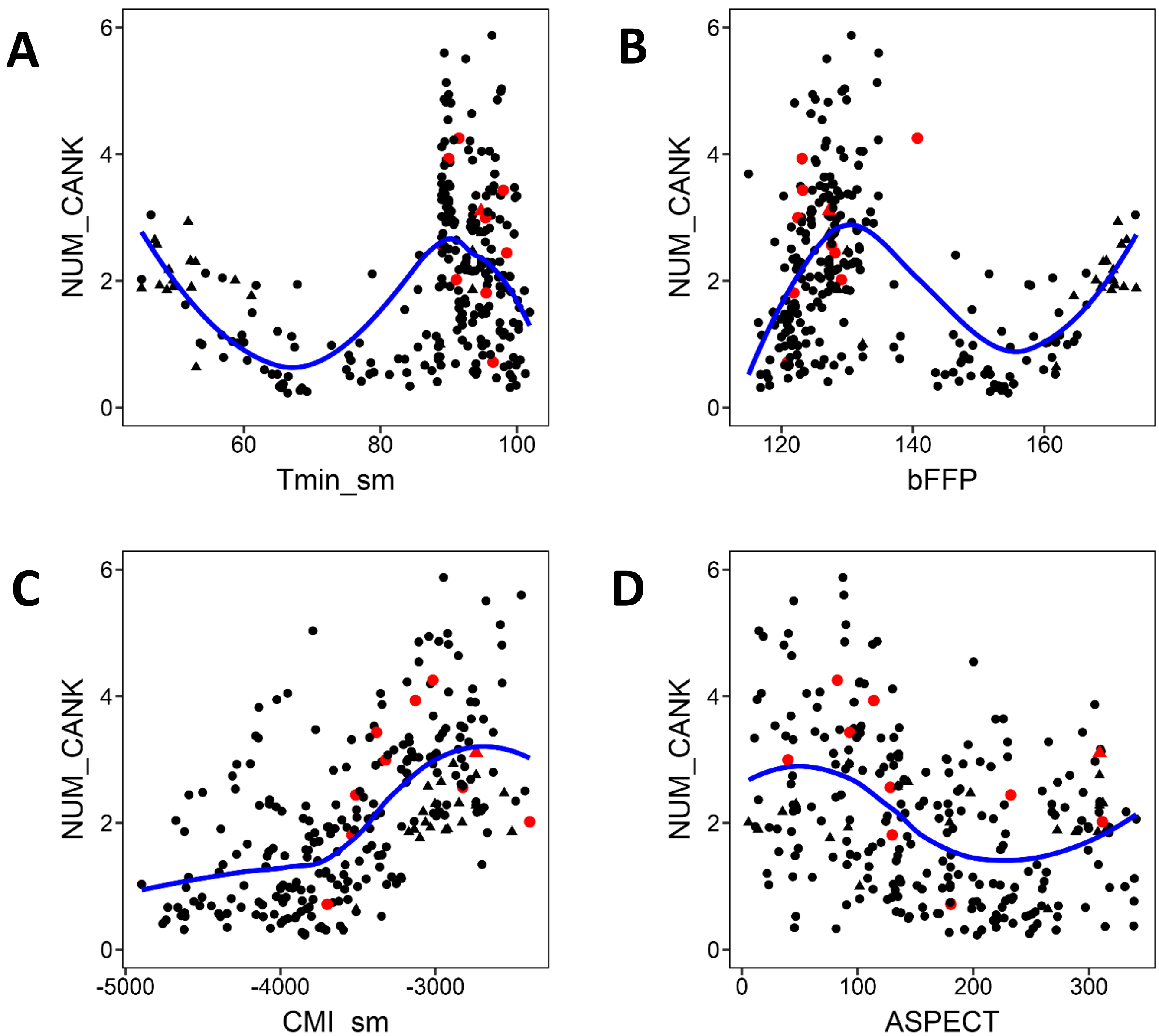

Figure 6: Partial dependency plots showing the relationships between NUM_CANK versus the environmental variables listed in Table 4. Relationships between the number of cankers per tree (NUM_CANK) versus (A) summer mean minimum temperature (Tmin_sm, °C), (B) day of the year on which the frost-free period begins (bFFP, Julian date), (C) summer Hogg's climate moisture index (CMI_sm, mm), and (D) aspect (ASPECT, degrees). Black points are the values for the naturally-regenerated sites of sugar pine (SP, ●) and western white pine (WWP, ▲). Red points are the values for the rust-resistant sites of sugar pine (RRSP, ●) and western white pine (RRWWP, ▲).

4.1.3 Which environmental variables were most closely associated with rust hazard?

A second objective was to identify which environmental variables were most closely associated with rust hazard. I used correlations and RF models to identify the relative importance of independent environmental variables for predicting rust traits. As described above, I used CANK% and NUM_CANK as the dependent variables, and environmental variables as the independent variables. One purpose of these analyses was to identify the best climate variables to use for future projections of rust incidence and severity (see below).

Based on univariate correlation coefficients, CANK% and NUM_CANK were associated with climate variables and ASPECT (Figures 3, 4 and 7). CANK% was positively associated with RH_sm and RH_at, with correlation coefficients of 0.57 and 0.56, respectively ($p < 0.001$). CANK% was also positively associated with NFFD_wt, EMT, and Tmin_sm, but these correlations were relatively low (i.e., 0.33, 0.32, and 0.21, respectively, $p < 0.001$). In contrast, CANK% was negatively correlated with variables representing climate moisture deficit (CMD and CMD_sp), with correlation coefficients of -0.52 and -0.49, respectively ($p < 0.001$). CANK% and NUM_CANK were greater on sites with northern, eastern, and northeasterly aspects. That is, CANK% was negatively associated with ASPECT, with a correlation coefficient of -0.21 ($p < 0.001$). NUM_CANK was positively associated with Tmin_sm and CMI_sm (Figures 4 and 7). The correlation coefficients were low for Tmin_sm (0.15) and CMI_sm (0.38) ($p < 0.001$). NUM_CANK was negatively associated with bFFP and ASPECT. The correlation was very low for bFFP (-0.12) and low for ASPECT (-0.23) ($p < 0.001$).

Next, I calculated variable importance (VI) scores using randomForest to judge the relative importance of the independent variables. In contrast to the univariate correlations described above, these analyses accounted for the multivariate relationships among the independent variables.

Among the independent variables, the climate variables had higher VI scores than did the topographic variables (Figures 8-9). Based on the CANK% model with environmental independent variables, the top-ranked variables were climate variables, followed by ASPECT (Figure 8A). The important climate variables were associated with temperatures in the winter and summer (EMT, NFFD_wt, and Tmin_sm), relative humidity in the fall and summer (RH_at and RH_sm, and climate moisture index (CMD_sp and CMD) (Figure 8A; Table 3). The VI score for the low temperature variable (EMT) was greater than the VI scores for the relative humidity variables (RH_sm and RH_at) (Figure 8A).

Based on the NUM_CANK models, the climate variables had higher VI scores than did the topographic variables (Figure 9). For example, the top-ranked variables were climate variables, followed by ASPECT (Figure 9). Using only the environmental variables as predictors, the most important climate variables were associated with moisture in the summer (CMI_sm) and temperatures in the summer and spring (Tmin_sm and bFFP) (Figure 9A, Table 3). The VI score for the summer moisture variable (CMI_sm) was greater than the VI score for the summer temperature variable (Tmin_sm) (Figure 9A).

Overall, CANK% and NUM_CANK tended to be higher at warmer and less-droughty sites (Figures 3-6). Based on analyses of CANK% and NUM_CANK, ASPECT was an important topographic variable. ASPECT occurred in models for both traits, ranking higher in VI score than did the other topographic variables, SLOPE and ELEV (Figures 8 and 9).

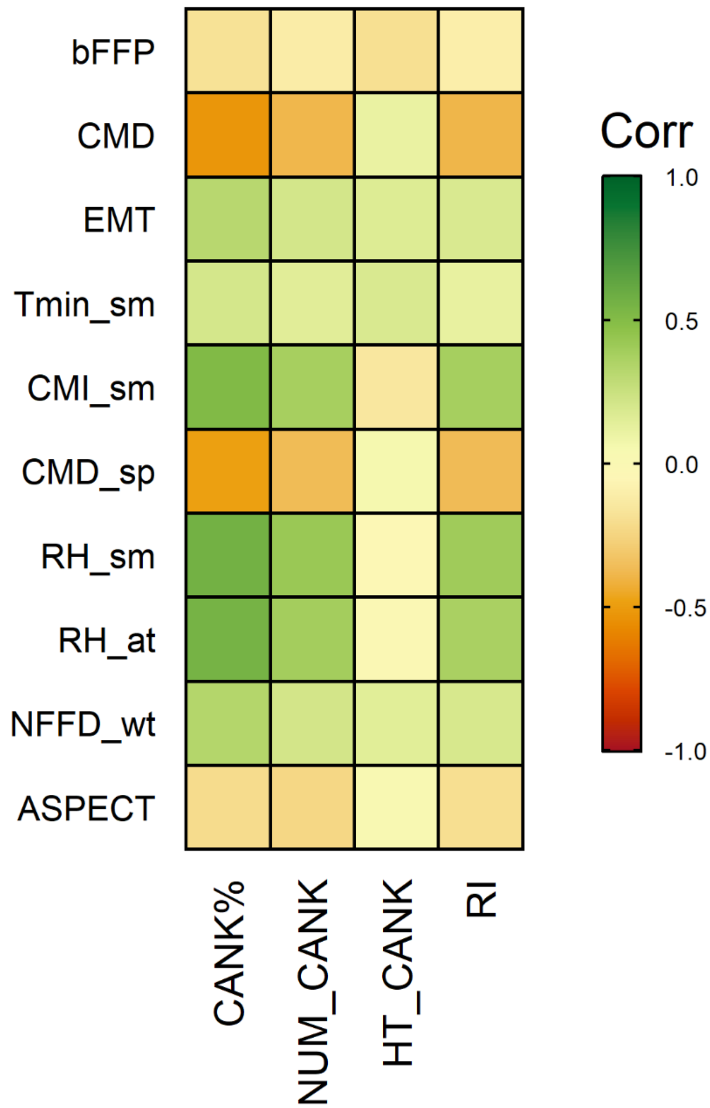

Figure 7: Heat map of correlation coefficients among rust and environmental variables. Tree variables are described in Table 1, and environmental variables are described in Tables 2-3. Correlation coefficients were calculated among 265 study sites of western white pine, sugar pine, rust-resistant western white pine, and rust-resistant sugar pine. Cool and warm colors of the heat map cells represent positive and negative correlation, respectively—the darker the color stronger the correlation.

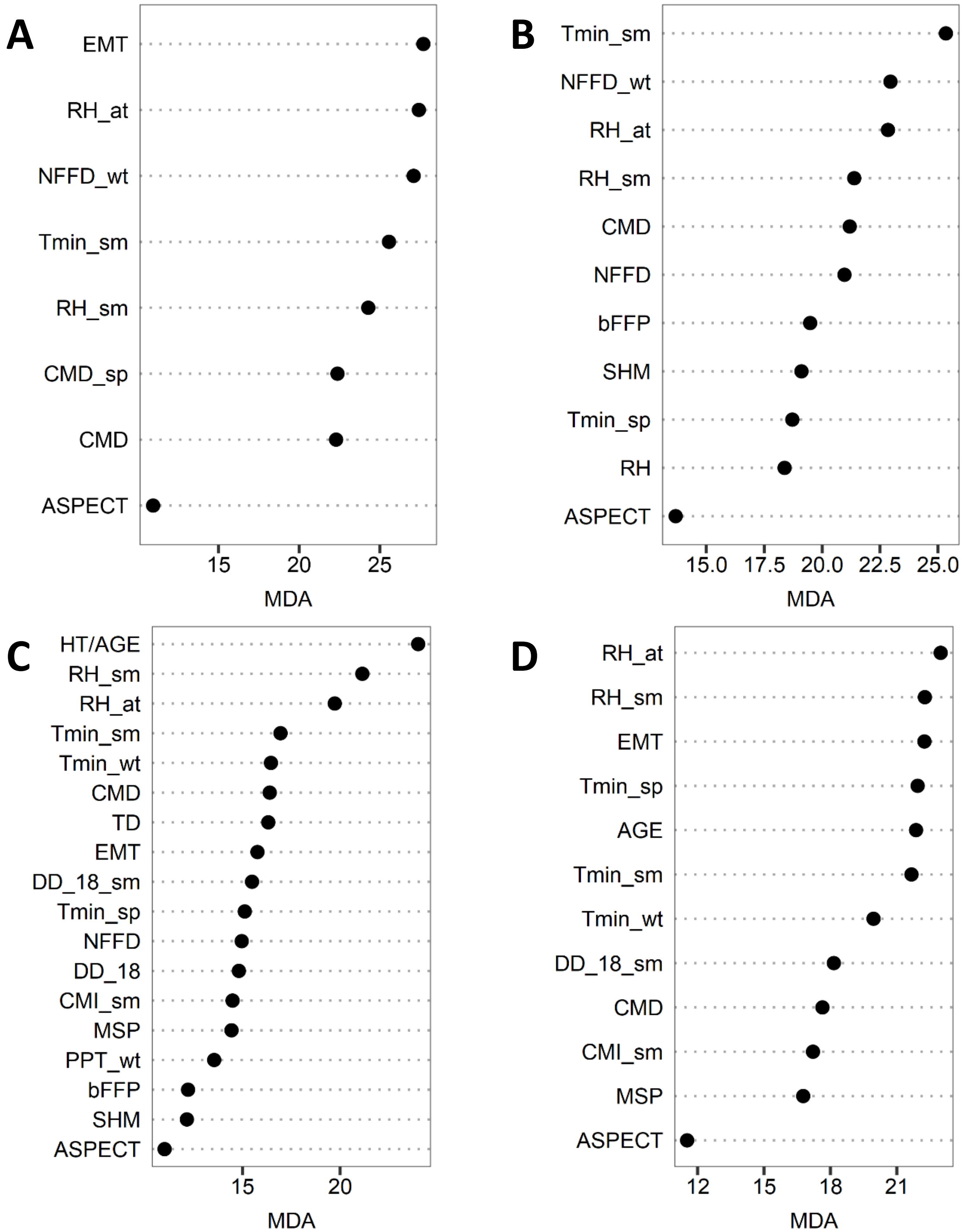

Figure 8: Variable importance (VI) rankings for CANK% based on Random Forest regression models. Variable importance values of independent variables for predicting the percentage of trees with a stem canker (CANK%) were based on the mean decrease in accuracy (MDA). Independent variables used in the four Random Forest models were (A) environmental variables, (B) environmental and tree size variables, (C) environmental and tree growth variables, and (D) environmental and tree age variables. These variables are described in Tables 1-3.

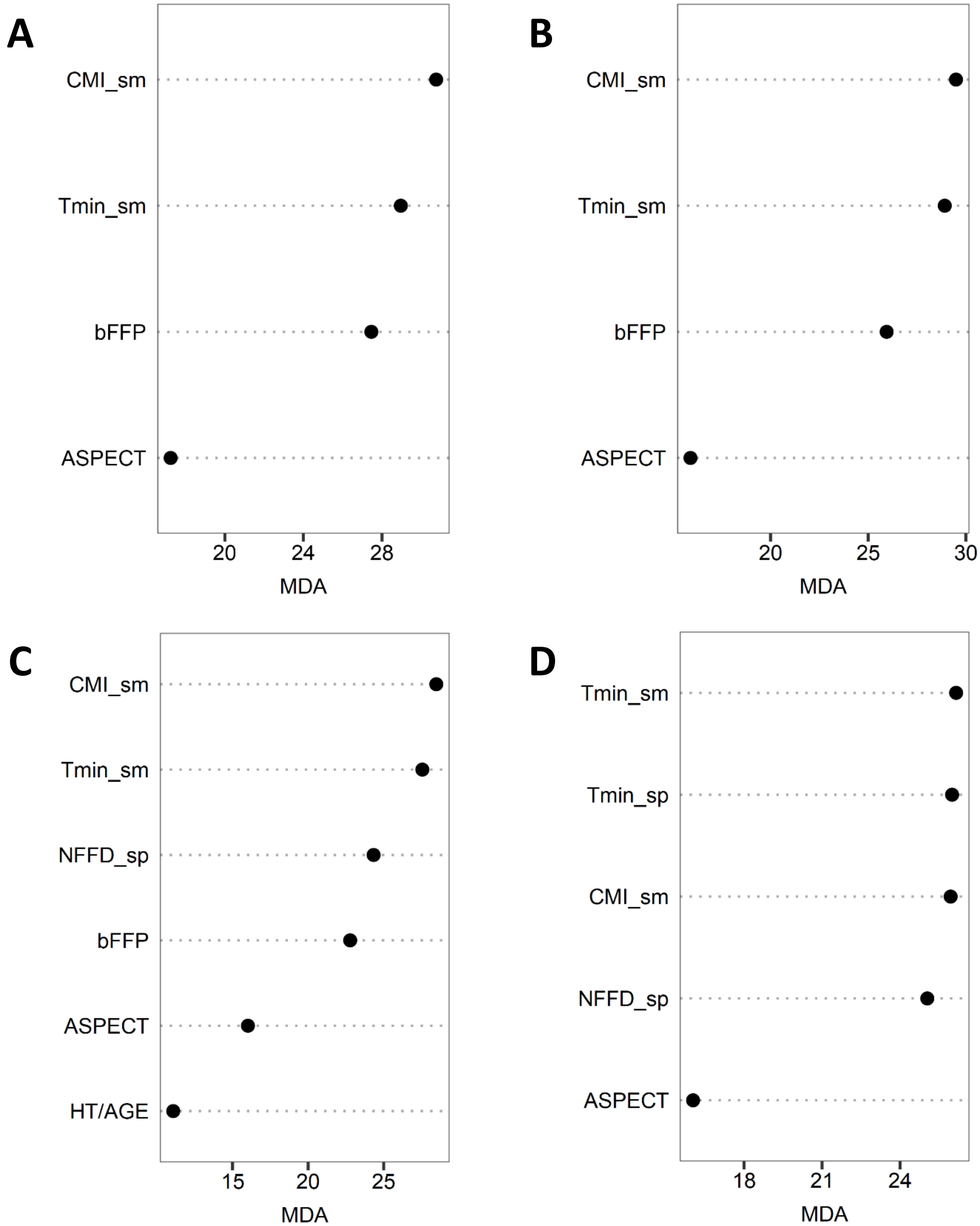

Figure 9: Variable importance (VI) rankings for NUM_CANK based on Random Forest regression models. Variable importance values of independent variables for predicting the number of cankers per tree (NUM_CANK) were based on the mean decrease in accuracy (MDA). Independent variables used in the four Random Forest models were (A) environmental variables, (B) environmental and tree size variables, (C) environmental and tree growth variables, and (D) environmental and tree age variables. These variables are described in Tables 1-3.

4.1.4 How were rust traits affected by tree characteristics?

I used correlations and RF models to infer the relative importance of tree characteristics to the incidence and severity of rust disease. For these analyses, rust traits were the dependent variables, and tree characteristics and environmental variables were the independent variables. First, I calculated correlation coefficients between rust traits versus tree growth (HT/AGE), tree age (AGE), and tree height (HT). Correlations between rust traits and HT/AGE were weak, ranging from -0.16 to 0.22 (Figure 10). CANK%, NUM_CANK, and RI had weak positive correlations with HT/AGE, whereas HT_CANK had a weak negative correlation. Correlations between rust traits and AGE were stronger than they were for HT/AGE (Figure 10). HT_CANK had a strong positive correlation with AGE (0.65), but CANK% and RI had moderate negative correlations (-0.37 and -0.35, respectively). HT_CANK was the only rust trait that had a relatively strong positive correlation with HT (0.44) (Figure 10). The correlations were low negative for CANK% (-0.10) and NUM_CANK (-0.05), and low moderate for RI (-0.30). Next, I calculated variable importance (VI) scores to judge the relative importance of the independent variables. The growth trait, HT/AGE, was included in the RF models for all four rust traits (Table 5). For example, using CANK% as the dependent variable, HT/AGE had the highest VI scores among the independent variables (Table 5). For the other rust traits, the VI rank for HT/AGE varied relative to the environmental variables. HT was included in the RF models for HT_CANK and RI (Table 6). Based on VI scores, HT was the most important variable in the HT_CANK RF model, followed by the climate variable, bFFP. HT was less important in the RF model for RI (Table 6). AGE was included in the RF models for CANK%, HT_CANK, and RI, but not for NUM_CANK (Table 7). For example, AGE was the top-ranked variable for HT_CANK, followed by climate variables (Table 7). However, AGE had lower VI scores than did the climate variables for CANK% and RI (Table 7).

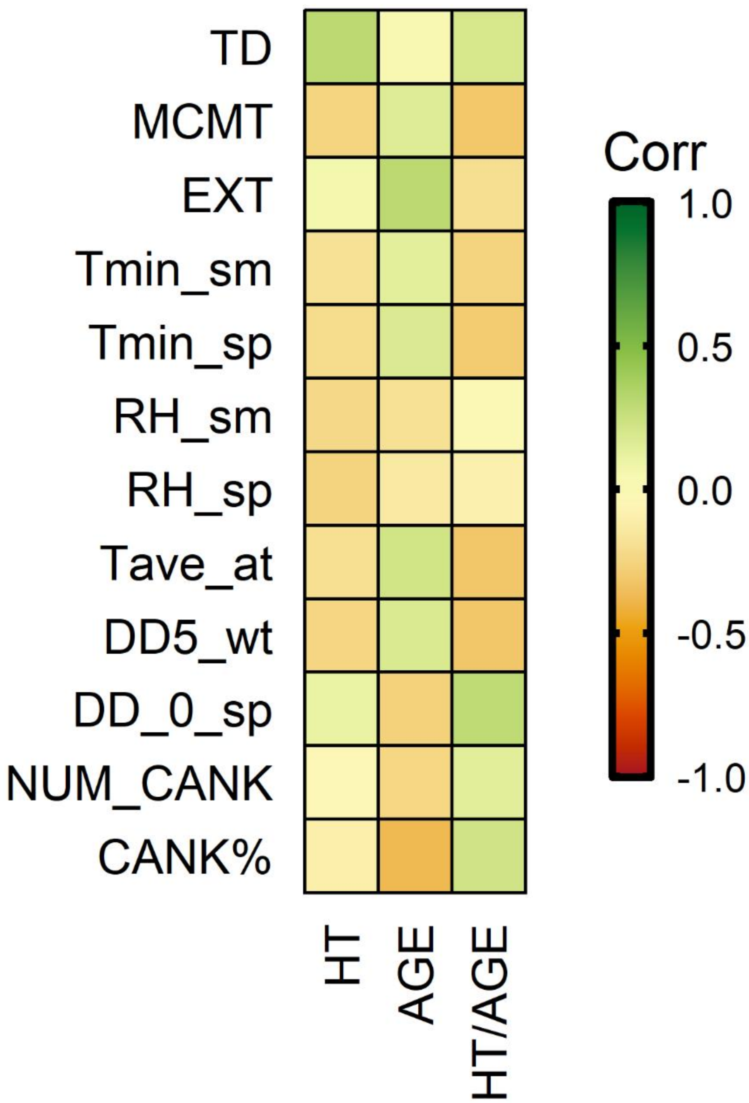

Figure 10: Heat map of correlation coefficients among tree and environmental variables. Tree variables are described in Table 1, and environmental variables are described in Tables 2-3. Correlation coefficients were calculated among 265 study sites of western white pine, sugar pine, rust-resistant western white pine, and rust-resistant sugar pine. Cool and warm colors of the heat map cells represent positive and negative correlation, respectively—the darker the color stronger the correlation.

4.1.5 How was tree growth affected by environmental variables and rust traits?

I calculated correlations and developed RF models using tree growth as the dependent variable and rust traits and environmental variables as the independent variables. One objective of these analyses was to identify the best independent variables to use for future projections of tree growth (see below).

First, I calculated correlation coefficients between tree growth (HT/AGE) versus the environmental variables. HT/AGE had weak negative correlations with climate variables (i.e., -0.31 to -0.03), except for DD_0_sp (0.30) and TD (0.20) (Figure 10; $p < 0.001$). Next, I calculated variable importance (VI) scores to judge the relative importance of the independent variables on tree growth. I developed two RF models for HT/AGE. The RSQ of the first model, which included only environmental independent variables, was much lower (32%) than the RSQ of the second model, which included the rust variables, too (Table 8).

In the first model, the temperature variable had a higher VI score than did moisture variable (Figure 11A). The important variables were associated with low temperatures in fall (Tave_at), spring relative humidity (RH_sp), low temperatures in the summer and spring (Tmin_sm and Tmin_sp), mean coldest temperature month (MCMT), extreme maximum temperature over 30 years (EXT), and high temperatures in winter (DD5_wt) (Figure 11A; Table 3). CANK% and NUM_CANK were included in the second HT/AGE RF model, but the climate variables had higher VI scores than did these rust variables (Table 8, Figure 11B).

For the second HT/AGE model, the most important climate variables were associated with low temperatures in spring (DD_0_sp), high temperatures in winter (DD5_wt), extreme maximum temperature over 30 years (EXT), mean coldest temperature month (MCMT and TD), relative humidity in summer (RH_sm), and low temperatures spring and summer (Tmin_sp, Tmin_sm) (Figure 11B, Table 3). Once the important rust traits and climate variables were identified, they were used for future projections of tree growth (see below).

Table 8. Random Forest models used to predict tree growth from environmental and rust independent variables.

Dependent variable	Reduced model* RSQ (%)	Reduced model* MSE	Full model† RSQ (%)	Full model† MSE	Variable importance score ranking of independent variables‡
Environmental independent variables					
HT/AGE	14.64	0.026	6.240	0.028	Tave_at, RH_sp, Tmin_sm, MCMT, EXT, DD5_wt, Tmin_sp
Environmental and rust independent variables					
HT/AGE	21.41	0.024	14.28	0.026	DD_0_sp, NUM_CANK, DD5_wt, CANK%, EXT, MCMT, RH_sm, Tmin_sp, TD, Tmin_sm

* The reduced models included tree growth and independent variables listed in the variable importance score column. RSQ is R-squared and MSE is mean square error.

† The full models included tree growth and rust variables described in Table 1 and environmental variables described in Tables 2-3.

‡ Independent variables are listed in order of variable importance from highest to lowest based on %IncMSE.

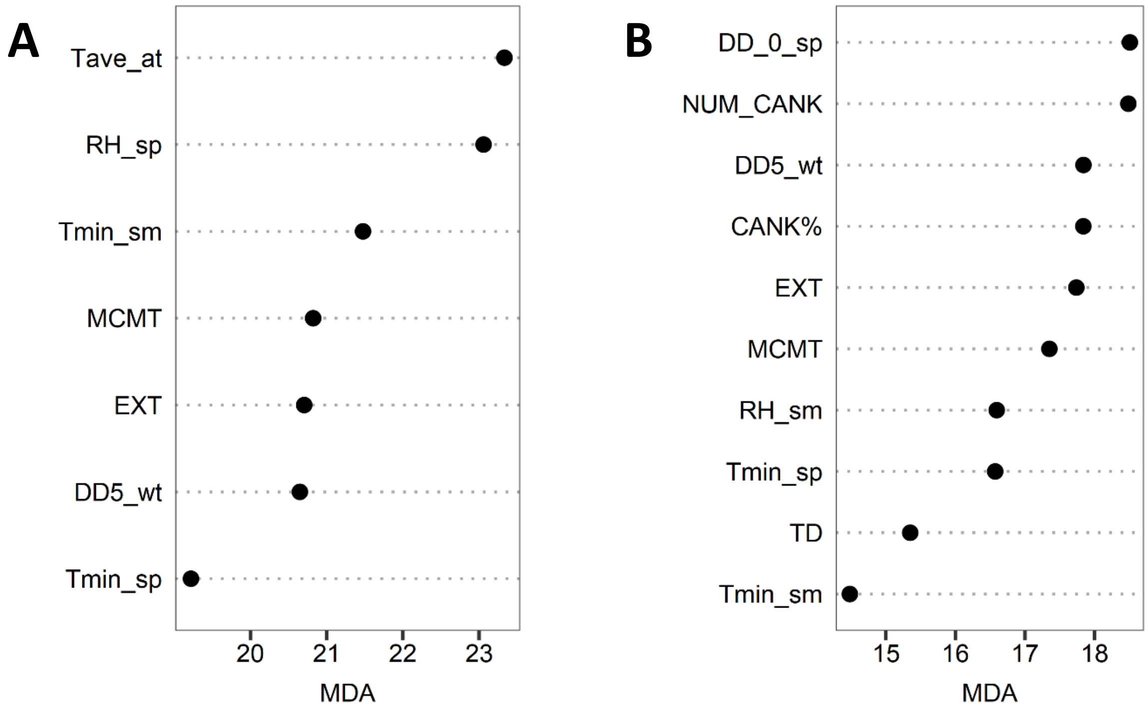

Figure 11: Variable importance (VI) rankings for HT/AGE based on Random Forest regression models. Variable importance values of independent variables for predicting (HT/AGE, feet/years) were based on the mean decrease in accuracy (MDA). Independent variables used in the two Random Forest models were (A) environmental variables and (B) environmental and rust variables. These variables are described in Tables 1-3.

4.1.6 How will rust traits change under future climates?

I used the CANK% and NUM_CANK prediction models to project how rust traits will change under future climates. For the CANK% prediction model, the predictors were seven future climate variables and ASPECT (Table 4). For the NUM_CANK prediction model, the predictors were a different set of three future climate variables and ASPECT (Table 4).

Overall, projected changes in the rust traits were small. Among all SSPs and years, differences in CANK% were no more than 2%. That is, the minimum and maximum values were 29% and 31% of trees with cankers (Figure 13). Among all SSPs and years, differences in NUM_CANK were no more than 0.9 cankers per tree (Figure 13).

Projected changes were also inconsistent between rust traits (Figures 12 and 13). For CANK%, there was no significant change in CANK% by the end of the century under any of the SSPs (i.e, year 2085, Table 9, Figure 12). In contrast, there was a significant decrease in NUM_CANK between 1985 and 2085 under all SSPs (Table 9, Figure 13). Thus, these two rust traits tell different stories.

Finally, projected changes in CANK% were inconsistent among the years. Compared to 1985 and 2085, there was a small decrease in CANK% in the mid-years (i.e., 2025 and 2055) (Table 9, Figure 12). Because projected changes in the rust traits are expected to be gradual over time, this pattern of change was unexpected (Figure 12). The main conclusion from these results is that projected changes in rust disease are uncertain, but will probably not be large.

Table 9. One-way analyses of variance (ANOVA) for measured and projected rust and tree growth variables under historical climate (1930-1990) and 12 climate change scenarios consisting of 4 Shared Socioeconomic Pathways (SSPs) and three future time periods (Years = 2011-2040, 2041-2070, and 2071-2100). CANK% is the percentage of trees with a stem canker, NUM_CANK is number of cankers per tree, and HT/AGE is tree growth.

	Year (treatment)*			**Residual (error)***			**F-test***	
Scenario[†]	**Df**	**Sum sq**	**Mean sq**	**Df**	**Sum sq**	**Mean sq**	**F-value**	**Pr**
CANK%								
SSP126	3	981	327	1052	135863	129.1	2.53	0.0557
SSP245	3	1041	347.1	1052	126308	120.1	2.89	0.0345
SSP370	3	1532	510.7	1052	133275	126.7	4.03	0.00728
SSP585	3	757	252.4	1052	120770	114.8	2.20	0.0866
NUM_CANK								
SSP126	3	59.30	19.77	1052	1050.7	0.999	19.80	$1.7\ 10^{-12}$
SSP245	3	70.50	23.51	1052	986.4	0.938	25.08	$1.13\ 10^{-15}$
SSP370	3	84.70	28.23	1052	1073.1	1.02	27.68	$<2\ 10^{-16}$
SSP585	3	105.90	35.29	1052	918.7	0.87	40.41	$<2\ 10^{-16}$
HT/AGE								
SSP126	3	0.27	0.08888	1052	3.617	0.00344	25.85	$3.87\ 10^{-16}$
SSP245	3	0.25	0.08323	1052	3.30	0.00314	26.53	$<2\ 10^{-16}$
SSP370	3	0.25	0.08178	1052	3.473	0.00330	24.77	$1.73\ 10^{-15}$
SSP585	3	0.25	0.08333	1052	3.045	0.00289	28.79	$<2\ 10^{-16}$
HT/AGE[†]								
SSP126	3	0.539	0.17951	1052	6.074	0.00577	31.09	$<2\ 10^{-16}$
SSP245	3	0.560	0.18672	1052	5.792	0.00551	33.91	$<2\ 10^{-16}$
SSP370	3	0.654	0.21811	1052	5.727	0.00544	40.06	$<2\ 10^{-16}$
SSP585	3	0.834	0.27793	1052	5.174	0.00492	56.51	$<2\ 10^{-16}$

[*]Df is degrees of freedom, Sum sq is sum of squares, Mean sq is mean square, F-value is F-statistic, and Pr is the p-value from one-way analyses of variance (ANOVA).

[†]Historical and future climate variables were obtained using ClimateNA v.7.01 and v.7.10 (Wang et al. 2016). Future climate variables were projected from the General Circulation Models (GCMs) of the Coupled Model Intercomparison Project (CMIP6) of the IPCC sixth assessment report (AR6).

[‡]CANK% and NUM_CANK were projected using only environmental variables as predictors. HT/AGE was projected using environmental variables and rust variables as predictors. These variables are described in Tables 1-3.

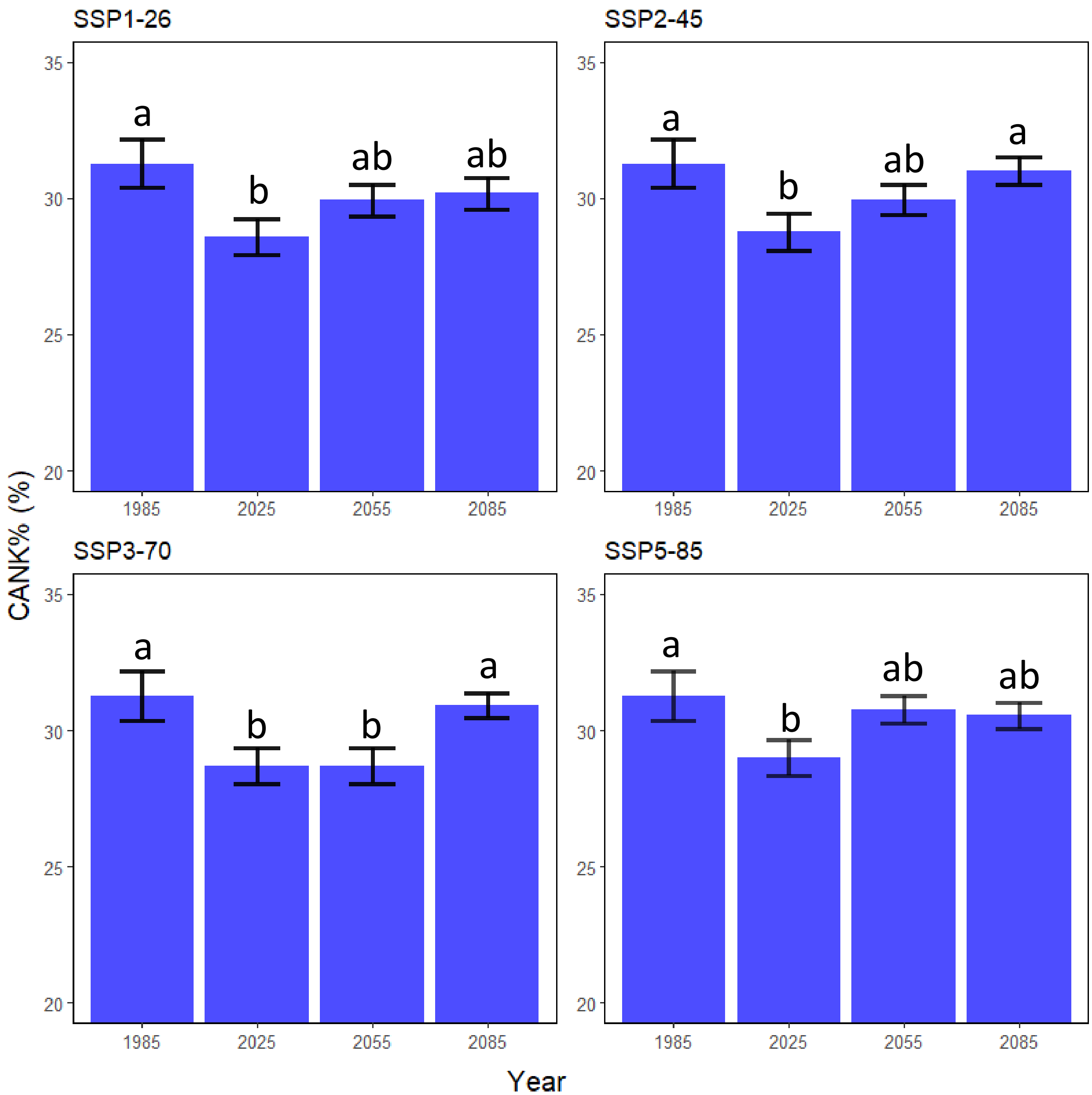

Figure 12: Historical and future projected percentages of trees with a stem canker (CANK%). CANK% was predicted using historical climate variables, 12 climate change scenarios, and other environmental variables. The climate change scenarios consisted of 4 Shared Socioeconomic Pathways (SSPs) and 3 future time periods (years = 2011-2040, 2041-2070, and 2071-2100). Environmental variables are described in Tables 2-3. Blue bars represent variable means, and error bars show the standard errors of the means for 265 study sites. Different letters indicate significant differences among means according to Tukey's honestly significant difference test.

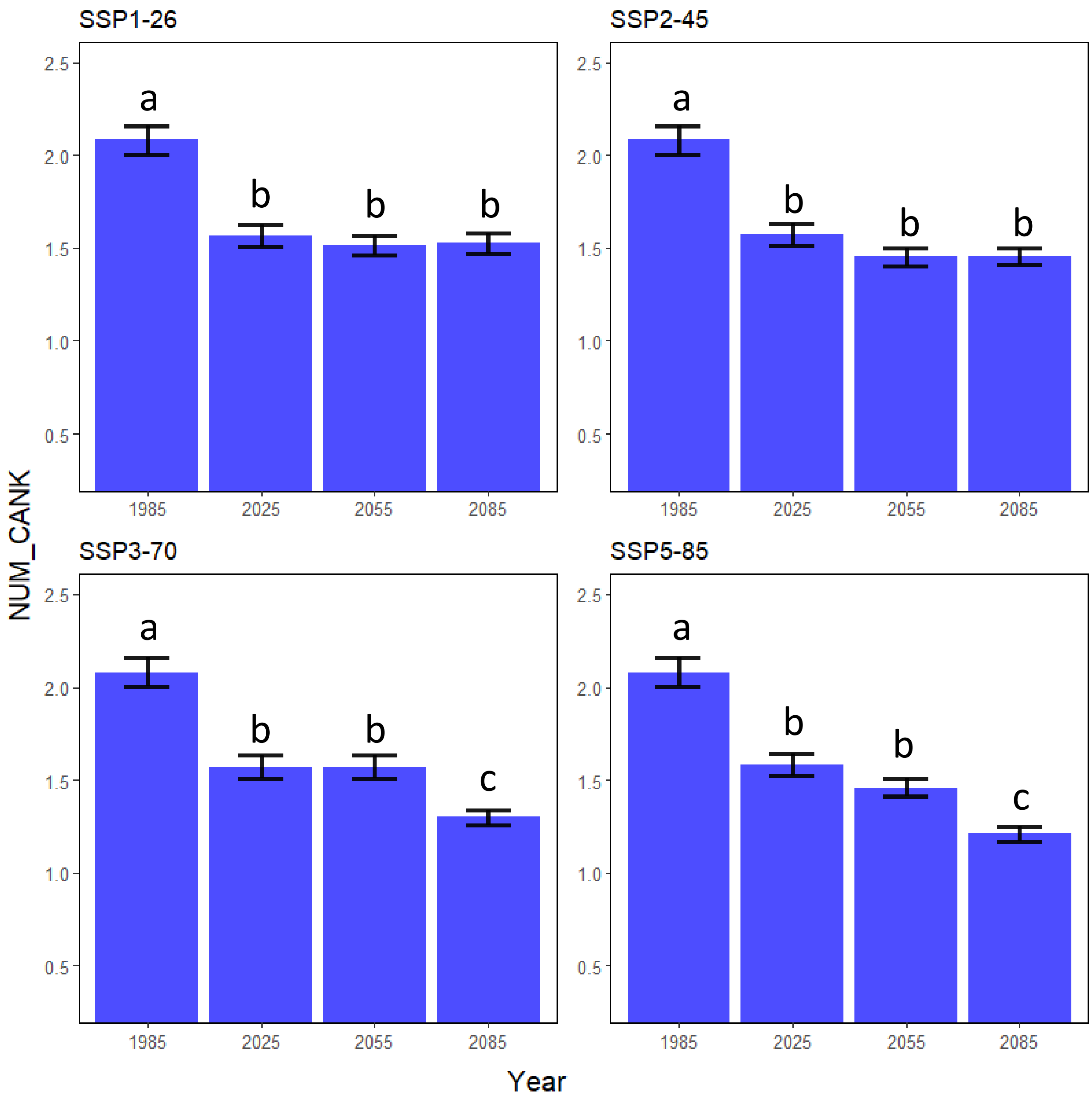

Figure 13: Historical and future projected numbers of cankers per tree (NUM_CANK). NUM_CANK was predicted using historical climate variables, 12 climate change scenarios, and other environmental variables. The climate change scenarios consisted of 4 Shared Socioeconomic Pathways (SSPs) and 3 future time periods (years = 2011-2040, 2041-2070, and 2071-2100). Environmental variables are described in Tables 2-3. Blue bars represent variable means, and error bars show the standard errors of the means for 265 study sites. Different letters indicate significant differences among means according to Tukey's honestly significant difference test.

4.1.7 How will tree growth change under future climates?

I used two tree growth prediction models to project future tree growth based on climate, topographic, and rust variables. For the first HT/AGE prediction model, I used seven future climate variables as predictors (Table 8). For the second HT/AGE prediction model, I used a different set of eight future climate variables, CANK%, and NUM_CANK (Table 8). Compared to 1985, there was a small increase in HT/AGE for prediction models by 2085 (Figures 14 and 15). The increases in HT/AGE were expected to be about 0.07 (feet/year) among all SSPs and years (Figures 14 and 15). The results were consistent among SSPs (Table 9, Figures 14 and 15). Overall, I observed a small increase in tree growth in the future compared to the past (Table 9, Figures 14 and 15). At the end of the century, HT/AGE was projected to be very slightly greater using the second model that included rust traits (Table 9, Figures 14 and 15). For example, there was a 0.05 (i.e., 0.51 versus 0.56) (feet/year) difference in HT/AGE between the two models under the most extreme SSP, which is SSP5-85 (Table 9, Figures 14 and 15). The main conclusion from these results is that the average growth rate will probably increase, but this increase will not be large.

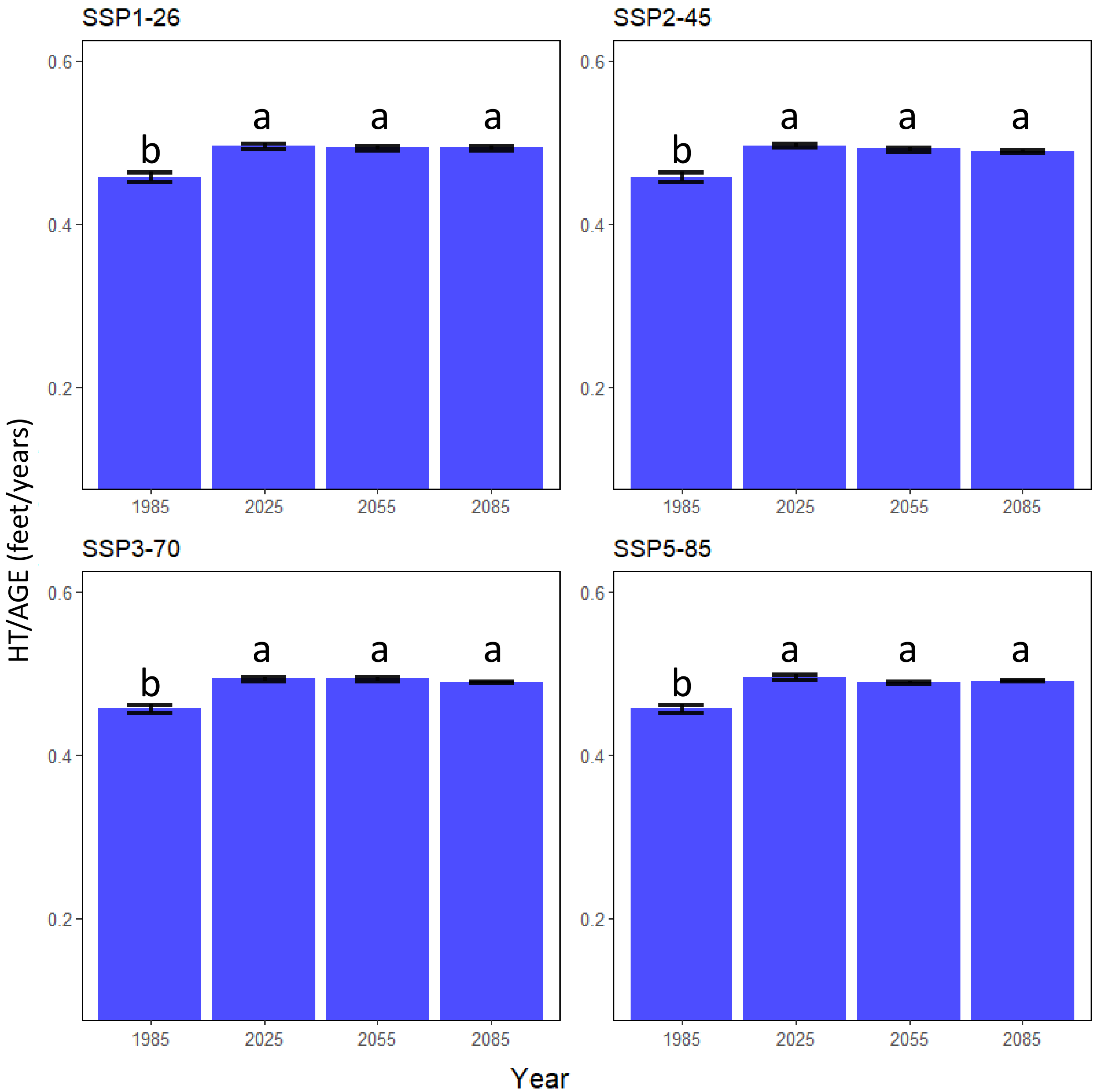

Figure 14: Historical and future projected tree growth (HT/AGE).
HT/AGE was predicted using historical climate variables, 12 climate change scenarios, and other environmental variables. The climate change scenarios consisted of 4 Shared Socioeconomic Pathways (SSPs) and 3 future time periods (years = 2011-2040, 2041-2070, and 2071-2100). Environmental variables are described in Tables 2-3. Blue bars represent variable means, and error bars show the standard errors of the means for 265 study sites. Different letters indicate significant differences among means according to Tukey's honestly significant difference test.

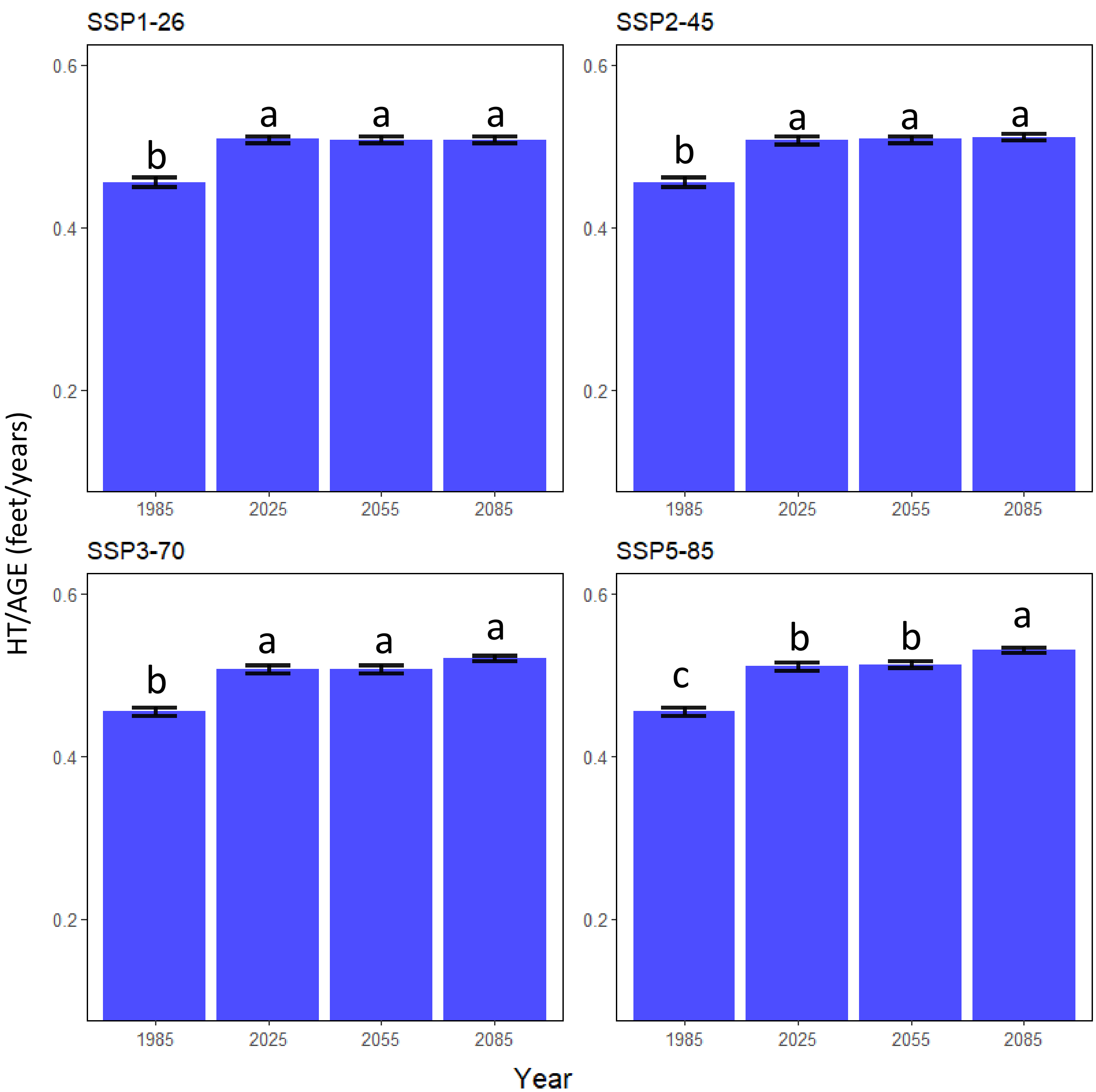

Figure 15: Historical and future projected tree growth (HT/AGE).
HT/AGE was predicted using historical climate variables, 12 climate change scenarios, rust variables, and other environmental variables. The climate change scenarios consisted of 4 Shared Socioeconomic Pathways (SSPs) and 3 future time periods (years = 2011-2040, 2041-2070, and 2071-2100). Rust variables are described in Table 1. Environmental variables are described in Tables 2-3. Blue bars represent variable means, and error bars show the standard errors of the means for 265 study sites. Different letters indicate significant differences among means according to Tukey's honestly significant difference test.

5. Chapter 5

5.1 Discussion

5.1.1 Approach

One of my objectives was to determine which rust traits are best for characterizing rust hazard. Among the rust traits, RI has been historically and widely used to measure and predict rust hazard (McDonald et al. 1981; Hagle et al. 1989; Koester et al. 2018). However, rust hazard might be measured using other rust traits as well. My second objective was to identify which environmental variables are most closely associated with rust hazard. As discussed in the Introduction, the pathogen requires certain environmental conditions to inoculate and spread (Geils et al. 2010). Thus, I expect that rust disease incidence and severity differ among sites. My third objective was to project changes in rust disease and tree growth using RF prediction models and 12 climate change scenarios. This information may provide new understanding of rust-environment interactions that can be used to manage WPBR. To address these questions and achieve the objectives described above, I used data from Koester et al. (2018), ClimateNA, and DEMs to build RF regression models for rust traits and tree growth.

5.1.2 Which rust traits were best for characterizing rust hazard?

I studied the relationships between rust traits versus environmental variables and tree characteristics to identify which rust traits were best for characterizing rust hazard. Various rust indices have been used to measure rust hazard of sites (Van Arsdel 1961; Hagle et al. 1989; Steele 1996). Van Arsdel (1961) recommended using an index to categorize rust hazard of sites to better manage WPBR. A rust hazard index is an indicator of the existing or potential infection level of a site, optimally reflecting both rust incidence and severity (Van Arsdel 1961; Hagle et al. 1989; Steele 1996). There are four characteristics of a good rust hazard index. A good rust hazard index is (1) closely associated with tree damage and death, (2) easy to measure precisely and accurately, (3) not confounded by non-rust tree variables, and (4) easy to predict from environmental variables. Because certain environmental conditions are required for rust disease development (Geils et al. 2010), rust hazard should be estimated considering environmental conditions (Van Arsdel 1961; Hunt 1983; Steele 1996; Geils et al. 1999).

Initially, the number of "cankers per tree" was used as a proxy for rust infection and damage (Stillinger 1943). Later, the number of pine needles was added to the measurement of rust hazard (Buchanan 1936) because the pathogen enters and infects through the stomata of the needles (Van Arsdel 1961; Geils et al. 2010). Individual needle bundles of western white pine were counted and multiplied by five to obtain the total number of needles (Buchanan 1936; Buchanan and Kimmey 1938). However, this measurement is not convenient and might be biased by different estimation approaches among observers. Buchanan (1936) and Buchanan and Kimmey (1938) estimated the number of needles from tree crown height and width, and then used the number of cankers per 1000 needles per year as an index of rust infection rate. McDonald et al. (1981) developed a computer program that can be used to analyze rust disease epidemics for western white pine using rust infection rate by estimating leaf (infection) surface area (cm2) of *Ribes*. Hagle et al. (1989) used tree age, tree height, and the number of cankers per tree to develop a rust index (RI). Measured trees must be at least 10 years old and less than 35 feet tall. This is because sites with trees less than 35 feet tall have a higher likelihood of current and future infections (Hagle et al. 1989). The units of the resulting RI are the number of cankers per 1000 needles per year. Hagle et al. (1989) concluded this index was reliable for estimating rust hazard and making effective management decisions for white pines. However, they also suggested that information on *Ribes* populations could be used to estimate rust hazard, but only if it was impossible to calculate rust index itself (e.g., for sites with no white pine trees). Koester et al. (2018) and I used the rust index described by Hagle et al. (1989) (i.e., RI = number of cankers per 1000 needles per year).

Below, I discuss RI, CANK%, NUM_CANK, and HT_CANK in relation to the characteristics of a good rust hazard index (described above). RI is a complex measure that integrates information on tree age, tree height, and the number of cankers per tree. The final units are number of cankers per 1000 needles per year. CANK%, the percentage of trees with a canker, is believed to reflect the severity of the disease and the distance from *Ribes* populations. For example, the percentage of trees with cankers decreased as the distance from alternate hosts increased (Buchanan and Kimmey 1938). NUM_CANK, the number of cankers per tree, is a component of RI, but does not include estimates of tree age, tree height, or indirectly, the number of needles per tree. HT_CANK, the height of the highest canker on the tree, may provide information about how the tree was infected. If cankers occur high in the crown, the trees are more likely to have been infected via basidiospores carried by the wind (McDonald et al. 1981). If the cankers are close to the bottom of the tree, the trees are more likely to have been infected by alternate hosts nearby (McDonald et al. 1981). I used the RF regression RSQ and correlation coefficients to identify which rust traits were best for characterizing rust hazard. RSQ is the percentage of among-site variation explained by the RF model. The main assumption underlying this approach is that rust traits with higher RSQ values were more closely associated with the environmental and tree independent variables.

A good rust hazard index is associated with tree damage and death. Each of my rust traits provides information on tree damage because they are based on the presence of cankers. Cankers occur on tree branches and bole, damaging and possibly killing the tree. The pathogen, which requires living tissue to survive, enters through the needles or bark, grows through the branches, and into the bole (McDonald et al. 1981; Geils et al. 2010). If branches die before the pathogen reaches the bole (e.g., via natural or manual pruning), the pathogen affects only the branches and does not cause stem cankers (McDonald et al. 1981; Geils et al. 2010). Trees with stem cankers are likely to die sooner than trees with only branch cankers (Hagle et al. 1989). Although branch cankers typically cause only the branches to die, a large abundance of branch cankers may also cause tree mortality (Mielke 1943; Burns et al. 2008). Overall, rust damage and mortality depend on the locations of cankers and the number of cankers on the tree. CANK% and HT_CANK may be less closely related to tree damage than are the other rust traits (RI and NUM_CANK) because they do not account for the number of cankers per tree. CANK% is the percentage of trees with at least one canker, and HT_CANK is the average height of the highest canker. NUM_CANK is the average number of cankers per tree. Hagle et al. (1989) and Mielke (1943) concluded there is a positive relationship between the number of cankers and the likelihood of tree death. One reason is that branch cankers are more likely to become stem cankers as the number of cankers increases. Hagle et al. (1989) concluded that information on the number of stem cankers improves the prediction of rust hazard. Thus, Hagle et al. (1989) integrated the number of cankers per tree into their RI metric.

A good rust hazard index is easy to measure precisely and accurately. RI requires multiple inputs to be measured; tree age, tree height, and the number of cankers per tree (Hagle et al. 1989), and each measurement may add error. For example, Koester et al. (2018) estimated tree age by counting whorls. In the calculation of RI, tree age and tree height are used to estimate the number of needles. Although the prediction accuracy for the number of needles was not reported, it is probably not high. Moreover, each variable needed to calculate RI requires time, money, and personnel to be measured. Thus, RI is difficult to measure precisely and accurately. Compared to RI, the other rust traits are easier to measure. CANK%, the easiest trait to measure, is estimated by counting trees having at least one canker on the stem. Stem cankers have distinctive shapes and are generally large enough to recognize from a distance. Stem cankers have discolored bark, yellow-orange canker margins, and resin leakage. NUM_CANK is more complex to measure because one must count the number of cankers anywhere on the tree (Koester et al. 2018). HT_CANK is not as complex as RI, but one must measure the height of the highest canker. However, Koester et al. (2018) found that HT_CANK was generally below 8 feet. Thus, CANK%, NUM_CANK, and HT_CANK can be measured more easily and accurately than RI can be.

A good rust hazard index is not confounded with non-rust tree variables. A good rust hazard index should reflect the potential of the site to develop WPBR, even if no white pine trees are present. Likewise, a good rust hazard index should be unrelated to the age and height of the existing trees. Based on correlations with AGE, the rankings of the rust traits were HT_CANK > CANK% > RI > NUM_CANK. That is, RI and NUM_CANK were the least closely related traits to tree age. Based on correlations with HT, the rankings of the rust traits were HT_CANK > RI > CANK% > NUM_CANK. That is, CANK% and NUM_CANK were the least closely related traits to tree height. Not surprisingly, HT_CANK had the strongest correlations with AGE and HT. In contrast, NUM_CANK had the weakest correlations with non-rust tree variables. The prediction models also support these conclusions. For example, AGE and HT did not occur in the NUM_CANK prediction models, and only AGE occurred in CANK% prediction model. Thus, overall, NUM_CANK and CANK% are less likely to be confounded with non-rust tree variables than are HT_CANK and RI.

A good rust hazard index is easy to predict from environmental variables. A good rust hazard index should be strongly associated with environmental variables that are responsible for site-to-site differences in rust hazard. I used the RSQ values to identify these rust traits. Based on the RSQ values, CANK% and NUM_CANK had the highest RSQs. That is, CANK% and NUM_CANK were the rust traits most closely associated with the environmental variables. In contrast, RI had the lowest RSQ among the rust traits, probably because of the errors associated with measuring RI (discussed above). HT_CANK had a low RSQ, probably because of the strong relationships with tree age and height (discussed above). Overall, CANK% and NUM_CANK had the strongest associations with environmental variables, and RI and HT_CANK had the weakest. The rust traits with the highest RSQ values (CANK% and NUM_CANK) were used for future projections of rust hazard (see below).

Based on the rust hazard criteria and my results, CANK% and NUM_CANK seem to be the best variables for measuring rust hazard. Both variables are relatively easy to measure precisely and accurately compared to RI. CANK% is easy to measure and had the highest RSQ, indicating the strongest association with environmental variables. NUM_CANK is somewhat harder to measure and had the second-strongest association with environmental variables. CANK% and NUM_CANK were also less confounded with non-rust tree variables. Thus, as direct measures of rust hazard, CANK% and NUM_CANK should be useful for improving management of sugar pine and western white pine sites that are climatically similar to the ones I studied. More importantly, the prediction models I developed should be useful for predicting rust hazard without measuring trees in the field. These prediction models could be used to create rust risk maps that would allow managers to consider management options. These management options might include identifying the optimum planting stock and sites for planting white pines, and applying silvicultural treatments in a timely and affordable manner. For example, forest managers could apply silvicultural treatments to sites where the disease is likely to occur, but before the disease becomes established.

5.1.3 Which environmental variables were most closely associated with rust hazard?

I studied the relationships between rust traits versus environmental variables to identify which environmental variables were most closely associated with rust hazard. I identified environmental variables associated with WPBR infection at the sites in southern Oregon. One purpose of these analyses was to identify the best climate variables to use for future projections of rust incidence and severity (see below). This information sheds light on the biology of rust infection, and the resulting RF regression models can be used to improve rust hazard maps.

The wind-borne aeciospores on infected pines can travel long-distances (~700 km) to infect *Ribes* species in spring (Mielke 1938; Mielke 1943; Campbell and Antos 2000). Mielke (1943) stated that aeciospore production on western white pines differs by seasonal environmental conditions. The pathogen produces basidiospores on the undersides of leaves of *Ribes* species, and these basidiospores reinfect pines in late summer and early autumn (Van Arsdel 1961). Basidiospores are short-lived and can be transmitted via only wind as far as ~2 km (Van Arsdel et al. 1956; Kinloch 2003; Geils et al. 2010). High relative humidity and mild temperatures are important for the pathogen to produce spores and complete its life-cycle (Van Arsdel et al. 1956; Geils et al. 2010). Thus, I predicted humidity and temperature variables would be associated with rust hazard.

Among the environmental variables, climate variables were more closely associated with rust traits than were the topographic variables—slope, aspect, and elevation. Based on the climate variables, my study indicated that rust hazard was greater at sites with milder temperatures and sufficient moisture. The potential reasons for these relationships are discussed below.

My first major conclusion was that rust hazard was greater at sites with milder temperatures in winter, spring, and summer. I found that CANK% and NUM_CANK were positively correlated with EMT and Tmin_sm. EMT is the extreme minimum temperature, and Tmin_sm is the minimum temperature in summer. Thus, a positive correlation indicated that increased rust disease was associated with milder temperatures in winter and summer. CANK% and NUM_CANK were positively correlated with NFFD_wt and negatively correlated with bFFP, indicating that increased rust disease was associated with longer growing seasons. NFFD_wt is the number of frost-free days in winter, and bFFP is the beginning of the frost-free period. The positive correlations with NFFD_wt indicate that more frost-free days in winter were associated with more rust disease. The negative correlations with bFFP indicate that earlier growing seasons were associated with more rust disease.

Why was rust disease associated with milder temperatures? The pathogen takes advantage of milder spring temperatures and longer growing seasons. Favorable climatic conditions allow the pathogen to produce spores frequently (Van Arsdel et al. 1956), resulting in a higher rust hazard. For example, spring temperatures impact the initial phase of spore development of the pathogen on *Ribes* (Mielke and Kimmey 1935; Larson 2011). Larson (2011) observed that rust infection was higher at sites with warmer spring temperatures. A positive correlation with milder winter temperatures was related to a longer growing season for the pathogen (Mielke 1943). For example, the pathogen grew from needles of western white pine to the bark during dormant seasons that had milder winter temperatures (Chapman 1934). Rust infections were observed until October in Idaho, resulting in more cankers on potted western white pine trees at test sites that had milder winters (Mielke 1943). Moreover, mild temperatures may allow basidiospores to enter pine needles more readily through the stomata. In contrast, Larson (2011) observed more rust infections at sites with colder winter temperatures in the northern Rockies, where the whitebark pine host was abundant. In this case, the relationship between rust disease and winter temperature may have been confounded with other weather or climatic differences among the sites.

Rust hazard was greater at sites with sufficient moisture in spring, summer, and autumn. CANK% and NUM_CANK had moderate positive correlations with relative humidity (RH_sm and RH_at) and Hogg's climate moisture index (CMI_sm). Hogg's climate moisture index, which is the difference between annual precipitation and potential evapotranspiration (PET), is higher for sites that are less droughty. Hargreaves climatic moisture deficit (CMD, CMD_sp) was negatively correlated with CANK% and NUM_CANK, which is consistent with these other relationships. Hargreaves CMD, which is annual evaporative demand that exceeds available water, is greater at droughty sites.

As for other fungal pathogens, *Cronartium ribicola* requires abundant moisture to complete its life-cycle. Conditions that are too dry are harmful for rust spore germination and production, particularly for the short-lived basidiospores (Van Arsdel et al. 1956; Van Arsdel 1972). Then, the higher the relative humidity, the longer time rust spores can be transmitted in the air during late summer and early autumn (Mielke 1943; Schwandt 2001; Smith et al. 2001). Because basidiospores infect pine trees in late summer and early autumn (Van Arsdel 1972), moisture conditions in these seasons affect rust hazard. Thus, the higher the relative humidity, the higher the expected spread and occurrence of blister rust disease (Mielke 1943; Schwandt 2001; Smith et al. 2001). For example, based on studies of tree islands in the Northern Divide

Ecosystem, Smith-Mckenna et al. (2013) concluded that high humidity increased rust infection rates for whitebark pine (*P. albicaulis*). Dudney et al. (2021) concluded that upper elevations create cool and moist conditions favorable for rust infection. In contrast, in arid regions, drier climates decrease the probability of rust infection, but once trees become infected, they are more likely to die (Dudney et al. 2021). Similar patterns were observed in southwestern Wisconsin (Van Arsdel et al. 1956) and the southern Lake States (Van Arsdel 1961), where the incidence of WPBR was lower in areas with drier climates. In the Greater Yellowstone Ecosystem, Thoma et al. (2019) concluded that relative humidity and temperatures in August and September were more influential than other site characteristics on blister rust disease. The other site characteristics they studied were latitude, longitude, elevation, slope, and aspect.

The forest management techniques aiming to alter the forest's climatic conditions could help reduce rust damage. For example, stand density could be reduced to decrease relative humidity and “leaf wetness duration” responsible for rust spore production and transmission (Bregaglio et al. 2011; Wyka et al. 2018). Moreover, reducing stand density (e.g., thinning) could provide more space for trees, reducing stress caused by drought and the pathogen.

Rust disease was greater at sites with northern, eastern, and northeasterly aspects. The pathogen favors cool and moist environments (see above), and northern, eastern, and northeasterly aspects are cooler and moister. Both rust variables, CANK% and NUM_CANK, were greater on sites with northern, eastern, and northeasterly aspects. However, the relationships between the rusts traits and ASPECT were weak, probably because other factors were more influential than aspect. For sites with northern and eastern aspects, wind patterns may add cool air, and lower solar radiation contributes to milder temperatures. These conditions provided the conditions needed for disease development in other regions with hot summers similar to southern Oregon (Van Arsdel et al. 1957; Smith-McKenna et al. 2013). For example, rust infections were common on north-facing sites of whitebark pine (*P. albicaulis*) (Larson 2011). In central and southeastern Wyoming and northern Colorado, disease incidence on limber pine (*Pinus flexilis*) was higher on sites with northern and eastern aspects (Kearns and Jacobi 2007). In contrast to aspect, elevation and slope did not occur in the rust models for CANK% and NUM_CANK. However, other researchers reported that sites on steeper slopes had greater rust disease, probably because they were cooler. For example, in British Columbia, more WPBR cankers were observed on WWP as the slope increased (Hunt 1983). However, no such relationship was found in central or southeastern Wyoming and northern Colorado (Kearns and Jacobi 2007).

In conclusion, my results suggest that climate variables were more influential than topographic variables for predicting rust hazard. Mild temperatures and sufficient moisture seem to be important predictors of rust hazard, probably because the rust pathogen is able to germinate, spread, and infect hosts better under these conditions. Northern, eastern, and northeasterly aspects support these climatic conditions, showing a small role for micro-topography for influencing rust infections in southern Oregon. These findings provide information about the interactions among the host, pathogen, and environment. This information may shed light on rust hazard in the future, under climate change. It should be possible to use climate projections to identify locations that are climatically suitable or unsuitable for rust establishment, enabling effective forest management decisions. For example, the white pine trees might be planted at sites with unfavorable climatic conditions for the pathogen (Van Arsdel 1961), allowing trees to avoid WPBR. Forest managers might use this climatic information to map potential planting sites for western white pine and sugar pine.

5.1.4 How were rust traits affected by tree characteristics?

I studied the relationships between rust traits and tree characteristics for three reasons. First, I wanted to understand how blister rust disease affects tree growth. Second, I wanted to understand how differences in tree characteristics among sites may affect the ability to estimate rust hazard. Finally, I wanted to understand the importance of tree characteristics in rust hazard because rust hazard metrics have been calculated using tree age, tree height, and the number of cankers per tree (Hagle et al. 1989).

Rust incidence and severity are related to tree characteristics (Geils et al. 2010). For example, McDonald et al. (1981) found a positive relationship between tree height and the probability of being infected. Generally, taller trees have wider crowns, with more foliage for the rust spores to reach and infect (McDonald et al. 1981; Conklin 2004). For example, Smith (2000) observed more serious rust infections higher in the tree crown in the Intermountain Region. Although the pathogen infects white pines at all ages, younger trees seem to be more vulnerable (Geils et al. 2010; Schoettle et al. 2011; Tomback and Sprague 2022). Thus, I studied the relationships between rust disease versus tree height and age as part of my research.

In my study, it appeared that the sites with faster growing trees had more rust disease. Based on the relative importance values, tree growth (HT/AGE) was an important predictor of rust hazard in southern Oregon. Furthermore, the two key rust traits, CANK% and NUM_CANK, had weak positive correlations with HT/AGE. Because it is unlikely that rust disease enhanced tree growth, this suggests fast-growing trees were more prone to be infected or develop cankers than were slow-growing trees. It also suggests the pathogen does not adversely affect tree growth as much as expected. For example, McDonald et al. (1981) found rapid decline in tree growth occurred only when the tree was close to death. This is because the cankered branches of trees die before the pathogen reaches the stem. Even trees with bole cankers appear to grow well for years even if they are mostly girdled and will eventually die (Schwandt et al. 2013; Schwandt 2013). An alternative explanation is that the environmental conditions that promoted tree growth were also favorable for the pathogen.

In my study, it appeared that sites with young trees had more rust disease. Based on the relative importance values, tree age (AGE) was an important variable for predicting rust hazard of the sites. Furthermore, the two key rust traits, CANK% and NUM_CANK, had moderate negative correlations with AGE. There are three possible explanations for these relationships. First, older trees were affected to the same extent when they were young, but either tended to recover or it is harder to detect cankers on older trees (i.e., measurements are biased). Second, the pathogen was more prevalent when the young trees were measured, and not as prevalent when the old trees were young. Finally, the older stands have a higher proportion of resistant trees because many of the susceptible trees have died. This latter explanation seems to be the most likely one.

There is a tendency for young trees to be infected and die (York 1927; Kinloch and Byler 1981). The distances between the pine needles and the stems of younger trees are shorter than those of older trees. Thus, the pathogen reaches the main stem of younger trees in a shorter time, resulting in more stem cankers on younger trees (Schwandt 2013). For example, a canker can reach the stem of a seedling in weeks, but it may take more than 40 years to kill mature trees (McDonald et al. 1981). Geils et al. (2010) concluded the pathogen causes faster death of young trees, and old trees may survive for years depending on the locations, abundance, and types of cankers. Childs and Kimmey (1938) also found more damage on smaller and presumably younger western white pine trees. Smith (2000) stated that the pathogen can girdle more of the cambium of young trees, resulting in more significant damage. Thus, he found more WPBR damage on younger trees. If susceptible trees die young, then mature stands are more likely to be populated by more resistant trees with fewer cankers. The greater rust-resistance of older trees is sometimes called "ontogenetic resistance" (King et al. 2010). Although susceptible young trees may have more symptoms of WPBR and die quickly, older surviving trees may have few or no symptoms of WPBR (King et al. 2010). In particular, a few cankers close to the ground are enough to kill small trees (Buchanan 1938; Mielke 1943), and these trees would then be missing from older stands.

In conclusion, based on CANK% and NUM_CANK, rust hazard was positively associated with tree growth and negatively associated with tree age, but had little relationship to tree height. These results demonstrate the potential problems of using both younger and older stands for measuring rust hazard. If susceptible trees died when the stand was young, the rust hazard of sites that have older stands will be underestimated. These results also emphasize that timely, appropriate, and intensive management techniques of WPBR are important. For example, pruning could be more effective for the sites with young trees. This is because removing branches of younger trees can reduce the occurrence of stem cankers. Thus, the trees with little or no genetic resistance to WPBR could survive at sites with high hazard. This may be undesirable for improving rust resistance, but could maintain genetic diversity for other traits (Hunt 1983; Hagle et al. 1989). From the financial point of view, applying the appropriate technique is important for the trees to reach merchantable age.

5.1.5 How was tree growth affected by environmental variables and rust traits?

Western white pine and sugar pine are fast-growing species, making them valuable for forest ecosystems and the timber industry (Goheen and Goheen 2014). However, variation in forest productivity is associated with abiotic and biotic factors, particularly climate, and in the case of white pines, blister rust disease. A better understanding of these abiotic and biotic factors could help to improve forest management of white pines. Thus, I studied the relationships between tree growth versus environmental variables and rust traits. One purpose was to identify the best climate variables to use for future projections of tree growth (see below). Another purpose was to evaluate the effects of rust disease on tree growth after accounting for climate.

First, I studied the associations between tree growth and environmental variables alone. Surprisingly, faster tree growth was associated with harsher temperatures. For example, tree growth was negatively correlated with mean coldest month temperature (MCMT), minimum temperatures in spring and summer (Tmin_sm and Tmin_sp), winter degree-days above 5°C (DD5_wt), and extreme maximum temperature (EXT). A possible explanation for these relationships is that rust damage reduced tree growth. As discussed above, rust disease was greater at sites with longer growing seasons and milder temperatures.

Second, I added rust variables to the environmental variables used above to infer the direct effect of rust disease on tree growth. The resulting model included many of the same variables as the model described above, but now that rust variables were added, CANK% and NUM_CANK were the most important predictors of tree growth. Contrary to expectations, however, tree growth was positively correlated with the percentage of trees with a canker (CANK%) and number of cankers per tree (NUM_CANK). As discussed above, this suggests that faster growing trees may be more susceptible to rust disease, and this effect was more pronounced than any adverse effects rust disease had on growth of the surviving trees. Alternatively, the sites that had the best climates for tree growth may have had climates that were more favorable for the pathogen.

In conclusion, the growth of western white pine and sugar pine seemed to be greater at the sites with harsher temperatures and moisture. Thus, I speculated this might be because there was less rust disease at these sites.

However, this conclusion was contradicted by the observation that sites with faster growing trees had more rust disease. Thus, the multivariate relationships between site climate, tree growth, and rust disease are not obvious.

5.1.6 How will rust traits change under future climates?

I studied the relationships between key rust traits, CANK% and NUM_CANK, versus future climate variables and ASPECT to identify how the rust traits will change under future climates. I aim to provide forest managers with the information needed to select future sites for white pine plantations based on rust hazard and climate projections. Climate change may alter the interactions among hosts, pathogen, and environment. This may accelerate the spread and inoculation potential of WPBR by expanding the duration of favorable climate conditions (Kinloch 2003; Wyka et al. 2018). In contrast, the shifts may inhibit the spread and inoculation potential of WPBR if drought or cold intensifies under climate change. Considering the expense of establishing, protecting, and sustaining forest plantations, identifying lower hazard sites should help retain sugar pine and western white pine on the landscape.

There are concerns that WPBR has been worsening with climate change (Keane et al. 2017). In contrast, other studies indicated WPBR would probably be lower in the future due to climate change (Kinloch 2003; Sturrock et al. 2011; Dudney et al. 2021). More specifically, Sturrock et al. (2011) concluded that pathogen pressure would decrease in the future because of warmer summers and springs due to climate change, inhibiting spore development and transmission (Frank et al. 2008).

My research indicates that changes in rust hazard are uncertain. I projected small but uncertain rust infections for western white pine and sugar pine under four climate change scenarios of warmer and drier future conditions. As discussed above, *Cronartium* requires moist air and relatively cool temperatures to infect trees and alternate hosts (Geils et al. 2010). Dudney et al. (2021) stated that a decrease in rust could be observed in some areas under future climate change scenarios. However, these changes may be nonlinear and differ across the landscape.

I projected a small decrease in rust hazard in a warmer and drier future. By the end of the century, I found a projected increase in temperatures in spring, summer, and winter, indicating a longer growing seasons. However, I also projected a decrease in relative humidity in summer and autumn under all SSPs. This suggests that springs and summers will probably be drier in the future. If true, this may inhibit initial spore development on pine and alternate hosts. However, I projected only a small decrease in rust traits in the future. Thus, I concluded that climate change will probably have little effect on WPBR in southwestern Oregon. Furthermore, I found projected changes in rust disease were inconsistent and uncertain. The potential reasons for this are discussed below.

Below, I discuss a number of caveats that probably affected the performance of my rust prediction models and reliability of future projections. The first caveat is that I studied correlations or the importance of variables in predictive models. Thus, I cannot draw direct cause-and-effects conclusions on the effects of environmental variables and tree characteristics on WPBR. However, the variables I used in RF analyses corresponded to those used in the studies that revealed cause and effect relationships between the environment and WPBR (Van Arsdel et al. 1956; Van Arsdel et al. 1957; Van Arsdel 1961; Hunt 1983).

The second caveat is that I studied rust hazard versus climate variables, which consisted of 30-year averages. Thus, my study did not provide information about the occurrence of specific wave years. Rust infection can occur yearly, but wave years occur when the weather is particularly suitable for rust development, resulting in rust epidemics (Mielke 1943; Peterson 1971; Kinloch 2003; R. Sniezko pers. comm.). The gap between wave years could be 4 to 10 years (Kinloch et al. 1996; Schwandt et al. 2013). The wave years are less likely to occur as the weather becomes warmer and drier (Kinloch 2003). However, the behavior of the wave years is not fully understood (Kinloch et al. 1996; Schwandt et al. 2013).

The third caveat is that I did not account for the alternate hosts. *Ribes* species are one of the main reasons for the occurrence, spread, and intensity of WPBR because they are alternate hosts (Geils et al. 2010). However, I had no information about the distribution of alternate hosts in the study area or their presence/absence at the sites I studied. Goheen and Goheen (2014) stated that infection was severe at sites in southwest Oregon with or without *Ribes* species. This may be because *Castilleja* and *Pedicularis* spp. acted as alternate hosts at these sites or *Ribes* species occurred near the surveyed stands. Due to the nature of the disease, I assumed *Ribes* species existed in the area I studied.

The fourth caveat is that I did not account for other environmental variables that might have improved the prediction models. For example, I did not include the abundance of water sources in the study areas and the distance of these water sources to the study sites. Smith-McKenna et al. (2013) concluded that areas with abundant water (e.g., near lakes and streams) had more WPBR. They stated these areas provided moisture for developing and establishing WPBR (Smith-McKenna et al. 2013). Additionally, I did not account for durations of free water on the surface of hosts' leaves, called 'leaf wetness duration' (Bebber 2015). Rust inoculation is only possible under a certain duration of wetness with specific temperatures (Van Arsdel et al. 1956).

Accounting for the plant's leaf wetness duration might increase the prediction model's accuracy. However, this would be complex because leaf wetness is estimated from daily temperature, precipitation, and humidity (Bregaglio et al. 2011), data which are typically unavailable. Furthermore, I did not use soil variables that provide information about available water capacity and other soil characteristics (USDA 2006). These data may be important to evaluate tree vigor associated with site quality.

Based on my results, future changes in rust hazard appear to be small and uncertain. Furthermore, climate change will complicate relationships among hosts, pathogens, and the environment. In particular, it would be valuable to include the current distributions of alternate hosts in the rust prediction models. Then, it would be possible to use future projections of alternate host distributions to better understand WPBR in the future. Rust infections generally occur on the undersides of *Ribes* leaves, but may occur on branch stems in some species (Kimmey 1938). Therefore, *Ribes* species have different levels of resistance to WPBR and provide different levels of inoculum, which influence WPBR incidence and severity on pines. Although researchers have conducted studies on the distributions of *Ribes* species, detailed information is still needed. For example, Kimmey (1938) studied the relative susceptibility of *Ribes* species to WPBR. Van Arsdel and Geils (2004) ranked *Ribes* species in relation to the spread and intensification of WPBR. They found that *Ribes nigrum* is the most susceptible with more telia production, and *Ribes cereum* is the most resistant with less telia production. Strunk (2020) mapped the distribution of some *Ribes* species in the PNW. Furthermore, the U.S. Forest Service (USDA) has a database of plant inventories for the U.S., including these alternate hosts.

The causes of wave years should be documented to improve our understanding of climate-pathogen interactions (Schwandt et al. 2013). Furthermore, it would be valuable to project the occurrence of wave years in the future. Because unusual weather conditions seem to be responsible for wave years, it may be possible to correlate wave years with climate. If so, prediction models could be used to project wave years in the future, which would improve our projections of rust hazard.

Finally, it might be helpful to add soil data to the prediction models to project where suitable sites for white pines might exist in the future. The sites with lower moisture and nutrient concentrations could be an option for pines to escape WPBR. This is because the growth and development of alternate hosts might be slower due to poor soil conditions (Kranabetter and Simard 2008). Moreover, the pathogen may adapt faster to climate change than pine and alternate hosts (Schoettle et al. 2022). Thus, it is only possible to make rough predictions of rust hazard presently. Based on my projections, southwestern Oregon could remain suitable for planting of sugar pine and western white pine, particularly if rust-resistant genotypes are used.

5.1.7 How will tree growth change under future climates?

I studied the relationships between tree growth (HT/AGE) versus future climate variables and rust variables, CANK% and NUM_CANK, to identify how tree growth will change under future climates. I aim to provide forest managers with the information needed to improve management options for white pine and identify future sites for white pine plantations based on potential tree growth in relation to climate change and WPBR.

Climate change alters species compositions and climatic habitat suitability. Loehman et al. (2011) projected an increase in western white pine populations with warming temperatures and increasing fire suppression. Western white pine uses fire to regenerate, which probably also helps trees escape from WPBR (Loehman et al. 2011; Hines 2013; Wang et al. 2023). Whitebark pine growth increased with warmer temperatures and extended growing seasons in the Northern Rocky Mountains without considering WPBR (Loehman et al. 2011). However, climate change may reduce tree growth in some regions, especially in warmer and drier areas. One of the main reasons for this is that available soil water will be reduced due to increased temperatures throughout the year (Keane et al. 2018). For the same reason, tree growth was projected to decrease in the southwestern and northwest United States (Harvey et al. 2020). Stern et al. (2021) predicted an increase in the growth rate of eastern white pine and eastern hemlock with higher temperatures in spring and fall. However, higher summer temperatures are expected to offset these growth benefits (Stern et al. 2021).

My main conclusion was that the average growth rate of sugar pine and western white pine will probably increase, but this increase will not be large. At the end of the century, I projected that changes in tree growth will be small under all SSPs. I have two possible explanations for this, including the effects of climate and WPBR. First, warmer and drier climates would inhibit initial spore development on pine and alternate hosts, possibly resulting in less rust damage (discussed above). Furthermore, many studies projected increases in tree growth in higher-elevation forests (Littell et al. 2011; Harvey et al. 2020; Schoettle et al. 2022; Halofsky et al. 2022). Warmer climates will increase the number of frost-free days at upper elevations (Little 1971), leading to increased growth at sites that are currently cold-limited. In contrast, a warming climate will probably cause earlier snowmelt, and then earlier depletion of soil water (Mahalovich 2013). The area of southwestern Oregon I studied is also water limited, resulting in water stress on trees (Halofsky et al. 2016; Halofsky et al. 2022). The confounding effects of climate change may explain the small increases in tree growth suggested by my results. My results suggest that climate change will probably have little effect on the growth of sugar pine and western white pine in southwestern Oregon.

A caveat for the tree growth prediction models is that I did not account for increases in CO_2 due to climate change. With sufficient moisture and nutrients, increases in atmospheric CO_2 result in higher net photosynthesis, facilitating tree growth. However, in southwestern Oregon, there is limited water during the growing season, and drought may increase because of less snowpack and earlier snowmelt (Restaino et al. 2016). Thus, trees in this region may not benefit from increased CO_2. Nonetheless, increased CO_2 could increase water use efficiency, potentially offsetting the effects of water stress during the growing season (Halofsky et al. 2022). Sugar pine and western white pine growth positively correlated with higher nighttime temperatures, probably because of increased CO_2 (Maloney et al. 2011). In addition, an increase in tree growth was positively associated with canker growth (Kearns 2009; Schoettle et al. 2022). Overall, including the effects of changes in atmospheric CO_2 in prediction models would probably have little effect on projections of tree growth. As for the rust prediction models described above, the tree growth prediction models might be improved by accounting for other factors. Western white pine and sugar pine populations in southern Oregon could be more vulnerable to climate change than northern regions because of limited water availability.

6. Chapter 6

6.1 General Conclusion

6.1.1 Future Work

Because my study is exploratory, it is only possible to make predictions in general. However, projection analyses help identify data patterns allowing exploratory analyses. RF regression models and ClimateNA could be considered for future research. RF is advantageous because it can handle missing values and identify linear and non-linear relationships between dependent and independent variables. RF could also select the most important independent variables from many independent variables. In addition, RF models provide relative importance of independent variables, allowing forest managers to prioritize the most important management strategies for WPBR.

Using RF models to project the effects of climate change on WPBR hazard can be a valuable approach for WPBR management and conservation efforts for white pines. Prediction models can be trained on historical data to project the future WPBR hazard under multiple climate change scenarios. ClimateNA generates historical and future climate variables based on different climate change scenarios. The percentage of trees with a stem canker, the average number of cankers per tree, the average height of the highest canker, rust hazard index, and average tree growth can be projected using RF models.

Overall, it is possible to project WPBR hazard and average tree growth in the future with appropriate data and approaches. The success of the projection depends on addressing the study caveats making projections uncertain. First, I recommend accounting for the distribution of *Ribes* species, the occurrence of wave years, and moisture-associated environmental variables. Second, I recommend updating the models as new data becomes available based on the latest version of climate change scenarios. Third, this study does not imply causation, and further analyses are needed to establish causal relationships better understand WPBR behavior. Finally, permanent plots could be established to monitor WPBR.

6.1.2 Conclusion

Forests have been one of the most important resources for humanity throughout history. Managing this vital resource sustainably and carrying it into the future is one of today's most critical issues. However, climate change disrupts the balance of forest ecosystem dynamics (Sturrock et al. 2011). Whereas this imbalance is advantageous for some forest disturbances, it poses a threat to tree species in general. WPBR incidence and severity may increase or decrease in the current regions, or the pathogen may move to new climatically-suitable habitats and cause epidemics due to climate change. In southwestern Oregon, mild temperatures and sufficient moisture were associated with higher rust infection. In areas with warmer and drier conditions with the longer growing season, WPBR may still be present. However, the impact on tree health may be less significant. Thus, drought during the growing season seems to be the most critical factor impacting both WPBR and average tree growth in the future. Understanding how the pathogen response to climate change is important for developing feasible and viable WPBR management techniques needed to manage white pines better to reduce the risk of WPBR and protect these important tree species.

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