Stand Structure and Understory Diversity of Restored Western White Pine Stands

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Authorization to Submit Thesis

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Abstract

Western white pine (*Pinus monticola* Dougl. ex. D. Don) once dominated the northern Rocky Mountains of the US and Canada. These forests were multi strata stands with white pine dominating in the overstory and more shade tolerant species occupying lower strata. In the early 1900s white pine blister rust (*Cronartium ribicola*) was introduced, which caused a major shift in forest management. White pine along with other shade intolerant species were preferentially harvested resulting in a forested landscape dominated by more shade tolerant tree species. These shade tolerant species are more susceptible to biotic and abiotic disturbances and have a less ecologic and economic value. Planting of blister rust-resistant white pine seedlings only became more frequent in the last 30 to 40 years, yet there has been little evaluation of ecology of these planted white pine stands. Therefore, the first objective of this thesis is to describe the structure, tree species composition, and tree growth of western white pine plantations. The second objective of this thesis was to examine the understory floristic diversity of planted white pine stands in relation to canopy characteristics and overstory species composition across the Northern Rockies. Twenty-seven stands planted on federal and private timberlands prior to 1991, were selected across northern Idaho. The majority of these stands were planted solely with western white pine, but similar aged, naturally regenerated stands with fewer western white pine were also selected. Results show these stands as containing an even-aged stratified mixture with an abundance of shade tolerant seedlings and saplings. We also found the total merchantable volume increased with an increasing amount of white pine in the stand. These planted stands also have a very diverse understory with species composition similar to that of historic stands, documented in previous literature. Results from this study will be used by forest managers to assess the effects of western white pine composition on stand structure, vegetation community diversity and will help direct future management efforts to reintroduce this iconic species into the forests of the region.

Acknowledgments

Most importantly, I must thank Andrew Nelson. None of this would have been possible without his guidance and patience answering my lists of questions I had prepared each week. Our meetings kept me on track and greatly enhanced my knowledge of statistics, coding and silviculture. My committee members, Theresa Jain and Eva Strand, thank you for her helpful comments and reviews of this thesis.

The field data collection would not have been possible without John Byrne, Andria Miller and Tori Enger. John Byrne spent several days crawling through steep slopes of tall shrubs in a full rain suit. Without his stubbornness and guidance, I would have never found enough stands for this thesis. I am incredibly grateful for Andria and Tori's patience. Several times, they hiked miles through the rough terrain of northern Idaho, only to turn around because the stand did not fit the minimum requirements. I am also grateful to the all the professors, researchers and fellow graduate students I have not mentioned but have given me much needed words of encouragement and advice.

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Chapter 1: Literature Review

Western White Pine in the Inland Empire

Western white pine, *Pinus monticola* Dougl. Ex. D Don, (hereafter white pine) is found in the Cascade, Sierra, and Northern Rocky Mountains of the western United States. and Canada (Figure 1.1; Graham 1990). This landscape was carved by glaciers, resulting in narrow canyons and a mixture of steep and gentle slopes (Jain and Graham 2015). Forested areas where white pine once occupied 15 to 80 percent of total number of stems or basal area were considered western white pine type forests (Harvey et al. 2008). Before the 1860s these white pine type forests made up 25 to 50 percent of the two million forested hectares in the Inland Northwest (Harvey et al. 2008). The greatest abundance of white pine was in the Inland northwest, including northern Idaho, eastern Washington, western Montana and southern interior British Columbia; here white pine was known to exceed 80 percent of trees within a stand. This unique area is very different than other parts of the inland western United States, and is moderated by the strong jet-stream that carries moist air from the Pacific Ocean over the Cascades (Neuenschwander et al. 1999).

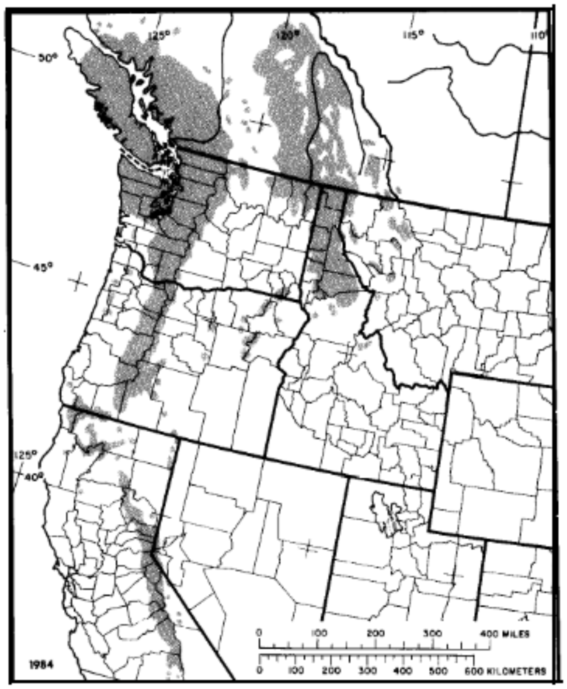

Figure 1.1 Native Range of western white pine in the United States and Canada (from: Graham 1990)

The northern Idaho climate is characterized by dry summers, with most of the 71 to 152 cm (28-60 in) of precipitation occurring in the fall and winter (Graham 1990). The annual average temperature ranges from 4 to 10 °C (40 to 50 °F) but can reach extremes of negative 40 and 42 °C (negative 40 and 107 °F) (Graham 1990). The growing season can last 60 to 160 days, depending on the year and stand location (Wellner 1965). In the Inland Northwest, western white pine is found at elevations between 500 and 800 m (1,640 to 5,910 ft). However, the occurrence of the species can range from sea level in the Puget Sound to over 3,000 m (10,000 ft) in the Sierra Nevada (Graham 1990).

White pine thrives in deep, porous soils, but is most often found in sandy soils with textures ranging from sandy loam to clay loam (Graham 1990). Specifically, in the Inland Empire, soil depths range from 25 to 230 cm (10-90 in) and are sourced from granite, schist, quartzite, argillite, sandstone and shale (Graham 1990). These soils are also influenced by a fine textured ash-cap that varies in depth across the area, but can be up to 62 cm thick (Page-Dumroese et al. 1997, Jain and Graham 2015). This ash-cap is a result of the eruption of Mt. Mazama (now Crater Lake) 7,500 years ago (Jain and Graham 2015). This geologic history as well as continued disturbance events have resulted in a range of topographic features and soils across the landscape (Quigley et al. 1996). White pine can grow on a variety of slopes and aspects; however, it is most common in moist creek bottoms, often on north facing slopes (Graham 1990). The soil pH of white pine forests ranges from 4.5 to 6.8 (Cooper et al. 1991).

White pine most often regenerates following disturbances such as wildfire or logging activity (Jain 2001). The species thrives in the mixed fire regime that burns between July and early September (Hann et al. 1997). There are frequent surface fires, every 15-25 years as well as less frequent, more intense crown fires, occurring every 20 to 150 years (Hann et al. 1997). White pine is able to establish well in these areas due to the abundance of seeds produced (Haig et al. 1941). Seeds overwinter in the duff and germinate in the spring (Haig et al. 1941, Jain 2001). White pine is well suited to regenerate after a variety of disturbances and soil substrates and can survive in a variety of light conditions (Haig et al. 1941). However, it grows best in full sunlight on northernly facing slopes (Haig et al. 1941). For white pine, the right environmental variables during the regeneration establishment phase is critical. Jain et al. (2004) found that canopy openness, as well as other environment characteristics have a significant effect on the regeneration establishment and growth of white pine. The amount of visible sky in addition to landform, elevation, aspect and soil characteristics were also found to influence height growth of white pine (Jain et al. 2002, Jain et al. 2004). Therefore, if the silvicultural goal is to have white pine as a significant part of the stand, it must be established before other species to ensure the area meets the minimum amount of visible sky required for establishment and growth (Jain et al. 2004).

White pine-dominated forests are one of the most productive forests in the western United States. According to Neuenschwander et al. (1999), a 100 year old white pine stand can yield 600 cubic meters per hectare of merchantable timber (100,000 board feet per acre), compared to a similar-aged stand without white pine, yielding less than 300 cubic meters per hectare (50,000 board feet per acre) under similar environmental conditions. White pine's growth characteristics allow the species to quickly dominate stands. It can exceed 38 cm (15 in) in stem diameter and 20 m (65 ft) in height at 30 years of age, commonly growing one meter per year. At 300 years old, white pine can reach 61 m (200 ft) tall and 152 cm (60 in) in diameter (Harvey et al. 2008). White pine can live 240-400 years even with endemic disturbances and diseases (Jain and Graham 2015).

Economic and Ecological benefits of Western white pine

White pine played such a significant role in historic stands due to its resistance to insects and disease, its longevity, seed producing ability and its ability to adapt to its environment (Jain and Graham 2015, Rehfeldt et al. 1984). The biophysical characteristics of the landscape, such as the climate, topography (dissected slopes with moist draws) and the ash-cap also allowed white pine to dominate the landscape. These characteristics, as well as white pine's ability to survive disturbances resulted in patchy stands with varying stand size, densities and composition (Jain and Graham 2015). Insects and pathogens killed the weakest trees within the stand, preserving only the strongest and further encouraged the dominance of white pine, prior to the introduction of the forest pathogen, blister rust (*Cronartium ribicola*) (Harvey and Morgan 2001).

The loss of white pine has altered historic stand dynamics and associated ecosystem benefits. Without white pine, late successional, shade tolerant species such as Grand fir (*Abies grandis*), Douglas-fir *(Pseudotsuga menziesii),* western red cedar *(Thuja plicata)*, and western hemlock *(Tsuga heterophylla)* often dominate (Hann et al. 1997). Harvey et al. (2008) claim that without white pine the forest ecosystem as a whole will be less productive and unstable, due to increased susceptibility to fire and insect damage. Forests composed of these shallow rooted tree species with very dense crowns will attribute more litter buildup as well as limited nutrient cycling when compared to forests composed of early successional species (Harvey et al. 1999). With these stagnated soils, it is possible for nutrients to be restricted to surface layers, and without disturbance the nutrients will be limited within a single rotation (Harvey and Morgan 2001). These forests will also provide less watershed protection and carbon sequestration potential (Harvey et al. 2008). These late successional forests are also more susceptible to root diseases, insects, and other disturbance such as drought, wind or fire (Neuenschwander et al. 1999).

White pine plays a role in maintaining the integrity and resilience in the moist forests of the Inland Northwest and provides several ecological, social and financial benefits. White pine can tolerate the very cold winters of the Inland Northwest as well as summer drought (Fins et al. 2002). Even when white pine is killed in more intense fires, it provides several important ecological benefits. Dead trees, both standing snags and los on the forest floor, can persist for more than 100 years, providing shelter for several wildlife species that use hollowed out trees for their dens (Fins et al. 2002). As these trees decompose, they also hold soil moisture and provide environments for fungi to thrive (Fins et al. 2002). White pine has also contributed to habitat for cutthroat and bull trout due to its ability to thrive on subsurface flows or near streams (Jain et al. 2002). White pine's large boles can shade the streams when they are standing and create deep pools in the stream if they happen to fall in the stream (Jain and Graham 2015, Fins et al. 2002). The loss of this iconic species has already negatively impacted several species that rely on white pine for food and shelter.

White pine wood quality is highly valued. It was referred to as "King Pine" by the settlers in the late 19th and early 20th centuries (Fins et al. 2002). It is a light but strong wood with straight grain (Wiedenhoeft 2010). It can be used for paneling and molding because it holds paint well and does not split easily (Harvey et al. 2008). White pine can also be used for doors, blinds, and home furniture like dressers, beds and tables (Fins et al. 2002). Historically, the species was used to make matches and toothpicks (Haig et al. 1941). According to Detwiler (1919), the value of the white pine timber standing in the North American forests was likely well over a billion dollars in the early 1900s.

Western White Pine Stand Structure and Composition

Western white pine was able to thrive and occupy a dominant canopy position prior to blister rust in the Inland Northwest due to the biophysical characteristics of the landscape, such as the ash cap and dissected slopes on varying aspects (Jain and Graham 2015). The species success can also be attributed to its resistance to disease and insects that thinned out the more vulnerable species (Jain and Graham 2015, Fins et al. 2002).

In a single-story stand of mature white pine, the overstory may be 15 to 80 percent white pine and have 247 to 1,235 trees per hectare (100-500 trees per acre) depending on stand age (Rockwell 1917). When the overstory density is low, yet dominated by white pine, the crown and needle architecture in the canopy is somewhat light porous and can encourage establishment of shade tolerant tree seedlings, shrubs, and forbs (Rockwell 1917). Composition of the lower strata depends on the light environment. While white pine thrives in open canopies, diffuse light conditions often found with early successional dominated overstories favor more shade tolerant species (Rockwell 1917; Cameron 1996). In the absence of white pine, Douglas-fir (*Pseudotsuga meziesii* var. *glauca*) held a dominant crown position (Cameron 1996). Western larch (*Larix occidentalis*), ponderosa pine (*Pinus ponderosa*), and lodgepole pine (*Pinus contorta*) are also common species in the upper stratum with white pine, while grand fir (*Abies grandis*), western hemlock (*Tsuga heterophylla*), and western red cedar (*Thuja plicata*) typically occupy lower strata (Graham 1990; Rockwell 1917, Tomback and Achuff 2010). When shade tolerant species are present under the overstory stratum, the canopy becomes too dense for vegetation to thrive in the understory (Rockwell 1917). Without subsequent stand-replacing disturbances, the lower strata of shade tolerant species replace the overstory white pine and other early successional species (Rockwell 1917).

Another characteristic of white pine stands are canopy gaps. Historically, fires and ice storms created openings of different sizes that white pine seedlings quickly dominated (Jain and Graham 2015, Fins et al. 2002). Marshall (1928) describes mature stands with a history of periodic severe fires as having distinct cohorts, due to the surviving trees providing seed to regenerate the recently burned area. This multistrata stand structure is typical of white pine forests, however if the overstory was killed by a fire prior to its prime seed producing years, it may result in an all aged stand (Marshall 1928). In this case, regeneration will be ongoing over the next 50 years and dependent on the few trees that survived the fire in the draws (Marshall 1928). Canopy openings created by a less intense fire are often not big enough to allow for establishment of white pine, instead shade tolerant species would fill in these smaller gaps (Marshall 1928). White pine stands may have open gaps in the canopy from blister rust mortality, the pathogen can kill numerous trees within a short period of time (Ban et al. 1998). Because the survival rate for improved white pine seedings is 66 percent, there is the potential for a large portion of white pine to die in a short period of time (Fins et al. 2002). After a gap forms, the regeneration within the opening depends greatly on the size of the opening. Shade intolerant species are able to dominate larger gaps, whereas shade tolerant species may be released from several years of suppressed growth in a small canopy opening (Hibbs 1982, Canham et al. 1994, Kobe and Coates 1997).

Harvest History

The first timber sale of white pine on federal land was in 1907 on the Kaniksu National Forest that spanned northern Washington, Idaho and Montana. It was a seed-tree cut that left only about 12 trees per hectare (five trees per acre) for reseeding (Haig et al. 1941). The seed trees fell over in a windstorm shortly after harvest, implying that white pine could not withstand wind when standing alone (Haig et al. 1941). Management of white pine quickly turned to leaving one to eight-hectare (2 to 20 acre) blocks of timber to ensure a seed bank; the cut area was then burned (Haig et al. 1941). The Coeur d’Alene National Forest was also using clear-cut methods at that time. It was found that partial cutting methods were too time consuming and the shaded areas from uncut areas would encourage undesirable species such as grand fir and western hemlock (Haig et al. 1941). During this time, the Inland Northwest went from producing one percent of the country's white pine in 1889, to 43 percent by 1929 (Neff 1933). Most of the white pine was from the Northeast, up until the mid-1800s, when it was moved to the Lake States (Larson 1949). However that supply was quickly exhausted and the industry moved west in the early 1900s (Strong and Webb 1970). Between 1900 and 1965, 10.2 million cubic meters (17.5 billion board feet) of lumber was milled in the Coeur d'Alene area of Idaho, much of which was white pine (Fins et al. 2002).

The marking rules were established in 1916 and included information about what makes a good seed tree. Foresters of the time relied on trees with at least a 14-inch diameter to reseed the cut area (Haig et al. 1941). They also found that there was no guarantee that there were enough seed in the duff to provide adequate regeneration (Haig et al. 1941). Areas with merchantable sized trees of undesirable species were left out of Forest Service timber sales. Leaving these areas uncut and encouraging reproduction of the less valuable species resulted in less white pine within the stand (Haig et al. 1941).

The introduction of white pine blister rust (*Cronartium ribicola*) in the early 1900s, resulted in less white pine within forest stands and changed the forest dramatically. After several methods failed to save the white pine, foresters turned to high grading and removing disease-susceptible white pine from the landscape (Fins et al. 2002, Ketcham et al. 1968). Blister rust continued infecting and killing non-resistant stock (Fins et al. 2002). Today only five percent of white pine remains in the historic range of the Inland Empire (Harvey et al. 2008, Fins et al. 2002).

The U.S Forest Service as well as private landowners are planting blister rust resistant seedlings across the native range of white pine (Fins et al. 2002). Those seedlings require full sunlight for at least two or three years after planting for ideal growth (Fins et al. 2002). Even with the improved seedlings, Fins et al. (2002) expects approximately 34 percent of the seedlings if they came from the Moscow Seed Orchard in Moscow, Idaho to be lost to blister rust.

As the stand grows, it may be subject to thinning or pruning depending on the management plan for a particular site (Halpern and Spies 1995). Thinning has the ability to shift species dominance to more early successional species by removing shade tolerant species. The increased availability of light and nutrients can result in the understory composition resembling that of old growth stands after thinning (Bauhus et al. 2009). Pruning the trees typically removes lower branches because most blister rust infections occur on the bottom third of the crown in saplings and pole sized trees (Hunt 1991). Hunt (1991) found that pruning reduced the number of white pine stems with blister rust, so it was recommended that white pine be pruned to a 1.5 meters (5 feet) height (Hunt 1991); if the stand is on a slope, it may be necessary to prune trees up to 3 meters (9 feet) (Hunt 1991). Pruning the trees allows light and air to enter the stand through the sides after removal of the lower branches (Van Arsdel 1961). This increased light availability after pruning may also significantly impact the understory composition.

White Pine Blister Rust

Western white pine is the most economically and ecologically valuable tree species in Inland Northwest forests despite the impact of white pine blister rust (Harvey et al. 2008). White pine blister rust which affects all five-needle pines, was introduced into North America in 1898 when infected pine seedlings were planted in the northeastern United States (Fins et al. 2002). Blister rust was independently introduced into western North America in 1910 through seedlings imported in British Columbia from France (Fins et al. 2002). The disease spread rapidly, and within ten years it was observed in Oregon and Idaho, becoming widespread by the 1940s (Harvey et al. 2008, Fins et al. 2002).

Bister rust is a fungus that requires living hosts, specifically five needle *Pinus* species (subgenus *Strobus*) and *Ribes* spp. (telial host) (Spaulding 1910). Blister rust causes a felt blight on *Ribes* leaves, which may result in defoliation when the infection is severe (Spaulding 1910). It also requires an aecial host, infecting the needles and progressing until it reaches the bole, ultimately creating a stem canker on white pine trees (Spaulding 1910). In the first part of the blister rust life cycle, the orange spores found on pine in the spring, known as aeciospores, are transported by wind to infect *Ribes* (Spaulding 1910). After a few weeks, spores of the second stage are produced on *Ribes* and then infect other *Ribes* plants in the summer. These spores are urediniospores (Spaulding 1910). This stage is repeated for several weeks (several generations), and eventually the rust makes brown, hair-like telia. These telia produce basidiospores, the spore that infect pine needles by wind (Figure 1.2) (Spaulding 1910). The affected pine producing aeciospores after several years of infection completes the blister rust cycle (Spaulding 1910). Without *Ribes*, the lifecycle of white pine blister rust wound not be complete.

In white pine, blister rust causes cankers on stems and branches, which are localized areas of swelling. Blister rust stem cankers can girdle trees, causing the foliage above the canker to die (Spaulding 1910). Rust spores land on the needles of the white pine, enter their stomata, grow down the needles and into branches, and eventually into the stem of the tree (Figure 1.2) (Spaulding 1910). Young trees may be killed very quickly once the main stem becomes infected due to the small surface area of the stem, but older trees may survive for decades after infection, depending on the location of the canker (Fins et al. 2002). Infections that are high in the crown of the tree may only kill branches or the portion of the tree located above the canker (Fins et al. 2002). Because cankers that are low on the tree are often fatal, pruning is a useful technique to control infection (Hunt 1998). Not only are these low cankers more fatal, the lower branches are also more likely to become infected due to the proximity to *Ribes* (Hunt 1991). Pruning is less effected on steep slopes due to the ability of the spore to travel (Hunt 1991). Pruning is also thought to be effective because the spores that infect the branches require cool, moist environments (Spaulding 1910). The spores are very delicate and are no longer viable after being exposed to sunlight (Kinloch 2003).

Early attempts to save the white pine included removing all *Ribes* from the forest (Fins et al. 2002). Because of the mountainous terrain of the Inland Northwest, it was soon realized that it was not possible to remove all *Ribes* to stop the spread of blister rust. Therefore, *Ribes* eradication was concentrated on the most productive sites across the white pine region but eventually stopped (Ketcham et al. 1968).

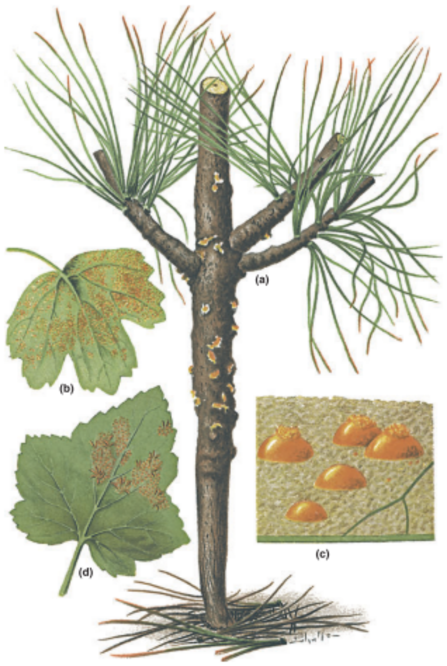

Figure 1.2 Cronartium ribicola (white pine blister rust) on Pinus strobus and Ribes (a) 4-year-old white pine with blister rust. (b) Leaf of Golden currant (Ribes aureum) with spores (c) enlarged picture of spores (d) Leaf of American black currant (Ribes americanum) with spores (From: Geils et al. 2010).

Once *Ribes* eradication was abandoned, various methods were developed to control blister rust. Injecting antibiotics into the infected trees' bark was tested as an attempt to save the species but was unsuccessful (Fins et al. 2002). In 1967, all efforts to control blister rust were stopped after spending 150 million dollars over 50 years (Fins et al. 2002). What was left of the valuable white pine was pre-salvage harvested before it was infected and killed by blister rust. This harvest inevitably removed the natural seed source and the potential rust resistance by natural selection (Fins et al. 2002). At this time, stands that were previously white pine were now regenerating with other species and planting and thinning efforts that favored white pine were abandoned (Ketcham et al. 1968). This sudden removal of disease-susceptible and potentially disease-resistant white pine, combined with fire suppression, resulted in dramatically altered forests, to the point where only 5 percent of white pine remains in the historic range of the Inland Empire (Harvey et al. 2008, Fins et al. 2002).

The white pine species of North America are much more vulnerable to blister rust than the European and Asian white pine species. This is most likely because the rust coevolved with the white pines in Europe and Asia (Hoff and McDonald 1980, La 2009). Sugar pine (*Pinus lambertiana*), western white pine, southwestern white pine (*Pinus strobiformis*), and limber pine (*Pinus flexilis*) all have documented single gene-related complete resistance (Kinloch 2002, Kinloch and Littlefield 1977, Kinloch et al. 1999). Western white pine is more resistant then sugar pine (Kinloch 2003, Sniezko et al. 2004), however whitebark pine (*Pinus albicaulis*) has even higher natural resistance compared to white pine (Kinloch 2003). Resistance to blister rust in some species of white pine can be attributed to needle shed. Needle shed is a defense system where the tree sheds the affected needles to avoid infecting the stem of the tree (Hoff and McDonald 1980). Other types of resistance include suppressing the growth of cankers, infected needles not infecting the stem, bark reactions, and limiting the spread of lesions on the needle after inoculation with rust spores (Fins et al. 2002, Geils et al. 2001).

A robust, well-funded blister-rust genetics program began in the 1960s that continues today (Bingham 1983). This began when Richard Bingham noticed healthy trees in blister rust-infected stands, suggesting natural resistance in white pine (Bingham 1983). Bingham and colleagues showed evidence of genetic blister rust control by crossing two disease–free trees (Bingham 1983). In 1957, Bingham crossed his more resistant seedlings together and started a breeding orchard on the campus of the University of Idaho (Bingham 1983). The resulting seedlings were the F_2 generation and tests showed that after inoculating the seedlings with blister rust, 66 percent were still free of blister rust cankers after 2.5 years (Fins et al. 2002). The seed orchard on the University of Idaho campus is still producing operational quantities of rust-resistant seed and as of 2001 produced more than 200 million seeds since 1970 (Fins et al. 2002). In addition, other seed orchards are in place that are designed to enhance blister rust resistance. More than 69,000 hectares (170,000 acres) across federal lands has been planted with blister rust resistant seedlings in Idaho, Montana, Oregon and Washington (Mahalovich 2010). Research on several aspects of white pine resistance to blister rust is ongoing. More recent research explains the extent of the spread.

Kinloch (2003) stated that blister rust has not been found in mainland Mexico, or in Transverse or Peninsula Ranges in Southern California. Geneticists are working on identifying specific genes that have desirable mechanisms of blister rust resistance but the enormous size of the *Pinus* genome makes this a difficult task. Genetic diversity in conifers is mostly within populations, where there is limited genetic differences among populations (Hamrick and Godt 1996). However, Kim et al. (2010) found the majority of the variation in western white pine to be among the populations. This is important because blister rust has the ability to further influence the genetic diversity within the species depending on the level of pressure on individual populations (Kim et al. 2010). Kim et al. (2010) also found that where pressure from blister rust was high, the population had lower genetic diversity. Studies like this provide the groundwork for identifying management and restoration techniques that will aid in the reintroduction of the species.

Understory Diversity

Little is known about understory complexity of western white pine stands. Understory diversity in general can increase disturbance resilience, nutrient cycling, carbon sequestration, and soil fertility (Puettmann et al. 2009, Nilsson and Wardle 2005, Chastain et al. 2006). More specifically, Nilsson and Wardle (2005) found that dwarf shrubs, mosses and lichens in the Swedish boreal forests were major ecosystem drivers and act as filters to tree regeneration by altering soil fertility, nutrient availability and understory growth.

Understory composition is likely limited by both above and below ground processes. Above ground light and precipitation are both filtered by the canopy (Waring and Running 2007). The canopy also influences the temperature and relative humidity within the stand (Riegel et al. 1995). Belowground there is competition for water and nutrients; both can be key limiting factors within the Inland Northwest (Riegel et al. 1995). A study in northeastern Oregon found that after reducing the root competition of overstory species, the biomass of the understory increased significantly (53-94%). The understory also became water limited two months later than the average end of the growing season. They concluded this understory response was due to the below ground limiting factors, mostly water and nitrogen, but not light (Riegel et al. 1992).

How light influences the understory has been studied extensively. Naumburg and Dewald (1999) examined how the light environment influenced the presence and abundance of understory species in ponderosa pine (*Pinus ponderosa)* stands of the southwest. They found that species presence was positively correlated with tree diameter, due to an increased amount of light getting through the canopy in stands with larger diameter trees. This happens as an increased amount of diffuse and direst radiation reaches the forest floor as the tree crown gets further away from the ground. The authors also attribute an increased number of understory species to the management history. They suggest that having smaller diameter trees within the stand implies a recent disturbance that has left mineral soil exposed. Exposed mineral soil was key in allowing new species to colonize the stand (Naumburg and Dewald 1999). Messier et al. (1998) found that the light availability in mixed broad leaf, conifer forests of Quebec, Canada, was influenced by stand composition, distribution of the understory vegetation and the soil type. They concluded that shade intolerant tree species allow more light through when compared to tree species that are shade tolerant. Interestingly, *Pinus* and *Larix,* both shade intolerant genera, have been found to increase the number of understory species (Barbier et al. 2007). This is most likely due to the spatial arrangement of the leaves or needles in the canopy (Planchais and Sinoquet 1998).

Another environmental variable that may influence the understory diversity is the depth of the duff layer. A study done in the Choctawhatchee National Forest, on the panhandle of Florida examined the effect of the forest floor depth on long leaf pine (*Pinus palustriss)* (Hiers et al. 2007). They found that burning had a significant positive effect on density and species richness, whereas management practices such as felling, girdling, and herbicides had no significant effect. They also attributed fewer understory species to the amount of litter on the forest floor. Litter on the forest floor acts as a physical barrier to understory growth. Understory species whose morphology does not allow them to break through the litter will not survive. The litter will also change the temperature, light and water availably. Lastly, the shade of the duff layer may not allow seeds to break dormancy due to lack of light Although this study examines longleaf pine and oak duff, the concept may still be applicable to pine duff of the inland northwest.

Previous research describes western white pine stands of the Inland Empire as having "strikingly rich in other woody and herbaceous flora" (Graham 1990). According to Graham (1990), huckleberry (*Vaccinium membranaceum*), willow (*Salix spp*.) honeysuckle (*Lonicera spp.),* currants *(Ribes spp.),* Rocky Mountain maple (*Acer glabrum*), Greenes mountain ash (*Sorbus scopulina*), princes-pine (*Chimapila umbellata*), snowberry (*Amelanchier alnifolia*), ninebark (*Physocarpus malvaceus*), rustyleaf menziesia (*Menziesia ferruginea*), spirea (*Spiraea betulifolia*), pachistima (*Pachistima myrsinites*), and twinflower (*Linnaea borealis*) are shrubs associated with western white pine type forests. Forbs associated with white pine cover include: false solomons-seal (*Smilacina spp*.), twistedstalk (*Streptopus spp*.), coolwort (*Tiarella spp*.), violet (*Viola spp*.), wild ginger (*Asarum caudatum*), queenscup (*Clintonia uniflora*), western goldthread (*Coptis occidentalis*), bunchberry *(Cornus canadensis*), sweetscented bedstraw (*Galium trifiorum*), white trillium (*Trillium ovatum*), and Brewers lupine (*Lupinus breweri*) (Graham 1990).

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Chapter 2: Structure of Planted Western White Pine Stands in the northern Rocky Mountains

Abstract

Western white pine (*Pinus monticola* Dougl. ex. D. Don) type forests of the northern Rocky Mountains are one of the most productive forests in the west. The introduction of white pine blister rust (*Cronartium ribicola*) and extensive harvesting during the 20th century decimated the species, shifting composition across the landscape to shade tolerant species that are less desirable (ecologically and economically) and more susceptible to disturbance and disease. Today, disease-resistant white pine have been planted across the region in hopes to restore these valuable ecosystems and provide economic value through timber production. This chapter examined stand structure indicators including diameter distributions, seedling occurrence and stand level characteristics to describe the current western white pine stands structure and growth over time post-blister rust introduction. The majority of stands sampled were planted prior to 1991 with almost 100 percent white pine by stem number. Additional stands of similar age dominated by late successional species were also sampled on private and federal forest land. Results show (1) these stands are an even-aged stratified mixture with small gaps that are dominated by shade tolerant tree species regenerating under the canopy, (2) seedling and sapling presence is influenced by management history (i.e. whether the stands were thinned and pruned), and (3) the total merchantable volume increased with an increasing amount of white pine in the stand. This active forest management with a particular emphasis on regenerating early successional species is becoming more common, resulting in enhanced forest complexity and providing a host of ecosystem benefits to the region.

Introduction

Reintroducing western white pine and other early successional species across the landscape is a common management goal in the Inland Northwest, USA. Since the early 1900s, several attempts to protect white pine from the devastating effects of blister rust failed and many stands were subsequently salvage harvested (Ketcham et al. 1968, Harvey et al. 2008). This changed white pine dominated forests dramatically (Harvey et al. 2008, Fins et al. 2002, Jain et al. 2015). Of the two million hectares of the northern Rocky Mountains that were once white pine forest type, only 5 percent remains today (Fins et al. 2002). This loss was eventually followed with white pine reintroduction efforts in the 1960s. Currently, blister rust resistant white pine seedlings are being planted by private land owners as well as state agencies and the US Forest Service, but the species still only makes up a minor component of its historic range in the region (Witt et al. 2018, Harvey et al. 2008)..

The loss of western white pine across northern Idaho, in combination with fire suppression encouraged stands with a lower strata of shade tolerant tree species to replace the overstory of early successional species (Rockwell 1917). This has created a more homogeneous landscape of shade tolerant tree species that are more susceptible to abiotic and biotic disturbances (Fins et al. 2002, Tomback and Achuff 2010, Bormann et al. 2015).

Historically, the mixed-fire regime, as well other native disturbances such as snow, ice, insects, and disease influenced the white pine type forests of northern Idaho and resulted in heterogenous forests with openings of various sizes (Jain and Graham 2015). Stands with larger openings from natural disturbances, or artificial gaps from thinning and regeneration establishment harvests can result in a stand with increased structural diversity (Deal and Tappeiner 2000). Seedling regeneration within these openings depends on the size of the gap. Shade intolerant species tend to thrive in large gaps, whereas shade tolerant species may have been suppressed in a closed canopy for several years and released when a small canopy gap opens (Hibbs 1982, Canham et al. 1994, Kobe and Coates 1997). Gaps also increase structural diversity by removing, either by natural disturbance or selective thinning, the suppressed and lower vigor trees of each cohort (Deal and Tappeiner 2000). Deal and Tappeiner (2000) demonstrated this by maintaining a stand with trees in several diameter classes 60 years after a selective thinning in southeastern Alaska. In addition to adding structural complexity, canopy gaps in uniform stands also provide important wildlife habitat (Wilson and Puettmann 2007). Complex forest structures, such as canopy gaps, are associated with increased songbird use, increased cover for protection, and higher visibility for spotting prey (Hagar et al. 2004, North et al. 1999, Wilson and Puettmann 2007).

Diameter distributions are a good way to describe stand structure due to their correlation with volume, stand composition, and density (Bailey and Dell 1973).

Most forests around the world have a history of past management and are influenced by current management practices (Kuuluvainen et al. 2002). Management inherently affects stand structure (i.e. the vertical and horizontal arrangement of trees and tree characteristics such as crown length) and tree species composition that varies by the management objectives. Stand structure is important for natural variability of fire regime, landscape connectivity, and distribution of wildlife habitats (Kuuluvainen et al. 2002). Forest management practices can generate complex stands and wildlife habitat that more closely resembles an ecosystem that functions similar to ecosystems prior to Euro-American management (Kuuluvainen et al. 2002).

Planted, even-aged pure composition stands (i.e. plantations) are typically dense with uniform height and diameter distributions (Ashton and Kelty 2018, Fins et al. 2002). Complex structures often found in old growth stands are typically absent in these even-aged stands (Deal and Tappeiner 2000). Management practices such as thinning and group selection harvesting can also increase stand yield (Puettmann et al. 2013). Deal and Tappeiner (2000) showed increased tree and stand growth after only the strongest spruce and hemlock were left post-cutting. Even aged stands can also be managed to promote increased yield of wood products or stand complexity. If the management goal is timber production, thinning at varying intensities allows for increased light and nutrients to become available, therefore increasing the growth of crop trees and increasing the yield of the stand long term (Bauhus et al. 2009, Deal and Tappenier 2000).

Patterns of stand structure as a result of stand dynamics, blister-rust induced mortality, and growth have not been studied in planted white pine stands in the Inland Northwest. Examining stand structure will help understand if current planting efforts are achieving the management objective of reintroducing white pine across the region. The objective of this study is to describe the structure, tree species composition, and tree growth of western white pine plantations. This study tested four hypotheses: (1) Blister rust reduced western white pine abundance and shifted overstory species composition to shade tolerant species. (2) Pruning significantly reduced evidence of blister rust bole cankers in western white pine trees, (3) Understory (seedling and sapling) regeneration was influenced by environmental characteristics such as overstory density and composition, duff depth, overstory mortality, and management history. (4) Species composition and management history will have a significant effect on the 5-year growth increments and predicted volume yield of stands when modeled to age 60.

Methods

Study area

Twenty-seven stands in northern Idaho were selected for this study. They were located on the Idaho Panhandle National Forests and Nez Perce-Clearwater National Forests, as well as private land owned by PotlatchDeltic Corp. and Stimson Lumber Company. Overstory (≥ 12.7 cm (5 in) DBH (diameter at breast height, 1.37 meters from the ground (4.5 feet)) species composition of the stands ranged from 0 to 100 percent western white pine by stem number, with an average of 65 percent western white pine. The stands were planted between 1960 and 2000, with a quadratic mean diameter of 22 cm (8.6 in) across all stands.

All stands sampled in 2018 (21 stands) met the following requirements: (1) average 12.7 centimeter (5 in) diameter at breast height (DBH) or larger (2) greater than 50 percent western white pine by stem number, and (3) reasonably accessible by road. In 2019, an additional six stands with western white pine composition between 25 and 50 percent by stem number were added (some individual plots had less than 25 percent white pine due to variability within the stand).

Sampling Design

The plot design resembled the sampling design used by the US Forest Service, Forest Inventory and Analysis program (FIA 2018). A random point was chosen as plot center of plot one (p1; Figure 2.1). The subsequent plots were located 36.6 m (120 ft) apart (slope distance) at azimuths of 0, 120 and 240 degrees (Figure 2.1). All four plots were within the stand boundary and not in a drainage, old landing or skid trail. All four plots locations were established before starting the first plot to guarantee all plots fit within the stand. If all four plots would not fit within the stand using the FIA design, the distance between plots was shortened to 30.5 meters (100 feet) or the design was stretched to a linear design. If all plots did not fit using these options, the stand was not sampled.

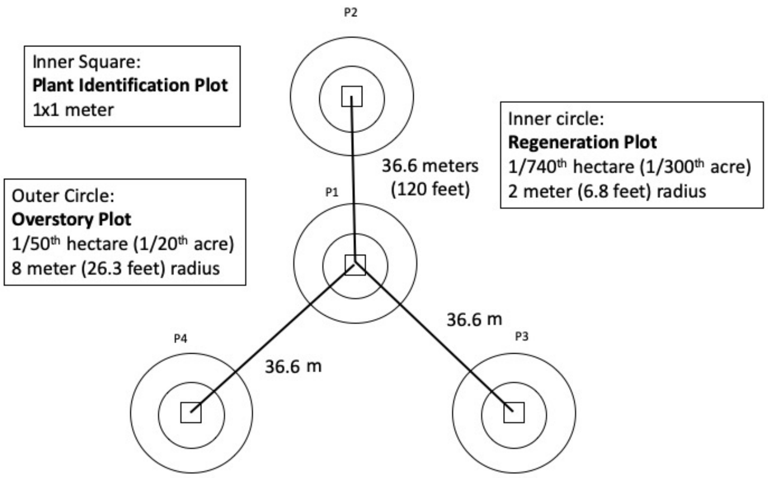

Figure 2.3 Nested plot layout design established in 27 planted western white pine stands across northern Idaho to measure stand structure and species composition

The stands were in three regions across northern Idaho (Figure 2.2.). The three regions included the Clearwater Mountains, Priest Lake area, and the Coeur d'Alene Mountains. The Clearwater Mountains stands ranged from east of Moscow, Idaho to south of Elk River, Idaho. The Priest Lake region included stands near Priest Lake on the Kaniksu National Forest. The Coeur d'Alene Mountains included stands on the Coeur d'Alene National Forest northeast of Coeur d' Alene, Idaho.

Live and dead standing overstory trees (≥ 12.7 cm (5 in) diameter at breast height [DBH; 1.37 m (4.5 feet) from the ground]) were measured in the four, 1/50th hectare (1/20th acre; 7.2-meter radius) plots. For each tree, I measured species, DBH, crown ratio (calculated from crown length and tree height) and mortality. The slope (%), aspect (degrees), and habitat type were also measured within each overstory tree plot. Habitat type was determined using the Cooper et al. (1991) habitat types for northern Idaho. Eleven stands occurred within the *Thuja plicata* habitat type series, eight within *Tsuga heterophylla* series, and eight in the *Abies grandis* series.

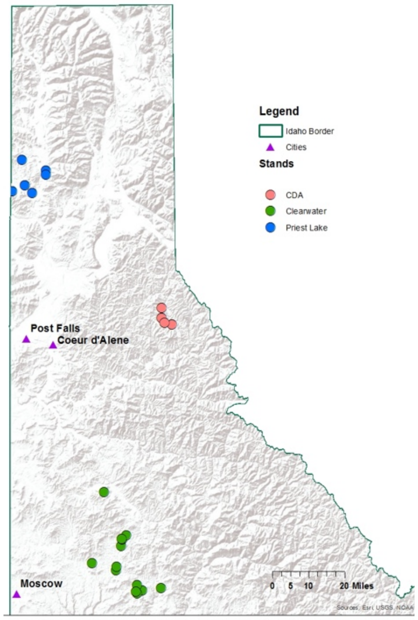

Figure 2.4 Map of stands sampled across northern Idaho. Pink (Coeur d'Alene Mountains), green (Clearwater Mountains) and blue (Priest Lake area) dots show stand locations in the three regions. Purple triangles indicate the location of major towns or cities.

A subsample of two trees per species in every plot were cored on the uphill side of the tree at breast height. Entire cores were taken of white pine (i.e. cored to the pith of the tree), while shorter cores were collected for two of all other species to examine five-year stem growth increments. The selection of subsampled trees started in the northeast quadrant and moved clockwise, selecting the first two trees of each species. The cores were transported back to the University of Idaho, mounted, and sanded. White pine cores were used to accurately age the stand. The height and crown length of the cored trees was also measured in the field.

Canopy cover was estimated using a GRS Densitometer^{TM} (Geographic Resource Solutions, Arcata, CA). A cloth tape was laid across the overstory plot oriented north to south with another cloth tape across the plot, oriented east to west. At each of the 30 locations within the plot (Figure 2.3), the densitometer was used to determine if foliage or open sky was overhead. The number of points intercepting foliage were divided by 30 and multiplied by 100 to calculate canopy cover. Canopy cover averaged 68 percent across all stands sampled and ranged from 27 to 93 percent.

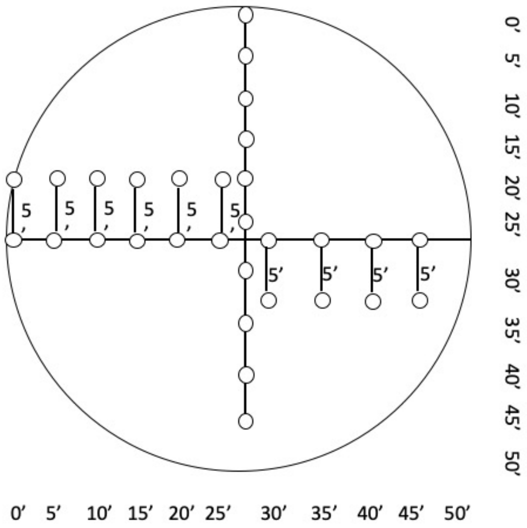

Figure 2.5 Sampling design used to measure canopy cover using a GRS Densitometer^{TM} within each plot. Data was collected at each point along two transects, one running north to south and the other east to west. Distances are shown in feet.

A regeneration 1/800th hectare (1/300th acre) plot was nested within the center of each overstory plot where all seedlings and saplings taller than 15 cm (6 in) but less than 12.7 cm (5 in) DBH were recorded. Seedlings were placed into height classes if they were below 135 cm. The height classes were 15 – 43 cm, 44 – 73 cm, 74 – 104 cm, 105 – 136 cm. Trees greater than or equal to 135 cm tall, but less than 12.7 cm DBH were put into diameter classes. The diameter classes were 135 cm tall – 4.4 cm DBH, 4.5 – 6.4 cm DBH, 6.5 – 8.4 cm DBH, 8.5 – 11.4 cm DBH, 11.5—12.7 cm DBH.

Data analysis

Age, basal area, trees per acre , quadratic mean diameter, mortality, management, and understory diversity metrics were calculated using the methodology shown in Table 2.1. Data analysis was done at the stand level (for every one stand there were four plots) The stand ages ranged from 19-58 years old with an average age of 31. The average number of overstory (trees ≥ 12.7 cm in DBH) trees per hectare across all stands was 647 and ranged from 247 to 1,235. Mortality averaged 11 percent across all stands and ranged from 0 to 55 percent.

Composition of white pine within the stand was calculated as the proportion of white pine divided by the total stem density in the overstory plot. Standing mortality (i.e. snags) within the stand was calculated as the number of standing dead trees divided by the total number of standing alive and dead. Dead trees on the ground were not measured.

Table 2. 1 Variables measured in the field or calculated from field measurements used in the analysis of stand structure in planted western white pine stands.

Variable	Description
Age	Tree cored at DBH, rings counted, added 5 years [1]
Basal Area per acre (BA)	$(0.00007854 \times DBH^2) \times$ trees per hectare
Trees per hectare (TPH)	Number of live trees (greater than 12.7 centimeters in diameter) in plot × 49.4
Quadratic mean diameter (QMD)	$\sqrt{\frac{BA}{TPH}} \times 0.00007854$
Standing Mortality	Number of standing dead trees ÷Total number of standing trees
Canopy Cover (%)	Number of "Canopy, yes" observations ÷ 30 (total number of observations) × 100
Management	If white pine were pruned, management= "YES"
Blister Rust (%)	Number of white pine with blister rust ÷ Total white pine × 100
Understory Species Richness	Count of understory species (shrubs and forbs) within the 1 by 1-meter plot up to 6 feet tall
Seedlings	Trees between 15 cm and 136 cm tall
Saplings	Trees between 135 centimeters tall and 12.7 cm at DBH
[1]Steele and Cooper 1983	

Exact management history after planting was not available for any of the stands. In order to estimate stand age, western white pine trees were cored at DBH and 5 years was added to the ring count to estimate total age (Steele and Cooper 1983). Even though thinning history was not available for the stands, it was assumed the stands on the Forest Service lands had been thinned if the western white pine trees were pruned, as this is the common practice across the region to minimize the impact of blister rust (Hagle et al. 1989). The resulting variable for management history was binary, either “Managed” or “Not Managed”. Of the 27 stands, 17 were not thinned and pruned and 10 were managed.

Diameter distributions were used to characterize the effects of blister rust and age of the stand on the distribution of tree size classes. Diameter distributions were developed because tree diameter is often representative of stand volume and may be an indicator of economic and biological values (Bailey and Dell 1973). Diameter distributions also offer easy interpretation of stocking, minimum tree diameter, maximum tree diameter, and skewness of the distribution towards large or small trees. Reverse J-shaped distributions result from natural disturbances or heavy cuttings that create gaps in the canopy and stimulate regeneration and ingrowth of seedlings and saplings (O’Hara 2014). Diameter distributions only included trees in the overstory ≥ 12.7 centimeter (≥ 5 in) DBH, therefore the distributions are left truncated. However, because the truncation point is so close to the minimum stand diameter, these data are still a valid representation of the stand diameter distributions (Zutter et al. 1986).

Diameter distributions grouped the data into blister rust abundance and age classes. Low blister rust abundance, evaluated as evidence of a stem canker, ranged from 0 to 20 percent of trees within a plot, while moderate to high blister rust infection ranged from 21 to 100 percent of trees with a canker. The three age classes were based on a combination of the data collected and biological relevance. The youngest age group ranged from 19 to 25 years old. The middle and older classes ranged from 26 to 35 and 36 to 58, respectively. Diameter distributions were created to show species groups of white pine, other shade intolerant species and shade tolerant species. The other shade intolerant species group comprised Douglas-fir, grand fir, lodgepole pine, western larch, ponderosa pine and Engelmann spruce (*Picea engelmannii*). Western red cedar, western hemlock, and grand fir were classified as shade tolerant species.

Logistic regression was used to evaluate the presence of seedlings (of any species), a binary response variable. Seedlings were not grouped by shade tolerance or species due to the low sample size. All calculations were done in R statistical software version 3.6.1 (R Core

Team 2017). The *trtools* package was used to calculate the predicted probabilities and odds ratios (*trtools* package, R v 3.6.1). An odds ratio of one represents no effect of the explanatory variable. To ensure the chosen model provided a good fit to the data, the model with the lowest Akaike's Information Criterion (AIC) was chosen (Ott and Longnecker 2010).

Mixed effects models were used to account for the hierarchical nature of plots within stands. Plots were not independent of each other because they are in the same stand with similar management histories (Ott and Longnecker 2010). This was done using the *nlme* package in R (*nlme* package, R v 3.6.1). Analysis of Variance (ANOVA) was used to evaluate the sapling abundance response to explanatory variables. Assumptions were checked via diagnostic plots. The residuals vs fitted plot showed a horizontal line with no pattern or significant deviation. The Normal QQ plot showed the data was normally distributed, therefore no transformations of the dependent variable were required (Ott and Longnecker 2010).

The Forest Vegetation Simulator (FVS) was used to predict the yield (in merchantable cubic meter and merchantable board feet volume) of individual stands at 60 years of age. FVS is an individual-tree forest growth model that is used across the United States (Crookston and Dixson 2005). The program uses a geographic specific version when calculating tree growth, in this case the Inland Empire (Keyser et al. 2019, Crookston and Dixson 2005). Stand data, such as stand identification number, region, age, habitat, slope, aspect, and density were imputed to FVS. Individual tree data (all trees within the 1/50th hectare (1/20th acre) plot, and all trees over 1.37 meters (4.5 feet) in the 1/800th hectare (1/300th acre) plot, was also imputed into FVS. Because the diameters of this data were ranges, they were assigned to the midpoint diameters of each class (e.g., 4.5 cm, 6.5 cm, 9 cm, and 12 cm). Information from the 1/50th hectare plot included species, DBH and crown ratio. For a subset of trees (two of each species at every overstory (1/50th hectare) plot) 10-year diameter increment and tree height were imputed. Data from the 1/800th hectare plot included the assigned diameter, and species.

The output from FVS aged each stand in 10-year increments, predicting the volumes in year 2029, 2039, 2049, 2059, and 2069. I used the volumes when the stands were between 60 and 69 years old. For example, the first stand was 23 years old in 2019 so the volume used was from year 2059, when the stand will be 63 years old. An ANOVA was used to evaluate the volume of merchantable timber in response to explanatory variables (composition at time of sampling, management history and density). The data was entered into FVS at the plot level, but the program used the four plots to get averages across the stand, therefore there was no need to use mixed effects models to treat the plots as a random effect.

Results

Overstory Structure After the Introduction of Blister Rust

Age class had a strong effect of shifting diameter distributions to the right, while blister rust abundance increased the number shade tolerant trees, except for the youngest age class (Figure 2.4). The young age class (19 to 25 years old) had trees with DBHs between 15 and 60 cm (5-16 in). When blister rust abundance was low in the young stands, the distribution was highly skewed to the left, while younger stands with high blister rust abundance had a slightly more normal distribution. The middle age class, ages 26 to 35, had diameters ranging from 15 to 45 cm (5-18 in), and distributions were right skewed for both classes of blister rust abundance. The 36 to 45-year age class had a relatively uniform distribution with low abundance of blister rust and a slight right skew distribution in the high blister rust abundance class. When blister rust was abundant there were more other species besides white pine. The older stands, aged 45 to 60, had flat, relatively uniform distributions with diameters ranging from 15 to 60 cm (6-24 in). Interestingly stands with high blister rust abundance showed a bimodal distribution where most smaller trees were shade tolerant species.

There were numerous saplings in all stands except for stands with low blister rust that were 36 years or older (Table 2.2). There was minimal difference in the number of saplings between low and high blister rust stands from age 19 to 35, while at older ages stands with higher blister rust had more saplings than low blister rust stands.

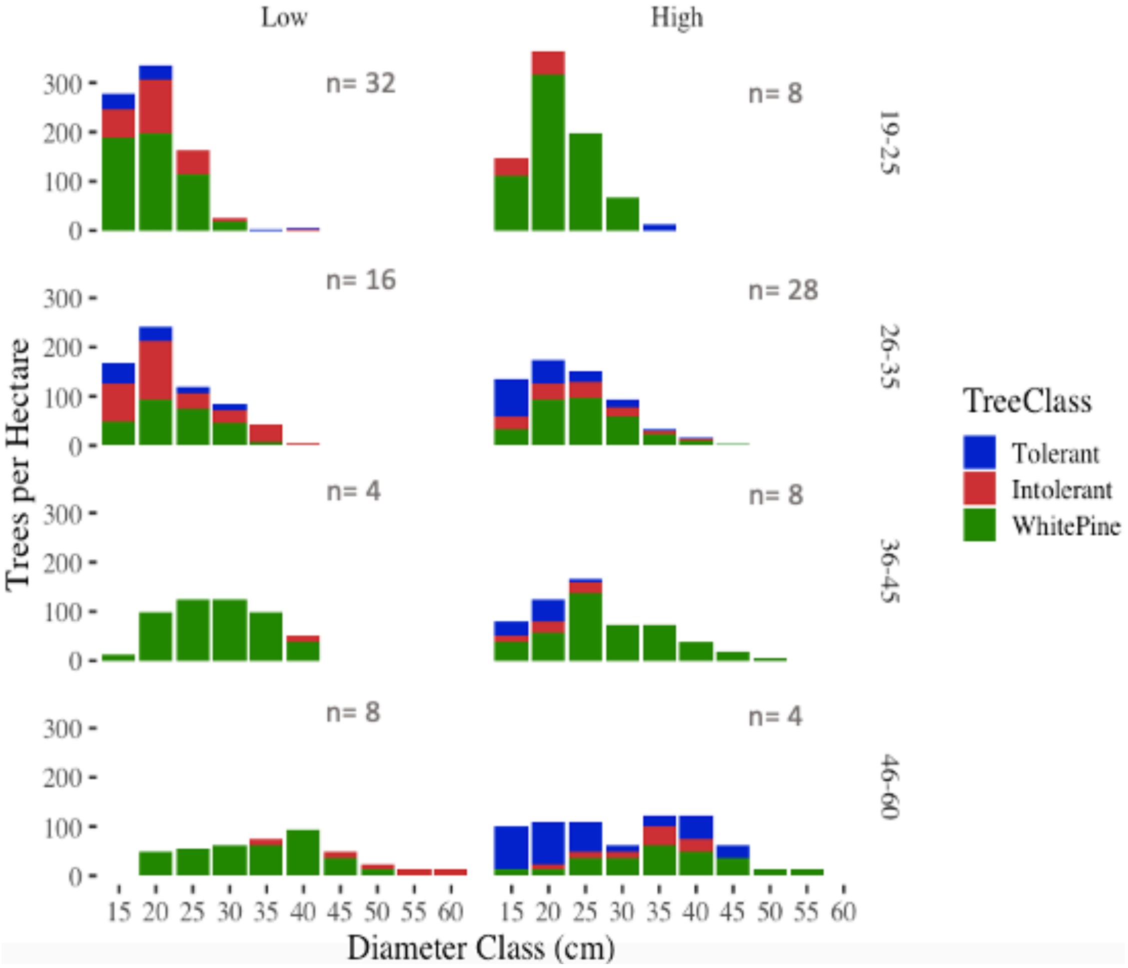

Figure 2.6 Average diameter distributions across all plots by age class and blister rust abundance (low blister rust abundance:0-20%, high 21-100%) (n is equal to the number of plots sampled). Green bars show white pine and red bars show other shade intolerant species (western larch, lodgepole pine, ponderosa pine, Engelmann spruce, Douglas-fir). Shade tolerant species are in blue; grand fir, western red cedar and western hemlock.

Table 2. 2 Average number of saplings (trees between 137 cm in height to 12.4 cm in diameter at breast height) per hectare in each age and blister rust class (low:0-20%, high 21-100%)

Age Class	**Low blister rust abundance**	**High blister rust abundance**
19-25	556	741
26-35	904	1,030
36-45	0	1,946
46-60	94	556

The greatest abundance of blister rust in the unpruned stands occurred in the two younger age classes (19-35 years old) (Table 2.3). Blister rust abundance in these two age classes was less if the stands had evidence of pruning, with abundance 22.1% lower in the 19-25 age class and 5.7% lower in the 26-35 age class. However, because of the high standard deviations, there was not significant difference in blister rust abundance regardless whether it was pruned or not pruned. There were no older stands that were pruned to compare blister rust abundance with unpruned stands, but the oldest age class (46-60 years old) had the lowest abundance possibly because trees died in the past and were not available to measure.

Table 2. 3 Summary of average blister rust abundance (% of trees affected) by age class. (Evidence of blister rust; bole canker, na= no stands sampled). Same letters within a row indicate significant differences between pruned and not pruned for a given age class at the α = 0.05 level when tested with analysis of variance.

Age Class	Average abundance of BR (Pruned)		Standard deviation	Average abundance of BR (Not Pruned)		Standard deviation
19 - 25	5.0	a	9.1	27.1	a	23.6
26 - 35	28.7	a	19.9	34.4	a	36.0
36 - 45	Na		na	21.0		23.0
46 - 60	Na		na	17.5		18.1
All	14.5	a	18.5	27.3	a	28.3

Seedling and Sapling Regeneration

The probability of seedling presence was predicted using a logistic regression model. The full logistic regression model included age, percent white pine by stem number, quadratic mean diameter, percent of standing dead trees (mortality), percent canopy cover, duff depth, and management history as explanatory variables and presence/absence of naturally regenerated seedlings as the dependent variable. Percent white pine, standing mortality, percent canopy cover, duff depth and the interactions were not significant ($p > 0.05$) and were dropped from the final model that included only the significant variables: stand age (p = 0.010) and management history (p = 0.047) (Table 2.4). The AIC of this model was 135.1. The odds ratio for age was 0.93, indicating that for every one-year increase in age, the odds of finding a seedling in the stand decreases by 7%. If the stand was thinned, the odds of finding a seedling increases by 158%. As stand age increased, the predicted probability of a seedling being present decreased (Figure 2.5). At each age, the probability of finding a seedling is higher when thinned. The estimates between thinned and not thinned get closer as the standages got older and the effect of thinning was no longer significant after age 40 (p > 0.050) (Table 2.5).

Table 2. 4 Summary table for predicted probabilities of seedling presence based on logistic regression.
CI are the 95% confidence intervals of the parameter estimates.

Variable	Estimate	p-value	2.5% CI	97.5% CI	Odds Ratio
Intercept	2.031	0.029	1.327	53.310	7.621
Age	-0.071	0.010	0.878	0.979	0.931
Management	0.949	0.047	1.028	6.782	2.583

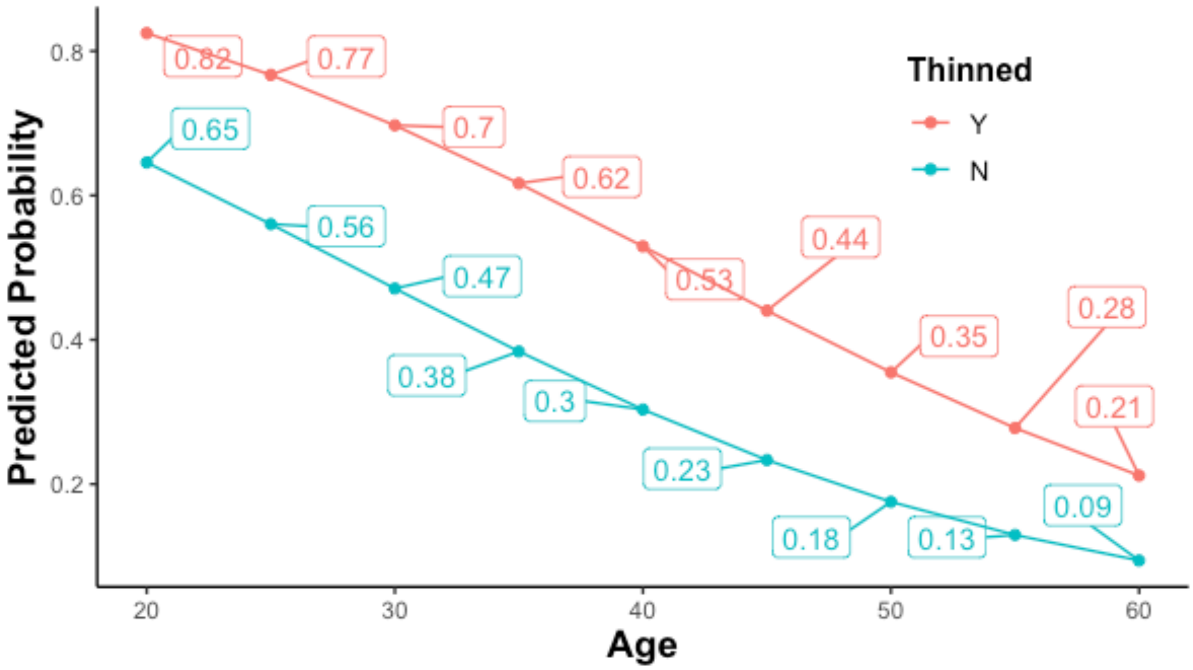

Figure 2.7 Predicted probability of seedling (trees between 15 to 137 cm in height) presence by stand age and management history (thinned and pruned). "Y' indicates the stand was thinned, while "N" indicates the stand was not thinned.

Table 2. 5 Estimates of differences of predicted probability of seedling presence between thinning and not thinning at different ages based on predictions of the logistic regression model.
P-values based on paired t-test and indicate significant difference between thinning and not thinning at each age, with p ≤ 0.05 considered a significant difference

Age	Estimated Difference	p-value
20	0.179	0.060
25	0.206	0.041
30	0.226	0.035
35	0.233	0.039
40	0.226	0.053
45	0.207	0.084
50	0.179	0.137
55	0.148	0.209
60	0.118	0.287

Mixed Effects Linear Regression was used to determine the variables that had a significant effect on the number of naturally regenerated saplings present. The full mixed effects linear regression model included the following explanatory variables: percent white pine, trees per hectare, duff depth, management history and mortality. Only significant variables ($p \leq 0.05$ Table 2.6) remained in the final model. The interactions of the explanatory models were tested but were not included in the model because they were not significant ($p>0.05$). The only significant variable was management history ($p=0.05$, Table 2.6), which accounted for 56 percent of the variance within the data ($R^2=0.56$, Table 2.6). The model indicates that the stands that were managed (thinned and pruned) had 249 more saplings per hectare (Table 2.6, Figure 2.6).

Table 2. 6 Linear mixed effects ANOVA model. Number of saplings per hectare within the sample plot vs significant ($p \leq 0.05$) explanatory variables Sapling; trees 134 cm in height to 12.7 cm in diameter at breast height

Variable	Estimate	Std. Error	DF	p-value
Intercept	238.2	75.9	81	0.002
Managed-Yes	249.3	124.7	25	0.05
Fixed effects generalized R^2			0.08	
Fixed+ Random generalized R^2			0.56	

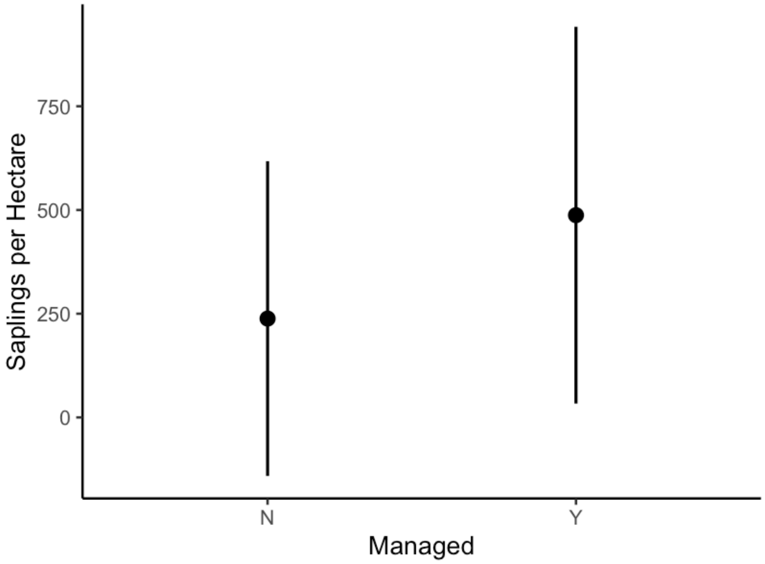

Figure 2.6 Number of saplings per hectare vs management history

Growth and Predicted Yield

A linear regression model was used to determine the variables that had a significant effect on the predicted volume (cubic meters per hectare) of the stands. To do this, I projected the volume of each stand at ages 60 to 69 years with FVS. Age at the start of the simulation did not significantly affect the predicted volume ($p > 0.05$). Explanatory variables in the full model included; management history, trees per acre (at predicted age), and percent white pine. Only significant variables, percent white pine ($p \leq 0.05$ Table 2.8), remained in the final model. The interactions of the explanatory models were tested but were not included in the model because they were not significant ($p>0.05$). The significant variable, percent white pine ($p=0.03$, Table 2.8) accounted for 14 percent of the variance within the data ($R^2=0.14$, Table 2.8). The model suggests that with a one percent increase in the percent white pine composition volume increased by 1.7 cubic meters per hectare (Table 2.8, Figure 2.7). Stands sampled and aged to between ages 60 and 69 had predicted volumes ranging from 85 to 634 with a mean of 308 merchantable cubic meters per hectare (Table 2.8, Figure 2.7).

Table 2. 7 Predicted QMD and volume per hectare at 60-69 years old

Stand	Managed	Age (2019)	Predicted year	Age at predicted volume	Percent white pine	QMD (cm) at 60-69 years old	Predicted merchantable cubic meters per hectare (at 60-69 years)
Angry Wolf	No	23	2059	63	99	24.9	499
Ewe Creek	No	25	2059	65	90	13.8	402
Fern Falls	Yes	32	2049	62	52	17	382
Flat Creek	Yes	28	2059	68	48	18.6	516
Gleason	Yes	25	2059	65	48	14.8	359
Ida Creek	No	37	2049	67	97	14.2	417
Little Tyson	No	25	2059	65	39	17.6	215
Lost Creek	No	25	2059	65	29	18.1	235
Middle Miner	Yes	29	2059	69	73	16.1	421
Nat Brown	No	23	2059	63	68	23	478
North Porc	Yes	19	2069	69	90	22	628
Oviatt Creek	Yes	25	2059	65	40	17.8	331
Peterson	No	53	2029	63	79	34.7	577
Purdue Creek	Yes	25	2059	65	41	15.3	331
Quartz Mt	Yes	32	2049	62	13	20	370
Robideaux	No	19	2069	69	98	22.4	634
Seed Orchard	No	36	2049	66	98	18.4	389
Shadow Falls	No	35	2049	65	18	18.9	401
Sleepy Wolf	No	32	2049	62	97	17.2	334
Snow Creek	No	58	2029	68	41	24.4	666
South Porc	Yes	21	2059	61	36	17.7	309
Spud Patch	No	65	2059	65	67	20.4	454
Stimson	No	29	2059	69	87	25.2	491
Tired Wolf	Yes	24	2059	64	98	23.5	512
Two	No	30	2049	60	35	22.1	542
Vassermeadows	No	43	2039	63	63	21.4	491
VQ PREF	No	48	2039	68	100	17.4	549
All Stands:	Average predicted merchantable cubic meters per hectare (at 60-69 years old)				442	Standard deviation	117

Table 2. 8 Linear regression ANOVA model.
Predicted merchantable volume (Cubic meters per hectare) of each stand sampled vs significant ($p \leq 0.05$) explanatory variables.

Variable	Estimate	Std. Error	p-value
Intercept	331.4	52.58	<0.0001
Percent white pine	1.7	0.75	0.03
Adjusted R^2			0.14

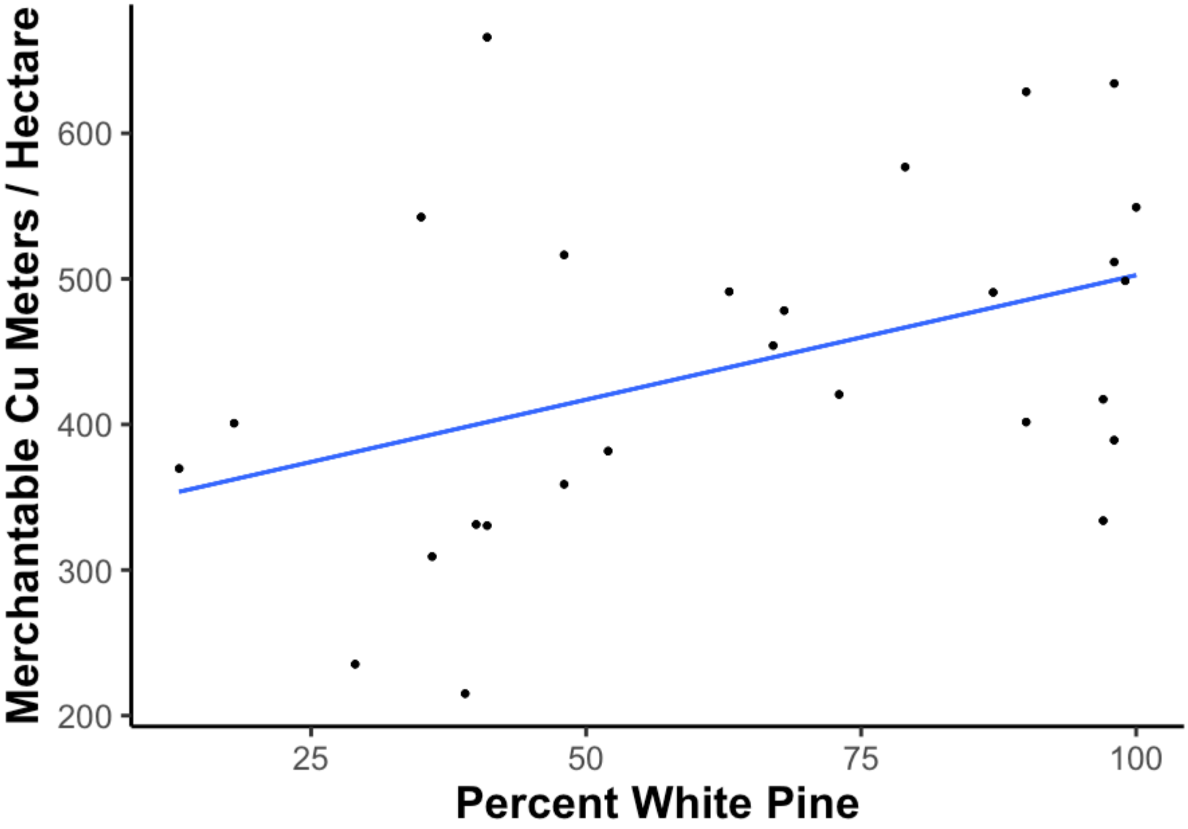

Figure 2.7 Merchantable cubic meters per hectare vs percent white pine at age 60 (Age 60 represents trees aged (by FS VEG) to 60-69 years old).

Discussion

Overstory structure after the introduction of blister rust

Pure stands of white pine in the Inland Northwest were not historically common but often intermixed with other conifer species such as Douglas-fir, western larch, lodgepole pine, and Engelmann spruce (Rockwell 1917). The introduction of blister rust combined with intense pre-salvage harvesting resulted in the loss of white pine across much of the region (Ketcham et al. 1968). In addition, composition of other early successional species declined over time due to selective harvesting followed by fire suppression and lack of active forest management. The result is a landscape comprised of middle-aged stands dominated by late successional tree species that likely were uncommon across the broad swath present today. Active management with a particular emphasis on regenerating early successional species is becoming more common, enhancing forest complexity and providing a host of ecosystem benefits to the region.

White pine stands planted across northern Idaho in the late 1990s and early 2000s are the result of efforts to reestablish these early successional stands. My data shows a uniform diameter distribution and an abundance of seedlings and saplings in the stands sampled, suggesting these stands are an even-aged stratified mixture. Even-aged stratified mixtures have a dominant overstory cohort with potentially several lower crown layers and are typically represented by a right-skewed diameter distribution (Ashton and Kelty 2018). In even-aged stratified stands, different species often occupy different strata due to a combination of differential height growth, differing shade tolerances, and advance regeneration (Ashton and Kelty 2018).

The diameter distributions indicate two different processes affecting stand dynamics in these white pine stands. The high number of smaller diameter trees in the younger stands is from a combination of planted seedlings and natural regeneration. These trees are strongly competing for resources to achieve dominant crown positions. In the absence of blister rust mortality, the more vigorous trees would out compete the weaker trees for light and soil resources (Ashton and Kelty 2018). This would result in a uniform stand with complete canopy closure and trees with small crowns (Ashton and Kelty 2018). Graham (1990) states the composition of white pine stands is decided in the first 30 years after establishment. During this time, lodgepole pine and western larch can grow one and a half times faster than white pine (Graham 1990). Western larch often remains superior in height growth, however lodgepole pine slows down after 50 years. Grand fir and Douglas-fir also compete with white pine in the first 30 years but are often overtopped (Graham 1990).

Western hemlock can match the growth of white pine, but only on shaded, north facing slopes (Graham 1990).

In the older stands there was evidence of canopy gaps resulting in either stratified even aged structures or multi-aged stands with seedlings that regenerated following gap formation, both with an understory of shade tolerant species. These canopy caps are characteristic of current white pine stands due to blister rust. These stands may have canopy gaps from blister rust mortality that can kill numerous trees within a short period of time (Ban et al. 1998). Because the survival rate for improved white pine seedings is approximately 66 percent, there is the potential for numerous white pine trees to die in a short period of time (Fins et al. 2002). After a gap forms, the regeneration within the opening depends greatly on the size of the opening. Shade intolerant species are able to dominate larger gaps, whereas shade tolerant species may be released from several years of suppressed growth in a small canopy opening (Hibbs 1982, Canham et al. 1994, Kobe and Coates 1997). My study supports this idea of shade tolerant species dominating gaps from blister rust, shown in Figure 2.4. Therefore, there is evidence to reject the first null hypothesis and conclude the introduction of blister rust has shifted the overstory composition over time. More specifically, the stands with low blister rust abundance were dominated by white pine or shade intolerant species in all age classes. Whereas, the stands with high blister rust abundance showed shade tolerant species present in the lower diameter classes of the older stands (36 to 45 and 46 to 60 years).

Some of the stands sampled were pruned to 3 meters (9 feet), in order to reduce the impact of blister rust (Hunt 1991). Pruning is thought to significantly reduces the risk of blister rust infection and this study supports that. My study showed evidence of pruning significantly reducing the evidence of blister rust in the western white pine sampled over all age classes. Because pruning was done in association with thinning, it created a different light environment than canopy gaps from blister rust.

Seedling and sapling regeneration

When timber production is the main focus of the forest management, thinning the stand to 500-740 trees per hectare (200-300 trees per acre) would increase wood production and encourage regeneration of seedlings (Graham et al. 1994, Ashton and Kelty 2018). In a light thinning, the canopy will quickly fill in the gaps and shade out understory species that would compete for nutrients (Hibbs 1982, Kobe and Coates 1997). Deal and Tappeiner (2000) found that after a heavy cutting, resembling a stand with large canopy gaps, resulted in a more complex stand with greater seedling diversity. The species and growth of these new cohorts that were established in heavily cut areas depended on the number and species of trees left post harvest (Deal and Tappeiner 2000). More specifically, their study found that heavy cutting (>50% basal area removed) favored the establishment of seedlings (trees shorter than 1.3 meters in height). When less than 50 percent of the basal area was cut, there were no seedlings present, instead the trees left after cutting expanded their crowns to fill in the canopy gaps (Deal and Tappeiner 2000). If management goals were focused more on resiliency and complex structure, the use of large canopy gaps would promote the establishment of shade intolerant species, compared to smaller canopy gaps encouraging the establishment of western hemlock and grand fir (Graham et al. 1994, Jain 2004). Stands composed of these shade tolerant species may become overstocked and vulnerable to insect and disease attacks, as well as increase the risk of a stand replacing fire (Graham et al. 1994).

The gaps in these white pine stands were not large enough to encourage intolerant seedlings to regenerate. Especially in these stands, where the gaps are formed due to a handful of tree deaths (or a thinning) and are quickly filled by lateral crown growth (Ban et al. 1998, Hibbs 1982). The shade tolerant species have an advantage to these conditions because they are present but suppressed in the understory. When light becomes available they are able to release (Woods 2008). Even in small gaps, shade tolerant species will go through several periods of suppression before they are released whereas shade intolerant species are not able to survive when they are suppressed (Hibbs 1982, Canham et al. 1994, Kobe and Coates 1997). Kobe and Coates (1997) found that in smaller gaps (less than 75 square meters), only western red cedar, western hemlock, and subalpine fir could survive (Kobe and Coates 1997), while shade intolerant species, such as lodgepole pine, and white pine require gaps greater than 2400 square meters (Kobe and Coates 1997). These findings support the results of this study. My results show seedling regeneration in this study was dependent on the age of the stand and management history, whereas sapling regeneration was only dependent on the management history. This supports my hypothesis: understory regeneration was found to be significantly influenced by management history and stand age. However, variables such as overstory composition, duff depth and mortality did not have a significant effect on the number of seedlings and saplings present.

Seedling and sapling presence in this study was influenced by the age of the stand and whether the stand had been thinned and pruned. Younger stands had a higher probability of seedling presence. The probability of finding a seedling was even higher if the stand had been thinned. This finding is well supported by past studies. A study done in the Priest River Experimental Forest in northern Idaho found that seedling density was much greater 11 years after thinning compared to unthinned controls and persisted 50 years after thinning (Shen et al. 2019). In my study, thinning increased the probability of seedling presence at all ages although the effect of thinning became less significant as the stand ages. At age 40, the effect of thinning was no longer significant (p = 0.053). Bailey and Tappeiner (1998) suggest that subsequent thinning may be needed to promote future growth of seedlings and saplings due to closure of the overstory canopy several years after thinning.

Growth and predicted yield

Pure white pine stands were historically not common across northern Idaho and there are documented benefits to mixed species stands (Rockwell 1917). Generally speaking, mixed stands reduce the risk of poor performance or loss of market for a particular species (Ball et al. 1995). Mixed species stands are also more resilient because in a single species stand you risk losing the entire rotation to a single pathogen (Ball et al. 1995). Another risk of single species plantations is possible site quality decline after repeated rotations of a single crop trees (Ball et al. 1995). All of these risks can be easily managed through good forestry practices and sustainable forest management (Ball et al. 1995). Mixed stands may also offer greater diameter growth. A study by Waskiewicz et al. (2013) found that using silviculture treatments in the Northeast United States that sought to maintain a forest evenly mixed with eastern white pine (*Pinus strobus*) and red oak (*Quercus rubra L.*) may be more productive than single species stands of either species. Mixed stands, differing in root and crown structure, shade tolerance as well as other traits may show improved productivity due to complementary resource use (Kelty 1992). Ball et al. (1995) recommends encouraging native understory shrubs and forbs under the desired crop tree as a middle ground to pure and mixed plantations.

We know that historically these western white pine-dominated stands were one of the most productive forests in the western United States and this study shows evidence that the number of white pine in the overstory is positively corelated with the total merchantable volume in the stands sampled. Specifically, this study found that percent western white pine within the stand was a significant indicator of yield of stands when grown to ages between 60 and 69. With an increasing amount of white pine in the stand, the total merchantable volume also increased. This finding is not surprising. Neuenschwander et al. (1999) stated that older white pine stands can yield 600 cubic meters (100,000 board feet per acre), whereas similar-aged stands without white pine, yield less than half that volume under similar environmental conditions. The growth characteristics of western white pine, as well as its longevity, genetic adaptability and seed producing ability allow the species to quickly dominate and thrive in a variety of stands (Rehfeldt et al. 1984, Graham 1990, Jain et al. 2015). Specifically, western white pine has the ability to thrive in a mixed stand due to its deep roots, when compared to the shallow roots of grand fir, western hemlock, western red cedar and Douglas-fir (Rockwell 1917).

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Chapter 3: Understory Diversity in Planted Western White Pine Stands of the Northern Rockies

Abstract

Moist forests of the northern Rocky Mountains cover 2.4 million hectares in the US and Canada and are one of the most diverse conifer forests in the world. These forest that are commonly associated with andic soils were once dominated by western white pine *(Pinus monticola* Dougl. Ex. D Don), an early-successional species. The introduction of white pine blister rust (*Cronartium ribicola*) followed by extensive harvesting during the 20th century decimated western white pine, no mature white pine-dominated forests were left. Since the 1950s, an active breeding program for blister-rust resistant white pine has resulted in resistant seed orchards producing seed and proliferation of white pine plantations across the region. Little information on the understory floristic diversity of stands planted with blister-rust resistant trees exist even though planting has been common since the 1980s. My objective is to examine the understory floristic diversity of planted white pine stands in relation to canopy characteristics and overstory species composition across the Northern Rockies. I selected stands that were planted with nearly 100% white pine prior to 1991 and similar aged naturally regenerated stands with late successional dominance on federal and private forest land. Understory vegetation was measured to the species level followed by measurements of tree structure and composition, and canopy openness. Results show white pine stands have a high diversity of vascular plant species that thrive under the moderate light conditions compared to unplanted stands with much lower diversity. The species found in these stands were representative of species associated with historic stands as mentioned in previous literature.

Introduction

Introduced forest pathogens have altered composition of forests across the world (Waring and O'Hara 2005). Often a single tree species among many within a stand is affected by the introduced pathogen, altering stand dynamics and forest succession (Ellison et al. 2005). These introduced pathogens and pests are leading to the demise of essential tree species around the world (Ellison et al. 2005). These pathogens have the ability to reduce biodiversity, displace natives and disrupt the entire ecological system (Mack and Lonsdale 2001). In a forest with few keystone species that perform critical ecological functions, there is little redundancy and because there is not a species to perform the same successional role within the stand, there is a risk of the rapid loss of the unique habitat associated with the species (Ellison et al. 2005, Ashton and Kelty 2018). More specifically, the loss of one species can change the watershed hydrology and affect wildlife and invertebrate populations as well as surrounding vegetation (Ellison et al. 2005, Snyder et al. 2002). For example, the loss of whitebark pine (*Pinus albicaulis*) due to blister rust (*Cronartium ribicola*) in the Northwestern USA has the ability to increase streamflow because it can no longer moderate snowmelt and runoff (Ellison et al. 2005). Similarly, streams that have lost the shade of the eastern hemlock (*Tsuga canadensis*) due to the hemlock woolly adelgid (*Adelges tsugae*) can no longer support unique assemblages of fish, salamanders and invertebrates (Snyder et al. 2002). In addition to the pathogens mentioned, there are over twenty introduced pathogens attacking woody plants in the United States (Liebhold et al. 1995).

The introduction of white pine blister rust in the early 20th century is a classic example of an introduced pathogen affecting forest composition, dynamics, and ecosystem functionality in western North America. This pathogen reduces vigor and kills trees within the *Pinus* subgenus *strobus*. Numerous white pine species within this subgenus occur across the region, including western white pine (*Pinus monticola*), sugar pine (*Pinus lambertiana*), whitebark pine, and limber pine (*Pinus flexilis*). In the northern Rocky Mountains, the greatest loss to date has occurred for western white pine that once dominated these forests. Prior to the introduction of blister rust, the species occupied 60 percent or more of the density within the stand, with average tree sizes of one meter in diameter in undisturbed stands (Fins et al. 2002). The loss of this important species has prompted management objectives that look to restore white pine stands as well as the ecosystem benefits they offer.

Forest management objectives and practices continue to evolve where multiple objectives in addition to timber production are often desired. There is increasing interest in managing forests for complex structure and composition, of which understory diversity plays a critical role (Puettmann et al. 2009). There are several benefits of complex understories in forested stands, including resiliency to disturbance, nutrient cycling, carbon sequestration, and soil fertility (Bauhus et al. 2009; Chastain et al. 2006; Nilsson and Wardle 2005). Silviculture techniques can manipulate environmental factors to restore ecosystems, improve biodiversity, and manage for more complex and resilient ecosystems (Puettmann et al. 2009).

When managing for complexity, overstory characteristics, such as species composition can be manipulated to change the understory microclimate, which can influence the floristic diversity of the understory. Shade intolerant species in the overstory allows more light to penetrate the canopy compared to shade tolerant species (Messier et al. 1998) due to their foliage arrangement (Horn 1971). Previous literature shows most pine species have needle and arrangement characteristics that allow for light transmittance through the canopy (Horn 1971; Bolstad and Gower 1990; Barbier et al. 2007). *Pinus* as well as *Larix* species are shade intolerant conifer species and have foliage clumped within fasicles and at the end of branches, thus they allow more light to penetrate to the understory and positively influence understory diversity (Barbier et al. 2007). A shade tolerant species, western hemlock (*Tsuga heterophylla*), has short, flat foliage that captures the majority of incoming light if the species is in the overstory and reduces light penetration to the understory (Bond et al. 1999; Niinemets et al. 2002). Therefore, it may be possible to enhance light in the understory environment by favoring shade intolerant species, such as western white pine (*Pinus monticola*; hereafter white pine), in the overstory.

Diversity, or the number of species, in the understory is but one metric of understory responses to microclimatic conditions created by different overstory structure and composition. Species assemblages can also differ, which provides additional understanding of microclimates that make these stands so floristically diverse (Kraft et al. 2015). Species assemblages are driven by the functional traits and their correlation with environmental factors like canopy openness and duff depth through environmental filtering (Kraft et al. 2015).

The overall goal of this research is to examine the effects of stand structure, overstory composition, and environmental variables on understory diversity of vascular plants in young but closed-canopy planted western white pine stands across northern Idaho. The study sought to test three hypotheses: (1) understory species richness of vascular plants increases with greater white pine composition due to more light penetrating the understory through the porous foliage arrangement of the branches (2) understory richness will be negatively correlated with stand density and overstory canopy cover but positively correlated with mortality (due to gap formation) and post-establishment thinning and pruning, and (3) species assemblages in planted white pine stands will be similar to assemblages found in white pine stands prior to blister rust.

Methods

Study area

A total of 27 stands across northern Idaho were selected for this study. All stands were either planted with white pine between 1960 and 2000 or of a similar age and naturally regenerated. Stands were primarily on USDA Forest Service land, but ten stands were on private timberlands (Chapter 2).

Stands selected had an average diameter greater than 12.7 cm (5 in), more than 25 percent white pine by stem number and were reasonably accessible by road (Chapter 2).

Four plots were installed in each stand using the plot design of the USDA Forest Service Forest Inventory and Analysis program (Chapter 2). Each plot was 1/50th hectare (radius = 8 m (26.3 ft)), where all living and standing dead trees were identified to species and measured for diameter at breast height (DBH; 1.37 m from the ground on the uphill side of the tree). The presence of blister rust was noted for all white pine trees. A random sample of two trees per species were selected for measurement of total height and crown length.

Understory sampling

Understory vegetation was sampled within a 1 × 1 meter square plot oriented in the northeast quadrat with the southwest corner of the sampling frame at the plot center (Figure 3.1). All vascular plant species less than 1.82 m (6 ft) tall within the 1 m^2 plot were identified to the species level except R*osa* spp., *Viola* spp*., Mitella* spp*., Epilobium* spp. and grasses. Unknown species were collected in a press, given an identification number and brought back to the lab for proper identification. Ocular estimates of percent foliar cover of each individual species were recorded to the nearest five percent, with one percent indicating a trace amount of cover. The total cover for the vegetation plot could exceed 100 percent due to layering of vegetation. The number of understory species found within a stand ranged from 0 to 19 species with an average of 11 species per stand (Appendix 4). At the northwest and southeast corners of the 1 m^2 plot, duff depth, including litter was measured to the nearest millimeter using a ruler. To reach the bottom of the duff, the needles and organic matter were excavated until bare mineral soil was found. Duff depths ranged from 0 to 105 mm, averaging 41 mm (Appendix 1).

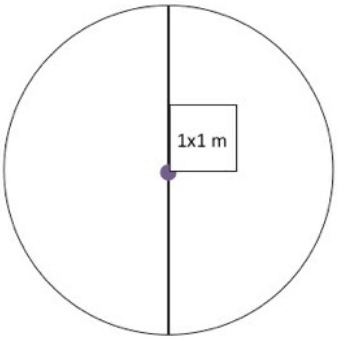

Figure 3.8 Plot design showing the location of the 1x1 m understory vegetation quadrat in the northeast quadrat of the 1/50th hectare plot.

A GRS Densitometer^{TM} (Geographic Resource Solutions, Arcata, CA) was used to measure canopy cover. Two 16 m (entire diameter of the overstory plot) transects were walked across the overstory plot, one north to south and one east to west, taking a reading every 1.5 meters (Chapter 2).

Data Analysis

Methodology for calculating trees per hectare, percent white pine, duff depth, management, mortality, crown cover and understory metrics is described in Table 3.1. Composition of white pine within the stand was calculated as the proportion of white pine divided by the total stem density of live trees in the overstory plot (trees > 12.7 cm DBH). Standing mortality (i.e. snags) within the stand was calculated as the number of standing dead trees over 12.7 cm (5 in) in diameter divided by the total number of standing trees (alive and dead) (Chapter 2).

Table 3. 1 Variables measured in the field or calculated from field measurements used in the analysis of stand structure in planted white pine stands.

Variable	Description
Trees per hectare (TPH)	Number of live trees (greater than 12.7 cm (5.0 inches) in diameter) in plot × 49.4
Standing Mortality	Number of standing dead trees (greater than 12.7 cm (5.0 inches) in diameter) ÷ Total number of standing trees
Canopy Cover (%)	Number of "Canopy, yes" observations ÷ 30 (total number of observations) × 100
Management	If white pine were pruned, management= "YES"
Blister Rust (%)	Number of white pine with blister rust ÷ Total white pine × 100
Understory Species Richness	Count of understory vascular plant species within the 1 by 1 meter plot up to 2 m (6 ft) tall

Because exact management history after planting was not available for any of the stands, it was assumed the stands on the Forest Service lands had been thinned if the western white pine trees were pruned (Chapter 2). The resulting binary variable for management history was either “Managed” or “Not Managed”. Of the 27 stands, 10 had been managed and 17 had not been managed.

All calculations and data analysis were done in R statistical software version 3.6.1. Linear mixed effects regression was performed using the *nlme* package (*nlme* package, R v 3.6.1). Mixed effects models were used to account for the hierarchical nature of plots within stands since plots were not independent of each other because they are in the same stand with similar management histories. Plot was the only variable included as a random effect. Analysis of Variance (ANOVA) and Analysis of Covariance (ANCOVA) were used to evaluate the understory richness response to the explanatory variables. The R package *emmeans* was used to calculate the estimated marginal means for a combination of factors within a linear model (*emmeans* package, R v 3.6.1). Assumptions were checked via diagnostic plots. The residuals vs fitted plot showed a horizontal line with no pattern or significant deviation. The

Normal QQ plot showed the data was normally distributed, therefore no transformations of the dependent variable was required.

I used percent pine instead of percent white pine as the response variable in the ANCOVA because of the high incidence of lodgepole pine within some plots (Appendix 2). Lodgepole pine, a shade intolerant species, has similar needle characteristics to white pine and allows for similar canopy light transmittance due to comparable spatial arrangement of the needles (Barbier et al. 2007). Percent pine was converted into a categorical variable based on breaks within the data. Because approximately 1/3 of the plots were 100 percent white pine, I chose to break the data into thirds. The lower percent pine class includes plots with 0-60 percent pine, the second class was 61-99 percent pine and the last class includes plots that were 100 percent pine.

Diversity counts and diversity indices do not account for the traits associated with individual species. Therefore, a multivariate analytic approach was used to evaluate what environmental and stand characteristics had the greatest effect on the presence of individual species (Halpern and Spies 1995). Relationships between species abundance and environmental variables were evaluated using Canonical (constrained) Correspondence Analysis (CCA) ordination. Constrained indicates the ordination only shows variation within the community data that can be explained by the environmental variables (constraints) (Gardener 2014). CCA combines properties of correspondence analysis and linear regression and is a recommended constrained ordination technique (Gardener 2014). CCA was performed using the *vegan* package in R (Gardener 2014) (vegan package, R v 3.6.1). CCA used Chi-squared distances to create a map of environmental explanatory variables and seedling height and species class combinations (Gardener 2014).

The CCA resulted in a graph where the red crosses represented the individual species, black circles represented the stands, and vectors represented each explanatory variable. The length of the environmental vectors are their Eigenvalues; the longer the vector the more important it is in explaining the variance within the data. The angle of the vector in relation to the X and Y axes represents the correlation with the axes. The vector angles in relation to each other indicates correlations among the environmental variables.

Vectors that are perpendicular to each other are independent and vectors that are opposite each other are highly correlated.

The CCA Eigenvalues are used in conjunction with the plot to evaluate how much of the variance within the data is explained by the axes. Larger Eigenvalues (e.g., 0.37 – 0.55) indicate the axis contributed significantly to species assemblages, while smaller Eigenvalues contributed little explanation (e.g., 0.12-0.16) (Aubert et al. 2003)

The vegetation matrix was comprised of 108 observations of 90 species (Appendix 4) and the explanatory matrix was comprised of 108 observations of 5 variables. (Appendix 5) The environmental variables used in the CCA included trees per hectare, percent white pine, standing mortality, crown cover, and duff depth.

Results

Mixed Effects, Linear Regression Results

The full mixed effects, linear regression model of understory diversity included variables representing overstory tree composition, tree density, average tree size, standing mortality, and duff depth. Not all variables that represented tree density were included in the final model due to the significance of their interactions ($p < 0.05$). There were also high correlations between basal area and trees per hectare, basal area and quadratic mean diameter, and quadratic mean diameter and trees per hectare and canopy cover and trees per hectare. The correlation coefficients were 0.32, 0.64 and 0.44, respectively. Trees per hectare was chosen to represent tree density because it resulted in the highest R^2 value of the model ($R^2 = 0.33$). The final linear mixed effects model of understory diversity included trees per hectare, percent white pine and management history and explained 33% of the variance when random effects were included and 26% for the fixed-effects only (Table 3.2).

Trees per hectare, percent white pine, duff depth and management were all significant factors in the model ($p \leq 0.041$ Table 1). The interactions of the explanatory variables were tested but were not included in the model because they were not significant ($p>0.05$). The model shows that for each one percent increase in white pine, the number of understory species increased by 0.046 species, or that it required a 21.7 percent increase in white pine to see an increase of one species (Figure 3.1a). Similarly, the model predicted that in order to observe a one species decrease required an additional 333 trees per hectare.

Table 3. 2 Linear mixed effects ANOVA model. Number of understory Species vs white pine percent, trees per hectare, duff depth and management history.

	Estimate	Std. Error	Pr(>|t|)
Intercept	10.251	1.430	<0.0001
White pine (%)	0.046	0.011	0.0001
Trees per hectare	-0.003	0.001	0.0342
Duff depth (mm)	-0.050	0.017	0.0041
Managed- Yes	2.306	0.753	0.0052
Fixed effects generalized R^2		0.2621	
Fixed + Random generalized R^2		0.3309	

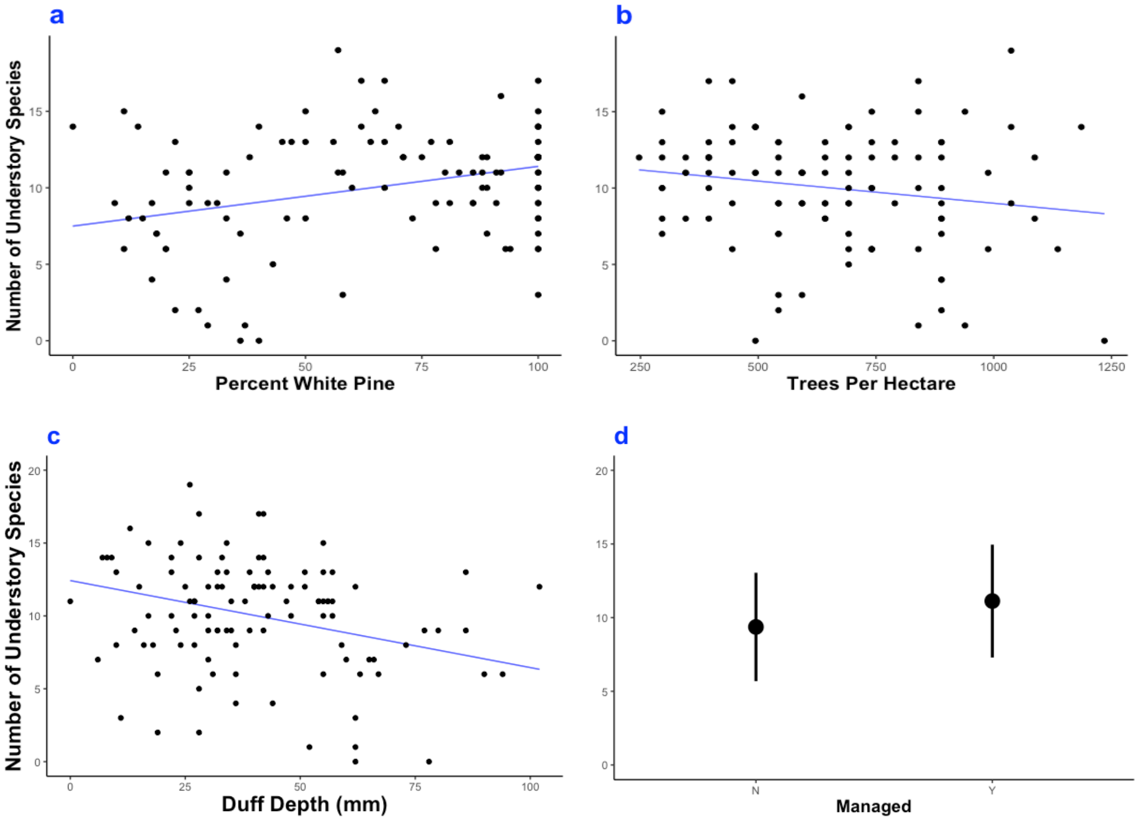

Figure 3.9 Number of understory species vs percent white pine, holding trees per hectare and duff depth constant at their means (a), trees per hectare, holding percent white pine and duff depth constant at their means (b), Duff depth, holding trees per hectare and percent white pine constant at their means (c), and management history, thinned or unthinned (d).

ANCOVA Results

Of all the variables examined, trees per hectare was the only variable in the ANCOVA that was marginally significant (p = 0.060, Table 3.3). In stands with mixed composition of pine and other species, species diversity decreased with the number of trees per hectare (Figure 3.4). There was a difference in understory diversity between a low proportion of pine and a moderate-to-high proportion of pine, where diversity was higher with more pine (p = 0.064, Table 3.4). Interestingly, understory diversity increased with trees per hectare in the pure pine stands.

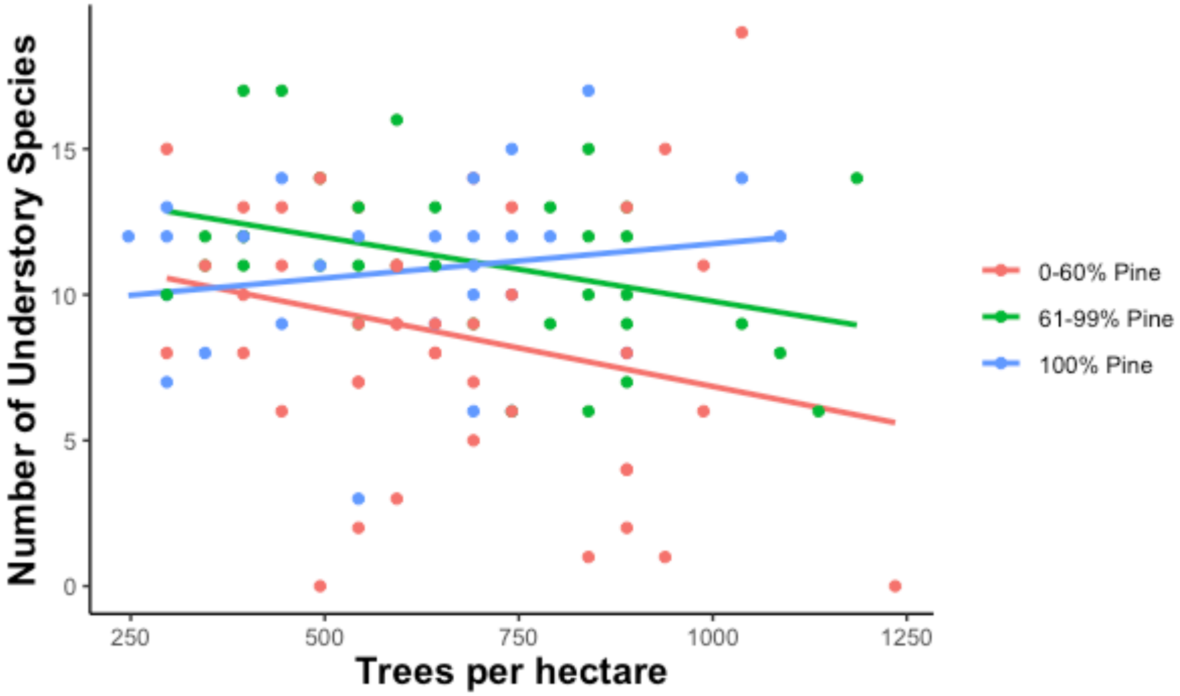

Figure 3.10 ANCOVA of Number of understory species vs Percent pine group and trees per hectare.

Table 3. 3 ANCOVA of Number of understory species vs white pine group and trees per hectare.

Variable	p-value
Intercept	<0.0001
Trees per hectare	0.060
Percent Pine Group	0.025
Trees Per hectare: Percent Pine Group	0.071
R^2	0.44

Table 3. 4 Estimated marginal means (emmeans) for number of understory species vs trees per acre hectare and white pine group ANCOVA

Contrast		Estimate	p-value
0-60	**61-99**	-2.390	0.0149
0-60	**100**	-2.553	0.0642
61-99	**100**	0.137	0.988

CCA Results

The CCA shows one obvious cluster of species and several species strongly associated with the environmental variables. The total inertia of the CCA plot was 4.161 (Table 3.5). The proportion explained for the CCA1 through CCA5 axes were 0.38, 0.28, 0.16, 0.09 and 0.09, with the first two CCA axes explaining 66 percent of the variance in the data. The CCA's are derived from a combination of the explanatory variables. Table 3.6 shows the biplot scores, or the location of the tip of the vector representing the explanatory variable (Gardener 2014). The larger the biplot score, the more variance that variable explains within that CCA (Gardener 2014). For example, for CCA1, the majority of the variance is explained by the percent canopy cover (0.83; Table 3.6), followed by duff depth (0.60), mortality (0.46), percent white pine (0.13) and trees per hectare (-0.11).

The cluster of species in the lower left corner of the CCA plot (Figure 3.4) included oxeye daisy (*Leucanthemum vulgare),* white clover (*Trifolium repens*), little buttercup (*Ranunculus uncinatus), and* common yarrow *(Achillea millefolium)*. Due to the species location in relation to the labeled vectors, we can conclude, these species were associated with lower trees per hectare, lower canopy cover, and higher mortality of white pine, which makes sense as they are typically associated with disturbed areas.

Species associated with an increased percentage of white pine include serviceberry (*Amelanchier alnifolia*), creeping Oregon grape (*Berberis repens*), bunchberry (*Cornus canadensis*), mitella (*Mitella* spp.), viola (*Viola* spp.), false solomons-seal (*Smilacina stellata*), mountain sweet-cicely (*Osmorhiza chilensis*), and sweet-scented bedstraw (*Galium triflorum*). Again, this conclusion is based on the location of these species in relation to the explanatory vector, "WPPercent". Table 3.7 shows a list of shrubs associated with white pine cover by past literature and this current study and Table 3.8 shows a list of forbs associated with white pine cover.

Most of the species are clustered together and do not group out to a particular variable. But some species are closely grouped with mortality include western hemlock (*Tsuga heterophylla*), Rocky Mountain maple (*Acer glabrum*), oakfern (*Gymnocarpium dryopteris*), and heartleaf arnica (*Arnica cordifolia*).

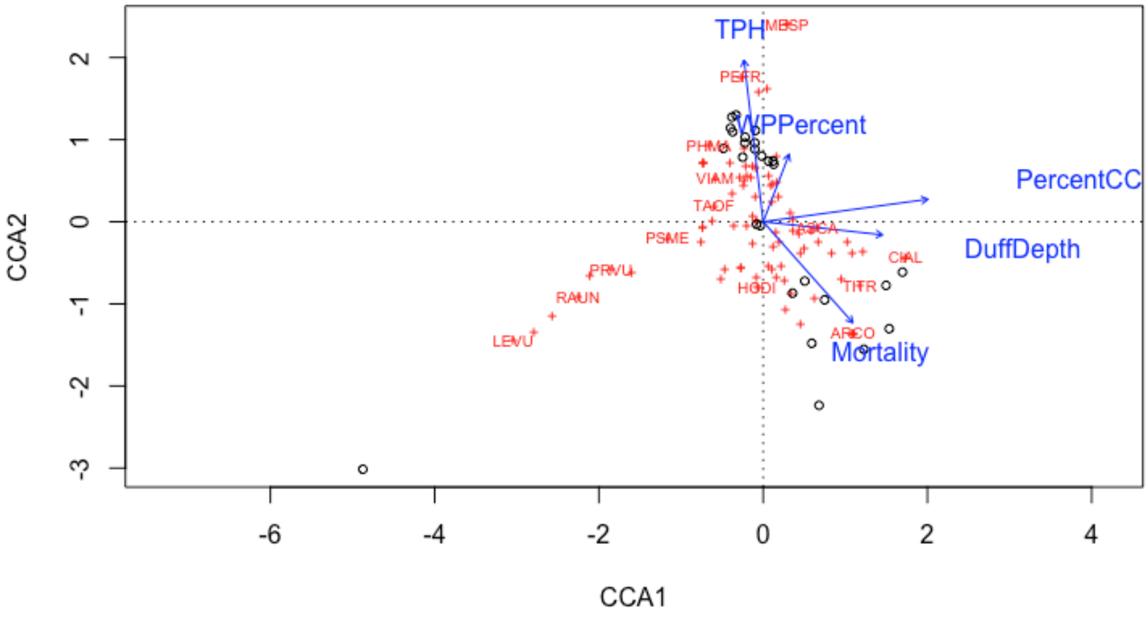

Figure 3.11 Understory CCA. Vectors represent constrained explanatory variables. Species are represented by species codes, species names and codes can be found in Appendix 3.

Table 3. 5 Summary of Undersroey CCA Eigen values and proportion explained associated with the CCA.

	CCA1	CCA2	CCA3	CCA4	CCA5
Eigenvalue	0.4638	0.3349	0.1874	0.1120	0.10313
Proportion Explained	0.3861	0.2788	0.1560	0.0932	0.08585
Cumulative Proportion	0.3861	0.6649	0.8210	0.9142	1.00000

Table 3. 6 Biplot Scores for Constraining Variables.

Variable	CCA1	CCA2	CCA3	CCA4	CCA5
WPPercent	0.13	0.34	0.87	0.26	-0.22
TPH	-0.11	0.81	-0.46	0.25	0.23
Standing Mortality	0.46	-0.52	0.19	0.70	0.004
PercentCC	0.83	0.12	-0.29	-0.30	0.34
DuffDepth	0.60	-0.06	0.23	-0.02	-0.76

Table 3. 7 Shrub species associated with white pine cover in Graham 1990, Haig et al. 1941 and this study.

Scientific Name	Common Name	USDA Plant Code	Haig et al. 1941	Graham 1990	This investigation	Number of Observations in this study
Acer glabrum	Rocky Mountain maple	ACGL	✓	✓		14
Alnus sp.	Alder	ALSP	✓	✓		2
Amelanchier alnifolia	Serviceberry	AMAL		✓	✓	7
Berberis repens	Creeping Oregon grape	BERE			✓	3
Ceanothus sp.	Ceanothus	CESP	✓			1
Holodiscus discolor	Oceanspray	HODI		✓		6
Linnaea borealis	Twinflower	LIBO		✓		39
Lonicera sp.	Honeysuckle	LOSP	✓	✓		12
Paxistima myrsinites	Myrtle boxleaf	PAMY	✓			35
Physocarpus malvaceus	Ninebark	PHMA		✓		1
Ribes Sp.	Currant	RISP	✓	✓		1
Rubus parviflorus	Western thimbleberry	RUPA	✓			18
Salix sp.	Willow	SASP	✓	✓		3
Spiraea betuifolia	Spirea	SPBE		✓		29
Vaccinium membranaceum	Huckleberry	VAME	✓	✓		32

Table 3. 8 Forb species associated with white pine cover in Graham 1990, Haig et al. 1941 and this study

Scientific Name	**Common Name**	**USDA Plant Code**	**Haig et al. 1941**	**Graham 1990**	**My study**	**Number of Observations in this study**
Asarum caudatum	Wild ginger	ASCA	✓	✓		19
Clintonia uniflora	Queenscup	CLUN	✓	✓		43
Coptis occidentalis	Western goldthread	COOC	✓	✓		47
Cornus canadensis	Bunchberry	COCA		✓	✓	20
Galuim triflorum	Sweet-scented bedstraw	GATR		✓	✓	37
Mitella sp.	Mitrewort	MISP			✓	33
Osmorhiza chilensis	Mountain sweet-cicely	OSCH			✓	47
Pyrola sp.	Pyrola	PYSP	✓			5
Smilacina stellate	False solomons-seal	SMST		✓	✓	70
Streptopus amplexifolius	Twistedstalk	STAM		✓		13
Tiarella trifoliata	Coolwort	TITR	✓	✓		7
Trillium ovatum	White trillium	TROV	✓			9
Viola sp.	Violet	VISP	✓	✓	✓	48

Discussion

Environmental variables effect on understory species richness

Stand structure (i.e. tree density, tree size, canopy openness) strongly influences understory vegetation diversity and plant associations (Koop 1989). This study aligns with these general findings, but the results are unique in that this is the first detailed investigation focused on forests planted with western white pine to restore the species across northern Idaho. Planting of blister rust resistant white pine only began with high frequency in the last 30 to 40 years, therefore only recently has such a study been possible. White pine is becoming a major component of forests across the region again and the species found in the understory align with assemblages found prior to the regionwide loss of the species.

This study found overstory characteristics influenced the diversity of understory vegetation in the white pine-dominated stands across northern Idaho. In particular, as the number of trees per hectare increased the understory diversity decreased, while understory diversity increased with a greater proportion of white pine in the overstory. Messier et al. (1998) and Barbier et al. (2007) both show evience of understory diversity being influenced by overstory characteristics. Messier et al. (1998) found that a greater proportion of shade tolerant trees in the overstory decreased understory diversity in mixed wood boreal forests, which they attributed to less light reaching the forest floor. My research supports a similar process in white pine stands in northern Idaho. Field observations showed evidence of a lush, floristically diverse understory in white pine stands but a bare understory in stands with less white pine of similar ages dominated by grand fir, western hemlock, and western red cedar.

I further examined the relationship between understory diversity, trees per hectare and pine cover with an ANCOVA. The 0-60 percent pine class had significantly less understory spcecies when compared to the 61-99 percent pine class. The most interesting part of this relationship is the positive correlation between trees per hectare and the number of understory species in the pure pine group. Because of this finding, I was unable to reject my first hypothesis that understory diversity is positively correlated with white pine composition in the overstory. Thus, concluding that stand characteristics of white pine stands modify the understory environment in a way that increases floristic diversity. As planted western white pine stands are not well studied, there is no information regarding light interception on the forest floor in these forests, but results could be comparable to eastern white pine (*Pinus strobus*). Vose and Swank (1990) found light interception below 32-year-old closed canopies of eastern white pine ranged from 2 to 55 percent during the growing season. Comparatively, light interception beneath closed canopies of very shade tolerant eastern hemlock (*Tsuga canadensis*) were less than 1 percent (Canham et al. 1994).

The white pine stands sampled in this study ranged from 247 to 1235 trees per hectare. It has been established that understory biomass is negatively correlated with overstory density (Cannell and Grace 1993; Ricard and Messier 1996). As tree density increases, the canopy intercepts most incoming light and limits penetration to the forest floor (Hale 2003) and shades out any understory species that were present. Results of the ANOVA in this study show an increase in trees per hectare decreases the number of species in the understory. This supports my second hypothesis, understory diversity is negatively correlated with stand density. This relationship can be attributed to increased competition for above and belowground resources, with the most limiting factor being canopy light transmittance (Lieffers et al. 1999; Naumburg and Dewald 1999; Riegel et al. 1995). Past studies have shown that less light transmittance through the canopy will discourage the growth of some understory species (Lieffers and Stadt 1994; Ricard and Messier 1996). Lieffers and Stadt (1994) found *Calamagrostis canadensis,* a native grass, was eliminated from the plot with light levels lower than eight percent of full light. Similarly, Ricard and Messier (1996) found *Rubus idaeus*, red raspberry, had a very low abundance under 10 percent canopy photosynthetic flux density. Every species has individual light requirements for establishment and growth and managers should take the light requirements of target species into account before thinning to a specific overstory density (Lieffers and Stadt 1994).

Understory environments can also be manipulated through management. Thinning not only frees up resources and opens up the canopy, it can also expose bare mineral soil for different vegetation species to colonize (Naumburg and Dewald 1999). Literature shows evidence of understory growth differing significantly between thinned and unthinned ponderosa pine stands but the intensity of thinning was not a significant variable (McConnell and Smith 1965). Halpern and Spies (1995) found that species richness initially decreased after management in forests of the Pacific Northwest, but the species richness of their plots surpassed the pre-management richness after only two years. There was a continuous increase in the number of understory species for the remainder of the 28 year study (Halpern and Spies 1995). My study confirms a similar process in white pine stands, supporting my second hypothesis, white pine stands that have been managed had significantly higher species richness in the understory. Pruning the white pine has the ability to create a more open understory and allowing light to reach the understory from all directions in addition to the available light created by thinning (Ashton and Kelty 2018).

Species Assemblages in White Pine Stands

The only obvious cluster of plant species in the CCA included *Leucathemim vulgare, Trifolium repens*, *Ranunculus uncinatus*, and *Achillea millefolium.* The location of the cluster is associated with low canopy cover and low trees per hectare. *L. vulgare* and *T. repens* are introduced plants and *A. millefolium* has both native and introduced varieties (USDA 2019). *R. uncinatus* is native to the state of Idaho, although Parish et al. (1996) describes it as being common in "disturbed, trampled areas". Parish et al. (1996) describes *A. millefolium* as being "weedy on disturbed sites". *T. repens* and *L. vulgare* are also common on disturbed soils (Parish et al. 1996). Because of the location of this cluster, relative to the variables on the CCA and the species characteristics, I am confident this is a cluster associated with disturbance and openings in white pine stands.

Of the 14 shrub species listed by Graham (1990) and Haig (1941) only one species, *Amelanchier alnifolia* was most associated with white pine based on my CCA. *Berberis repens* was also associated with white pine cover but was not listed as an associated species by Graham (1990) or Haig (1941). Of the 11 forb species listed by Graham (1990) and Haig (1941) only four species, *Smilacina stellata, Viola* spp*., Cornus canademsis* and *Galuim trifiorum* were most associated with white pine based on my CCA. It is important to note that all of the stands sampled are considered white pine stands as described by Haig (1941) (all stands were between 15 and 100% white pine by stem number). The fact that my CCA did not identify all of the species mentioned in previous literature does not suggest the species are not associated with white pine cover. Instead, the species not included in my white pine cluster were more closely related to other variables within the model, such as tree density or mortality. All of the species mentioned by Graham (1990) and Haig (1941), however were found in at least one plot of my study. Therefore, there is evidence to support my third hypothesis; species assemblages in planted white pine stands are similar to assemblages found in white pine stands prior to blister rust. However, some species are more influenced by other stand characteristics such as stand density and standing mortality.

Tsuga heterophylla was a tree species found in the understory plot and most closely related to standing mortality in the CCA. *T. heterophylla* is a shade tolerant tree species, capable of germinating and surviving in small (<75 m^2) gaps (Kobe and Coates 1997). Shrubs are also able to thrive in these small gaps (Swanson et al. 2011). *Amelanchier alnifolia* and *Berberis repens* are shrubs associated with standing mortality in my CCA. Layers of tree regeneration and shrub establishment driven by gap-formation in these stands increases the complexity of the stand (Bauhus et al. 2009). Churchill et al. (2013) describes the spatial patterns of pre-settlement era reference stands as a mosaic of clumps and openings and providing “fences of high resistance”. These areas of complexity and high resilience are capable of reducing the susceptibility of an ecosystem to insects and disease, and supports a more natural fire regime (Churchill et al. 2013). Complexity in spatial patterns may also enhance the ability to adapt to a changing climate (Churchill et al. 2013).

Not only does the complexity associated with these white pine stands enhance resilience to disturbance, the diverse plant community provides ecosystem benefits such as wildlife forage and increased seed dispersal (Piper 1986; Swanson et al. 2011). Shrubs, grasses and forbs, all abundant in these stands, provide nectar, seeds and fruit (Swanson et al. 2011). Early successional species, in particular are associated with wildlife species (Swanson et al. 2011). In this study, *Smilacina stellata, Rubus sp., Amelanchier alnifolia*, and *Vaccinium membranaceum* are great examples of fruiting forbs and shrubs that provide for wildlife. These species, as well as *Prunus* spp. and *Ribes* spp. are all fruiting species used by Native American tribes (Lynn et al. 2013; Wynecoop et al. 2019) and are considered a super food based on today’s nutritional standards (Seeram 2008). These white pine stands and their associated stand characteristics allow for gap formation where early successional species can thrive, while providing other non-timber forest products (Swanson et al. 2011; Lynn et al. 2013).

Conclusions

While the objective of planting white pine stands in the northern Rocky Mountain region is not to recreate historic white pine forests, restoring these stands aims to enhance forest resilience and improve habitat quality by increasing stand complexity. I provide evidence that stand characteristics of white pine, such as the porous canopy and gap-dynamics, along with overstory density and management history can modify the understory environment in a way that increases floristic diversity. White pine understories provide structural diversity by encouraging the growth and establishment of forbs, shrubs and shade tolerant tree regeneration. The diverse group of species associated with white pine, in this study as well as previous studies, provide an assortment of habitat and ecological benefits to the stand.

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Appendix 1: Stand Characteristics

Stand	Habitat Series	Pruned/ Thinned	Slope (%)	Aspect (degrees)	Age	White Pine (%)	Number Understory Species	Number Seedlings per Hectare	Number Saplings per Hectare	Trees per Hectare	Canopy Cover (%)	Duff Depth (mm)
Angry Wolf	ABGR	No	16	16	23	99	8	927	0	778	57.5	71.8
Ewe Creek	TSHE	No	27	27	25	90	10	1297	1483	840	70	38.3
Fern Falls	TSHE	Yes	50	50	32	52	13	3521	1668	383	74.25	55.5
Flat Creek	TSHE	Yes	33	33	28	48	9.5	926	1482	729	87.25	58.5
Gleason	TSHE	Yes	6	6	25	48	9.5	3521	2965	519	64	38.5
Ida Creek	TSHE	No	14	14	37	97	10	3150	2780	519	69	50.5
Little Tyson	ABGR	No	5	8	25	39	11.75	0	741	457	40.75	8.8
Lost Creek	ABGR	No	22	77	25	29	7.75	185	0	852	62.5	24.3
Middle Miner	TSHE	Yes	52	52	29	72	12	3335	2038	432	71.75	39.0
Nat Brown	ABGR	No	16	17	23	68	12.75	2594	927	815	69.25	26.3
North Porc	THPL	Yes	22	22	19	90	10.25	1482	1112	1025	69.25	39.5
Oviatt Creek	THPL	Yes	37	65	25	39	15.25	1112	371	827	69.25	15.0
Peterson	ABGR	No	33	30	53	79	8.75	0	185	469	64	73.5
Purdue Creek	THPL	Yes	36	67	25	41	9.25	185	926	864	68.75	20.0
Quartz Mt	TSHE	Yes	34	34	32	13	9	927	556	556	79.25	23.3
Robideaux	THPL	No	18	18	19	98	9.5	185	0	642	69.75	40.5
Seed Orchard	THPL	No	7	7	36	98	11.75	185	0	506	54.25	35.8
Shadow Falls	TSHE	No	32	32	35	18	7.5	371	371	593	70	39.0
Sleepy Wolf	THPL	No	15	15	32	97	12.25	185	185	753	56	41.8
Snow Creek	THPL	No	18	18	58	41	3	0	556	729	75.5	64.0

South Porc	THPL	Yes	40	40	21	36	9.25	4633	741	753	73.25	36.5
Spud Patch	THPL	No	29	56	25	67	10.5	1483	556	432	61.75	57.8
Stimson	ABGR	No	4	4	29	87	9.25	556	185	692	70	40.8
Tired Wolf	ABGR	Yes	10	10	24	98	14.25	556	185	692	59.25	31.3
Two	THPL	No	43	43	30	35	5.25	371	927	778	85.75	27.0
Vasser Meadows	ABGR	No	10	10	43	63	10.25	556	1112	580	77.75	41.0
VQ PREF	THPL	No	34	40	48	100	11	0	0	358	60.25	50.5

Appendix 2: Tree Species Composition (%) by Stand

Stand	White Pine	Grand fir	Douglas fir	Engelmann Spruce	Lodgepole pine	Ponderosa pine	Western red cedar	Western hemlock	Western Larch
Angry Wolf	99	0	0	0	1	0	0	0	0
Ewe Creek	90	0	0	0	10	0	0	0	0
Fern Falls	52	19	10	0	19	0	0	0	0
Flat Creek	48	12	21	5	3	0	0	9	0
Gleason	48	16	7	0	11	0	15	0	3
Ida Creek	97	3	0	0	0	0	0	0	0
Little Tyson	39	0	0	0	61	0	0	0	0
Lost Creek	29	9	2	0	60	0	0	0	0
Middle Miner	73	0	0	21	0	0	0	4	0
Nat Brown	68	1	0	1	29	0	0	0	0
North Porc	90	3	4	0	0	0	3	0	0
Oviatt Creek	40	1	51	0	0	0	4	0	4
Peterson	79	0	13	0	0	7	0	0	0
Purdue Creek	41	0	39	0	0	0	0	0	20
Quartz Mt	13	26	57	0	4	0	0	0	0
Robideaux	98	2	0	0	0	0	0	0	0
Seed Orchard	98	0	0	0	0	2	0	0	0
Shadow Falls	18	68	11	0	0	0	0	2	0
Sleepy Wolf	97	0	3	0	0	0	0	0	0
Snow Creek	41	10	1	0	0	0	38	0	8
South Porc	36	1	57	0	2	0	0	2	1
Spud Patch	67	10	11	0	0	0	4	0	7
Stimson	87	8	4	0	1	0	0	0	0
Tired Wolf	98	0	0	0	2	0	0	0	0

Two	35	21	24	0	5	0	13	0	3
Vasser Meadows	63	28	0	0	9	0	0	0	0
VQ PREF	100	0	0	0	0	0	0	0	0

Appendix 3: USDA Plant Code, Scientific and Common Name

Original Code	*Scientific Name*	Common Name
ABGR	*Abies grandis*	grand fir
ACGL	*Acer glabrum*	Rocky Mountain maple
ACMI	*Achillea millefolium*	common yarrow
ADBI	*Adenocaulon bicolor*	pathfinder
alder	*Alnus sp.*	alder
AMAL	*Amelanchier alnifolia*	serviceberry
ANPI	*Anemone piperi*	windflower
APAN	*Apocynum androsaemifolium*	spreading dogbane
ARCO	*Arnica cordifolia*	heartleaf arnica
ARMA	*Moehringia macrophylla*	bigleaf sandwort
ARNU	*Aralia nudicaulis*	wild sarsaparilla
ARUV	*Arctostaphylos uva-ursi*	kinnikinnick
ASCA	*Asarum caudatum*	wild ginger
BEPA	*Betula papyrifera*	paper birch
BERE	*Mahonia repens*	creeping oregon grape
CASP	*Castelleja sp.*	Indian paintbrush
CHLE	*Leucanthemum vulgare*	oxeye daisy
CHME	*Chimaphila menziesii*	Menzies' prince's pine
CHUM	*Chimaphila umbellata*	prince's pine
CIAL	*Circaea alpina*	dwarf enchanter's nightshade
CISP	*Cirsium sp.*	thistle
CLUN	*Clintonia uniflora*	queen cup beadlily
COCA	*Cornus canadensis*	bunchberry dogwood
DIHO	*Prosartes hookeri*	Hooker fairy-bell
EPSP	*Epilobium sp.*	epilobium

FAFY	*Fabaceae family*	pea family
FRVE	*Fragaria vesca*	woodland strawberry
GABO	*Galium boreale*	northern bedstraw
GAOV	*Gaultheria ovatifolia*	Oregon wintergreen
GATR	*Galium triflorum*	sweetscented bedstraw
GYDR	*Gymnocarpium dryopteris*	oak fern
HIAL	*Hieracium albiflorum*	white-flowered hawkweed
HISP	*Hieracium sp.*	hawkweed
HODI	*Holodiscus discolor*	ocean-spray
HYPE	*Hypericum perforatum*	common St. John's wort
LAFY	*Laminaceae* family	mint family
LAOC	*Larix occidentalis*	western larch
LIBO	*Linnaea borealis*	twinflower
LOUT	*Lonicera utahensis*	Utah honeysuckle
MEFE	*Menziesia ferruginea*	fool's huckleberry
Mentha	*Mentha sp.*	mint
MISP	*Mitella sp.*	mitrewort
OSCH	*Osmorhiza berteroi*	mountain sweet-cicely
PAMY	*Paxistima myrsinites*	myrtle boxwood
PEFR	*Penstemon fruticosus*	bush penstemon
PHMA	*Physocarpus malvaceus*	ninebark
PICO	*Pinus contorta var. latifolia*	lodgepole pine
PIEN	*Picea engelmannii*	Engelmann spruce
PIMO	*Pinus monticola*	western white pine
PIPER2	*Piperia sp.*	rein orchid
PIPO	*Pinus ponderosa*	ponderosa pine
POGR	*Potentilla gracilis*	cinquefoil
PREM	*Prunus emarginata*	bittercherry

PRVU	*Prunella vulgaris*	self-heal
PSME	*Pseudotsuga menziesii*	Douglas-fir
PTAQ	*Pteridium aquilinum*	bracken fern
PYAS	*Pyrola asarifolia*	common pink wintergreen
PYSP	*Pyrola sp.*	wintergreen
RAUN2	*Ranunculus uncinatus*	little buttercup
ROSA	*Rosa sp.*	rose
RUOC	*Rudbeckia occidentalis*	western coneflower
RUPA	*Rubus parviflorus*	western thimbleberry
SADO	*Clinopodium douglasii*	yerba buena, savory
SMST	*Maianthemum stellatum*	starry Solomon's seal
SOSP	*Solidago sp.*	goldenrod
SPBE	*Spiraea lucida*	spiraea
STSP	*Stellaria sp.*	starwort
SYAL	*Symphoricarpos albus*	common snowberry
TAOF	*Taraxacum officinale*	common dandelion
THMO	*Thermopsis montana*	Montana golden pea
THOC	*Thalictrum occidentale*	western meadowrue
THPL	*Thuja plicata*	western redcedar
TITR	*Tiarella trifoliata*	coolwort foamflower
TRCA	*Trautvetteria caroliniensis*	false bugbane
TROV	*Trillium ovatum*	trillium
TRRE	*Trifolium repens*	white clover
TSHE	*Tsuga heterophylla*	western hemlock
VAGL	*Vaccinium membranaceum*	thinleaf huckleberry
VESP	*Veronica sp.*	speedwell
VIAM	*Vicia americana*	American vetch
VIGL	*Viola glabella*	pioneer violet

VIOLA	*Viola sp.*	violet
XETE	*Xerophyllum tenax*	beargrass

Appendix 4: Understory Species Matrix by Stand (% foliar cover)

	Angry Wolf	Ewe Sheep	Fern Falls	Flat Creek	Gleason	Ida Creek	Little Tyson	Lost Creek	Middle Miner	Nat Brown	North Porc	Oviatt Creek	Peterson	Purdue Creek	Quartz Mt	Robideaux	Seed Orchard	Shadow Falls	Sleepy Wolf	Snow Creek	South Porc	Spud Patch	Stimson	Tired Wolf	Two	Vasser Meadows	VQ PREF
ABGR	0	11	2	0	3	2	0	0	13	10	1	3	0	0	1	1	0	8	0	0	5	4	0	4	0	14	0
BEPA	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
PIMO	0	0	0	0	0	0	0	0	5	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0
PSME	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
THPL	0	0	3	0	2	2	0	0	0	0	3	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
TSHE	0	4	10	3	5	36	0	0	17	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
ACGL	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	11	0	0	0	1	1	0	1	0	3
AMAL	0	0	0	1	0	0	0	2	0	0	0	1	0	0	0	1	0	0	0	0	0	0	2	1	0	0	0
ARUV	0	0	0	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
CHME	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
CEVE	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
CHUM	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	1	0	2	0	0	0	0	0	0	0	0	0
GAOV	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
HODI	0	0	1	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	4
LIBO	0	1	21	2	12	5	0	0	20	1	7	21	0	2	0	2	2	3	0	0	7	0	1	10	0	0	0
LOUT	1	0	0	0	0	0	0	0	0	0	0	3	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0
LOCI	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
BERE	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0
MEFE	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
PAMY	1	1	6	2	0	0	1	4	9	0	1	2	0	0	0	1	0	5	1	0	1	4	0	0	0	0	0

PEFR	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
PHMA	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
RIVI	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
ROSP	0	0	0	0	0	0	0	1	0	5	1	0	3	0	1	1	6	3	0	0	0	10	4	1	1	0	4
RUPA	0	2	6	0	0	0	0	0	2	0	0	1	1	0	1	0	0	0	0	0	0	9	0	0	0	0	15
RUID	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
SADO	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0
SASC	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
SARA	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
SPBE	1	0	2	1	1	0	1	0	7	0	0	0	0	0	0	3	3	0	3	0	0	0	1	0	0	1	0
SYAL	24	6	1	0	0	0	2	54	1	28	14	46	9	45	2	28	24	1	21	0	15	24	25	18	7	24	2
SYMO	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
VAME	4	0	5	1	10	0	0	0	11	0	0	2	0	0	0	0	1	14	3	0	0	12	3	2	0	0	0
ASCO	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
ACMI	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
ADBI	0	3	0	0	0	9	0	0	0	0	0	0	0	0	1	0	0	0	0	14	0	0	0	1	0	0	5
AMPI	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
ANPI	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
APAN	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
ARCO	0	0	14	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
ARNU	0	0	0	0	1	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	19
ASCA	0	0	0	0	0	5	0	0	1	4	0	0	0	1	1	0	0	0	0	2	0	0	0	1	0	1	0
CASP	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
CIAL	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
CISP	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
CLUN	0	0	8	1	9	1	0	0	2	1	0	4	0	0	14	0	0	2	2	1	2	1	0	1	0	0	8

COCA	0	0	0	0	1	0	0	0	0	9	2	2	0	0	0	0	0	0	5	0	9	0	0	1	0	0	0
COMA	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
COOC	1	0	18	20	1	6	0	0	4	0	3	2	0	0	1	0	1	2	2	0	6	0	1	1	2	0	4
DIHO	0	0	0	1	0	1	0	0	1	0	0	1	2	0	1	0	0	0	0	0	0	0	0	0	0	0	1
EPSP	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	1	0	0	1	0	0	0	0	0	0
FRVE	8	7	2	0	0	1	3	5	1	2	1	9	1	3	0	15	11	0	7	0	6	0	6	13	0	3	0
GABO	0	0	0	0	0	1	0	1	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0
GATR	0	2	0	0	0	3	0	0	1	2	0	1	3	1	0	1	1	0	2	2	0	1	0	1	0	0	2
GYDR	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
HASP	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
HISP	0	0	0	0	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
HIAL	0	4	0	0	0	0	42	0	1	0	0	0	1	0	0	1	0	0	0	0	1	0	0	0	0	0	0
HYPE	0	0	0	0	0	0	1	0	3	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
LAFY	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
LEVU	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
SMST	5	5	1	1	1	2	0	9	7	4	10	3	24	8	7	3	1	2	1	4	5	6	14	8	4	1	4
MESP	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
MISP	2	1	0	1	0	1	0	0	1	1	0	0	0	3	0	2	2	0	1	0	2	1	1	1	0	1	0
ARMA	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1
OSCH	1	0	0	0	0	1	1	0	0	3	2	0	9	0	1	1	2	0	2	1	0	0	3	3	0	2	0
POGR	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
PIPER2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
PRVU	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
PTAQ	9	0	0	1	6	0	1	0	0	1	0	0	21	24	0	4	0	0	9	0	0	3	0	13	0	0	2
PYAS	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
PYSP	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

RAUN	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
RUOC	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
SOSP	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
TAOF	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0
TITR	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
THOC	0	0	0	0	0	0	0	0	0	6	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0
THMO	5	0	0	0	0	0	0	0	0	1	0	3	0	0	0	5	1	0	5	0	0	1	2	8	0	2	0
TRCA	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
TRRE	0	0	0	0	0	0	12	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0
TROV	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
VESP	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
VIAM	0	0	0	0	0	0	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
VISP	0	1	0	1	1	2	1	0	0	3	1	1	0	1	2	1	1	0	1	0	0	1	0	8	1	1	1
VISP2	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
XETE	0	0	0	2	0	0	0	0	2	0	0	0	0	0	0	0	0	33	0	0	0	0	0	0	0	0	0

Appendix 5: Explanatory Variable Matrix for CCA

Stand	WPPercent	TPH	Mortality	PercentCC	DuffDepth
Angry Wolf	99	778	3	58	72
Ewe Creek	90	840	9	70	38
Fern Falls	52	383	16	74	56
Flat Creek	48	729	11	87	59
Gleason	48	519	7	64	39
Ida Creek	97	519	29	69	51
Little Tyson	39	457	7	41	9
Lost Creek	29	852	13	63	24
Middle Miner	73	432	15	72	39
Nat Brown	68	815	4	69	26
North Porc	91	1025	6	69	40
Oviatt Creek	40	827	0	69	15
Peterson	80	469	9	64	74
Purdue Creek	41	865	0	69	20
Quartz Mt	13	556	7	79	23
Robideaux	98	642	7	70	41
Seed Orchard	98	506	9	54	36
Shadow Falls	18	593	18	70	39
Sleepy Wolf	97	753	29	56	42
Snow Creek	41	729	25	76	64
South Porc	36	753	2	73	37
Spud Patch	67	432	6	62	58
Stimson	87	692	11	70	41
Tired Wolf	98	692	8	59	31
Two	35	778	15	86	27

Vasser Meadows	64	580	15	78	41
VQ PREF	100	358	17	60	51