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The Effects of Western Dwarf Mistletoe (Arceuthobium campylopodum) on Radial Growth of Ponderosa Pine (Pinus ponderosa) in Managed Stands in Eastern Oregon

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THE FIRE ECOLOGY OF MATURE PONDEROSA PINE (*PINUS PONDEROSA*) STANDS INFECTED WITH WESTERN DWARF MISTLETOE (*ARCEUTHOBIUM CAMPYLOPODUM*)

by

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DISSERTATION APPROVAL

The abstract and dissertation of Sharon Marie Stanton for the Doctor of Philosophy in Biology were presented March 14, 2007, and accepted by the dissertation committee and the doctoral program.

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ABSTRACT

An abstract of the dissertation of Sharon Marie Stanton for the Doctor of Philosophy in Biology presented March 14, 2007.

Title: The fire ecology of mature ponderosa pine (*Pinus ponderosa*) stands infected with western dwarf mistletoe (*Arceuthobium campylopodum*)

Dwarf mistletoes (*Arceuthobium* spp.) are native flowering plants that parasitize a range of conifer species throughout western North America. Dwarf mistletoes are considered destructive forest pathogens, but recent research indicates that mistletoes play a key role in structuring plant communities by increasing structural diversity and providing wildlife habitat. The primary objective of my research is to quantify the structural and functional differences between infected and uninfected forest communities.

I investigated the effects of mistletoe (*Arceuthobium campylopodum*) on host community dynamics and the interaction between mistletoe infection and fire in old-growth ponderosa pine (*Pinus ponderosa*) forests. Fifty study plots were established in Crater Lake National Park and Lava Cast Forest, Oregon. I compared fuel composition, broom formation, and flammability between infected and uninfected stands. I also compared mortality rates following prescribed fire treatments and variation in climate response between infected and uninfected trees.

My results indicate that mistletoe increases fine fuel accumulations. It is a weak predictor of fine fuels compared to stand structure measures such as basal area. I also found evidence that infected branches do not persist lower in the crown or live longer than uninfected branches, but it is difficult to accurately age old-growth branches. Prescribed fire results show that plots infected with mistletoe burned at higher temperatures for shorter periods than uninfected plots. There is no difference in fuel reduction between the two groups. Post-fire mortality rate was 35%, but there was no difference in mortality between uninfected and infected plots. Burn chamber tests indicate that infected branches lost a greater proportion of their mass during burns, primarily as needle combustion. Results from the climate response study show that mature trees infected with dwarf mistletoe have higher radial growth rates, exhibit greater sensitivity, and respond more strongly to climate variation. The results of this work indicate that the influence of dwarf mistletoe on ponderosa pine fire ecology is complex and often indirect. My results suggest that managers should consider mistletoe abundance when modeling fire behavior in unmanaged ponderosa pine stands, but do not need to consider different prescriptions for fire treatments in intensively managed stands.

DEDICATION

For my husband Michael Leeson, who has supported and encouraged me throughout this process. Michael sparked my interest in science and helped me gain the confidence to pursue a career in biology.

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OVERALL INTRODUCTION

CHAPTER 1

INTRODUCTION

Parasitic plants exhibit a diversity of life forms (trees, shrubs, vines) across a broad range of habitats (Musselman and Press 1995). There are over 4000 species of parasitic plants, including 1% of all angiosperm species (Nickrent et al. 1998, Press et al. 1999). The majority of research on parasitic plants investigates their role as agricultural pests and their physiological and developmental effects on host plants. The effects of parasitic plants on community and landscape ecology have received less attention, especially within the context of natural communities (Smith 2000, Watson 2001, Pennings and Callaway 2002, Press and Phoenix 2005). Parasites can have a major influence on ecosystem structure and function despite their relatively small contribution to biomass.

Parasitism among plants plays a key role in structuring plant communities. Parasitism alters host growth and reproduction, leading to changes in the competitive relationships among host and non-host species, which could ultimately influence community structure, succession, and disturbance regimes. Pennings and Callaway (2002) draw parallels between parasitic plants and herbivores and note their similarities as modifiers of plant community structure and dynamics. The presence of parasites and their effects on host plants also influence other types of organisms in the community, such as herbivores, pollinators, and dispersers of the host and parasite (Pennings and Callaway 2002, Press and Phoenix 2005). Abiotic components of a community may be altered by the presence of parasitic plants. Parasites can indirectly affect water availability (Sala et al. 2001), nutrient availability and cycling (Quested et al. 2005, Press 1998), local temperature, and carbon dioxide concentrations (Press and Phoenix 2005).

Mistletoes are an example of parasitic plants that act as keystone species and strong predictors of alpha diversity (Watson 2001). Mistletoes are a polyphyletic group of obligate hemiparasitic flowering plants that includes over 1300 species (Calder 1983, Nickrent 2001) across five families within the Santales (Nickrent and Soltis 1995). An endophytic system inside host branches allows mistletoes to obtain water, minerals and carbohydrates. Evidence suggests the aerial shoot parasitic habit evolved independently four or five times (Nickrent et al. 1998, Nickrent 2001). The majority of mistletoes parasitize trees and shrubs, and the highest diversity of mistletoes is found in forest communities (Kuijt 1969, Calder 1983, Hawksworth 1983).

Dwarf mistletoes (*Arceuthobium* spp.) are considered the single most destructive pathogen of conifers valued for timber in western North America (Hawksworth and Wiens 1996). Mistletoe is blamed for increased mortality rates, reduced height and diameter growth, and reduction of wood quality. The dwarf mistletoes evolved in the Old World as obligate parasites on members of the Pinaceae and Cupressaceae (Hawksworth and Wiens 1996). Dwarf mistletoes are believed to be the most evolutionarily advanced members of the Viscaceae, with unique features such as highly reduced flowers and shoots, and an explosive mechanism for seed dispersal (Hawksworth and Wiens 1996).

A common host reaction to infection by dwarf mistletoe is the formation of "witches' brooms" (Figs. 1.1 and 1.2). Brooms are one of the most complex, important and least understood aspects of the relationship between this obligate parasite and its host. Branches undergo extensive swelling at the point of infection and a loss of apical dominance allows dormant buds to become active. The result is increased numbers of twigs growing in abnormal patterns and orientation from a swollen main limb, but the mechanisms driving broom formation are unclear. Schaffer et al. (1983) examined cytokinin levels in two different *Arceuthobium* species, one that induces broom formation and one that does not. Higher concentrations of cytokinin were present in the mistletoe that leads to broom formation, but the source of the hormone was not determined. Paquet (1979) also examined cytokinin levels, finding higher concentrations in dwarf mistletoe tissue than in the host. The source of these hormones remains unspecified and there is still debate over whether these imbalances result from the host response to infection or from the mistletoe itself (Mathiasen 1996).

Several studies have summarized the differences between healthy and broomed tissue. Broomed branches tend to show reduced cone and seed production (Bonga 1964, Kuijt 1969). Tinnin and Knutson (1980) studied the growth characteristics of mistletoe induced brooms on Douglas-fir and determined that broomed branches had twice as many twigs as healthy branches and infected branches were 50% longer on average. Overall biomass of infected branches was 250% greater than uninfected, but the biomass of needles was 25% lower on infected branches. Broshot et al. (1986)

also demonstrated that brooms on lodgepole pine have reduced number, length and mass of needles as compared to healthy tissue.

Brooms may have negative effects on host tree growth, but they also have some positive effects on forested ecosystems. Tinnin et al. (1982) view brooms as mutually adaptive to the host and the parasite, facilitating the perpetuation of infected forests that act as highly integrated systems that sustain the coexistence of hosts and parasites. Mathiasen (1996) notes the emergent properties of infested stands and suggests that infested stands are more ecologically complex than healthy stands and represent a distinct ecosystem. Godfree et al. (2003) find that mistletoe strongly influences canopy structure of lodgepole pine stands and ultimately increases structural diversity.

Fire exclusion, grazing, and timber harvesting during the past century have resulted in dramatic shifts in the stand structure and composition of ponderosa pine forests of the American West (Weir 1959, Cooper 1960, Covington and Moore 1994, Belsky and Blumenthal 1997, Dahms and Geils 1997). Among these changes are increased tree density, increased levels of insect and dwarf mistletoe infestation, and an accumulation of highly flammable fuels. Fire suppression has resulted in higher levels of insect and disease infestation, but how these agents influence fire behavior and susceptibility remains poorly understood.

Tinnin (1984) suggests forest stand conditions that historically experience cool surface fires could be altered in several ways by dwarf mistletoe infestation. Host tree death or senescence of broomed branches would result in stands that support more intense fires. Intense fires dramatically alter stand structure, potentially resulting in local eradication of mistletoe and its host species. Alternatively, intense fires can create conditions that foster the regeneration of seral stands of the host species rather than non-host climax species, facilitating the persistence of mistletoe infestation (Tinnin 1984). Zimmerman and Laven (1984) investigated the relationship between mistletoe and fire histories in lodgepole pine stands in Colorado and report that fire is the primary ecological factor that drives mistletoe frequency and severity. They also found that active fire suppression has not resulted in increased mistletoe severity in their study sites. Zimmerman and Laven (1984) note that it is difficult to quantitatively assess the relationship between fire and dwarf mistletoe and caution against assuming the same relationships exist in other locations.

Mistletoe may ultimately amplify fuel loading and fire susceptibility in ponderosa pine stands (Geils and Hawksworth 2002). Mistletoe increases both surface and aerial fuels in young ponderosa pine stands, depending upon stand structure and the degree of infection (Koonce 1981). High fuel loadings in young infected stands are considered a consequence of increased branch size on both the ground and persisting in the crown. Given sufficient time, witches' brooms may form in response to infection; these brooms are massive and resinous relative to healthy branches (Hawksworth and Wiens 1996). Fuel loadings under infected mature trees have not been characterized, and there is a lack of data comparing the fuel characteristics of brooms to infected, but unbroomed branches.

It is unclear if brooms self-prune at the same rate as healthy branches. Personal observations and other evidence (Weir 1916) indicate that brooms have longer life spans than healthy branches, and once dead, they appear to persist in the crown. One consequence of broom persistence in the crown is the potential to provide a fuel ladder for surface fires to become crown fires (Koonce and Roth 1980, Koonce 1981, Koonce and Roth 1985). Broomed branches often remain attached to the main stem, but droop close enough to the ground to act as a fire ladder. Alternatively, if brooms persist in the crown longer than healthy branches do, they will not be available as fuel for a low intensity ground fire.

Individual trees are stressed by dwarf mistletoe (Hawksworth 1961) and other competitors such as understory species and neighboring trees (Barrett 1973). These stressors can result in high mortality rates (Maffei 1989, Hawksworth and Geils 1990). One consequence of high mortality rates is the accumulation of fuel in the form of dead standing or downed trees, as documented by Wanner and Tinnin (1989) in infested stands of lodgepole pine. My two study sites include mature ponderosa pine trees (300-600 years old) that appear to be surviving mistletoe infection, indicating that mistletoe–induced mortality may not be contributing to fuel accumulation in these forests.

Managers have employed prescribed fire and "let burn" policies in fire-prone forests to reduce understory competitors and accumulated fuels. However, the presence of dwarf mistletoe in a stand seems to complicate the use of fire in management. Between 1976 and 1986, Crater Lake National Park staff burned several areas of mixed conifer forest in an attempt to selectively remove understory trees and retain mature ponderosa pine trees. These fires resulted in high mortality (45%) of large ponderosa pine trees (Thomas and Agee 1986, Swezy and Agee 1991). Recent observations reveal that many of the dead trees were infected with dwarf mistletoe, which may have influenced mortality rates. Harrington and Hawksworth (1990) cite higher fire-mortality rates among heavily infected ponderosa pine, whereas lightly infected trees had a greater probability of survival, potentially becoming new centers of infection as regeneration proceeds in the gaps.

OBJECTIVES & SIGNIFICANCE

My research focuses on the ecological interrelationships between dwarf mistletoe and fire in mature ponderosa pine forests of the western United States. Previous research (Tinnin 1984) noted that dwarf mistletoe causes observable differences in community structure, but forest ecologists and pathologists have not identified the relationship between changes in pattern and changes in process. My goal is to quantify the effects of dwarf mistletoe on host community dynamics and to assess the interaction between a low-intensity, chronic disturbance agent (mistletoe infection) and fire, a disturbance agent of greater intensity and lower frequency.

The specific objectives of my research are to further our understanding of the complex ecological relationships among dwarf mistletoe and host tree growth, broom development, fire susceptibility and fire behavior (Fig.1.3). My hypotheses are:

1. Stands infested with dwarf mistletoe have higher accumulations of fuel than uninfected stands.
2. Brooms have greater longevity and persistence in the crown than healthy branches.
3. Infected stands and trees are more flammable than uninfected stands and trees.
4. Post-fire mortality is higher among infected trees than uninfected individuals.
5. Infected trees show greater variation in climate response than healthy trees.

Fuel Composition

I will test the hypothesis that stands infested with mistletoe have higher accumulations of fuel, particularly litter and small diameter woody debris dropped from brooms. Mistletoe interacts with a variety of biotic and physical factors that indirectly influence the quantity, quality, flammability and distribution of fuel in the forest (Fig.1.4). Mistletoe directly influences tree growth, ultimately influencing fuel accumulation. Vigor and growth rates typically decrease in infected trees, resulting in altered crown structures and higher mortality rates for severely infected trees (Hawksworth and Wiens 1996). Mortality of host species also alters stand composition and the successional trajectory of infected stands. The successional stage and structure of a stand will determine the composition of fuels.

Broom Longevity

Personal observations and preliminary data suggest that brooms in ponderosa pine trees have longer life spans and persist in the crown longer than healthy or unbroomed branches under similar conditions. Brooms in lodgepole pine and Douglas-fir typically break from the crown and accumulate at the base of infected trees, but this is not the case with ponderosa pine (Wicker and Leaphart 1976). Infected trees growing in dense stands may be more likely to prune their brooms (Wicker and Leaphart 1976, Godfree 2000), but observations suggest that brooms in old-growth ponderosa pine trees persist longer than healthy or infected but unbroomed branches. The influences of stand characteristics and fire history on broom development and longevity also need investigation.

Infected ponderosa pine branches do not always develop into brooms, and the mechanism behind broom formation is unknown. Preliminary age determinations revealed live broomed branches at Lava Cast Forest dating back to 1620. Currently there is no reliable method for dating the initial infection or the onset of brooming. My research examines the usefulness of standard dendrochronological techniques for dating infection and the onset of brooming.

Flammability and Mortality

I hypothesize that broomed branches are more flammable than healthy limbs because previous research suggests brooms have dense growth, altered distribution of biomass and chemical composition. If brooms are highly flammable and lead to increased fuel loads, it would follow that infected trees are more vulnerable to fire-related mortality. Flammability represents the ease with which a material ignites and sustains combustion (Wein and MacLean 1983). Wind, drying, stand composition and the fuel complex at the point of ignition all influence flammability at the stand level (Knight 1987). Vigor, crown structure and transpiration rates affect flammability at the tree scale. Dwarf mistletoe is directly related to the factors mentioned above, and consequently has indirect effects on flammability.

Brooms may have a direct relationship with flammability at the scale of tree and stand. Brooms that persist low in the crown often have a pendulous form that may act as a fuel ladder, allowing a surface fire to move into the crown and cause more severe damage to the tree before spreading to the crowns of other trees, regardless of their infection level. Brooms are thought to be more resinous and dense than healthy branches, which may translate into higher flammability. I will test the hypothesis that brooms are more flammable than uninfected branches.

Climate response

Dendrochronologists typically avoid sampling trees with evidence of physical damage or disease (Fritts 1976, Stokes and Smiley 1996). Diseased trees, including those infected with dwarf mistletoe, may experience anomalous growth that confounds the reliability of climate reconstructions based on variations in ring widths. Despite the common practice of avoiding infected sample trees, little is known about how parasitic plants alter the usefulness of host trees for dendrochronological studies.

My study investigates the influence of dwarf mistletoe on host tree response to climate to determine if it is necessary for dendrochronologists to avoid sampling infected trees. I expect infected trees to have lower growth rates because of the well-documented negative influence of mistletoe on radial growth. Decreased growth rates should result in a stronger response to climate variation because infected trees experience increased moisture stress and nutrient sinks in from mistletoe infection. Therefore, I hypothesize that infected trees will have more sensitive ring-width series and stronger correlations with climate variables.

Significance

Ecosystem-based management currently views pathogens as integral parts of forested communities. The focus of land managers is shifting from the control and eradication of these organisms toward maintaining a balance among pathogens, their hosts, and other species in the landscape. There is a need for baseline information on the ecological role of mistletoe so that infected stands can be managed effectively for multiple uses, such as timber, wildlife habitat, and recreation. Historically, brooms have been considered undesirable because of the perceived impacts on growth reduction, fire hazard, and the spread and intensification of mistletoe on a stand level. Brooms are now being considered as critical elements of habitat diversity (Parks et al.

1999, Watson 2001, Shaw et al. 2004). Management strategies are shifting away from broom removal in many cases, highlighting the need for more information on the relationship between mistletoe and fire.

Dissertation Outline

This dissertation includes six additional chapters, four of which are written as stand-alone manuscripts. Chapter 2 provides a description of the study sites and outlines the field and lab methods used for all parts of the project. I examine the influence of dwarf mistletoe on fuel accumulation in relation to several biotic and abiotic variables in Chapter 3. Chapter 4 presents my investigation into the longevity and persistence of broomed and uninfected branches. I analyze the response of infected trees and branches to fire in Chapter 5. In this chapter, I also identify whether mistletoe increases the flammability of host trees and the vulnerability of infected trees to damage during prescribed fire treatments. Chapter 6 presents a study of the climate response of infected trees, illustrating that host trees provide useful samples for dendrochronological research. Finally, I discuss the general conclusions about the interrelationships between dwarf mistletoe and fire in mature ponderosa pine forests in Chapter 7. Suggestions for future research are addressed in the final chapter.

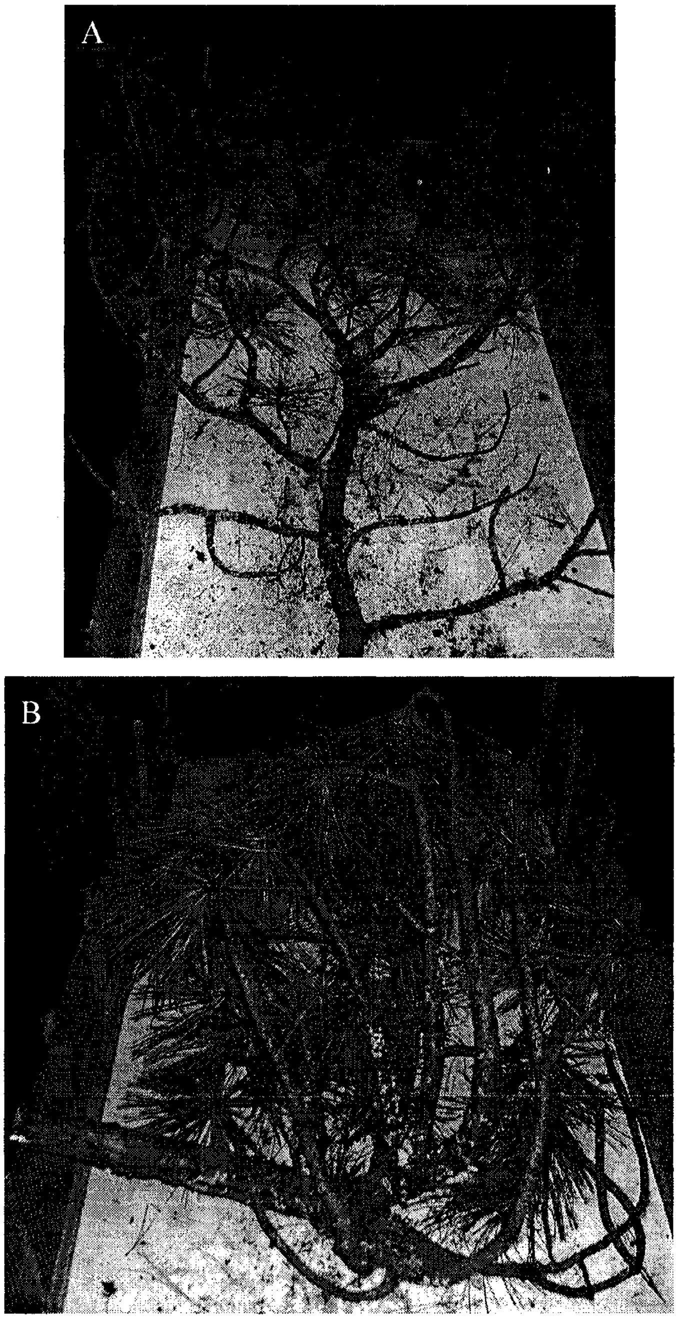

Figure 1.1: A healthy ponderosa pine branch (A) and an infected, broomed branch (B). Note the unusual shape of the broom, the swollen stem where the majority of twigs originate, and the increased number of twigs and needles.

Figure 1.2: A ponderosa pine tree infected with western dwarf mistletoe (A) and a healthy, uninfected tree (B). Note the brooms throughout the infected crown and the dead top.

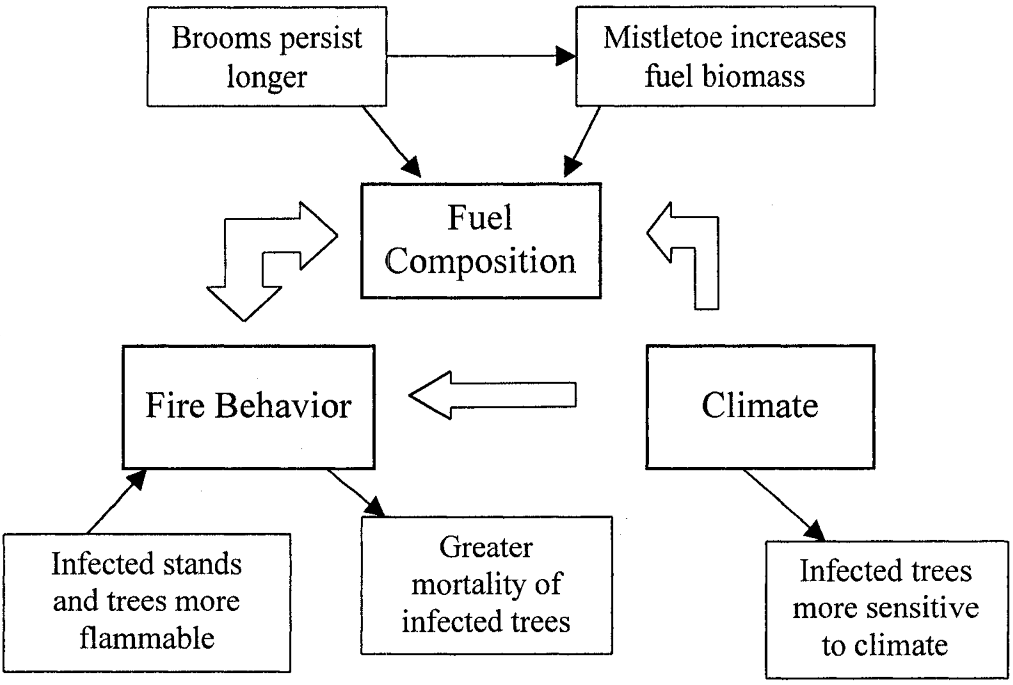

Figure 1.3: Conceptual diagram of the three general areas of study and the five related hypotheses.

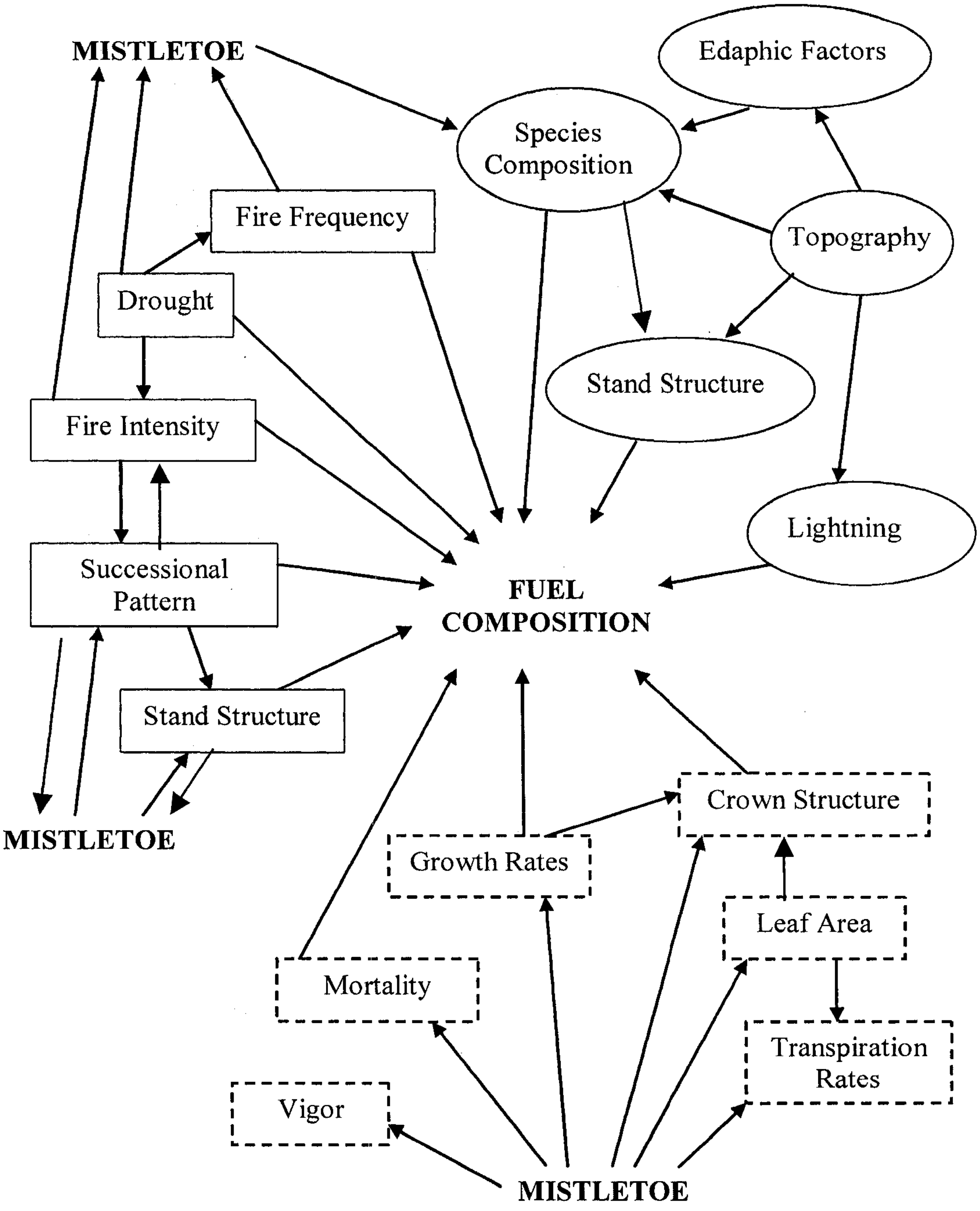

Figure 1.4: Conceptual diagram of the physical and biotic factors influencing the quantity and quality of the fuel complex, including the complex role of mistletoe in the accumulation of fuels. Factors in dashed boxes pertain to the tree scale; circles the stand scale; and solid boxes the landscape scale. Modified from Knight (1987).

CHAPTER 2

SITE DESCRIPTIONS AND PLOT ESTABLISHMENT

This chapter presents background information for my study sites and summarizes my research design. I also present the details of how plots were established and sampled at each study site. Subsequent chapters include detailed descriptions of my field and laboratory methods relevant to individual aspects of the research, and reiterate relevant site characteristics.

Study Sites

I conducted this research in two areas in central Oregon, Lava Cast Forest and Crater Lake National Park (Fig. 3.1). Both areas support mature, mixed-conifer forests dominated by ponderosa pine with varying levels of dwarf mistletoe infection. Previous research established fire histories for each site (McNeil and Zobel 1980, Arabas et al. 2006).

The semi-arid climate and short growing season at Lava Cast Forest provide stand and tree conditions that increase the likelihood of finding old trees with sensitive ring series for dendroclimatic sampling. Mistletoe infection levels vary across Lava Cast Forest, allowing me to sample both infected and non-infected trees from the same or similar stands.

Crater Lake National Park provided a unique opportunity to study fire behavior in a mature ponderosa pine stand with varying levels of mistletoe infection. A fire management plan was already in place, with scheduled fall season prescribed burns to reduce fuels and promote pine regeneration. Park staff was willing to alter their burn plans to meet my experimental needs as well as their own management objectives.

The park also allowed me to establish permanent plots and tag mature trees to monitor long-term changes in stand composition and mistletoe infection.

Lava Cast Forest

The Lava Cast Forest Geological Area (LCF) is located in central Oregon, within the Newberry National Volcanic Monument administered by the Deschutes National Forest (Fig. 3.1). LCF is situated approximately 8km northwest of the Newberry Crater caldera and is characterized by 11 kipukas (forested islands) isolated among shallow, mid-Holocene lava flows (Peterson and Groh 1969). Two surface flows of basaltic andesite 6600 years ago covered 800 ha to the north of Newberry Crater, creating an area of fragmented forest growing on isolated cinder cones. The kipukas range from 0.4 to 113 ha, with elevations from 1590 to 1820 m. A few logs and stumps resulting from recent fire suppression efforts are the only evidence of anthropogenic disturbance among the kipukas (Hadley and Arabas in prep).

The climate of the study area is strongly influenced by the rainshadow effect from the Cascade Mountains to the west. The moisture regime is semi-arid, with the majority of precipitation occurring as snow during the winter (October to March). Average annual precipitation $\approx$ 300mm, and average temperatures range from a low of 0° C in January to a high of 17.3° C in July (OCF 2005).

The soils underlying the Newberry Crater site are characterized by large deposits of Mazama ash and pumice with younger Newberry pumice on top. Soil depth varies with pre-eruption topography. The ash and pumice soils of central

Oregon are slightly acidic because of the porosity and high allophane content of parent material (Franklin and Dyrness 1988). Pumice soils are characterized by low bulk densities, thermal conductivities, and nutrient content (Youngberg and Dyrness 1965; Cochran et al. 1967).

Forest composition on the kipukas consists of three major dominant species that appear to be topographically and edaphically controlled (Hadley and Arabas in prep). Ponderosa pine (*Pinus ponderosa* var. *ponderosa*) is most common on south-facing slopes, while north-facing slopes and interior stands are dominated by white fir-grand fir hybrid (*Abies concolor – A. grandis*). Flat areas are often covered in dense stands of lodgepole pine (*Pinus contorta* var. *murryana*). Western white pine (*Pinus monticola*) and quaking aspen (*Populus tremuloides*) are found at a few locations. Understory vegetation is dominated by snowbrush (*Ceanothus velutinus*), green manzanita (*Arctostaphylus patula*), and bitterbrush (*Purshia tridentata*). There are also large areas of bare ground.

Two species of dwarf mistletoe occur in the study area – *Arceuthobium campylopodum* is found on ponderosa pines, and *A. americanum* on lodgepole pines. The distribution and density of dwarf mistletoe across the study area is highly variable, with some kipukas currently lacking mistletoe and others having mistletoe in the majority of pine stands. The stands with mistletoe are moderately to severely infested, where the majority of trees support mistletoe in over half of their crowns.

Fire history for the Lava Cast Forest is available from both historical records and a tree-ring reconstruction (Arabas et al. 2006). Mean fire return interval for the kipukas is 6 years, with both the number of fires and fire frequency being higher on the kipukas when compared to the surrounding, non-fragmented forest. Evidence of the last major fire in stands I sampled dates to 1918 (Arabas et al. 2006).

Crater Lake Panhandle

Crater Lake National Park is located in the southern Cascade Mountains of Oregon. The Panhandle site is along the east flank of the Cascades and slopes gently (3%) with a south-facing aspect, ranging in elevation from 1340-1400 meters. Crater Lake was designated a national park in 1902, but the panhandle region was not managed by the Park Service until 1932. U.S. Forest Service records and physical evidence indicate that logging occurred between 1909 and 1927. The National Park Service suppressed wildfires in the park for most of the 20th century, with the last wildfire to burn in the study site occurring in 1902. In the 1970s, park managers implemented a prescribed burn plan to reduce accumulating fuels in the panhandle region and to promote regeneration of sugar and ponderosa pines. The management program was active until the 1988 Yellowstone National Park fires instigated the suspension of all federal fire management activities.

The climate at the Crater Lake study site is strongly seasonal. Average annual precipitation is 51.3cm (1971-2000) at Chiloquin located 30 km to the southeast at similar elevation, with the majority of precipitation occurring as snow between November and March. Mean annual temperature is 14.7°C, with the warmest months being July and August and the coldest months December and January.

Soils at Crater Lake are similar to those at LCF. The soils of the study are characterized by thick layers of pumice deposits from the eruption of Mt. Mazama approximately 7000 years ago (Olsson 1970). There are deposits of rounded pumice cobble and gravel in a sand matrix, resembling the Lapine series (Dyrness and Youngberg 1966).

Vegetation in the panhandle region of Crater Lake National Park is dominated by ponderosa pine – white fir forest. Dominant tree species are ponderosa pine and white fir. Sugar pine (*P. lambertiana*) and lodgepole pine are common, with occasional incense cedar (*Calocedrus decurrens*) and Douglas-fir (*Pseudotsuga menziesii*). Common understory species include wax currant (*Ribes cereum*), snowbrush (*Ceanothus velutinus*), dogbane (*Apocynum androsaemifolium*), pinemat manzanita (*Arctostaphylos nevadensis*), grasses and sedges.

Western dwarf mistletoe is more abundant in lower elevation stands at the south end of the park. There are several stands of ponderosa pine further north in the panhandle that do not support dwarf mistletoe infections, indicating the infestation in my study area is independent of host density. The northwest corner of the study area includes lodgepole pine infected by *A. americanum*.

A several-hundred year fire history is available for the panhandle region of Crater Lake. McNeil and Zobel (1980) completed a dendrochronological assessment of fire scarred trees in the late 1970s, and historical records document natural and prescribed fires during the 1900s. McNeil and Zobel (1980) report mean fire return intervals of 9-42 years for the time period 1748-1902 for the area that includes my study site.

The management-ignited fires of the 1970s resulted in unexpectedly high mortality of large trees for 2 to 5 years following fire. Mortality rates were higher when burns were implemented in the spring, killing up to 45% of trees larger than 112 cm in diameter (Agee and Thomas 1982, Thomas and Agee 1986). Park management later agreed to a fire management plan in the late 1990s with the objectives of reducing fuel loadings to protect against catastrophic wildfire, and to restore the forest structure and fire regimes to projected conditions that existed between 1500 and the 1850s. Specifically, the goals were to reduce total fuel loading at least 25%, reduce the density of white fir seedlings by 5 to 60%, and increase density of ponderosa pine seedlings by 20 to 40%. The plan called for low intensity broadcast burns during the fall season of 2003.

Research Plot Establishment

Plots were established at both study sites to collect background data summarizing stand structure and general characteristics (Table 2.1). My sampling included 36 plots at Lava Cast Forest (14 severely infected, 14 uninfected, and 8 lightly infected) and 14 plots at Crater Lake (7 infected and 7 uninfected). Plots sizes vary (15m^2 to 50m^2), based on the minimum area needed to include at least 20 live trees. All plots are located in stands where ponderosa pine, the host species for western dwarf mistletoe, has the greatest basal area. The lightly infected plots at Newberry Crater are underrepresented compared to the other two groups because of the lack of stands with low levels of mistletoe infection.

Plot selection was stratified to ensure equal representation of infected and non-infected samples. Within each stratum, plot locations were chosen subjectively to include the largest ponderosa pine trees in the area. I located infected and non-infected plots as close to each other as possible to control for the variability in biotic and abiotic factors that could influence the results. The dispersal mechanism of dwarf mistletoe coupled with the range of stand ages and lack of recent disturbance made it to difficult to find adjacent areas with different levels of infection. Several plots at Newberry Crater coincide with research plots previously established by Hadley and Arabas (in prep).

Table 2.1: Data collected for each plot to summarize general stand characteristics and structure.

Type of information	**Plot sampling method**
Stand density	Trees/hectare (total and by species), extrapolated from trees per plot
Species composition	Identify species of trees, shrubs and forbs
Age class distributions	Increment cores from all living trees (> 4cm dbh)
Diameter classes	Diameter at breast height (dbh) for all trees in plot, live and dead
Regeneration patterns	Counts of seedlings (<1.4 m tall) and saplings (>1.4 m tall, but < 4 cm dbh) by species, including dead individuals
Mistletoe infection level	Hawksworth's dwarf mistletoe rating (DMR) and Tinnin's broom volume rating (BVR)

PART II

FUEL COMPOSITION

The following two chapters investigate the role of dwarf mistletoe on fuel composition in mature ponderosa pine forests. The first chapter quantifies surface fuel loads (litter, duff, and woody debris ranging from small twigs to logs) and compares fuel composition between infected and uninfected sites. The second chapter investigates the vertical distribution of fuels in the form of limbs attached to the main stem of sample trees. Previous research suggests that limbs infected with mistletoe live longer and persist in the crown rather than self-pruning as healthy limbs typically do, thereby contributing to aerial fuel loads and facilitating crown fires. I compare heights between infected and uninfected limbs, as well as estimate ages of infected limbs in old-growth ponderosa pine trees to quantify the role of mistletoe on the vertical distribution of fuels.

CHAPTER 3

FUEL ACCUMULATION IN MATURE PONDEROSA PINE (*PINUS PONDEROSA*) STANDS INFESTED WITH DWARF MISTLETOE (*ARCEUTHOBIUM CAMPYLOPODUM*)

ABSTRACT

Management practices during the past century have resulted in dramatic shifts in the stand structure and composition of ponderosa pine (*Pinus ponderosa*) forests of the American West, including increased tree density, increased levels of insect and dwarf mistletoe infestation, and an accumulation of highly flammable fuels. I examined the relationship between fuel accumulation and stand characteristics in old-growth ponderosa pine stands at varying levels of mistletoe infection. Fuel composition and stand structure were sampled for 14 plots (7 infected and 7 uninfected) in Crater Lake National Park (CLP) and 36 plots (22 infected and 14 uninfected) in Lava Cast Forest (LCF), Oregon. T-tests indicate that mistletoe has no influence on mean fuel accumulation at CLP, but increases the biomass of fine fuels at LCF. Redundancy analysis reveals mistletoe infection explains a significant amount of the variation in fuel composition at CLP, but fir (*Abies concolor*) basal area is a stronger explanatory variable. In contrast, basal area of ponderosa pine and stand age explain the greatest amount of variation in fuel accumulation at LCF, while mistletoe explains a small but significant amount of fuel variation. These results indicate that mistletoe infection does not drive overall fuel accumulation in these forests but results in greater accumulations of fine surface fuels and should be considered as a parameter in local fuel and fire behavior models.

INTRODUCTION

Fire exclusion, grazing and timber harvesting during the past 150-years have resulted in dramatic shifts in the stand structure and composition of ponderosa pine forests of the American West (Weaver 1959, Cooper 1960, Covington and Moore 1994, Belsky and Blumenthal 1997, Dahms and Geils 1997). Among these changes are increased tree density, increased levels of insect and dwarf mistletoe infestation, and an accumulation of highly flammable fuels (Agee 1993). Fire suppression has resulted in higher levels of insect and pathogens such as dwarf mistletoe (Dahms and Geils 1997, Fule et al. 2002), but the extent to which these agents influence fire behavior and susceptibility remains poorly understood.

Mistletoe interacts with a variety of biotic and physical factors, indirectly influencing the quantity, quality, flammability, and distribution of fuel in the forest. Mistletoe directly influences tree morphology by reducing vigor and growth rates (Hawksworth and Wiens 1996). Mortality of host species also alters stand composition and the successional trajectory of an infected stand. The successional stage and structure of a stand will determine the composition of fuels. One consequence of high mortality rates is an increased rate of fuel accumulation in the form of dead standing or downed trees in infested stands of lodgepole pine (Wanner and Tinnin 1989). However, mature ponderosa pine trees (300-600 years old) are surviving mistletoe infection dominate my study sites, indicating that the relationship between brooming, mistletoe-induced mortality, and fuel accumulation differs between ponderosa and lodgepole pine stands.

A common host reaction to infection by dwarf mistletoe is the formation of "witches' brooms." Branches undergo extensive swelling at the point of infection and a loss of apical dominance allows dormant buds to become active. The result is an increased numbers of twigs growing in abnormal patterns and orientation from a swollen main limb (Fig. 1.1). These changes in crown and branch structure are ecologically important for a variety of reasons (Tinnin et al. 1982, Godfree et al. 2002), including their potential influence on fire behavior and fuel composition, but there is a lack of research to elucidate the role of mistletoe in forest fire ecology.

Geils and Hawksworth (2002) suggest that mistletoe brooms lead to an increase in fuel loading and fire susceptibility in ponderosa pine stands. Brooms are massive and resinous relative to healthy branches, which may make them more flammable (Hawksworth and Weins 1996). Koonce (1981) quantified fuel loadings in young ponderosa pine stands and found that mistletoe increases both surface and aerial fuels, depending upon stand structure and the degree of infection. Koonce (1981) considered high fuel loadings in young infected stands a consequence of increased branch size on both the ground and persisting in the crown. Fuel loadings under infected mature trees have not been characterized, and there is a lack of information about the fuel characteristics of broomed branches.

It is unclear if brooms self-prune at the same rate as healthy branches. Preliminary data and field observations indicate that brooms have longer life spans than healthy branches, and once dead, they appear to persist in the crown. One consequence of broom persistence in the crown is the potential to provide a fuel ladder for surface fires to become crown fires (Koonce 1981, Koonce and Roth 1980, 1985). Broomed branches often remain attached to the main stem, but droop close enough to the ground to act as a fire ladder. Alternatively, if brooms persist in the crown longer than healthy branches, that fuel is not available for a low intensity surface fire. Brooms may result in more biomass in the stand, but that does not necessarily translate into more fuel on the ground.

My research investigates the influence of mistletoe infection on fuel accumulation. I will test the hypothesis that stands infested with mistletoe have higher accumulations of fuel, particularly litter and small diameter woody debris dropped from brooms. The objectives of this research are *i)* to determine if fuel accumulation is greater in ponderosa pine stands infected with dwarf mistletoe than in uninfected, *ii)* to identify which specific fuel types are most influenced by mistletoe infection, and *iii)* to determine the relative influence of mistletoe on fuel accumulation relative to other stand variables such as age and density. My general objective is to identify if parasitic plants play an important role in shaping large scale disturbance events such as fire and to determine if mistletoe should be considered when modeling fire behavior and setting management policies.

METHODS

Study areas

I conducted this research in two areas in central Oregon, Lava Cast Forest and Crater Lake National Park. Both areas support mature, mixed-conifer forests dominated by ponderosa pine with varying levels of dwarf mistletoe infection. Records of prescribed burns are available for CLP and previous research established a fire history for LCF (Arabas et al. 2006), allowing me to work from established fire history baselines for estimating rates of fuel accumulation.

Lava Cast Forest (LCF)

Lava Cast Forest is located in the Deschutes National Forest east of the Cascade crest (Fig. 3.1). My study site within the monument is the Lava Cast Forest Geological Area, which is characterized by 11 kipukas (forested islands) isolated among shallow, mid-Holocene lava flows (Peterson and Groh 1969). Kipuka areas range from 0.4 to 113 ha, with maximum elevations from 1590 to 1820 m. A rainshadow effect from the Cascade Mountains to the west strongly influences the regional climate of the study area. The moisture regime is semi-arid, with the majority of precipitation occurring from October to March, typically as snow during the winter. Average annual precipitation between 1971 and 2002 is ≈ 300 mm. and average temperatures range from a low of 0° C in January to a high of 17.3° C in July (OCS 2006).

Floristically, the kipukas are dominated by three tree species with distributions appearing to be topographically and edaphically controlled (Hadley and Arabas in prep). Ponderosa pine is most common on south-facing slopes, while north-facing slopes and interior stands are dominated by white fir-grand fir hybrid (*Abies concolor – A. grandis*). Flat areas are typically covered with dense stands of lodgepole pine. Western white pine (*Pinus monticola*) is found at a few locations on the kipukas. Typical understory species include snowbrush (*Ceanothus velutinus*), green manzanita (*Arctostaphylus patula*), and bitterbrush (*Purshia tridentata*). Two species of dwarf mistletoe occur in the study area – *Arceuthobium campylopodum* is found on ponderosa pine trees, and *A. americanum* on lodgepole pine. The distribution and density of dwarf mistletoe across the study is highly variable, with some kipukas lacking mistletoe while others support mistletoe in the majority of pine stands. The stands infected with mistletoe are moderately to severely infested, meaning that the majority of trees support mistletoe in over half of their crowns.

Historically, fires frequency is higher on the kipukas than in the forests surrounding them (Arabas et al. 2006). The mean fire return interval (MFRI) on the kipukas is 6 years, compared to 9 years in the surrounding forest (Arabas et al. 2006). Fire return intervals for the surrounding forest decreased following European settlement, probably as a result of anthropogenic disturbance. In contrast, MFRI for the kipukas remained constant before and after European settlement, providing further evidence that the study area represents relatively pristine forest conditions.

Crater Lake National Park (CLP)

The study site is an 81.5 ha unit located in the panhandle extending from the southern boundary of Crater Lake National Park (Figure 3.2). This site was selected because it includes large ponderosa pine with a mixed severity of dwarf mistletoe infection, and was scheduled for prescribed burning by National Park staff.

Crater Lake National Park is located in the southern Cascade Mountains of Oregon. The CLP study site is along the east flank of the Cascades and slopes gently (3%) with a south-facing aspect, ranging in elevation from 1340-1400 meters. Crater Lake was designated a national park in 1902, but the panhandle region was not managed by the Park Service until 1932. U.S. Forest Service records and physical evidence indicate that logging occurred between 1909 and 1927.

The climate at the Crater Lake study site is strongly seasonal. Average annual precipitation is 51.3cm (1971-2000) at Chiloquin located 30 km to the southeast at similar elevation, with the majority of precipitation occurring as snow between November and March. Mean annual temperature is 14.7°C, with the warmest months being July and August and the coldest months December and January.

Vegetation in the panhandle region of Crater Lake National Park is dominated by ponderosa pine – white fir forest. Dominant tree species are ponderosa pine and white fir. Sugar pine (*P. lambertiana*) and lodgepole pine are common, with occasional incense cedar (*Calocedrus decurrens*) and Douglas-fir (*Pseudotsuga menziesii*). Common understory species include wax currant (*Ribes cereum*), snowbrush (*Ceanothus velutinus*), dogbane (*Apocynum androsaemifolium*), pinemat manzanita (*Arctostaphylos nevadensis*), grasses and sedges.

Western dwarf mistletoe is more abundant in lower elevation stands at the south end of the park. There are several stands of ponderosa pine further north in the panhandle that do not support dwarf mistletoe infections, indicating the infestation in my study area is independent of host density. The northwest corner of the study area includes lodgepole pine infected by *A. americanum*.

The National Park Service suppressed wildfires in the park for most of the 20th century, with the last wildfire to burn in the study site occurring in 1902. A several-hundred year fire history is available for the CLP study site. McNeil and Zobel (1980) completed a dendrochronological assessment of fire scarred trees in the late 1970s, and historical records document natural and prescribed fires during the 1900s. McNeil and Zobel (1980) report mean fire return intervals of 9-42 years for the time period 1748-1902 for the area that includes my study site.

Sampling strategy

Plots were established at both study sites to collect background data summarizing stand structure and general characteristics. Sampling included 36 plots at Lava Cast Forest (22 infected, 14 uninfected) and 14 plots at Crater Lake (7 infected and 7 uninfected). Plots sizes vary (15m^2 to 50m^2) according to tree density, based on the minimum area needed to include at least 20 live trees. Plot selection was stratified to ensure equal representation of infected and non-infected samples. Within each stratum, plot locations were chosen subjectively to include the largest ponderosa pine trees in the area. I located infected and non-infected plots as close to each other as possible to control for variability in biotic and abiotic factors.

Environmental Variables

I measured environmental and forest structure variables within each plot to determine their relative influence on fuel composition in relation to dwarf mistletoe abundance. Environmental variables included estimates of slope aspect and angle, diameter measurements for all live and dead trees > 4 cm dbh (diameter at breast height, 1.4 m), as well as tallies of all saplings and seedlings growing within each plot. I used four 1 m^2 quadrats per plot to estimate percent cover and richness of understory plants. I visually estimated infection intensity using the dwarf mistletoe rating system (DMR), which ranges from 0 (uninfected) to 6 (severely infected) (Hawksworth 1977).

I collected a single increment core at 30 - 50 cm above the root collar of all live trees to determine their age. Increment cores were removed parallel to slope contours to minimize the influence of reaction wood on the ring patterns in each sample (Fritts 1976). Increment cores were dried and mounted following standard dendrochronological procedures (Stokes and Smiley 1996). I prepared the surface of each core by sanding with progressively finer sandpapers and steel wool until achieving clear, cellular resolution under standard 7–10x magnification (Orvis and Grissino-Mayer 2002). I crossdated all samples using a combination of skeleton plotting (Stokes and Smiley 1996) and the list method (Yamaguchi 1991). Skeleton plots are a graphical representation of ring widths that allows for pattern matching among different increment cores. The list method notes particularly narrow rings or latewood increments (marker years) that are compared among samples.

Arabas et al. (2006) provided fire history information for LCF that includes years since the last major fire and mean fire return interval for each stand. I define major fires as being sufficiently intense to scar trees or logs, or replace entire stands. Arabas et al. (2006) found that USDA Forest Service historical fire records include fewer events on the kipukas than the empirically-derived fire scar data revealed. Because this record is incomplete, I excluded low-intensity surface fires (i.e., those that did not scar trees) from the analyses. Fire history is not included in CLP analyses because park records indicate that the entire study area underwent prescribed burning in 1976.

Fuel biomass

Surface and ground fuels were measured in each plot using the planar intercept method (Brown 1974, Brown at al. 1982). The number of transects per plot ranged from one to five, varying according to plot size. Total transect length was 15 m, but sampling along this length depended upon fuel size. Size classifications are based on the time it takes for fuels of a certain diameter range to lose or gain ~66% of the difference between the initial and equilibrium moisture contents (Deeming et al. 1977). Fuels in the 1-hour size class (0-0.64 cm diameter) were sampled from 0-2 m along each transect; 10-hour fuels (0.65-2.54 cm) from 0-3 m; 100-hour fuels (2.55-7.62 cm) from 0-5 m; and 1000-hour fuels (> 7.62 cm) were sampled from 1–25 m. We used dbh to calculate the basal area of all snags in each plot and extrapolated to m^2/ha.

I measured litter and duff depth at 0, 3, and 6 m along each transect. Litter samples were collected from each transect and oven dried to obtain bulk density measurements. Fuel biomass calculations followed the procedures of Brown et al. (1982).

Data analysis

All fuel variables were square-root transformed to correct for skewed distributions and to avoid domination by the larger fuel types. Fuel data were standardized to adjust for different measurement units (biomass for ground fuels and basal area for snags). Environmental data were log transformed to normalize skewed distributions. Environmental variables were standardized using *z*-scores to account for inconsistency in units of measurement (e.g., count data versus area).

I used descriptive statistics and t-tests to compare fuel loads from each size class and environmental variables between the two study sites. Significant differences between LCF and CLP variables would indicate that it is inappropriate to analyze both data sets together. I used t-tests to compare mean fuel loads between infected and uninfected plots.

I used a combination of indirect and direct gradient analysis to quantify the importance of mistletoe in fuel composition. Principal components analysis (PCA), an unconstrained, indirect gradient analysis allowed me to identify patterns in fuel distribution among the samples. PCA revealed the covariance structure within the fuel data and identified the amount of variability in the fuels that can be interpreted with direct gradient analysis.

Redundancy analysis (RDA) is a constrained or direct gradient analysis used to identify which linear combinations of the environmental variables best explain the variation in fuel biomass among samples. RDA also approximates the distributions of fuel data along the range of sampled values for each environmental variable (ter Braak 1986). I chose a forward-selected RDA to determine which environmental variables accounted for the greatest amount of variance in the distribution of fuels and to reduce multicollinearity among the independent variables (CANOCO v.4.0, Ter Braak 1997). This iterative process selects variables that uniquely and significantly ($p \leq 0.05$) explain variation in the distribution of fuels. The significance of each added variable and the final canonical axes were verified using Monte Carlo permutation tests with 999 unrestricted permutations ($p \leq 0.05$).

RESULTS

Descriptive statistics and t-tests reveal the stand structure data for CLP and LCF study areas are too dissimilar to be pooled. All environmental variables, except fir basal area, differ significantly between CLP and LCF (Table 3.1). The majority of plots were located on gentle south or west-facing slopes. Slope and aspect demonstrated little variation among plots and were removed from subsequent analyses. Descriptive statistics and PCA revealed an outlier among the uninfected CLP plots. Litter and duff levels are unusually low in this plot, so it was removed from subsequent redundancy analysis.

Crater Lake Panhandle

Statistical tests revealed few differences between infected and uninfected plots at CLP. T-tests comparing environmental data between infected and uninfected plots show no significant differences (Table 3.2). T-tests of plot fuel loads show no significant differences between infected and uninfected plots at CLP (Table 3.3). Tree-level fuel data show that uninfected trees have significantly more litter accumulating at the base (Table 3.3).

The first four PCA axes explain 85% of the variance in fuel composition among the CLP plots. The first axis explains 36% of the variance in fuels, primarily with 10- and 100-hour classes (Table 3.4, Fig. 3.3). The second axis, representing a gradient of duff accumulation, explains an additional 22% of the variance in fuels. Infected plots form two distinct groups, representing low versus high accumulations of duff (Fig. 3.3). Infected plots tend to have higher than average accumulations of 1-, 10-, 100-, and 1000-hour fuels. Infected plots also show high variation in litter, duff, 1000-hour fuels, and snags. Uninfected plots show greater variation overall in fuel accumulation (Fig. 3.3).

Forward-selected RDA identified five significant environmental variables: fir basal area, mistletoe infection, ponderosa basal area, density of seedlings and saplings, and maximum tree age (Table 3.5). The initial forward-selected RDA model indicated that snag basal area was uncorrelated with mistletoe infection, therefore I removed snags as a dependent variable in the final model. The first four RDA axes explain 51% of the variance in fuel composition among CLP plots. The first constrained axis explains 28%, representing a gradient in fir basal area and mistletoe infection (Table 3.5 and Fig 3.4). The second axis explains less variation, 15%, representing basal area of ponderosa pine and density of seedlings and saplings (Table 3.5 and Fig 3.4). RDA reveals that infection is positively correlated with 10-, 100-, and 1000-hour fuels, but is negatively correlated with litter and duff accumulation (Fig. 3.4). Plots with high basal area of ponderosa pine tend to have high accumulations of litter and duff. In contrast, high basal area of fir is positively correlated with 1-hour fuel biomass (Fig 3.4). Density of seedlings and saplings at CLP is positively correlated with biomass of 1000-hour fuels (Fig 3.4).

Lava Cast Forest

T-tests indicate that infected and uninfected plots do not differ in total fuel loads, but infected plots have higher accumulations of 1-, 10-, and 100-hour fuels and litter (Table 3.3). T-tests comparing environmental data between infected and uninfected plots show that infected plots experienced more recent fires and have lower tree densities ($p<0.05$) (Table 3.2). Infected plots burned on average 96 (s.d. 66.9) years before sampling, compared to 136 (s.d. 68.1) years for uninfected plots. Mean stand density in infected plots is 310 (s.d. 202) trees/ha and 487 (s.d. 112) in uninfected plots. No other environmental variables differ between infected and uninfected plots at LCF.

The first four PCA axes explain 79% of the variance in fuels at LCF. The first axis, representing a gradient in 10- and 100-hour fuels, explains 34% of the variance in fuels (Table 3.6, Fig. 3.5). The second axis explains 20% of the variance among LCF plots, representing 1000-hour fuels and litter (Fig. 3.5). The ordination diagram does not reveal any clear groupings of infected or uninfected plots, but the majority of infected plots have higher than average 1-, 10-, and 100-hour fuels (Fig. 3.5). Uninfected plots have the least litter, 1-, 10-, and 100-hour fuels. Infected plots appear to show more variation in fuel composition.

Based on initial PCA and RDA results, I removed snag basal area and 1000-hr fuels as a dependent variable in the final RDA model. PCA indicated that snags contribute little to the covariance structure of fuels at LCF, and the initial forward-selected RDA model showed that snag basal area and 1000-hr fuels are uncorrelated with mistletoe infection.

The final RDA model identified five significant environmental variables: maximum tree age, mistletoe infection, ponderosa basal area, time since the last fire, and average age of ponderosa pine trees (Table 3.7). The first four RDA axes explain 34% of the variation in fuel composition among LCF plots. The first axis explains 16% of the variance in fuels, representing two environmental variables, mistletoe infection and maximum tree age (Table 3.7; Fig. 3.6). Axis two explains 9% of the variance with years since the most recent fire and ponderosa pine average age (Table 3.7; Fig. 3.6). Ponderosa pine basal area is negatively correlated or uncorrelated with all fuel size classes (Fig. 3.6). Maximum tree age and average age of ponderosa pine trees are positively correlated with duff, 10- and 100-hour fuels. In contrast, tree age and time since last fire variables negatively correlated with litter accumulation (Fig. 3.6). Plots without recent fire, which also tend to have the oldest trees, have the highest accumulations of duff and the least litter.

Redundancy analysis shows that dwarf mistletoe infection is positively correlated with 1-hr and litter biomass, and negatively correlated with duff accumulations (Fig. 3.6). Mistletoe has weak positive correlations with 10- and 100-hour fuels (Fig. 3.6). Spearman's correlation coefficients also reveal significant positive relationships between DMR and litter, 10-, and 100-hour fuels ($p<0.05$).

DISCUSSION

Crater Lake Panhandle

Dwarf mistletoe appears to weakly influence fuel composition at CLP. Constrained ordination identified mistletoe abundance as a key environmental variable, but it explains relatively little of the total variance in fuel composition (28% when combined with fir basal area). Stand density and basal area of dominant tree species appear to be stronger predictors of fuel composition than dwarf mistletoe abundance at the Crater Lake study area.

Infected and uninfected plots at CLP are highly similar with respect to the measured environmental variables. The key difference between the two groups of plots is the presence or absence of mistletoe. This may explain why the redundancy analysis explained little of the total variance in fuel composition and identified infection level as a significant environmental variable.

Uninfected samples at CLP show greater variation in fuel composition than infected samples. Fuel loads in infected plots are more predictable, tending to have higher than average accumulations of fine and coarse woody fuels. Mistletoe abundance is negatively correlated with litter biomass, which may result from needle retention on broomed branches. Alternatively, the difference in litter accumulation may be a function of stand structure rather than a direct result of mistletoe infection. The more severely infected plots typically represent young, mixed cohorts of several species including white fir and lodgepole pine that possess smaller needles and more dense growth forms that may lead to less litter biomass as compared to long-needled species such as ponderosa pine. Mistletoe-related mortality of ponderosa pine trees could explain the shift in stand age and structure to non-host species, indicating an indirect connection between infection and litter accumulation. Litter accumulation is greater in infected plots with a high basal area of ponderosa pine, which tend to have low tree species diversity and contain older ponderosa and sugar pine trees. Both of these species are long-needled and tend to accumulate litter and duff at their base.

Infected plots at CLP tend to have more downed logs, saplings, and seedlings. This is not a function of mistletoe-induced mortality leading to open areas suitable for regeneration. Infected plots have large cohorts of immature shade-tolerant white fir, including high densities of fir seedlings and saplings, rather than the shade-intolerant host species. The 1000-hour fuels in these infected plots are likely the result of self-thinning among dense white fir cohorts growing in the understory of mature pines infected with mistletoe. Ponderosa pine regeneration is low in these areas because of diminished understory light levels and the exposure to mistletoe from infected overstory trees.

Lava Cast Forest

Mistletoe infection appears to increase fine fuel accumulation at Lava Cast Forest. Unlike its minimal effect at CLP, mistletoe infection at LCF is positively correlated with 1-, 10-, and 100-hour fuels and litter. Uninfected plots show lower variations in most fuel types and have the lowest accumulations of litter, 1-, 10-, and 100-hr fuels. The low variation within each fuel type seen in uninfected plots may be an artifact of the smaller sample size compared to infected plots, but the variation is comparable with CLP plots.

Mistletoe influences fuel loads at LCF both directly and indirectly. Mistletoe brooms may contribute to high accumulations of litter. Evidence indicates that mistletoe infection increases needle surface area (Tinnin and Knutson 1980; Wanner and Tinnin 1986), which may in turn increase the biomass of leaf litter on the ground. To date, no published research has examined the effects of mistletoe infection on needle morphology in brooms on ponderosa pine. Because infected plots have experienced more recent fire and have lower tree densities than uninfected plots, this suggests that infection and fire may lead to mortality of understory host trees, resulting in low stand density. One would expect recent fire and low density to decrease fine fuel loadings, but we see the opposite at LCF. One explanation for this may be that recent fire scorched low branches of standing trees, especially the brooms persisting low in the crown, resulting in high rates of needle and fine fuel accumulation following fire.

At LCF, mistletoe has little influence on the accumulation of coarse fuels such as downed logs and snags. One would expect the high mortality rates associated with mistletoe infection to result in higher biomass of coarse fuels, but infection at LCF does not appear to decrease growth or increase mortality rates among mature host trees (Stanton 2007). Tree age is more strongly correlated with coarse fuel loads. Older stands have more downed or standing dead trees, regardless of the presence of mistletoe, and there is no correlation between stand age and mistletoe infection level.

Comparison of Study Areas

Ten-hr and 100-hr fuels explain the greatest amount of variance in fuel accumulation at both CLP and LCF, yet the influence of mistletoe differs between the sites. These differences are primarily related to differences in stand structure and composition with large, pure stands of ponderosa pine characterizing LCF versus the mixed forest found at CLP. These differences are consistent with recent finding by Stanton and Arabas (in prep) that show different tree species contribute different fuel types. Consequently, my results may indicate that the non-host tree species common at CLP may be exerting a strong influence on fuel accumulation and obscuring the effect of mistletoe.

While the CLP plots include a variety of tree species, there is little variation in environmental variables or fuel loads, especially when compared to LCF plots. This lack of variation may explain why mistletoe abundance was a key explanatory variable in the constrained ordination analysis, yet did not explain any differences in univariate tests. The primary difference among sample plots at CLP is the presence or absence of mistletoe, while all other environmental variables are relatively constant among the plots. LCF possesses a variety of environments and successional stages, as well as greater variation in most fuel types. Mistletoe is a key explanatory variable for fuels at LCF also, but it explains far less of the variation compared to the CLP analysis. There is more variation to explain at LCF, and more variables emerge as explanatory.

The role of mistletoe at LCF may be exacerbated by climate and stand age. LCF experiences a more arid and extreme climate than CLP. The trees at LCF are older and experience more frequent drought, and infected trees grow poorly when under moisture stress (Chapter 6). The combination of age and moisture stress at LCF leads to reduced tree vigor and crown health, ultimately resulting in needle and branch loss as the crown dies back. The trees at CLP appear to have healthier crowns because they are younger and growing in a more mesic environment.

CONCLUSIONS

This study indicates that dwarf mistletoe results in higher fuel accumulations, but only for a subset of fuel types and under certain site conditions. Crater Lake exhibited a weak correlation between infection level and accumulations of litter, 1-, 10-, and 100-hour fuels. Increasing mistletoe infection contributes significantly to increasing fuel accumulation at CLP, but greater basal area of white fir exerted an equally strong influence. Infected plots at Lava Cast Forest also have higher accumulations of litter, 1-, 10-, and 100-hour fuels. Mistletoe explains a small but significant amount of the variation in fuels at LCF. Infection and maximum tree age explain most of the variation in fuel accumulations, with time since fir and ponderosa pine age also being strong predictors.

My results suggest that mistletoe infection leads to higher accumulations of fine fuels, but the influence of mistletoe is complex and often indirect. Environmental variables, including mistletoe infection level, explain little of the variance in fuel accumulation, indicating the absence of some key explanatory variables in my study. Stand history appears to play a critical role in fuel loadings, but the history or successional trajectory of a stand is difficult to quantify. Although I was able to measure plot-level variables related to the successional trajectory of the study stands, there are other important stand-related variables that need to be assessed. These variables include measures of mistletoe induced needle density, determination of how mistletoe influences tree stress and possible insect and pathogen infestation, and detailed, stand-level fire histories that include low-intensity surface fires.

This study illustrates the need to incorporate mistletoe abundance in fire behavior and fuel models. While I cannot attribute how much of each fuel type is a direct result of mistletoe infection, my results indicate that mistletoe infection increases fine fuel biomass in mature ponderosa pine stands, and therefore should be included as a parameter in fire models. Additional studies are needed to investigate the effects of mistletoe infection on fuel loads in other forest types.

Table 3.1: Mean (standard deviation) and t-test results for environmental (independent) and fuel composition (dependent) variables used in redundancy analysis. LCF = Lava Cast Forest, N = 36; CLP = Crater Lake National Park, N = 14.

Environmental Variables	**CLP**	**LCF**	**All Plots**
Basal area (m^2/ha) – all spp.	86.8 (24.2)*	48.4 (18.8)	59.1 (26.7)
Ponderosa pine	65.3 (22.6)*	37.8 (20.0)	45.5 (24.0)
White fir	13.8 (14.8)	7.7 (9.9)	9.4 (11.7)
Tree density (trees/ha)	782 (381)*	379 (192)	492 (313)
Tree ages (years)	97 (15)	194 (42)*	167 (57)
Maximum tree age (years)	295 (124)	413 (108)*	380 (123)
Ponderosa pine age (years)	183 (90)	250 (59)*	231 (74)
Sapling and seedling density (#/ha)	6176 (5905)*	261 (275)	1917 (4062)
Years since last fire	27 (0)	112 (69)*	88 (70)
Fuel Variables			
1-hour (Mg/ha)	0.13 (0.12)*	0.13 (0.12)*	0.11 (.011)
10-hour (Mg/ha)	0.68 (0.34)	0.68 (0.34)	0.67 (0.32)
100-hour (Mg/ha)	0.92 (0.70)*	0.92 (0.70)*	0.82 (0.64)
1000-hour (Mg/ha)	11.7 (12.9)*	11.7 (12.9)*	9.13 (11.69)
Litter (Mg/ha)	0.03 (0.05)	0.03 (0.05)	0.03 (0.04)
Duff (Mg/ha)	4.54 (3.35)	4.54 (3.35)	4.19 (3.35)
Total (Mg/ha)			
Snag basal area (m^2/ha)	4.83 (4.55)	4.83 (4.55)	5.15 (4.85)

* Significantly greater at this site ($p < 0.05$).

Table 3.2: Differences in environmental variables (mean and standard deviation) between uninfected and mistletoe-infected plots. BA = basal area; CLP = Crater Lake; LCF = Lava Cast Forest

Environmental Variables	**CLP uninfected**	**CLP infected**	**LCF uninfected**	**LCF infected**
BA (m^2/ha) all spp.	92.2 (12.3)	81.5 (22.2)	55.8 (18.4)	43.6 (17.9)
Ponderosa pine	75.6 (26.5)	55.0 (12.8)	43.6 (18.9)	34.0 (20.1)
White fir	11.4 (10.8)	16.3 (18.4)	8.9 (6.1)	7.0 (11.9)
Tree density (trees/ha)	875 (414)	688 (350)	487 (112)*	310 (202)
Tree ages (yrs)	91 (12)	102 (17)	185 (35)	200 (46)
Maximum tree age (yrs)	312 (128)	278 (128)	412 (126)	414 (97)
Ponderosa pine age (yrs)	99 (31)	105 (35)	266 (45)	240 (65)
Sap / seed density (#/ha)	6145 (6216)	6207 (6075)	302 (266)	235 (284)
Years since last fire	27 (0)	27 (0)	136 (68)*	96 (67)
N	7	7	14	22

* Significantly greater in this group ($p < 0.05$).

Table 3.3: Mean (standard deviation) of fuel loads (Mg/ha) and snag basal area (m^2/ha). *T*-tests were used to compare uninfected and infected plots within each study site. CLP = Crater Lake National Park; LCF = Lava Cast Forest.

Fuel Size	**CLP plot uninfected**	**CLP plot infected**	**CLP tree uninfected**	**CLP tree infected**	**LCF uninfected**	**LCF infected**
1-hr	0.06 (0.04)	0.06 (0.04)	0.04 (0.03)	0.04 (0.04)	0.05 (0.03)	0.17 (0.14)*
10-hr	0.53 (0.24)	0.76 (0.27)	0.80 (0.25)	0.75 (0.27)	0.53 (0.22)	0.78 (0.38)*
100-hr	0.41 (0.40)	0.66 (0.25)	0.67 (0.50)	0.64 (0.46)	0.60 (0.39)	1.13 (0.78)*
1000-hr	1.69 (1.83)	3.29 (1.83)	4.14 (3.28)	5.26 (4.17)	12.0 (16.2)	11.5 (10.6)
Litter	0.03 (0.01)	0.03 (0.01)	0.04 (0.01)*	0.03 (0.01)	0.02 (0.01)	0.05 (0.06)*
Duff	3.4 (3.0)	3.3 (3.8)	6.24 (3.65)	5.82 (5.62)	5.0 (3.6)	4.2 (3.2)
Total	6.1 (3.3)	8.1 (3.8)	11.9 (6.16)	12.6 (7.07)	18.2 (18.2)	17.9 (12.3)
Snags	4.3 (4.8)	7.6 (6.3)	n/a	n/a	4.8 (5.3)	4.8 (4.2)

* Significantly greater in this group ($p < 0.05$).

Table 3.4: Results from principal components analysis of fuel composition at Crater Lake Panhandle. Eigenvalues represent variance explained by each axis. Species scores indicate coordinates along each ordination axis.

	Axis I	**Axis II**	**Axis III**
Eigenvalues	0.36	0.22	0.17
Species Scores			
1-hour (Mg/ha)	0.68	-0.53	0.15
10-hour (Mg/ha)	0.85	-0.17	-0.07
100-hour (Mg/ha)	0.77	-0.25	-0.12
1000-hour (Mg/ha)	0.64	0.53	0.22
Litter (Mg/ha)	-0.22	0.34	0.72
Duff (Mg/ha)	-0.28	-0.80	0.36
Snag Basal Area (m^2/ha)	-0.17	-0.42	-0.76

Table 3.5: Results from forward-selected redundancy analysis for Crater Lake plots. Eigenvalues represent variance explained by each axis. Species-environment correlations indicate how well the included environmental variables explain the fuel composition among the samples. Inter-set correlations indicate the strength of the relationship between environmental variables and fuel composition along each axis.

	Axis I	**Axis II**
Eigenvalue:	0.28	0.15
Species-environment correlation:	0.86	0.72
	Inter-set Correlations	
Environmental Variables		
Fir basal area	0.43	0.12
Mistletoe infection	0.42	-0.43
Ponderosa pine basal area	-0.22	0.64
Sapling & seedling density	-0.26	-0.46
Maximum tree age	0.26	0.15

Table 3.6: Results from principal components analysis of fuel composition at Lava Cast Forest. Eigenvalues represent variance explained by each axis.

	Axis I	**Axis II**	**Axis III**
Eigenvalues	0.34	0.20	0.15
Species Scores			
1-hour (Mg/ha)	0.70	0.33	-0.05
10-hour (Mg/ha)	0.80	0.24	-0.07
100-hour (Mg/ha)	0.74	0.04	-0.13
1000-hour (Mg/ha)	0.52	-0.62	0.21
Litter (Mg/ha)	0.24	0.76	0.09
Duff (Mg/ha)	0.48	-0.28	0.68
Snag Basal Area (m^2/ha)	0.39	-0.44	-0.67

Table 3.7: Results from forward-selected redundancy analysis for Lava Cast Forest plots. Eigenvalues represent variance explained by each axis. Species-environment correlations indicate how well the included environmental variables explain the fuel composition among the samples. Inter-set correlations indicate the strength of the relationship between environmental variables and fuel composition along each axis.

	Axis I	**Axis II**
Eigenvalue:	0.16	0.09
Species-environment correlation:	0.63	0.68
	Inter-set Correlations	
Environmental Variables		
Maximum tree age	0.25	-0.22
Ponderosa pine basal area	-0.17	-0.10
Mistletoe infection	0.36	0.33
Time since last fire	0.05	-0.56
Ponderosa pine average age	0.20	-0.44

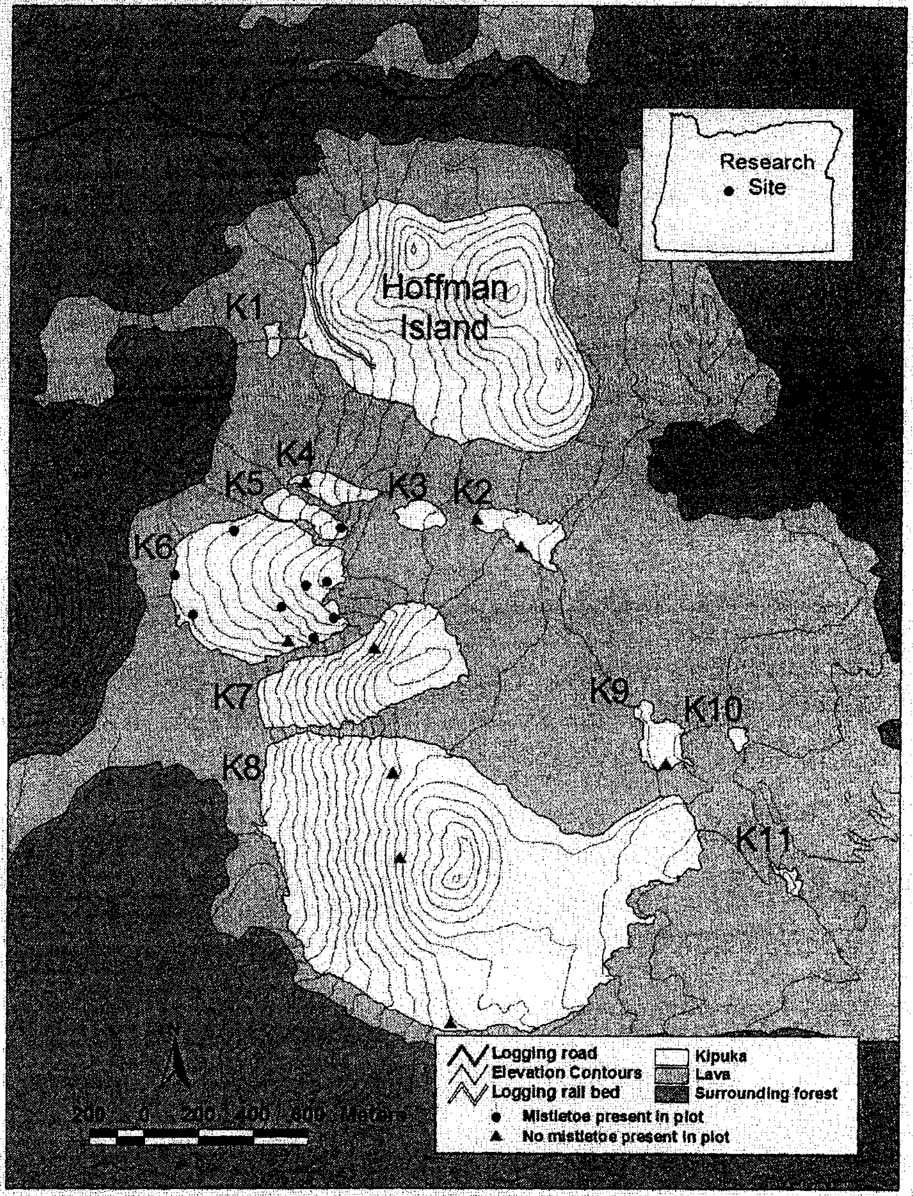

Figure 3.1: Lava Cast Forest study site. Dark symbols designate plots infested with mistletoe; light symbols are plots without mistletoe.

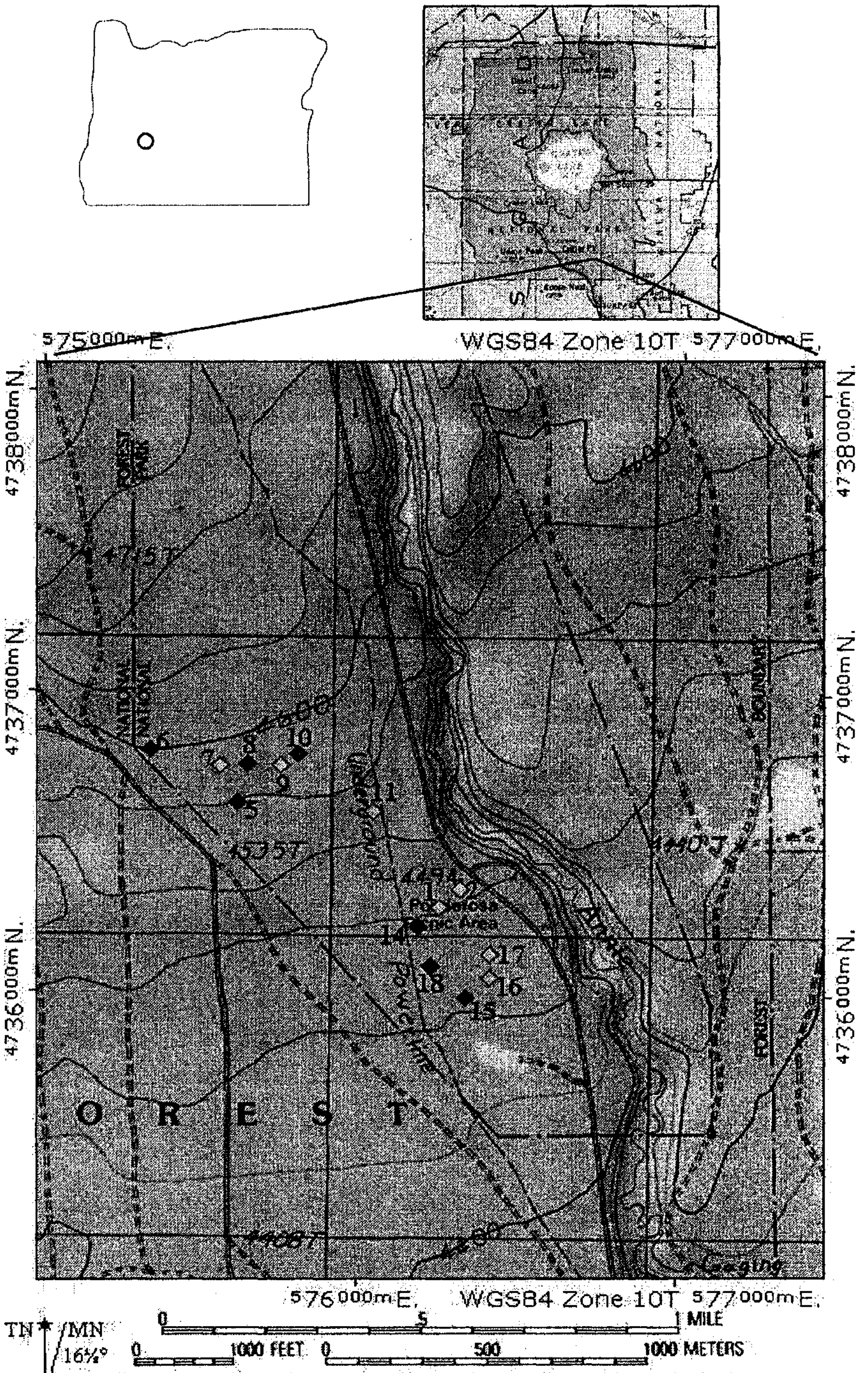

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Figure 3.2: Study site at Crater Lake National Park, Oregon. Dark symbols designate plots infested with mistletoe; light symbols are plots without mistletoe.

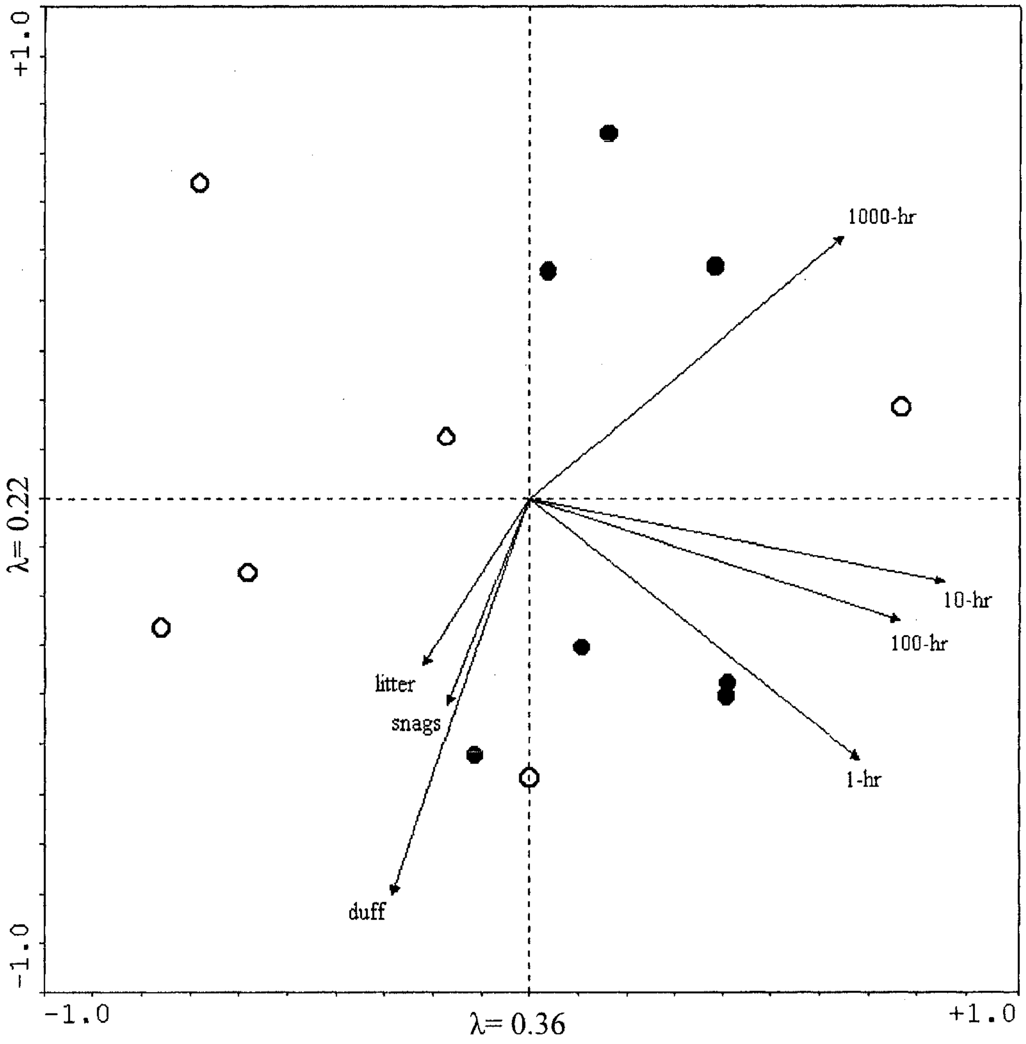

Figure 3.3: PCA diagram for fuel composition in Crater Lake plots. Dark circles represent plots infected with mistletoe; open circles represent uninfected plots. The first axis represents a gradient of 1-, 10-, and 100-hr fuels; the second axis 1000-hr fuels and duff.

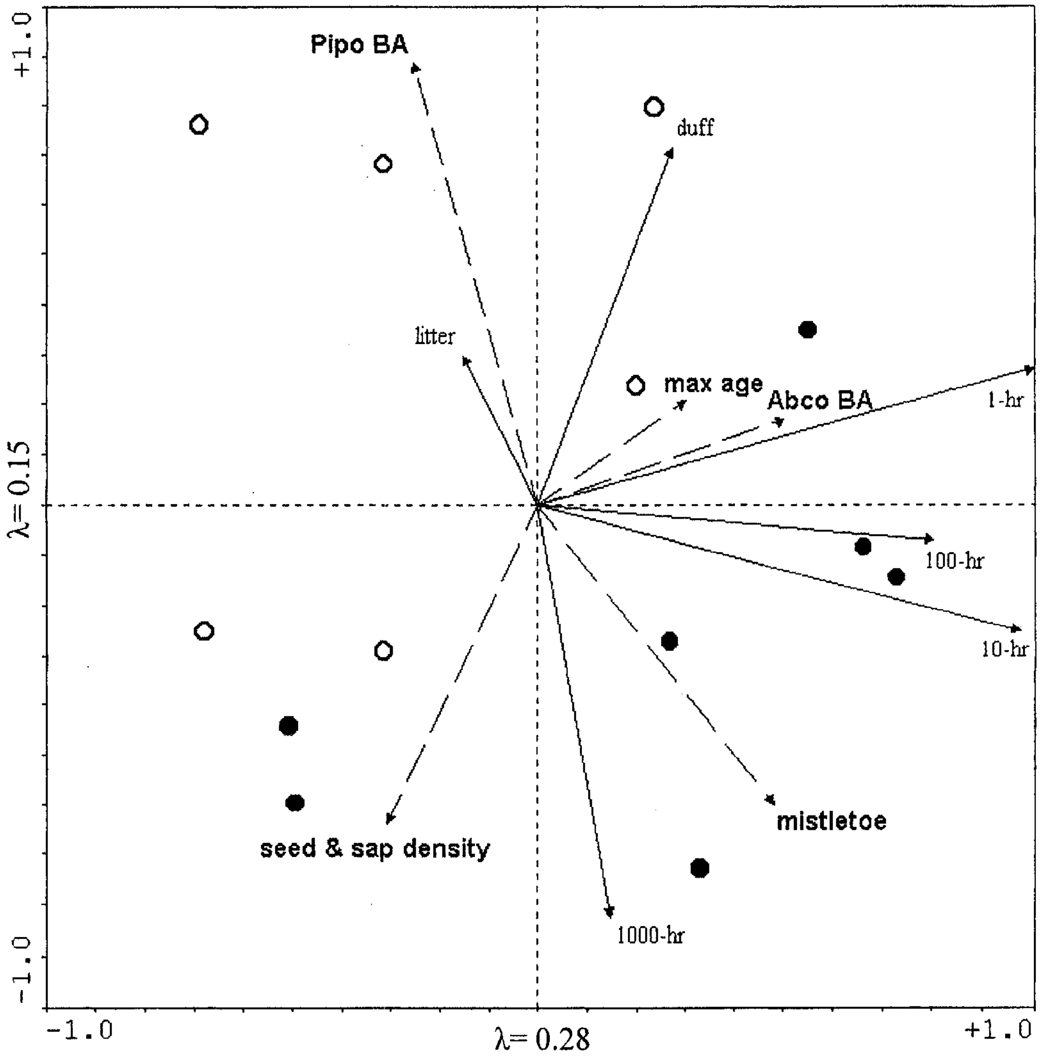

Figure 3.4: RDA diagram for Crater Lake plots. Dark circles represent plots infected with mistletoe; open circles represent uninfected plots. Environmental variables are indicated by bold text and dashed vectors. Fuel variables are indicated by solid vectors.
Pipo = ponderosa pine; Abco = white fir; BA = basal area; seed & sap = seedling and sapling density.

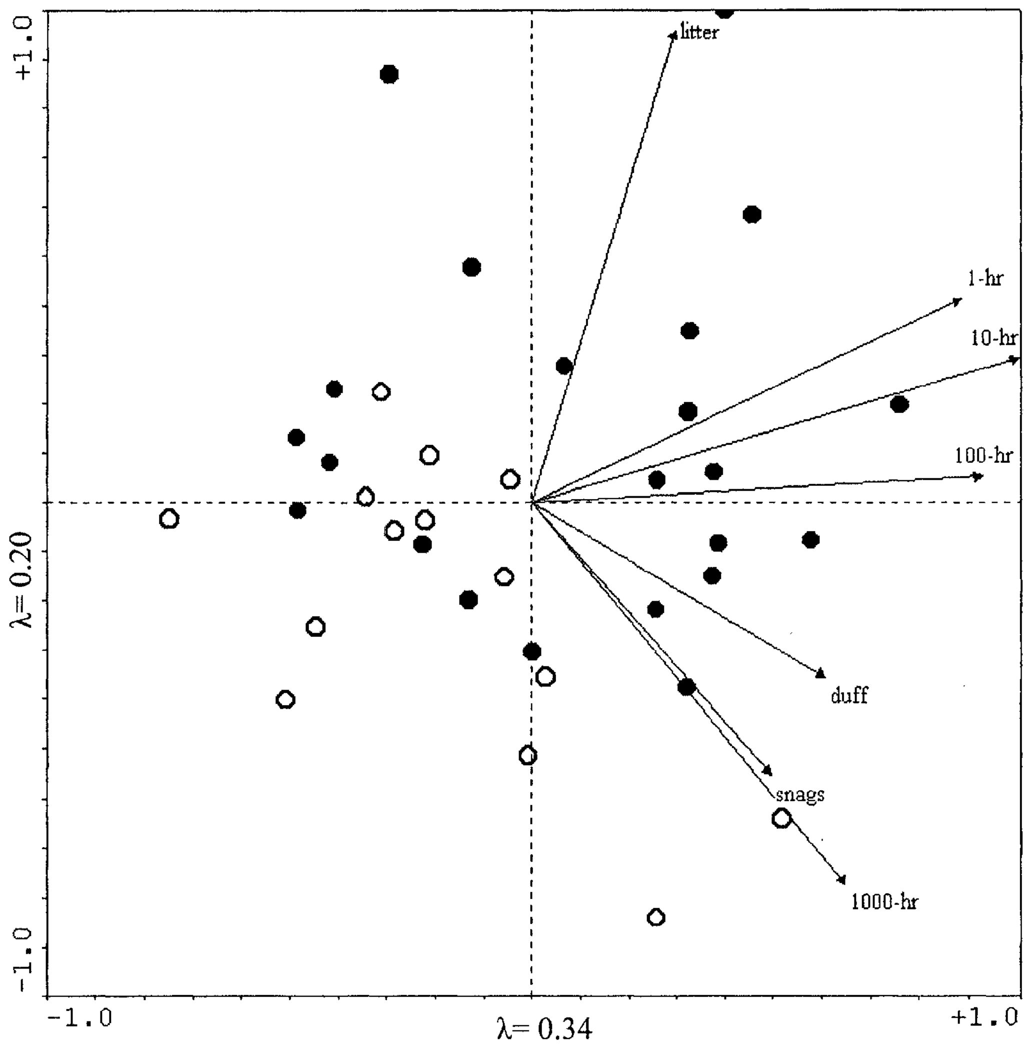

Figure 3.5: PCA diagram for fuel composition at Lava Cast Forest. Dark circles represent plots infected with mistletoe; open circles represent uninfected plots. The first axis represents a gradient of 1-, 10-, and 100-hr fuels; the second axis 1000-hr and litter.

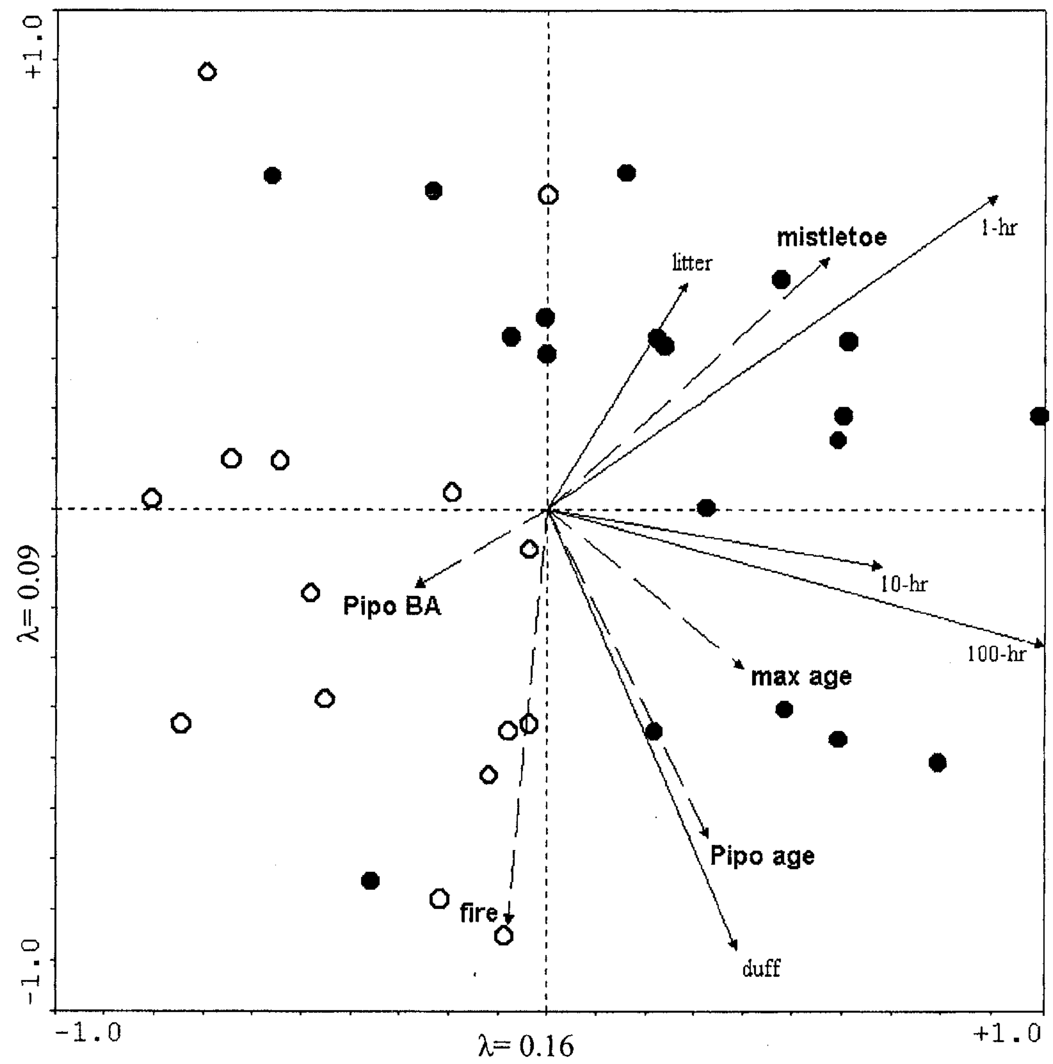

Figure 3.6: RDA results for Lava Cast Forest plots. Dark circles represent plots infected with mistletoe; open circles represent uninfected plots. Environmental variables are indicated by bold text and dashed vectors. Fuel variables are indicated by solid vectors.

Pipo = ponderosa pine; Abco = white fir; BA = basal area; seed & sap = seedling and sapling density.

CHAPTER 4

DWARF MISTLETOE BROOM DEVELOPMENT AND PERSISTENCE IN PONDEROSA PINE TREES

ABSTRACT

Dwarf mistletoe brooms add structural diversity to ponderosa pine stands and provide critical wildlife habitat, but they may also increase fire hazard. This study investigates infested stands of mature ponderosa pine to determine if brooms live longer and persist lower in the crown than healthy branches. I measured heights to the lowest limbs on 39 trees at Crater Lake National Park (CLP), 19 uninfected and 20 infected with mistletoe. I used increment cores to age 53 brooms on 29 different ponderosa pine trees at Lava Cast Forest (LCF). The lowest live limb on 17 of the CLP trees was infected and broomed, compared to 22 that were healthy, and there was no difference in mean height between the two groups. Twenty-six of the sample trees had dead limbs low in their crowns, and there was no significant difference between dead infected and uninfected branch heights. Sample trees from LCF ranged in age from 91 – 452 years with a mean age of 255 years. Limb samples did not crossdate well because of dense, asymmetrical, and resinous ring growth. Estimates of ages for infected branches ranged from 64 – 350 years. My results do not support previous reports that infected branches occur lower in the crown compared to healthy branches. Estimates of branch age from old-growth trees have limited accuracy. Future research will benefit from more accurate techniques to reconstruct infection histories at both the stand and tree level so that mistletoe can be linked to other disturbances such as fire.

INTRODUCTION

A common host reaction to parasitism by dwarf mistletoe is the formation of a “witches' broom" at the point of infection. Brooms result from a loss of apical dominance, which is usually caused by the death of the apical bud (Hawksworth 1961). The loss of apical dominance triggers dormant buds, resulting in masses of host twigs growing in a dense pattern of abnormal branching and orientation. Many biotic agents produce brooms in host trees, but the ability of dwarf mistletoes (*Arceuthobium* spp.) to induce broom formation is unusual among higher plants (Kuijt 1955).

Mistletoe infection in ponderosa pine (*Pinus ponderosa*) does not always result in brooming, and the specific physiological causes of broom formation are unclear. Several studies implicate hormonal signals. Schaffer et al. (1983) examined cytokinin levels in two different *Arceuthobium* species, one that induces broom formation and one that does not. Higher concentrations of cytokinin were present in the mistletoe that leads to broom formation, but the source of the hormone was not determined. Paquet (1979) also investigated cytokinins, finding higher concentrations in dwarf mistletoe tissue than in the host. The source of these hormones remains unspecified and there is still debate over whether these imbalances are the result of host responses to infection or are a result of release from the mistletoe itself (Mathiasen 1996).

Several studies have summarized the differences between healthy and broomed tissue. Broomed branches tend to have reduced cone and seed production (Bonga 1964; Kuijt 1969). Tinnin and Knutson (1980) studied the growth characteristics of mistletoe induced brooms on Douglas-fir and determined that infected twigs were 50% longer and there were twice as many of them as healthy twigs. They also found that overall biomass of infected branches was 250% greater than uninfected, but needle biomass was 25% lower on infected branches (Tinnin and Knutson 1980). Broshot et al. (1986) reported that needles on lodgepole pine brooms have reduced number, length and mass compared to healthy tissue.

Brooms may have negative effects on host tree growth, but they also have some positive effects on forested ecosystems. Tinnin et al. (1982) view brooms as mutually adaptive to the host and the parasite, perpetuating infected forests that act as highly integrated systems with processes in place that sustain the coexistence of hosts and parasites. Mathiasen (1996) also notes the emergent properties of infested stands, suggesting that infested stands are more ecologically complex than healthy stands and represent a distinct ecosystem. Godfree et al. (2003) found that mistletoe strongly influences canopy structure of lodgepole pine stands and ultimately increases structural diversity.

Stand structural diversity plays a critical role in enhancing habitat diversity for plants and animals. Several studies have demonstrated that brooms provide wildlife habitat. Many species of birds, including endangered northern spotted owls (*Strix occidentalis caurina*) and marbled murrelets (*Brachyramphus marmoratus*) prefer brooms for nesting and roosting platforms (Buchanan et al. 1993, Bull et al. 1997, Marshall et al. 2003). Other studies have found that small mammals use broomed branches for nesting sites (Tinnin et al. 1982, Parks and Bull 1997, Tinnin and Forbes

1999, Parks et al. 1999, Garnett 2002). Several researchers have identified interactions between invertebrates and dwarf mistletoe. Many species of insects feed on mistletoe shoots and seeds (Stevens and Hawksworth 1970, Scharpf and Koerber 1986). Brooms are now being considered as critical elements of habitat diversity (Watson 2001; Shaw et al. 2004), and more information on how brooms develop and interact with other disturbance agents would help managers retain and promote brooms as part of the forest structure.

Previous research and personal observation suggest that brooms have longer life spans than healthy limbs, and once dead, they seem to persist in the crown. Weir (1916) determined that broomed branches often live longer than unbroomed branches. Koonce and Roth (1985) found brooms to be larger, more resinous, and persisting in the crown longer than healthy branches. They report average height to the crown bottom was 21% of total height for infected trees, compared to 38% for uninfected trees. Harrington and Hawksworth (1990) studied host tree damage following prescribed fire treatments. They attribute increased crown scorch and subsequent mortality of infected trees to the presence of flammable witches' brooms and low live crowns, but they did not measure crown base height or clarify if infected trees tended to be smaller (Harrington and Hawksworth 1990). Godfree et al. (2003) found that infected lodgepole pine trees have more foliage in the lower canopy than uninfected individuals, but they did not find a difference in total canopy height or volume. Regression models developed by Godfree et al. (2002) predict that crown base heights for infected lodgepole pine trees are 37% lower than uninfected trees.

It is unclear if brooms self-prune at a similar rate as uninfected limbs. One consequence of broom persistence in the crown is the potential to provide a fuel ladder for ground fires to become crown fires (Koonce 1981, Koonce and Roth 1980, 1985). Broomed limbs often remain attached to the main stem, but droop close enough to the ground to act as a fire ladder. Alternatively, brooms will not be available as surface fuels if they persist in the crown longer than healthy limbs. Brooms in lodgepole pine and Douglas-fir typically break from the crown and accumulate at the base of infected trees, but this is not the case with ponderosa pine (Wicker and Leaphart 1976, Koonce and Roth 1981, Harrington and Hawksworth 1990). Infected trees growing in dense stands may be more likely to prune their brooms (Wicker and Leaphart 1976; Godfree 2000), but observations suggest that brooms in old-growth ponderosa pine trees persist longer than healthy or infected but unbroomed limbs.

The lack of a reliable and accurate method for dating mistletoe infection makes it difficult to assess the role of mistletoe in fire ecology. Previous studies that estimated ages of brooms and the timing of mistletoe infection included relatively young trees and brooms. Scharpf and Parmeter (1966) successfully estimated ages of brooms in red fir trees by identifying the first annual ring showing distortion caused by mistletoe haustoria entering the host xylem. Mallans et al. (2005) used the methods of Scharpf and Parmeter (1966) to estimate ages of brooms in Douglas-fir trees, but their sample trees were young, ranging in age from 81-176 years with brooms between 4 – 74 years old. Neither Parks et al. (1999) nor Mallans et al. (2005) found any relationship between broom volume and age of brooms or host trees. Other researchers (Zimmerman and Laven 1984) modeled infection histories in lodgepole pine based on current stand infection levels and estimates of spread and intensification (Hawksworth and Hinds 1964).

This research studies broom development in mature ponderosa pine trees to assess the influence of mistletoe on the spatial arrangement of aerial fuels. Specifically, I investigate if brooms persist lower in the crown than healthy branches and if brooms tend to live longer than healthy branches. I also attempt to accurately date the onset of mistletoe infection in mature host trees, which could then be linked to fire histories for a more complete understanding of the interaction between the two disturbance agents.

METHODS

Field and Analytical Methods

Limb height sampling at Crater Lake

I compared heights of infected and uninfected branches at the Crater Lake National Park study site (Chapter 2 and 3). Fourteen plots (7 infected and 7 uninfected) were selected by stratified random sampling to collect background data summarizing stand structure, mistletoe abundance, and fuel composition. A grid over a map of the entire panhandle study area defined the locations with which plots were positioned to capture the largest ponderosa pine trees in each grid cell. Plot sizes varied (ranging from 15 - 40 m^2) to include at least 20 live trees. Plot corners were marked with rebar and mapped using UTM coordinates, allowing for long-term research evaluating changes in stand structure, understory vegetation, and mistletoe abundance.

Within each plot, I permanently tagged and photographed 2-4 of the largest ponderosa pine trees to allow for long-term assessment of damage and mortality following the prescribed burns. A total of 19 uninfected trees and 20 infected trees were tagged. Mistletoe abundance was visually estimated with the aid of binoculars for all sample trees using Hawksworth's (1977) dwarf mistletoe rating (DMR) ranging from zero (no mistletoe) to six (severely infected).

I collected increment cores from the base of all sample trees. Increment cores were mounted and sanded following standard dendrochronological procedures (Stokes and Smiley 1996) and samples were crossdated using a combination of skeleton plotting (Stokes and Smiley 1996) and the list method (Yamaguchi 1991).

A laser rangefinder was used to estimate heights to the lowest limbs for each sample tree. I included both live and dead limbs and determined if they were infected with dwarf mistletoe and broomed (hereafter, brooms) or uninfected (hereafter, branches). I statistically tested for differences in tree ages and densities between infected and uninfected plots that would confound differences in crown structure. Mann-Whitney U-tests were used to determine if age ranges of infected and uninfected trees were similar and to test for equal stand densities between the two sample groups. I used *t*-tests to identify mean differences in broom and branch heights, and tested for correlations among heights of live and dead brooms or branches and tree age.

I used ordination techniques to assess the influence of mistletoe on crown structure. I examined the relationships among limb heights and tree age data using non-metric multidimensional scaling (NMDS) (PRIMER 5 v. 5.2.9). NMDS is a distance-based ordination that graphically represents community relationships derived from relative similarities among samples (Clarke 1993). NMDS is a useful exploratory approach that lacks the assumptions of eigenvector-based techniques and allows the user to choose the type of similarity coefficient used in the ordination. I used normalized Euclidian distances because the variables are quantitative (ordinal) and dimensionally homogeneous (Legendre and Legendre 1998). NMDS results were plotted in two dimensions and I used the stress value to assess goodness-of-fit and visually examined grouping of sample trees relative to infection levels to assess the influence of mistletoe infection on limb position. I used analysis of similarities (ANOSIM) to test for differences between ordination groups. ANOSIM is a non-parametric, multivariate analysis of variance (ANOVA) that tests for significant differences between within group and among group variability.

Broom age and size sampling at Lava Cast Forest

I collected data at Lava Cast Forest (Chapter 2 and 3) to assess if brooms tend to be older than branches growing at similar heights and to determine if size-age correlations exist in broom development. Sample trees were located in three areas on two kipukas. Twenty-nine trees were subjectively selected to include large, obvious brooms and healthy branches and to ensure safe canopy access. Infected but unbroomed branches were not sampled. I recorded tree dbh, DMR, and limb diameter and height of the limb above the ground, and collected increment cores approximately 20-30 cm from the limb axis for both branches and brooms. I removed cores from the top, bottom, and two sides of each limb to reduce aging difficulties related to asymmetrical growth. Increment cores were also removed from the main stem just above the attachment point of sample limbs and the base of each tree (30 – 50 cm above the soil surface) to determine tree age and aid with crossdating limb cores.

Increment cores were mounted and sanded following standard dendrochronological procedures (Stokes and Smiley 1996) and crossdated using a combination of skeleton plotting (Stokes and Smiley 1996) and the list method (Yamaguchi 1991). I recorded the range and mean of ring counts for the 4 radii of each limb sample. I used Spearman correlation analyses to identify relationships among limb ring counts, limb height, limb diameter, tree age and tree diameter. I looked for correlations between branch age estimates and the range of ring counts and limb diameter to determine if older or larger limbs are more difficult to accurately age.

RESULTS

Limb heights

There was no difference between ages of infected and uninfected trees at Crater Lake (U = 169.5, $p = 0.58$) and no difference in ages of trees with brooms low in the crown compared to those with uninfected branches at the base of the crown (U = 177.5, $p = 0.79$). The lowest live limb on 17 of those trees was broomed, compared to 22 that were uninfected branches. Mean height of the live branches (14.9 m, s.d. = 4.2) was not significantly higher than live broom heights (12.7 m, s.d. = 4.4), ($t = 1.6$, $p = 0.1$), (Fig. 4.1A). Twenty-six of the sample trees had dead limbs low in their crowns, 8 of them were broomed and 18 appeared to be uninfected branches. Heights of lowest dead limbs do not differ between branches (10.2 m, s.d. = 3.6) and brooms (8.9 m, s.d. = 2.1), ($t = 1.0, p = 0.3$), (Fig. 4.1B). Limb heights were not correlated with tree age ($p > 0.05$).

Infected and uninfected trees group separately in the NMDS diagram based upon a combination of the heights of the lowest live and dead limbs (Fig. 4.2). The infected and uninfected samples both ordinate into two groups based primarily on tree age, resulting in four distinct groups in the ordination diagram (Fig. 4.2). There is a young, currently uninfected tree that groups more closely to the older infected trees, but it has a low dead limb that appears to be broomed by mistletoe. ANOSIM results indicate that the four ordination groups (Fig. 4.2) are significantly different from each other ($p < 0.05$).

The NMDS stress value of 0.1 indicates a moderately robust ordination with a low chance of conveying false relationships (Clarke 1993). Stress values below 0.3 denote a more accurate representation of the relationships among samples in the ordination diagram. Stress values greater than 0.35 indicate that samples are essentially placed at random in the ordination diagram and do not reflect the original similarities among samples (Clarke 1993).

Broom age and size

I sampled 56 limbs from 29 different ponderosa pine trees and successfully counted rings from 53 limbs (46 brooms and 7 healthy branches); cores from 3 limbs were damaged or incomplete. Sample tree ages ranged from 91 – 452 years with a mean age of 255 years (Table 4.1). Limb samples did not crossdate well because of dense, asymmetrical, and resinous ring growth. I successfully crossdated 40% of the samples. The mean number of rings derived from the 4 increment cores from each broom (broom age) ranged from 64 – 350 years (Fig. 4.3), and the range in ring counts among the 4 cores for each limb was 6 - 190 years. I had little success crossdating limb cores with other cores from the same limb or with the main stem of the tree. There is a strong correlation between ring counts in limbs and ages of the tree at limb height (Spearman's rho = 0.73, $p < 0.001$), but several brooms have more rings than the main stem (Fig. 4.4).

There are no significant correlations between the broom age and range of broom ring counts or broom height. There is a significant relationship between broom age and three other variables, broom diameter (Spearman's rho = 0.43, $p = 0.006$), tree age (Spearman's rho = 0.74, $p < 0.001$) and tree DMR (Spearman's rho = 0.32, $p = 0.04$). The age range for uninfected branch samples shows a negative correlation with height (Spearman's rho = -0.79, $p = 0.04$).

DISCUSSION

My results from Crater Lake do not support previous reports noting that brooms occur lower in the crown than uninfected branches. The lowest live limb on any sample tree was broomed, but heights did not differ between broom and unbroomed branch sample populations. Stand density at Crater Lake is relatively high, leading to high crown bases as lower branches self-prune in response to competition for sunlight. A difference between broom and branch height may be more evident in less dense stands where ponderosa pine trees tend to self-prune at a slower rate.

Infected and uninfected sample trees ordinate into distinct groups based upon a combination of heights of lowest live and dead limbs and tree age, suggesting that infection leads to a unique crown structure. Multidimensional analysis is able to identify differences among all the variables measured for each sample. Bivariate tests (correlations and *t*-tests) are unable to capture the differences among samples because they examine only one variable at a time.

Brooms tend to be more spherical than healthy branches and sometimes have a pendulous, drooping morphology that would make their maximum distance from the ground less than healthy branches that tend to be more horizontal in form. I measured height to the point where limbs attach to the main stem of the tree, rather than the lowest physical point on the limb. My results suggest that brooms are closer to the ground than healthy branches because their point of attachment to the main stem is the same but broom shape tends to be less horizontal. The point of limb attachment indicates age, with older limbs occurring lower in the crown. Because there is no difference in the heights of limb attachment, my results do not support previous reports that broomed branches are older than healthy ones (Weir 1916, Koonce and Roth 1985, Harrington and Hawksworth 1990).

I was unsuccessful in accurately aging broom increment cores (only 40% crossdated) or identifying the year of initial mistletoe infection. Other researchers were able to identify distorted annual rings that represent the mistletoe tissue inserting itself into the host xylem, but the trees were much younger than my samples and they used destructive sampling techniques that removed complete cross-sections from each broom (Scharpf and Parmeter 1966, Mallans et al. 2005). My ages were estimated from increment cores from older limbs and mean limb ages were ≈ 200 years and poorly crossdated with other cores from the same limb or with the main stem of the tree.

Limb crossdating was difficult because of the large number of rings and irregular growth of broom samples. There was a wide range in the number of rings among the four increment cores removed from each broom. Annual incremental growth displayed strong asymmetry with numerous false and missing rings when compared to samples from the main stem. Many increment cores were inundated with pitch, making it difficult to achieve clear cellular resolution. These factors may have contributed to the lack of significant correlations between mean ring counts (broom age) and the range of ring counts (an estimate of error in dating) or the height of the broom (an indication of branch age). These results indicate that older brooms may not necessarily be more difficult to age accurately. I would expect to see a positive correlation between age estimates and the amount of error in my estimates if older branches are more difficult to age accurately. Only four of the brooms I examined were estimated to be less than 100 years old and the majority of them were older than 175 years. Personal observations suggest that branches less than 75 years in age have greater ring clarity that would facilitate accurate ageing.

Future research will need to address the difficulties in assessing the mistletoe infection history of mature host trees. Using cross-sections of infected limbs, rather than increment cores, provides more surface area for growth analysis but requires removing limbs from host trees. Chemical treatments to remove resin may improve ring clarity in increment cores. Alternatively, wood densitometry or stable isotope techniques may be useful both for crossdating brooms and identifying the onset of mistletoe infection. More accurate estimates of infection histories will allow researchers to investigate interactions between mistletoe and other disturbance agents such as fire, and assess the role of mistletoe in the successional pathways of host stands.

Table 4.1: Descriptive statistics for Lava Cast Forest sample trees and limbs (mean and s.d.). Tree ages were derived following statistical crossdating (100% crossdated); some limb ages are crossdated (40%) with the remainder derived from visual estimates of ring counts. Height was measured from the point of limb attachment to the main stem of tree. Tree diameter is at breast height (1.4 m); limb diameter is at the point of attachment to the main stem.

	N	**Mean age (yrs)**	**Mean height (m)**	**Mean diameter (cm)**
Sample trees	29	255 (82)	n/a	64.2 (23.8)
All sample limbs	53	190 (72)	4.7 (3.1)	15.1 (5.5)
Brooms	46	189 (64)	14.8 (5.5)	14.8 (5.5)
Branches	7	197 (116)	13.9 (1.9)	16.8 (5.3)

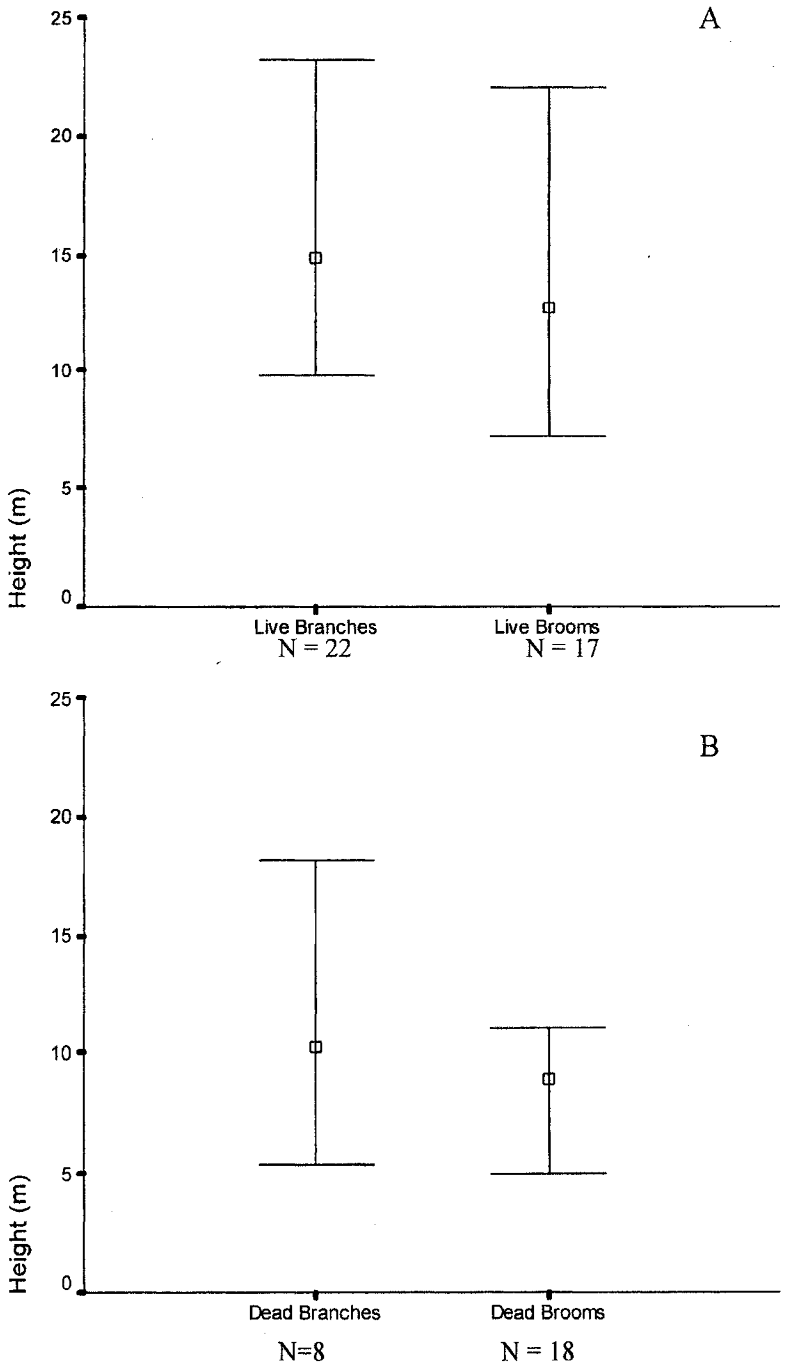

Figure 4.1: Mean and range of heights for live (A) and dead (B) branches and brooms at Crater Lake National Park. There is no significant difference between heights of live or dead branches and brooms.

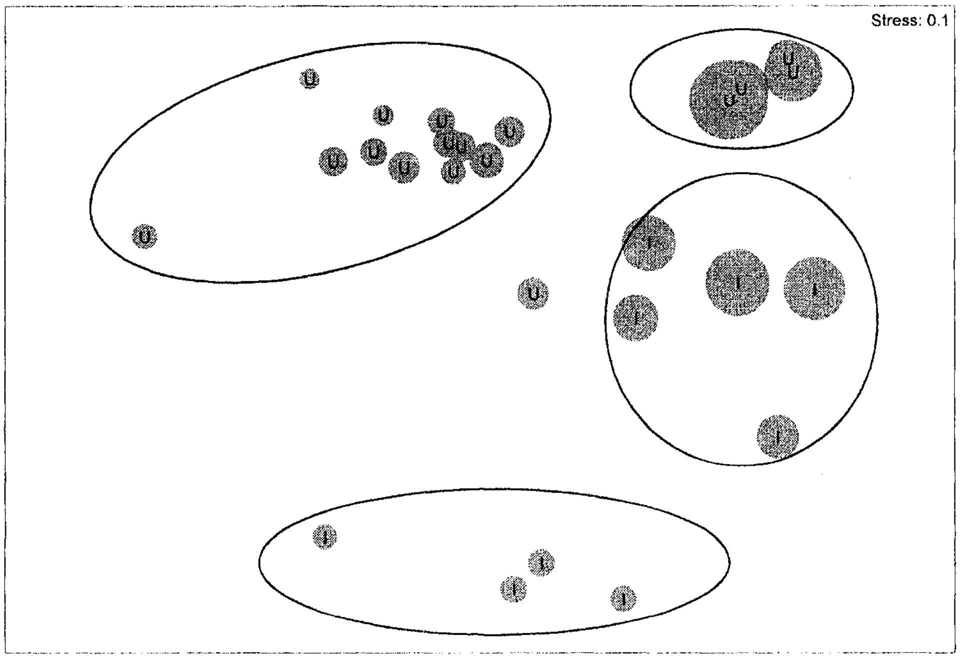

Figure 4.2: NMDS results for heights of lowest live and dead limbs at Crater Lake National Park. Bubble size represents relative tree ages. Letters inside the bubbles indicate if the tree was infected (I) or uninfected (U). The uninfected outlier is a currently uninfected tree with a broomed lowest dead limb.

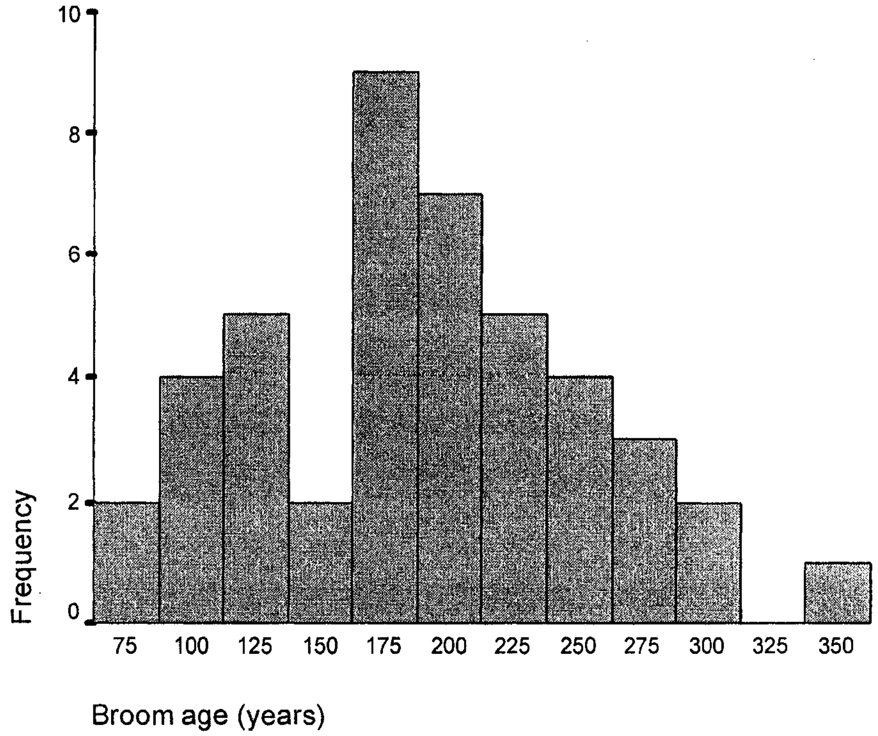

Figure 4.3: Histogram of broom age classes (25 yrs) estimated as means of annual ring counts among four increment cores sampled from each broom. N = 46.

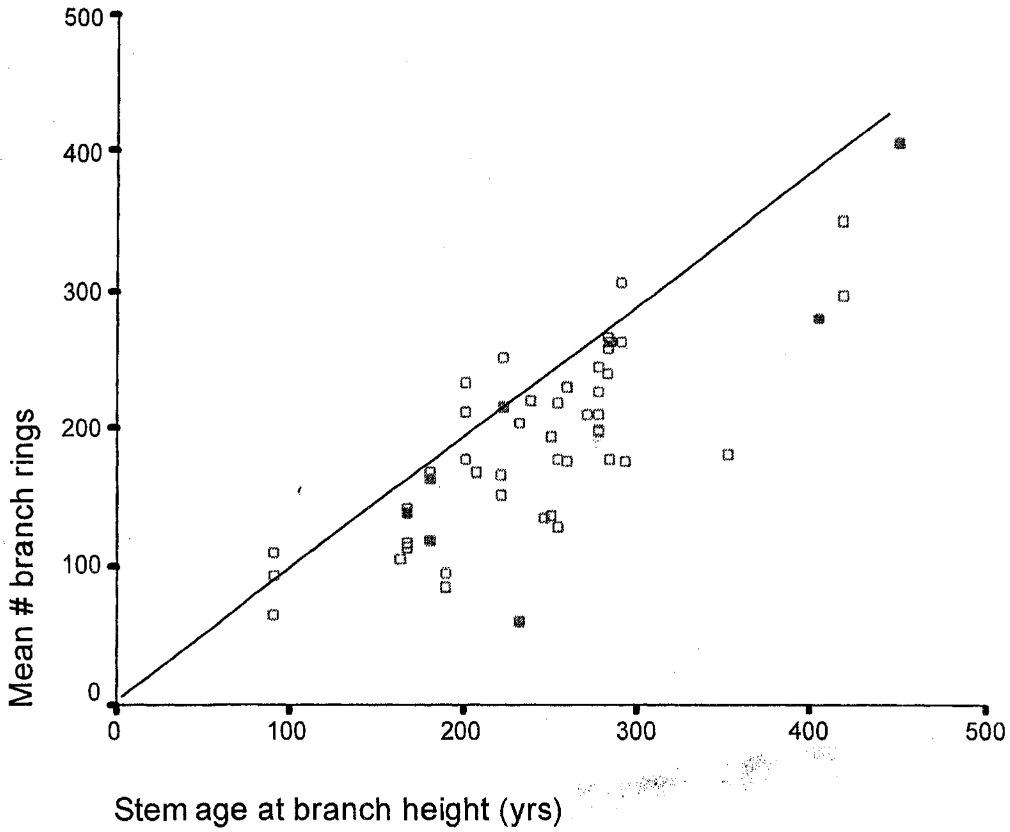

Figure 4.4: Relationship between mean numbers of rings from each sample limb (average of four increment cores) and the crossdated age of cores taken from the main stem at the height of sampled limbs. Samples above the reference line have more rings in the limb than the main stem of the tree. Open symbols represent brooms, and dark symbols uninfected branches.

PART III

FLAMMABILITY, FIRE BEHAVIOR, AND POST-FIRE MORTALITY

The following chapter investigates the influence of dwarf mistletoe on fire behavior and tree mortality following prescribed fire treatments. Part I indicated that mistletoe infection influences vertical distribution of fuels and is positively correlated with the accumulation of fine fuels on the forest floor. Part II uses prescribed fire treatments to distinguish differences in fire behavior and fuel consumption between infected and uninfected stands. I also monitor post-fire injury and mortality to determine if infected trees are more vulnerable to damage than uninfected individuals. It is difficult to monitor fire behavior in the field and to control for confounding variables (weather, ignition patterns), therefore I conducted a series of tests inside a burn chamber to more accurately quantify the influence of mistletoe infection on limb flammability.

CHAPTER 5

FIRE BEHAVIOR, FLAMMABILITY, AND MORTALITY IN PONDEROSA PINE STANDS INFECTED WITH DWARF MISTLETOE

ABSTRACT

This study investigates the influence of dwarf mistletoe on prescribed fire behavior, post-fire fuel accumulation and tree mortality, and limb flammability. Prescribed fire treatments were applied to fourteen plots (7 infected with mistletoe, 7 uninfected) at Crater Lake National Park in the fall of 2003. I measured stand structure variables and fuel composition prior to fire treatments, monitored fire behavior during treatments, and re-measured fuel composition and monitored tree mortality for several years following fire treatments. I also burned samples of infected and uninfected limbs ($n = 36$) under controlled conditions in a burn chamber to assess the influence of mistletoe infection on limb flammability. My results show that plots infected with mistletoe burned at higher temperatures for shorter periods than uninfected plots. Plots with greater duff biomass recorded higher temperatures during the prescribed burn and those with greater accumulations of litter burned longer. All plots experienced a significant reduction in total fuel loads, but there was no difference in fuel reduction between uninfected and infected plots. Three years following fire, 125 trees (35%) had died within the plots, with smaller diameter trees experiencing higher mortality. There was no difference in mortality between uninfected and infected sample trees. Burn chamber tests indicate that infected branches lost a greater proportion of their mass during combustion, but the majority of tissue lost was in the form of needles. My results suggest that managers do not need

to consider different prescriptions for fire treatments in intensively managed stands infected with mistletoe, but should consider mistletoe abundance when modeling fire behavior in unmanaged ponderosa pine stands.

INTRODUCTION

Dramatic shifts in the stand structure of ponderosa pine (*Pinus ponderosa*) forests since European settlement of the American West are well documented (Weaver 1959, Cooper 1960, Covington and Moore 1994, Belsky and Blumenthal 1997). These fire-adapted forests no longer reflect historic conditions and are currently characterized by accumulations of highly flammable fuels and greater vulnerability to catastrophic wildfire and non-native plant and insect invasions (Agee 1993, Arno et al. 1995, Fule et al. 1997, Agee and Skinner 2005). Increased levels of insects and pathogens such as dwarf mistletoe is another consequence of 150 years of anthropogenic disturbance (Dahms and Geils 1997, Fule et al. 2002), but how these biota ultimately influence fire behavior and risk has received little attention.

Despite a lack of direct evidence demonstrating the role of dwarf mistletoe in fire ecology, forest pathologists (*e.g.*, Geils and Hawksworth 2002) suggest that mistletoe increases fuel accumulation and fire susceptibility in ponderosa pine stands. Research by Koonce (1981) quantified fuel loadings in young ponderosa pine stands and found that mistletoe increases both surface and aerial fuels, depending upon stand structure and the degree of infection. While I found no difference in fuel loadings between uninfected and infected plots at Crater Lake, I did note higher biomass of smaller diameter fuels in infected old-growth ponderosa pine stands in central Oregon (Chapter 3).

A common host reaction to infection by dwarf mistletoe is the formation of "witches' brooms." Branches undergo extensive swelling at the point of infection and a loss of apical dominance allows dormant buds to become active. The result is increased numbers of twigs growing in abnormal patterns and orientation from a swollen main limb (Fig. 1.1). These changes in crown and branch structure are ecologically important for a variety of reasons (Tinnin et al. 1982, Godfree et al. 2002), including their potential influence on fire behavior and fuel composition. Brooms may have a direct relationship with flammability at the scale of tree and stand. Brooms that persist low in the crown can act as a fuel ladder, allowing a ground fire to move into the crown and cause severe damage to the tree before spreading to the crowns of other trees, regardless of their infection level.

If brooms are highly flammable and lead to increased fuel loads, host trees would be more vulnerable to post-fire mortality because of higher temperatures and more intense fire behavior. Most studies of the relationship between mistletoe and fire are primarily observational (not quantitative or experimental) and focus on the use of fire as a mechanism to control mistletoe spread and intensification (Hawksworth and Wiens 1996). Few studies compare mortality rates between infected and uninfected trees. Harrington and Hawksworth (1990) noted higher fire-related mortality among heavily infected ponderosa pine following prescribed fire treatments in Grand Canyon National Park.

In addition to direct effects from fire, mistletoe infection tends to reduce overall health and vigor of host trees, which would result in decreased resistance to fire damage, especially crown scorch or loss of cambium. Previous studies found that mistletoe shoots have higher transpiration rates than host tissue (Fisher 1983, Tocher et al. 1984) and infection decreases host respiration rates (Wanner and Tinnin 1986, Ryan 1990), leading to moisture stress and lower water use efficiency compared to uninfected individuals (Sala et al. 2001). Other research found that infected ponderosa pine seedlings experienced reductions in root volume (Knutson and Toevs 1972), but little is known about the effects of mistletoe on host root growth in mature trees. Host trees, which tend to be moisture stressed, may respond by producing more fine roots when the resources are available. Previous research at Crater Lake suggested damage to fine roots growing just below smoldering duff as a mechanism promoting mortality of large pines following prescribed burns (Swezy and Agee 1991, Agee 2003). High post-fire mortality would be expected among infected trees if they respond to moisture stress by increasing growth of fine root tissue that is uniquely vulnerable to damage during surface fire treatments.

Previous prescribed fire treatments at Crater Lake National Park resulted in high mortality (45%) of large ponderosa pine trees (Thomas and Agee 1986, Swezy and Agee 1991). This was an unexpected outcome because the thick bark and tall live crowns typically confer fire resistance to large trees (Peterson and Ryan 1986, Agee and Skinner 2005). However, decreased vigor and growth rates related to mistletoe infection may reduce bark thickness in host trees. Thick bark is a key feature of fire resistance in ponderosa pine trees, but there is limited information on the effects of mistletoe on host bark growth. Hawksworth et al. (1983) found no relationship between dwarf mistletoe infection and phloem thickness in lodgepole pine trees (*Pinus contorta*), which tend to have thinner bark and are less fire resistant than ponderosa pines. In contrast, Roe and Amman (1970) reported that lodgepole pine trees infected with mistletoe are less susceptible to mountain pine beetle attack because they have significantly thinner bark than trees without mistletoe.

Historically, mistletoe brooms have been considered undesirable by forest managers because of the perceived impacts on growth reduction, fire hazard, and the spread and intensification of mistletoe on a stand level. Brooms are now being considered as critical elements of habitat diversity (Watson 2001, Shaw et al. 2004). Management strategies are shifting away from broom removal in some cases, highlighting the need for more information on the relationship between mistletoe and fire.

My research investigates the influence of dwarf mistletoe on prescribed fire behavior, fire-related mortality, and flammability of branch tissue. I use a combination of field-based prescribed fire treatments and controlled laboratory burns to characterize the fire response of stands and trees infected with mistletoe. My specific objectives are to: (*i*) compare fire behavior and (*ii*) fuel consumption between infected and uninfected plots during prescribed fire treatments, (*iii*) test for increased postfire mortality rates among infected trees, and (*iv*) determine if brooms are more flammable than healthy branches.

METHODS

Study area

Crater Lake was designated a national park in 1902, but the panhandle region was not managed by the Park Service until 1932. U.S. Forest Service records and physical evidence indicate that logging occurred between 1909 and 1927. The National Park Service suppressed wildfires in the park for most of the 20th century, with the last wildfire to burn in the study site occurring in 1902. A several-hundred year fire history is available for the panhandle region of Crater Lake. McNeil and Zobel (1980) completed a dendrochronological assessment of fire scarred trees in the late 1970s, and historical records document natural and prescribed fires during the 1900s. McNeil and Zobel (1980) report mean fire return intervals of 9-42 years for the time period 1748-1902 for the area that includes my study site.

Between 1976 and 1986, Crater Lake National Park staff burned several areas of mixed-conifer forest in an attempt to selectively remove understory trees and retain mature ponderosa pine trees (Agee and Thomas 1982, Thomas and Agee 1986). Historically, ponderosa pine was the dominant tree species in the southern regions of the park (McNeil and Zobel 1980), but in the absence of fire over the last 150 years, dominance is shifting to shade-tolerant white fir (*Abies concolor*). The fire treatments successfully reduced understory tree density and surface fuel loads, but they also resulted in high mortality (45%) of large ponderosa pine trees (Thomas and Agee 1986, Swezy and Agee 1991).

Field Methods

Sampling strategy

I collected stand structure, mistletoe abundance, and fuel composition data prior to prescribed fire treatments to characterize pre-burn forest conditions (Table 5.1). Plot locations were determined by superimposing a grid over a map of the panhandle study area and identifying an equal number of infected and uninfected plots (7 of each) using stratified random sampling. Plot sizes varied ($225m^2$ to $780m^2$) according to tree density, with a minimum of 20 live trees included in each plot. Within each plot, I permanently tagged and photographed 2-4 of largest ponderosa pine trees to allow for long-term assessment of damage and mortality following the prescribed burns. A total of 19 uninfected trees and 20 infected trees were tagged.

Stand structure

I measured several environmental and forest structure variables within each plot. Environmental variables included estimates of slope aspect and angle. Forest structures variables included diameter measurements for all live and dead trees greater than 4 cm DBH (diameter at breast height, 1.4 m), as well as tallies of all saplings and seedlings growing within each plot. I used four 1 m^2 quadrats per plot to estimate percent cover and richness of understory plants.

I collected a single increment core from 30 - 50 cm above the root collar of all trees to determine their age. Increment cores were removed along slope contours to minimize the influence of reaction wood on the ring patterns in each sample (Fritts 1976). Increment cores were air dried and glued to wooden core mounts following standard dendrochronological procedures (Stokes and Smiley 1996). I prepared the surface of each core by sanding with progressively finer sandpipers (ANSI 80 - 400-grit) (Orvis and Grissino-Mayer 2002). A final polish was applied to each sample by buffing the surface with superfine steel wool, resulting in clear, cellular resolution under standard 7–10x magnification. To ensure accurate dating, I crossdated all samples using a combination of skeleton plotting (Stokes and Smiley 1996) and the list method (Yamaguchi 1991). Skeleton plots are a graphical representation of ring widths that allows for pattern matching among different increment cores. The list method notes particularly narrow rings (marker years) that are compared among samples.

Mistletoe abundance was visually estimated with the aid of binoculars for every ponderosa pine tree in each plot using Hawksworth's (1977) dwarf mistletoe rating (DMR). DMR ranges from zero (no mistletoe) to six (severely infected) (Hawksworth 1977). I averaged individual tree DMRs into plot-level dwarf mistletoe indices DMI).

Fire behavior

Fire treatments were applied on October 31 and November 1, 2003 following a burn prescription developed by Crater Lake National Park fire ecologists. Drip torches were used to ignite strip headfires within each plot that were allowed to smolder until extinguishing naturally. Park personnel monitored weather conditions, flame length, and rate of spread. I monitored fire temperatures with high-temperature thermocouples attached to data loggers enclosed in insulated stainless steel housing and buried below the soil surface (Fig. 5.1). I replaced the soil and fine fuels above the steel housing, leaving the thermocouple exposed for several centimeters above the soil and litter. Thermocouples were placed at the dripline of tagged trees and temperatures recorded every 30 seconds.

Fuel composition

Surface and ground fuels were measured in each plot and at the base of each tagged tree during the summers preceding and following prescribed burning. I used the planar intercept method to estimate fuel biomass (Brown 1974, Brown et al. 1982). Total transect length was 15 m and the number of transects per plot ranged from one to five, varying according to plot size. I anchored four transects at the base of each tagged tree, oriented to each cardinal direction. Sampling distances along each transect varied depending on fuel size. Fuels in the 1-hour size class were sampled from 0-2 m along each transect; 10-hour fuels from 0-3 m; 100-hour fuels from 0-5 m; and 1000-hour fuels were sampled from 1–15 m. Size classifications are based on the time it takes for fuels of a certain diameter range to lose or gain ~66% of the difference between the initial and equilibrium moisture contents (Deeming et al. 1977). I measured litter and duff depths at three points along each transect - 0, 3, and 6 m. Litter samples were collected from each transect and oven dried at 80°C to obtain bulk density measurements, which were then used to derive litter biomass. All biomass calculations or woody surface fuels followed the procedures of Brown et al. (1982).

The summer following fire treatments, I measured fuel biomass with the same procedures used to determine initial fuel composition in each plot and at the base of each tagged tree. Three years following fire, I assessed overall tree mortality in each plot, and measured stem char heights, and noted any other signs of damage to tagged trees.

Analytical Methods

Limb flammability

I conducted combustion experiments in a controlled setting to determine whether or not brooms are more flammable than uninfected branches. I collected 18 samples of each branch type from ponderosa pine trees in the Rock Creek Reservoir area, near the western edge of Mount Hood National Forest (670 m elevation, 45°12'N and 121°23'W). Samples were stored at ambient temperatures in Portland, Oregon for 20 days before being transported to the U.S. Forest Service Fire Science Lab in

Missoula, Montana for burning in a large combustion chamber. Each sample was weighed to the nearest tenth of a gram immediately following pruning and prior to burning to quantify moisture loss.

The fuel bed in the combustion chamber consisted of 1m x 3m fire-resistant ceramic fiber tiles. I placed each branch horizontally on a layer of fine grade excelsior wood fibers (shredded aspen) of approximately equal depth and bulk density. The excelsior fibers were ignited from opposite ends of the fuel bed, ultimately igniting the branch sample. I estimated maximum flame height (combustibility) above the highest point of branch tissue and the length of time until flames extinguished (sustainability). I used digital video and photographs to record combustion of each sample for future reference. Following flame extinction, I weighed any remaining tissue to estimate consumption of each sample (consumability).

Three components of flammability were characterized during the combustion chamber experiments: combustibility, sustainability, and consumability (Martin et al. 1994). Flame height was used as a proxy for combustibility or burn intensity. Sustainability of the fire was measured by the length of time until flames extinguish, then until embers completely extinguish. The percent of tissue consumed by the fire and the mean rate of weight loss provided an estimate of consumability. I used nonparametric correlation coefficients to identify relationships among flammability variables. I compared moisture content, combustibility, sustainability, and consumability of brooms and branches using Mann-Whitney U-tests.

Stand Structure

Tree diameter and tally data were used to calculate importance values, basal area, and density. I used *t*-tests to identify any differences in environmental or forest structure variables between uninfected and infected plots that may explain subsequent differences in fuel composition, fire behavior, or mortality.

Prescribed fire treatments

I used Spearman's rho correlation coefficients to identify relationships between fuel loads and maximum temperatures or duration of high heat during prescribed burns. Mann-Whitney U-tests were used to identify any differences in temperatures or duration between the two ignition dates and between uninfected and infected plots.

Fuel variables were square-root transformed to correct for skewed distributions. I used descriptive statistics and t-tests to compare mean fuel loads between uninfected and infected plots, both before and after prescribed burning. I also used *t*-tests to test for a significant reduction of fuel biomass resulting from prescribed fire and to compare reduction of fuels between uninfected and infected plots. I assessed differences in plot-level tree stem char heights and mortality using Mann-Whitney U-tests. I used a Chi-square test and Fisher's exact test of proportions to compare mortality rates between uninfected and infected ponderosa pines.

RESULTS

Stand structure

T-tests comparing mean differences in stand variables between infected and uninfected plots show no significant differences prior to prescribed burning (Table 5.1). A total of 358 trees were sampled within the 14 plots. Ponderosa pine trees make up 76% of the stand basal area and represent the oldest trees within the study site. The oldest uninfected ponderosa pine is 550 years old, compared to an infected tree at 424 years.

Fire behavior

Weather at the time of ignition was cool, ranging from 2 to 12 °C, with winds below 4 mph. Relative humidity ranged between 40 and 58%. The average flame length within the study plots was 25 cm, typically ranging from 4 to 53 cm with occasional torching of intermediate canopy white fir trees. Most of the flames were extinguished by snowfall starting on the evening of November 1, but some patches of duff and coarse fuels continued to smolder under several centimeters of snow for at least a week.

Thermocouple data indicate that areas infected with mistletoe burned for shorter periods of time and recorded the highest temperature. Uninfected plots tended to burn for longer time periods (Fig 5.2). Mean maximum temperature was 156 (s.d. = 101) °C in uninfected plots, and 214 (s.d. =153) °C for infected plots, but Mann-

Whitney U-test results indicate no significant difference in mean temperatures between the two populations. However, duration of high temperatures is significantly greater in uninfected plots, with an average duration of 438 (s.d. = 402) minutes compared to 129 (s.d. = 183) for infected plots ($p = 0.05$).

Eight plots were ignited on October 31 and the other 6 plots were ignited on November 1. Maximum temperatures were higher in the plots ignited on the first day ($p = 0.01$). Mean maximum temperature for October 31 ignitions was 269 °C, compared to 117 °C for November 1 ignition. Mann-Whitney U-test results reveal no significant difference in duration of high temperatures between the two ignition days ($p = 0.6$).

Fine fuels have the strongest relationship with temperatures and duration of prescribed fires. Maximum temperatures are positively correlated with duff biomass prior to burning (Spearman's rho = 0.58, $p = 0.004$), and there is a significant correlation between temperatures and duff consumption (rho = 0.46, $p = 0.03$). Duration of high temperatures is correlated with litter biomass (rho = 0.53, $p = 0.01$). Infection level is negatively correlated with duration (rho = -0.42, $p = 0.05$). There are no significant correlations between the prescribed fire variables and woody fuel classes.

Fuel composition

T-tests of plot-level fuel biomass before and after prescribed burning show no significant differences between infected and uninfected plots (Table 5.2). Prior to burning, tree-level samples showed more litter accumulating at the base of uninfected trees, with other fuel size classes being the same between the two groups (Table 5.3). Following the burns, infected trees had a greater residual accumulation of 100-hr fuels (Table 5.2)

Prescribed burning reduced fine woody fuel loads by an average of 54% and litter accumulation by 80% (Figs. 5.3. and 5.4). There was a significant reduction in total fuel loads for all plots and trees, and a significant reduction in all individual fuel size classes except sound 1000-hr at both the tree- and plot-levels of sampling, and 100-hr at plot-level only (Table 5.4). Uninfected samples experienced greater total fuel reduction (65%) than infected samples (53%) ($t = 1.96, p = 0.05$). All fuel size classes were reduced by an average of 67% but the relative contribution of litter, 1-, 10-, and 100-hr fuels to the total fuel load did not change following fire (Fig. 5.5). The proportion of duff was reduced by 22%, while the relative contribution of 1000-hr fuels increased by 26%.

Post-fire damage and mortality

Three years following fire, 125 trees (35%) had died within the plots (Table 5.5). White fir trees experienced the highest mortality, making up 38% of the dead trees. Only 20% of the dead trees were ponderosa pine, the primary host for western dwarf mistletoe. Smaller diameter trees of all species were more likely to be killed by the prescribed fire treatment, with some torching during the treatment. Half of the recently dead trees are less than 11 cm in diameter, and most of these were white fir or lodgepole pine (Fig. 5.6). Many intermediate diameter individuals smoldered at the base and fell over within 6 months. The largest 10% were ponderosa pine.

Four of the large, tagged sample trees were dead in 2006 - 2 uninfected and 2 infected. Three other infected tagged trees appear to be dying, exhibiting major needle loss and bark beetle damage (pitch tubes and frass). Mean mortality rates of all species in uninfected plots were 21%, and 39% in infected plots (Fig. 5.7). I found no significant difference in plot-level tree mortality rates between infected and uninfected plots (Mann-Whitney U-test $p = 0.3$). Infected ponderosa pine experienced 35% mortality, compared to 22% of uninfected pine (Fig. 5.8), but a Chi-square test revealed no significant difference between the two populations of trees ($X^2 = 2.4$; $p = 0.13$; d.f. = 1). Fisher's Exact test of proportions also showed no difference in the ponderosa pine mortality rate between infected and uninfected sample populations ($p = 0.07$).

All 39 tagged trees were charred at the base during prescribed fire treatments, with 34 (87%) experiencing char around the entire bole. Mean stem char height was 20 cm for both uninfected and infected trees. Stem char heights ranged from 15-160 cm for uninfected trees, compared to 12-250 cm for the infected population (Fig. 5.9). Maximum stem char height ranged from 12-250 cm, averaging 53 cm. Mann-Whitney U-tests indicate no significant difference between charring of uninfected and infected trees. There were no significant correlations between DMR and char variables.

The seven tagged trees that died or appear to be dying following fire experienced higher stem char heights than the individuals that survived. Mean char heights were 21 cm for trees that died, compared to 19 cm for those that survived (Mann-Whitney U-test $p = 0.05$). Maximum stem char heights and the circumference of bole damaged did not differ for trees that died post-fire.

Limb flammability

The broomed samples were more massive than the uninfected branches, but limb diameters did not differ between the two groups, and there was no significant difference in the proportion of water lost prior to burning between the branch and broom samples (Table 5.6). Limb diameter was negatively correlated with the amount of water lost (Spearman's rho = -0.57 for branches and -0.69 for brooms, $p < 0.001$).

Burning produced no significant difference in flame heights between broom and healthy branch samples (Table 5.6). Sustainability data show no correlation between burn duration and limb diameter, mass, or tissue consumption. *T*-test results indicate no difference in burn duration between brooms and healthy branches. There is a positive correlation between branch diameter and percent of tissue consumed (rho = 0.66, $p = 0.003$), but there is no such correlation for the broom samples ($p > 0.05$). Broom samples experienced more tissue consumption during the burn treatments compared to healthy branches (U = 89.0, $p = 0.02$) (Table 5.6) and broom consumption displayed greater variation than healthy branch samples (Fig. 5.10).

DISCUSSION

Fire behavior

A combination of low total fuel accumulations, low initial variability in fuels, and cool weather resulted in relatively low burn severity and low variability in fire behavior throughout most of the burn unit. Fire behavior was similar in uninfected and infected plots, primarily because there were no differences in fuel composition prior to burning. Infected plots tended to burn for less time with temperatures statistically related to fine fuels such as duff and litter.

Plots with the greatest duff biomass recorded higher temperatures and greatest reduction in duff during prescribed burns. Other researchers note that duff accumulations at the base of large trees result in extended periods of smoldering following surface fires (Sackett 1998, Stephens and Finney 2002). I found that plots with the highest litter biomass experienced longer burn durations, and the uninfected plots tended to have the most litter accumulation. Litter is a fine fuel that is consumed relatively quickly, but encourages combustion of woody fuels that tend to burn more slowly and experience more complete combustion.

Treatment temperatures were significantly higher during the first day of ignition. Because one-half of the plots representing infected and uninfected conditions were burned each day and there are no differences in stand structure variables between the two groups of plots, differences between treatments were not confounded by differences in fire behavior between the two ignition dates. A later ignition start time and lower relative humidity on the first treatment day could explain the higher temperatures.

Fuel composition

Mean biomass of downed woody fuels at the Crater Lake study site is slightly lower than those reported for mature ponderosa pine stands in Newberry National Volcanic Monument (Chap. 3) and Jeffrey pine-mixed conifer stands in Baja, California (Stephens 2004). Surface fuel loads at Crater Lake also have lower variability than those reported in other studies (i.e. Kauffman and Martin 1989, Stephens 2004, Chap. 3), likely the result of an unnatural fire regime and management practices at Crater Lake throughout the last century (cf. Stephens 2004).

Prescribed fire treatments in the late 1970s likely contributed to the relatively low accumulations of fuel at Crater Lake. By comparison, 75% of the plots at Lava Cast Forest burned at least 75 years before sampling (Chap. 3), allowing more time for fuels to accumulate. Fuels at Newberry National Volcanic Monument also show high variability and greater fuel loads in sites with dwarf mistletoe, suggesting that mistletoe may influence fuel composition in ponderosa pine stands under unmanaged conditions.

Fuel composition was similar among the uninfected and infected plots, both before and after the prescribed fire treatment. Infected plots at Lava Cast Forest have greater biomass of the smaller fuel size classes, but total fuel loads were similar to those at Crater Lake (Chap. 3). These results differ from Koonce and Roth (1985), who found higher total fuel loadings in infested stands of sapling and small-diameter ponderosa pine. These differences appear to be related to the changes in morphology and biomass allocation between mature and young trees infected with dwarf mistletoe.

Fuel biomass data from tree-level samples reveal significant differences between uninfected and infected trees. Prior to burning, uninfected trees had higher accumulations of litter than infected trees. Healthy trees tend to have more vigorous crowns, which one would expect to correspond with greater foliar biomass to ultimately contribute to needle litter. Korstian and Long (1922) demonstrated that uninfected ponderosa pine trees had longer and more abundant needles, and longer needle-bearing stems. I found no difference in age or basal area between my two sample populations, but did not collect height data. Several studies have shown that uninfected trees are taller than infected individuals and consequently may possess more branches that ultimately contribute to litter accumulation on the ground.

Infected trees experienced less reduction in 100-hr fuels during prescribed burns, resulting in a significantly higher residual fuel load at their base following fire. Uninfected plots burned for longer periods of time, which would facilitate more complete combustion of coarse woody debris. The shorter and hotter fires that occurred in infected plots would result in less consumption of larger diameter fuels, such as 100- and 1000-hr size classes. My findings of higher residuals of larger fuel sizes following fire appear to be a function of small diameter trees falling over after smoldering at the stem base. Other researchers have reported prescribed burn treatments leading to an increase in some fuel accumulations or attenuating the reduction of fuels consumed by the fire (Arabas 1997, Agee 2003, Perrakis and Agee 2006).

Recorded increases in duff and 1-hr fuels are likely an artifact of plot-level sampling procedures. Tree-level results show no increases in fine fuels. Tree-level fuels results may be more accurate for comparing pre- and post-fire fuel loads because transects were placed in the same locations at both sampling times. Plot-level transects were randomly placed within the plot, and locations may have changed enough between sampling dates to include anomalous areas of the plot following prescribed burns.

Post-fire mortality

The Crater Lake plots suffered relatively high mortality rates (35%) following prescribed fire treatments, but it is unclear if mistletoe directly increases postfire mortality of mature ponderosa pine. There was no difference in mortality rates between uninfected and infected plots, but five of the seven (71%) dead or severely damaged sample trees were infected with mistletoe and experienced higher stem char heights. Harrington and Hawksworth (1990) reported higher mortality among infected trees following prescribed fire treatments at Grand Canyon National Park, but primarily among young, small diameter trees. Previous prescribed fire treatments in my study area also resulted in high mortality, especially of large ponderosa pine trees (45%) (Thomas and Agee 1986, Swezy and Agee 1991). McHugh and Kolb (2003) found lower mortality rates (18%) following prescribed fires in northern Arizona, and Perrakis and Agee (2006) reported only 5% mortality in adjacent stands at Crater Lake. The majority of large trees that died during my study were infected ponderosa pine, but the sample size is too small (7 trees) to determine if the difference is significant. Continued monitoring may reveal longer term differences in mortality between uninfected and infected individuals because postfire mortality can be delayed beyond three years (McHugh and Kolb 2003, Agee 2003).

Post-fire mortality was negatively correlated with tree diameter, with the majority of dead trees being < 11 cm dbh. Other studies have reported bimodal distributions of mortality by tree diameter, with intermediate size trees being least likely to die following both prescribed fire and wildfire (Swezy and Agee 1991, McHugh and Kolb 2003). The J-shaped mortality-DBH curve at Crater Lake appears to be related to the relatively low severity of the fires, which caused charring at the base of smaller diameter stems but minimal crown damage to larger diameter trees. A similar distribution of mortality was seen in adjacent burn units at Crater Lake (Perrakis and Agee 2006).

Greater litter accumulation at the base of uninfected trees did not result in higher stem char heights on uninfected trees. The relatively cool, slow-burning fires in uninfected plots resulted in similar litter consumption and stem char as the hotter fires in infected plots. Stem char height was slightly greater for infected and uninfected trees that died following fire, indicating a greater probability of cambium damage. These results support other studies that found correlations between stem char and postfire mortality (Swezy and Agee 1991, Harrington 1993, McHugh and Kolb 2003).

The results of this study suggest a direct relationship between mistletoe and postfire mortality, and that mistletoe may indirectly influence tree mortality by increasing susceptibility to beetle attack. It is generally accepted that mistletoe infection weakens trees, making them more vulnerable to insect infestation (Hawksworth and Wiens 1996), but the relationship has not been clearly demonstrated in the literature. Several studies identified positive correlations between fire and insect activity, and mortality following earlier prescribed fire treatments was often attributed to bark beetle (Swezy and Agee 1991, Agee 2003), but the complex interactions among fire, mistletoe, and beetles remains poorly understood.

Limb flammability

Broomed branches experienced greater tissue loss during chamber burns, primarily needle biomass. Visual observations indicated that the brooms had more needle-bearing twigs and more needles overall (see Fig. 1.1). Additional work is needed to quantify needle and twig mass and volume in ponderosa pine brooms. Tinnin and Knutson (1980) found that brooming in Douglas-fir increases the number and length of twigs and produced more needles without a significant increase in total needle mass per annual growth segment. In contrast, Broshot et al. (1986) reported decreases in the number, length, and mass of needles in lodgepole pine brooms.

CONCLUSIONS

My results do not confirm the existing view that mistletoe infestation contributes significantly to fuel loading, fire behavior or fire hazard in mature ponderosa pine stands. Mistletoe appears to have little influence on prescribed fire behavior and post-fire mortality at Crater Lake National Park. Pre-treatment surface fuel loads did not differ among infected and uninfected plots. The high density of non-host tree species and recent prescribed fires (20-25 ybp) may explain the similarity in fuels between the two sample populations. Additional work is needed in larger areas of pure ponderosa pine with a more variable fire history. The lack of variation in fuel composition resulted in low variation in fire behavior during prescribed burn treatments. Mortality does not appear to be directly related to prescribed fire behavior, but mistletoe infection appears to result in a higher probability for mortality of mature host trees. Additional indirect influences may result from interactions with insects and other pathogens. Long-term monitoring of tree mortality and regeneration at the study site may increase our understanding of the indirect effects of mistletoe infection.

Future research would benefit from a morphological comparison between young and old infected trees, including variables such as photosynthetic surface area, length of needle-bearing branches, and needle length. Future burn chamber studies should remove needles prior to burning and use more dense fuel beds to burn the limbs at higher temperatures, but it should be noted that the logistics of burning inside under controlled conditions will limit the temperature and intensity of burns. Removing needles would allow for comparisons of needle volume and biomass between brooms and branches, as well as limit combustion to woody tissue. Burning at higher temperatures would allow for more complete combustion of the limbs than I achieved during burn chamber tests using an intermediate density fuel bed consisting of fine fibers that burned relatively hot and fast. The conditions were intended to be comparable to a surface fire in an open ponderosa pine stand, resulting in minimal combustion of woody tissue. While the conditions may be ecologically meaningful, they did not reveal differences in flammability that would be related to wood density or resin content in brooms.

The conclusions of this study are constrained by a limited data set resulting from inadequate areas of infected old-growth ponderosa pine, problems obtaining accurate fuel loads at an appropriate scale, and the difficult logistics involved with implementing prescribed fire treatments. Fuel composition is easily influenced by local topography and vegetation, making it difficult to obtain accurate estimates that represent a plot or stand. More fuel composition and fire behavior data are needed from other mature stands of infected ponderosa pine, particularly from those rare communities where disturbance regimes are relatively natural.

Table 5.1: Descriptive statistics (mean and standard deviation) for stand structure variables measured in each plot. *T*-tests show no significant differences between uninfected and infected samples ($p > 0.05$). Uninfected N = 7; infected N = 7.

Stand Variables	All plots	Uninfected	Infected
Basal area (m^2/ha) – all species	86.8 (24.2)	92.2 (26.6)	81.5 (22.2)
Ponderosa pine only	65.3 (22.6)	75.6 (26.5)	55.0 (12.8)
White fir only	13.8 (14.8)	11.4 (10.8)	16.3 (18.4)
Tree density (trees/ha) – all species	782 (381)	876 (414)	688 (350)
Tree ages (years)	97 (15)	91 (12)	102 (17)
Maximum tree age (years)	295 (124)	312 (128)	278 (128)
Ponderosa pine age (years)	183 (90)	98 (31)	105 (35)
Sapling and seedling density (#/ha)	6176 (5905)	6145 (6216)	6207 (6075)
Time since last recorded fire (years)	27	27	27
Understory richness (# of species)	11	12	10

Table 5.2: Mean (standard deviation) of plot-level fuel biomass (Mg/ha) for each fuel size class. *T*-tests show no significant difference in fuel loads between uninfected and infected plots before or after burning ($p > 0.05$). Uninfected N=7 infected N=7.

Fuel class	Pre-burn uninfected	Pre-burn infected	Post-burn uninfected	Post-burn infected
1-hr	0.06 (0.04)	0.06 (0.04)	0.01 (0.01)	0.03 (0.02)
10-hr	0.53 (0.24)	0.76 (0.27)	0.18 (0.09)	0.23 (0.12)
100-hr	0.41 (0.40)	0.66 (0.25)	0.26 (0.22)	0.46 (0.30)
1000-hr	1.69 (1.83)	3.29 (1.83)	1.69 (1.28)	3.28 (4.24)
Litter	0.03 (0.01)	0.03 (0.01)	0.005 (0.004)	0.007 (0.003)
Duff	3.4 (3.0)	3.3 (3.8)	0.75 (0.64)	1.22 (0.50)
Total				

Table 5.3: Mean (standard deviation) of tree-level fuel biomass (Mg/ha) for each fuel size class. Uninfected N=19, infected N=20. Prior to burning, there was significantly more litter at the base of uninfected trees compared to infected. After burning, there was significantly more 100-hr fuel at the base of infected trees.

Fuel class	**Pre-burn uninfected**	**Pre-burn infected**	**Post-burn uninfected**	**Post-burn infected**
1-hr	0.04 (0.03)	0.04 (0.04)	0.002 (0.001)	0.003 (0.004)
10-hr	0.80 (0.25)	0.75 (0.27)	0.19 (0.06)	0.23 (0.12)
100-hr	0.67 (0.50)	0.64 (0.46)	0.14 (0.15)	0.22 (0.17)*
1000-hr	4.14 (3.28)	5.26 (4.17)	2.56 (3.91)	3.77 (2.88)
Litter	0.04 (0.01)*	0.03 (0.01)	0.005 (0.003)	0.005 (0.003)
Duff	6.24 (3.65)	5.82 (5.62)	0.47 (0.60)	0.36 (0.41)
Total				

* Significantly higher biomass ($p < 0.05$).

Table 5.4: Mean differences in before and after fuel biomass for tree-level sampling. There was a significant ($p < 0.05$) decrease in all fuel sizes except sound 1000-hour fuel. There was no significant difference between infected and uninfected samples.

Plot type	**1-hr**	**10-hr**	**100-hr**	**Sound 1000-hr**	**Rotten 1000-hr**	**Litter**	**Duff**
Infected	0.04	0.52	0.42	-0.30	1.79	0.03	5.46
Uninfected	0.04	0.62	0.53	-0.15	1.72	0.04	5.77

Table 5.5: Means (standard deviations) of tree mortality by basal area (BA) and density, and comparison of values for all tree species to ponderosa pine (Pipo).

Plot type	BA m^2/ha All species	BA m^2/ha Pipo only	% trees/ha All species	% trees/ha Pipo only
Uninfected	12.3 (21.2)	9.4 (19.0)	21%	22%
Infected	18.0 (27.0)	10.8 (25.2)	39%	35%

Table 5.6: Descriptive statistics (mean and standard deviation) for limb flammability experiments. Diameter was measured at the base of each limb near the point of attachment to the main stem of the tree. Water loss is the percent reduction in mass between limb pruning and burning (~ 20 days). Mass before is the mass of limbs immediately prior to burning. Mass loss is the percent reduction in mass resulting from tissue consumption during the burn treatments.

Branch type	Diameter (cm)	Water loss (%)	Mass before (kg)	Mass loss (%)	Flame height (m)	Burn duration (min)
Healthy	4.2 (0.8)	14 (8)	2.7 (1.2)*	32 (7)*	1.7 (0.5)	10.3 (3.1)
Broomed	4.0 (0.9)	16 (7)	3.9 (1.7)*	38 (9)*	1.9 (0.7)	11.1 (6.9)

* Significant difference between branches and brooms ($p < 0.05$) as determined by

Mann-Whitney U-tests.

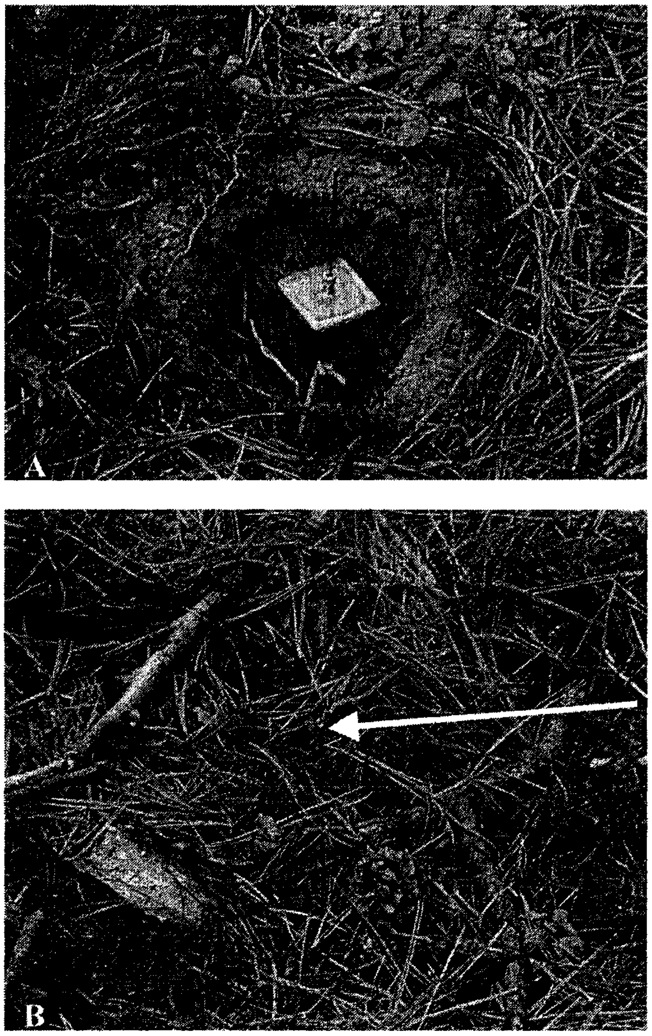

Figure 5.1: Fire temperature monitoring equipment. A: Stainless steel housing protects a data logger that is attached to the high temperature thermocouple protruding from the top. The housing is buried and fuels are replaced at the soil surface. B: Thermocouple (arrow) extending ≈ 5 cm above fuel bed.

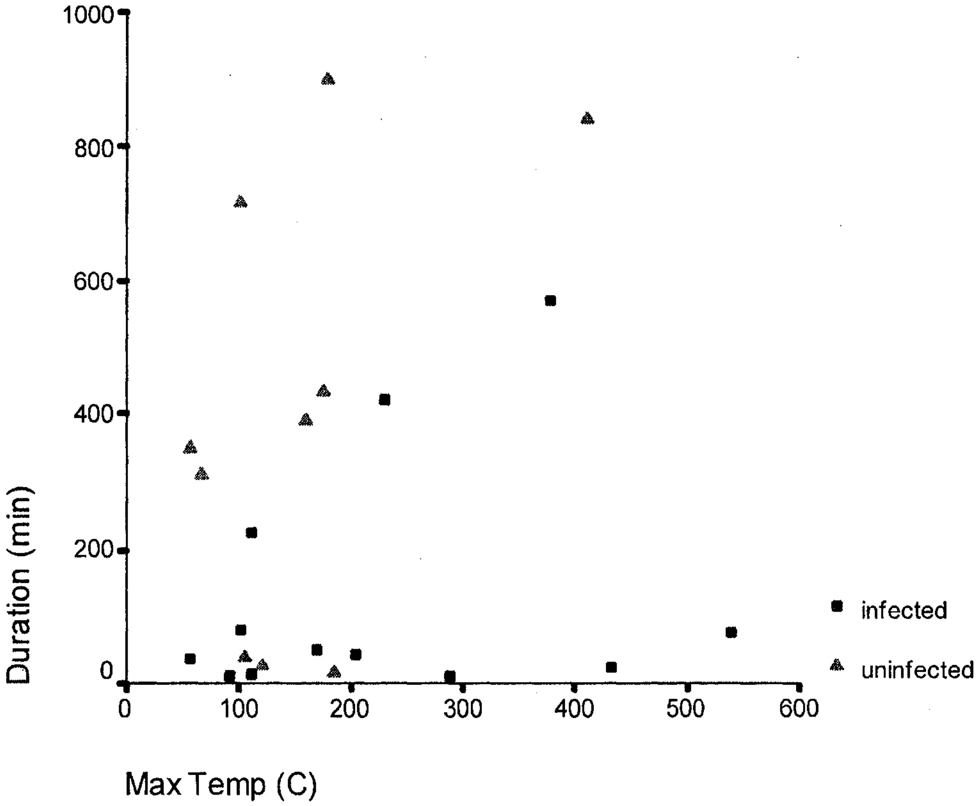

Figure 5.2: Relationship between mistletoe infection level and maximum temperatures and duration of high temperatures during prescribed burns at Crater Lake National Park.

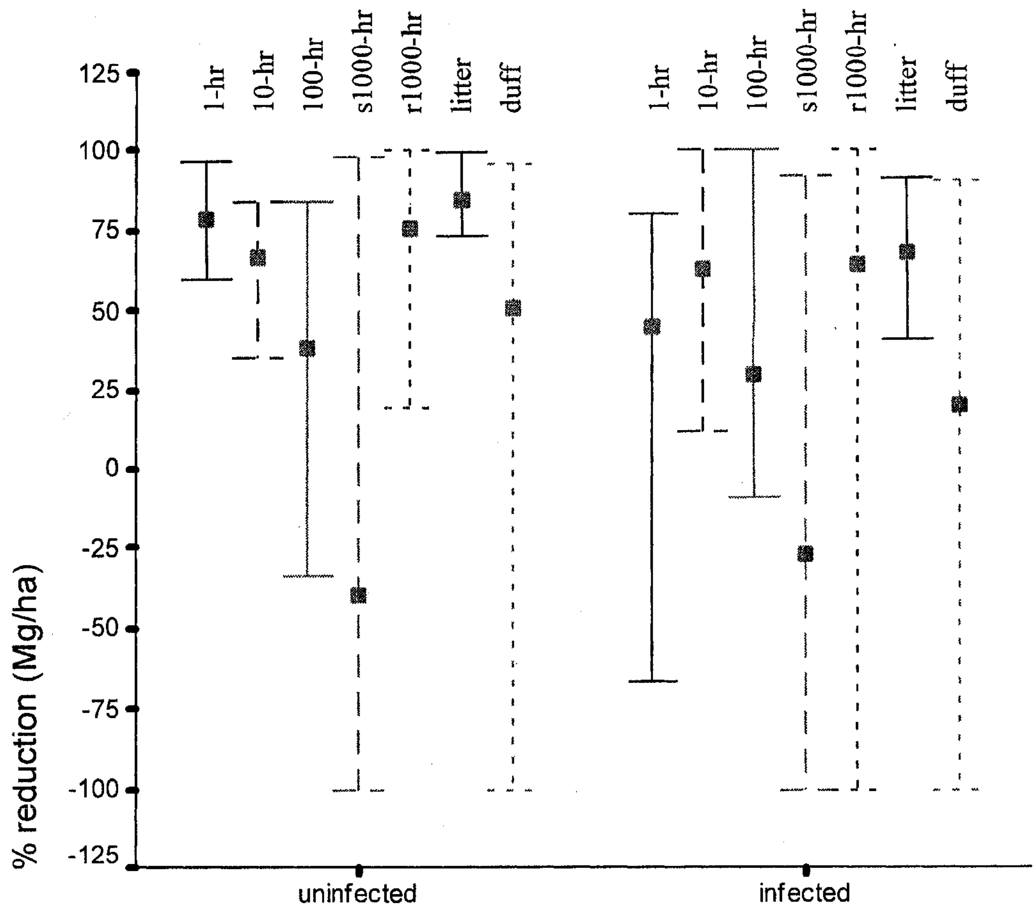

Figure 5.3: Plot-level surface fuel reduction (range and mean percent reduction) following prescribed fire. All fuel sizes except 100-hour and sound 1000-hour fuel showed significant ($p < 0.05$) decreases in biomass after prescribed burning. There was no significant difference between infected and uninfected samples

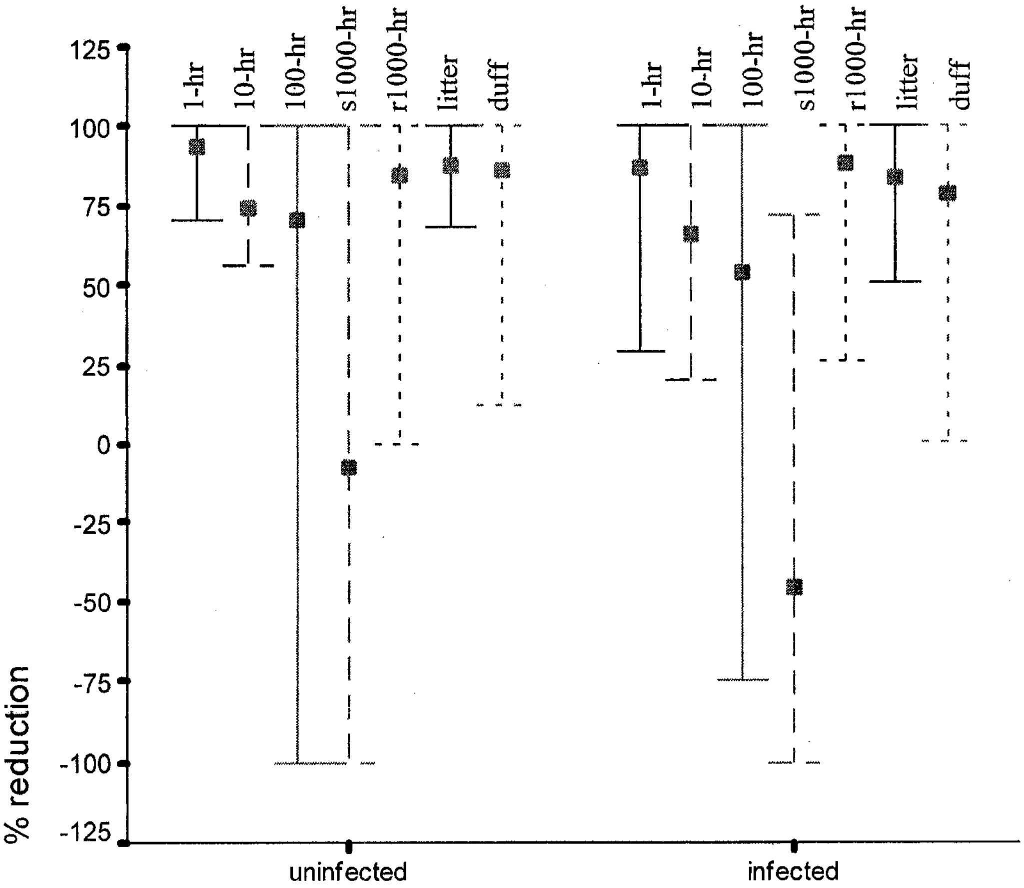

Figure 5.4: Tree-level surface fuel reduction (range and mean percent reduction) following prescribed fire. All fuel sizes except sound 1000-hour fuel showed significant ($p < 0.05$) decreases in biomass after prescribed burning. There was no significant difference between infected and uninfected samples

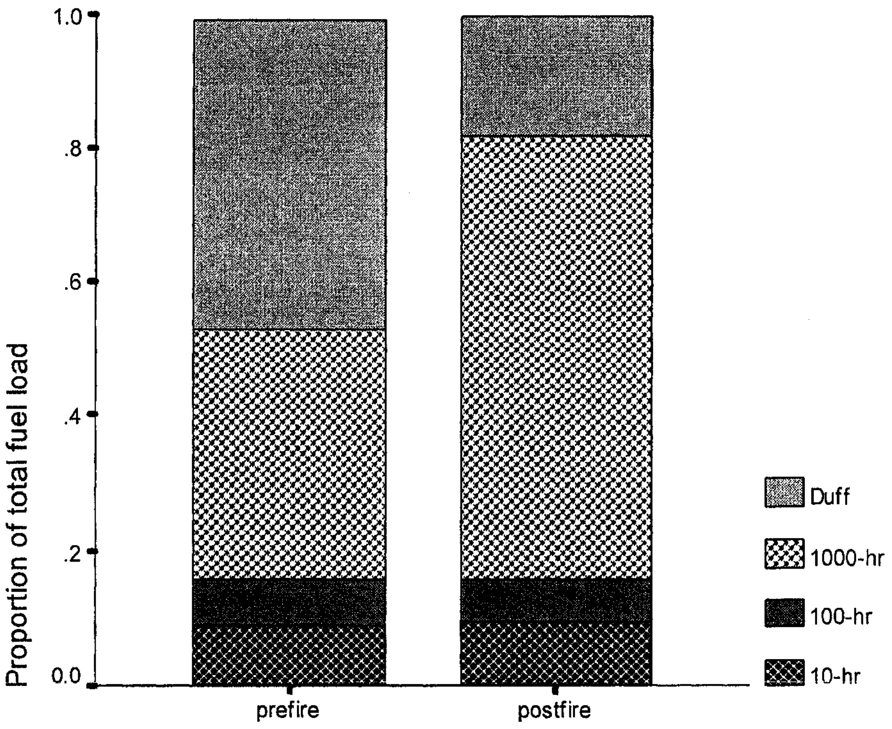

Figure 5.5: Relative contributions of each fuel size class to the total fuel loads before and after prescribed fire treatment. Litter and 1-hr fuels are omitted because they both represent < 1% of the total.

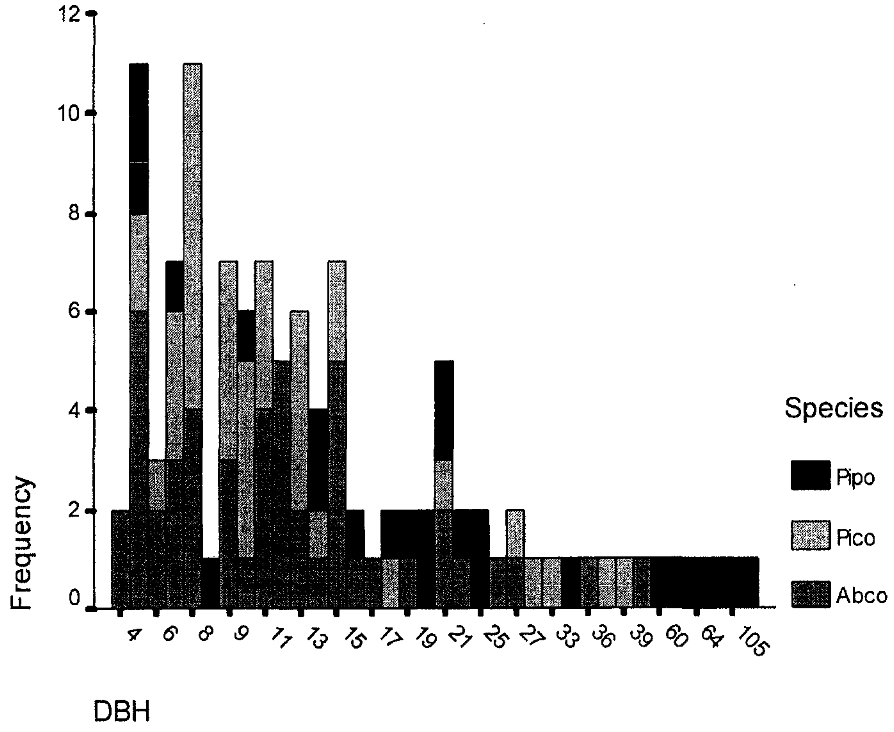

Figure 5.6: Tree mortality during or after prescribed burns. Pipo = ponderosa pine; Pico = lodgepole pine; Abco = white fir; DBH = diameter at breast height (cm).

Figure 5.7: Tree mortality following prescribed burns, represented as percent reduction in live tree density (trees/ha); each bar represents mortality in one plot. A Mann-Whitney U-test showed no significant difference in tree mortality between infected and uninfected plots ($p = 0.3$).

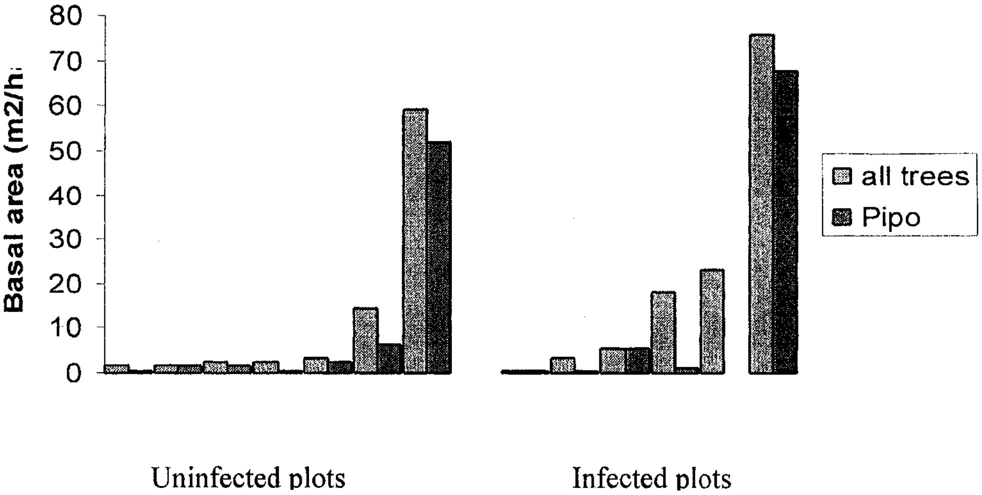

Figure 5.8: Basal area of trees that died during or after prescribed burns in each plot. Light gray bars include all tree species; dark gray bars include only ponderosa pine (Pipo), the mistletoe host species. A Mann-Whitney U-test revealed no significant difference in mortality between uninfected and infected plots ($p > 0.05$)

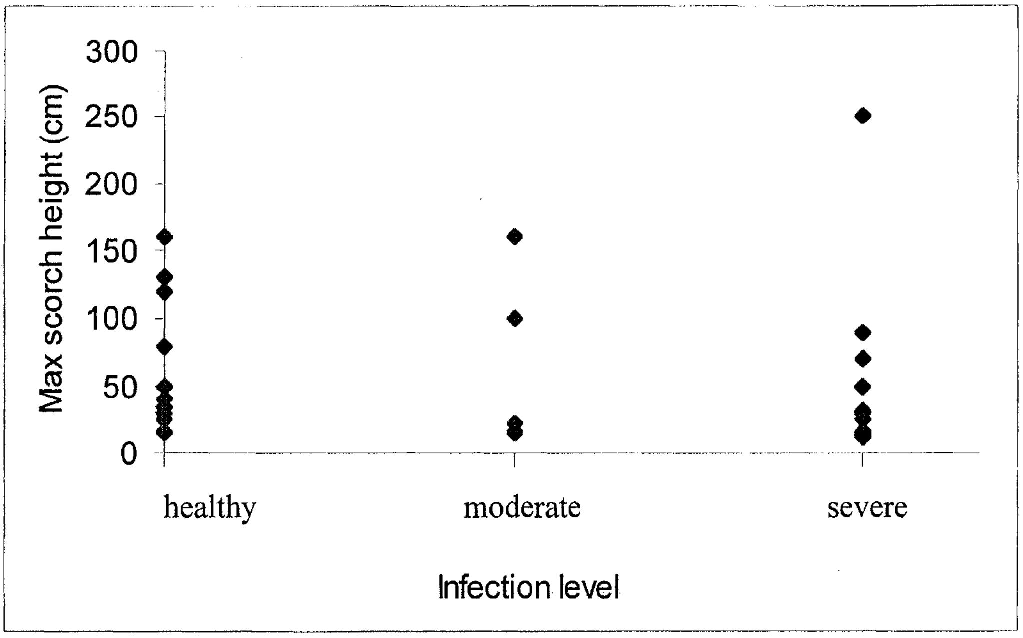

Figure 5.9: Relationship between mistletoe infection levels and stem char heights resulting from prescribed burns.

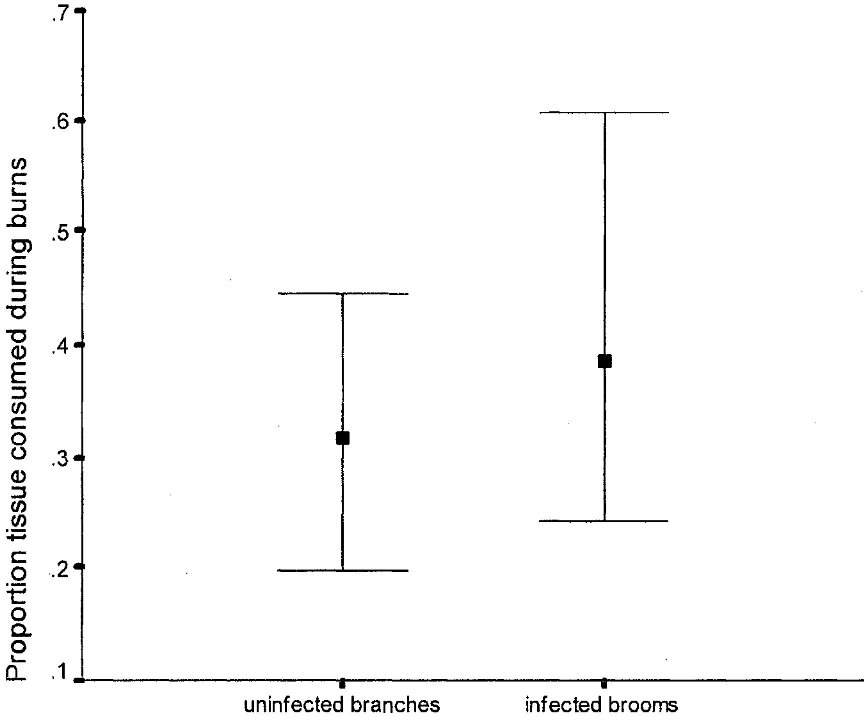

Figure 5.10: Range and mean of the proportion of limb tissue consumed during burn chamber treatments. Broom samples lost more mass during burns (Mann-Whitney U = 89.0, $p = 0.02$).

PART IV

CLIMATE RESPONSE

This chapter compares growth patterns in infected and uninfected old-growth ponderosa pine trees to identify any differences in annual response to precipitation and temperature. Mistletoe infection appears to influence the accumulation of fine fuels, which may be explained by an increased sensitivity to climatic variation. I compare infected and uninfected tree-ring chronologies to temperature, precipitation, and a drought severity index. I aged approximately 1200 trees for the studies presented in previous chapters. Working with those increment cores suggested to me that infected tree growth is more sensitive to climate variation, and should not be excluded from dendrochronological research projects. The following chapter quantifies the differences in climate response between infected and uninfected ponderosa pine trees.

CHAPTER 6

EFFECTS OF DWARF MISTLETOE ON CLIMATE RESPONSE OF MATURE PONDEROSA PINE TREES

ABSTRACT

This research examines the influence of western dwarf mistletoe (*Arceuthobium campylopodum*) infection on the radial growth response of mature ponderosa pines (*Pinus ponderosa*) and its effects on dendroclimatic reconstructions. I hypothesize that trees with mistletoe have lower annual growth rates than uninfected trees, but exhibit higher mean sensitivities and stronger relationships between growth and climate variation. I tested these hypotheses using correlation and regression analyses to compare 100-year crossdated and standardized tree-ring chronologies from 26 infected and 29 uninfected trees. I compared both chronologies to climate variation as measured by changes in total precipitation, minimum, mean, and maximum temperature, and the Palmer Drought Severity Index (PDSI). Results show that trees infected with dwarf mistletoe have higher radial growth rates, exhibit greater sensitivity, and respond more strongly to climate variation. Both infected and uninfected chronologies are significantly correlated with the respective climate variables, but exhibit different patterns. The strongest correlations are between infected trees and PDSI for all months tested; significant correlations between uninfected trees and PDSI are limited to May through December lagged from the previous year. These results suggest mistletoe-infected trees are more sensitive to climatic factors than uninfected trees and may be useful for dendroclimatic analyses.

INTRODUCTION

Site selection and targeting climate sensitive trees is an essential component of dendroclimatological research. It is important to select trees that have a specific factor that limits growth of annual rings. To reduce the influence of endogenous disturbances on ring formation in sample trees, dendroclimatologists historically avoid selecting trees with evidence of physical damage or disease, including infection by parasitic plants such as mistletoes (Fritts 1976, Stokes and Smiley 1996). Despite this protocol, little is known about how parasitic plants alter the usefulness of host trees for dendroclimatological studies. Mistletoes are widespread throughout western North America, and their explosive dispersal mechanism results in clumped distributions, which may make it difficult to find uninfected trees in certain locations.

The dwarf mistletoes are a group of obligate vascular hemiparasites found on a wide range of conifers in North America, Asia, Europe, and parts of Africa (Hawksworth and Wiens 1996, Geils and Hawksworth 2002). Mistletoes use an endophytic system inside host branches to uptake water, minerals, and carbohydrates from host trees (Knutson 1983, Lamont 1983), leading to several physiological and morphological changes in the tree. Increased host mortality rates, reduced height and diameter growth, and reduction of wood quality are typical results of mistletoe infection (Hawksworth and Wiens 1996, Thomson et al. 1997, Geils and Collazo 2001, Geils and Hawksworth 2002). Infection alters host foliage growth and respiration rates (Tocher et al. 1984), ultimately altering water relations within host tissue (Fisher 1983, Wilson and Calvin 1996).

Changes in host water relations and biomass allocation suggest that infected trees are more sensitive to annual changes in precipitation and temperature. Several studies have demonstrated that transpiration rates of dwarf mistletoe shoots are higher than those of host tissues, which may increase both water stress in the host and allocation of resources to mistletoe shoots (Fisher 1983, Tocher et al. 1984, Wilson and Calving 1996). Additional evidence indicates that infection increases needle surface area while decreasing volume (Tinnin and Knutson 1980, Wanner and Tinnin 1986). Such shifts in the distribution of biomass in the host crown could lower water use efficiency, resulting in lower tolerance to drought stress (Sala et al. 2001). Sala et al. (2001) also reported that foliage in infected branches has lower water use efficiency when compared to uninfected branches in Douglas-fir (*Pseudotsuga menziesii* Mirb.) and western larch (*Larix occidentalis* Nutt.), which differ from ponderosa pine in their morphological response to infection.

The majority of research on dwarf mistletoes focuses on host plant productivity (Wanner and Tinnin 1989), economic impacts (Hawksworth and Shaw 1984), and control of spread in second growth stands (Hawksworth and Wiens 1996). Studies of physiological effects of mistletoe on mature, unmanaged trees are also rare (Shea 1962, Childs and Wilcox 1966). Limited research exists that investigates the physiological response of host trees in terms of specific climate variables.

This study investigates the influence of dwarf mistletoe on host tree response to climate to determine the necessity or advantages for dendrochronologists to avoid sampling infected trees. Compared to uninfected trees, I expect infected trees to exhibit: 1) lower growth rates, 2) higher mean sensitivities, and 3) stronger correlations with climate variables. The negative influence of mistletoe on radial growth is well-documented (Geils and Hawksworth 2002), so I expect to see low growth rates among the severely infected individuals sampled. Decreased growth rates could result in a stronger response to climate variation as infected trees experience increased moisture stress and nutrient loss to mistletoe plants. Therefore, I hypothesize that infected trees will have more sensitive ring width series and stronger correlations with climate variables.

METHODS

Study area

Lava Cast Forest is located in the Newberry National Volcanic Monument in the Deschutes National Forest east of the Cascade crest (Fig. 3.1). My study site within the monument is the Lava Cast Forest Geological Area (LCF), which is characterized by 11 kipukas (forested islands) isolated among shallow, mid-Holocene lava flows (Peterson and Groh 1969).

The climate, topography, and lack of management make LCF ideal for investigating the influence of mistletoe on the growth of mature trees. The semi-arid climate and short growing season indicate that moisture is the limiting factor for tree growth at LCF, making it an appropriate location for dendroclimatic sampling. Sample sites are located on drought-sensitive southwest or west-facing slopes with angles ranging from 6 to 25°. Each sample site is located in mature (mean age >157 years) low density (≈ 330 trees/ha) stands to ensure adequate sampling of mature trees with sensitive ring series.

Field methods

I removed increment cores from 26 severely infected trees and 29 uninfected trees located on seven different kipukas (Fig. 3.1). Sample trees are all located in stands dominated by large, mature ponderosa pine. I selected infected and uninfected trees of similar size and from similar stand conditions in order to control for differences in growth unrelated to mistletoe infection. The samples I used are part of a larger study investigating disturbance and succession across a fragmented landscape (Arabas et al. 2006, Hadley and Arabas in prep). The cores for this larger study were used to establish age structures, therefore only one core per tree was removed 30 to 50 cm from the base.

Chronology development

Increment cores were prepared using standard dendrochronological techniques (Stokes and Smiley 1996). I crossdated samples using a combination of skeleton plots and the list method (Yamaguchi 1991). Ring widths were measured to the nearest 0.001 mm using a Velmex measuring system and Medir software (Holmes 1994). I used COFECHA (Holmes 1999) to verify crossdating of the infected and uninfected samples first together and then separately, as well as against a local climate reconstruction (Pohl et al. 2002). The measurement data were then truncated to begin in 1900 because of the unknown level of mistletoe infection prior to that time. Although I could not reconstruct historical mistletoe infection levels, mistletoes have long life cycles leading to relatively slow rates of spread (Hawksworth and Wiens 1996). Based on this knowledge, I assumed that a severely infected tree at present supported some level of mistletoe infection 100 years ago. The use of 100-year chronologies also provided sufficient data for robust statistical analyses.

I standardized the ring-width indices for each tree and averaged them into separate mean chronologies for the infected versus uninfected samples using the program ARSTAN (Cook 1985). Both standardized chronologies were detrended using a linear regression line. The truncated time series allowed for the use of linear regression detrending to remove low frequency signals unrelated to climate, without the need to remove growth trends.

Comparison of means

I tested for differences in annual growth variation between infected and uninfected chronologies. Paired t-tests were used to compare annual average ring width, expressed as the standardized ring-width index for each chronology. I compared mean sensitivities and series intercorrelations between the infected and uninfected chronologies with independent sample t-tests. Additionally, differences in sample stand basal area, and sample tree ages and diameters were evaluated using an independent sample t-test.

Correlations with climate variables

I used Spearman's rank-order correlation analysis and linear regression to examine the relationship between climate variation and mean ring-widths from the standardized chronologies. Climate variables used in the analyses included: Palmer Drought Severity Index (PDSI) and total precipitation for Oregon Climate Division 7 for 20 months (the year of tree growth plus 8 months lagged from the previous year), mean, minimum, and maximum monthly temperatures from Bend, Oregon for 12 months (the year of tree growth) (NCDC 2005). PDSI uses temperature, precipitation, soil moisture, and drought duration to measure the departure of moisture supply from average conditions (Palmer 1965). A positive PDSI indicates higher than average moisture availability, while a negative PDSI reflects lower than average moisture.

RESULTS

Comparison of means

Uninfected trees exhibit lower mean ring-widths than infected trees ($t = -8.1$, $p<0.01$, Table 6.1 and Figure 6.1). Mean sensitivity of the infected sample (0.253) is significantly higher than the uninfected sample (0.232, $p < 0.05$), but the series intercorrelations do not differ significantly between infected and uninfected samples

(Table 6.1). Mean sensitivities and interseries correlations are relatively low for ponderosa pine, but not unusual for the Pacific Northwest (Speer 1997, Pohl et al. 2002). Stand basal area and tree age and size do not differ between infected and uninfected samples (Table 6.1).

Correlations with climate variables

The dominant climate controls on growth differ between infected and uninfected trees. Palmer Drought Severity Index (PDSI) has the strongest relationship with both chronologies. The infected chronology is significantly correlated with PDSI for the current year and eight months lagged from the previous year (Fig. 6.2). PDSI explains 48% of the variance in the infected chronology, with the previous November and current year July being the strongest predictors of growth ($\beta = 1.36$ and 1.92, respectively). The uninfected chronology is significantly correlated with PDSI for the eight months lagged from the previous year and December of the current year (Fig. 6.2). PDSI explains 36% of the variance in the uninfected chronology, and July from both the previous and current growing year is the strongest predictors of growth ($\beta =$ 1.06 and 0.95, respectively). Strong correlations with PDSI indicate that the chronologies are robust.

Precipitation and temperature are significantly correlated with both chronologies. The infected chronology is positively correlated with precipitation from June, August, and November lagged from the previous year (Fig. 6.3). April precipitation is negatively correlated with the uninfected chronology (Fig. 6.3).

Average temperatures in March and July are negatively correlated with both the infected and uninfected chronologies, but correlations with the infected sample are stronger (Fig. 6.4). June average temperature is also significantly correlated with the infected chronology. Minimum temperatures for March, April, and June to September are negatively correlated with growth for both chronologies, but stronger relationships exist for the uninfected chronology (Fig. 6.5). Maximum temperatures have a weak relationship with tree growth, showing a significant correlation only between June temperatures and the infected chronology ($r = -0.25$, $p<0.05$) (Fig. 6.6).

Infected trees are more sensitive to variations in climate and appear to grow more rapidly when conditions are favorable. During periods of high soil moisture (1915-1923 and 1980s), infected trees grow more rapidly than uninfected trees (Fig. 6.7). Infected trees grow less rapidly than uninfected when moisture supply is low (1940s and early 1960s), but the growth difference is less than during high soil moisture years. During years of moisture stress as indicated by a very low PDSI (1930s and late 1960s), infected trees did not appear to have an advantage over uninfected trees and both grew poorly (Fig. 6.7).

DISCUSSION

Mean growth rates

The observation that infected sample trees tend to have higher radial growth rates than uninfected trees is not likely to be a function of age or competition because the sampled trees represent similar ages and are growing in comparable conditions. Several mechanisms may explain the unexpectedly high radial growth rates of infected trees. Previous studies demonstrated that mistletoe decreases respiration and transpiration rates of host trees, which may lead to lower water use efficiency and altered metabolic rates in infected trees (Fisher 1983, Tocher et al. 1984). Higher metabolic rates would result in faster growth during periods of abundant resources. Changes in metabolism may explain the higher growth rates of infected trees in a semi-arid environment during years of high moisture availability. Similar results have been reported by Knapp and others (2001) who found increased growth in western juniper resulting from atmospheric carbon dioxide fertilization. Increased growth rates were highest for trees experiencing moisture stress, suggesting that carbon dioxide fertilization could disproportionately influence growth of infected trees.

High growth rates could also be a function of changes in biomass allocation in infected individuals. Apical growth (height) tends to decrease with mistletoe infection (Knutson 1972, Thomson and Smith 1983), allowing resources to be reallocated to local growth of the main stem and infected branches. Previous studies have demonstrated increased bole taper in infected trees (Tinnin 2001), but I do not have measurements to verify a difference in height between the infected and uninfected samples.

High growth rates of infected trees could be an artifact of the preference of parasites for more vigorous hosts. Recent evidence indicates that the success of dwarf mistletoe depends largely upon the physiological condition of the host trees (Bickford et al. 2005), suggesting that the faster growing trees may be more suitable hosts for the mistletoe. Other studies, however, have found a greater abundance of mistletoe on trees growing in stressful conditions (Gehring and Whitman 1995). Cause and effect cannot be determined without experimental manipulation of infection levels and long-term study of host response.

Mean sensitivity

My results do not explain the differences in growth rates between infected and uninfected trees, but they do indicate that infected trees are more sensitive to climate. Infected trees at LCF exhibit higher mean sensitivities and stronger correlations with precipitation and temperature since 1900. This evidence suggests it may be unnecessary to avoid sampling infected trees for dendrochronological studies, and that infected trees may actually provide stronger climate signals than uninfected samples.

Higher mean sensitivity of infected trees may be a function of changes in water relations caused by mistletoe infection. Sala et al. (2001) found that foliage in infected Douglas-fir branches have lower water use efficiency, but infected trees do not have higher water use overall. Their results indicate that infected trees compensate for lower water use efficiency by increasing sap flow during times of moderate water availability. Increases in sap flux may not be possible during times of high moisture stress. Changes in sap flux in response to water availability may explain the higher sensitivity and lower growth rates of the infected samples. Piirto et al. (1974) found that annual rings of lodgepole pine infected with dwarf mistletoe had a higher ratio of early to late wood when compared to uninfected samples. A higher percentage of early wood would lead to greater sapwood volume, but more frequent cavitations during periods of moisture stress, increasing the sensitivity of infected trees to changes in aridity.

Correlations with climate

If infected trees are more sensitive to short-term changes in climate, they may respond more dramatically to global climate change. Consequently, models predicting changes in ponderosa pine distribution under different climate change regimes should consider the influence of dwarf mistletoe on potential range expansions or contractions. There is little information concerning the influence of mistletoe on mature trees or how infection may alter the climate response of host trees (Shea 1962, Hawksworth et al. 1992). If host vigor and productivity control mistletoe productivity, we need to improve our understanding of the interaction between host and parasite to accurately model their response to climate change. Two possible climate change scenarios are that trees in stressed situations will not support mistletoe populations, or moderate increases in precipitation and temperature could increase the number of trees able to support mistletoe infections, resulting in more widespread infestation.

CONCLUSIONS

These results indicate that infected ponderosa pine trees are more responsive to climate variation, as demonstrated in higher mean sensitivities and stronger correlations with moisture availability. Previous studies investigated the physiological and morphological effects of mistletoe on host trees, but this study is the first, to my knowledge, to identify the climate response of ponderosa pine trees infected with dwarf mistletoe. These results suggest that ponderosa pine trees infected with mistletoe may provide strong climate signals and do not need to be avoided in dendrochronological studies. It is not clear if the climate response of other mistletoe-host combinations follows the same pattern or if younger infected ponderosa pine trees respond to climate in the same way as our old-growth sample. Additional information about the influence of mistletoe infection on host response to moisture and temperature variation would help us generate more accurate models of the effects of climate change on vegetation in western North America.

We need to better understand how mistletoe alters the physiological response of the host tree throughout its development. The increased sensitivity of host tree-ring series may provide a mechanism for reconstructing mistletoe infection histories in old-growth stands. Dendrochronologists would benefit from being able to identify trees that once supported mistletoe but now have no visible signs of infection. Methods for reconstructing mistletoe infections would be useful for identifying historical changes in mistletoe distributions across western North America and correlating those changes with disturbances such as fire and management practices.

Table 6.1: Summary statistics (mean and standard deviation) and t-test results for the infected and uninfected chronologies. Ring width indices, representing growth rates, are the averaged and standardized annual growth increment for all sample trees in the chronology.

	Stand BA[a] (m^2/ha)	DBH[b] (cm)	Age[b] (yrs)	Series inter-correlation	Mean Sensitivity*	Ring width index*
Infected	48 (19)	55 (18)	284 (61)	0.54 (0.10)	0.25 (0.03)	0.75 (0.23)
Uninfected	54 (14)	52 (20)	303 (89)	0.52 (0.09)	0.23 (0.04)	0.64 (0.17)

* Infected and uninfected significantly different ($p < 0.05$)

[a] Mean basal area (BA) for the sample tree and 20 to 30 surrounding trees.

[b] Mean diameter at breast height (DBH) and age for sample trees only.

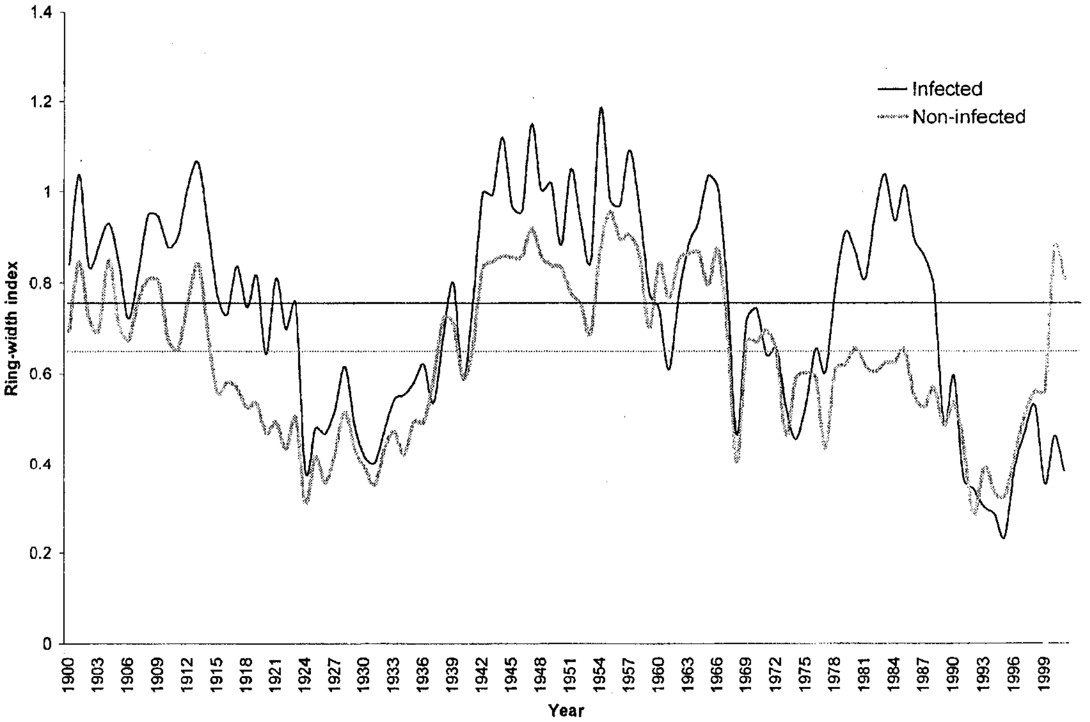

Figure 6.1: Mean ring-width chronologies for standardized, non-detrended measurements from 1900-2001. Horizontal lines indicate mean ring-width index for all series in the chronology (infected = 0.75 and uninfected = 0.64).

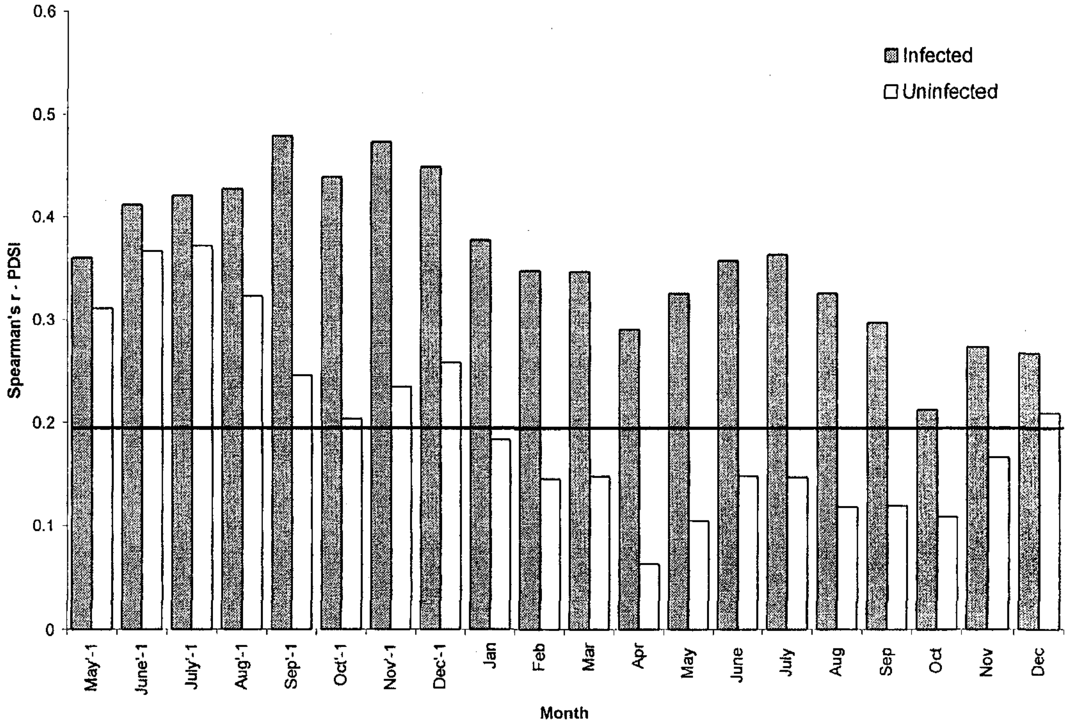

Figure 6.2: Spearman's correlation coefficients between standardized chronology index value for each year and Palmer Drought Severity Index for each year plus 8 months lagged from the previous year. The horizontal line indicates the 95% confidence interval; therefore all correlations above that line are significant ($p<0.05$).

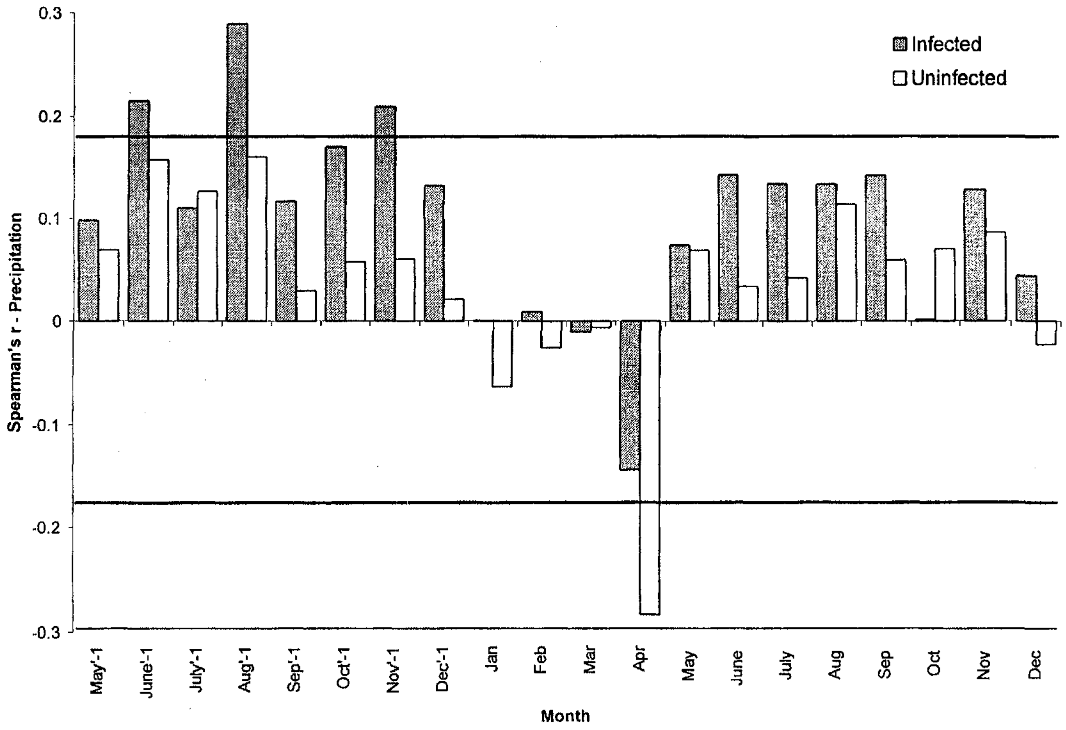

Figure 6.3: Spearman's correlation coefficients between standardized chronology index value for each year and total monthly precipitation for each year plus 8 months lagged from the previous year. Horizontal lines indicate the 95% confidence interval; therefore all correlations above or below the lines (outside the interval) are significant ($p<0.05$).

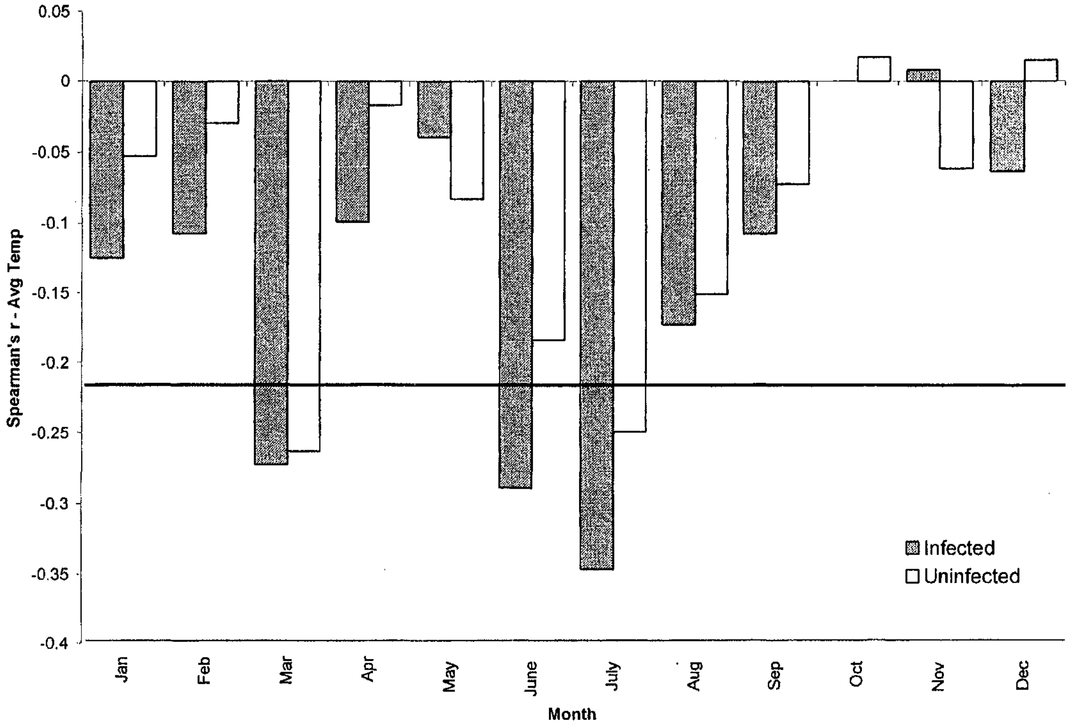

Figure 6.4: Spearman's correlation coefficients between standardized chronology index value for each year and average monthly temperature. The horizontal line indicates the 95% confidence interval; therefore all correlations below that line are significant ($p<0.05$).

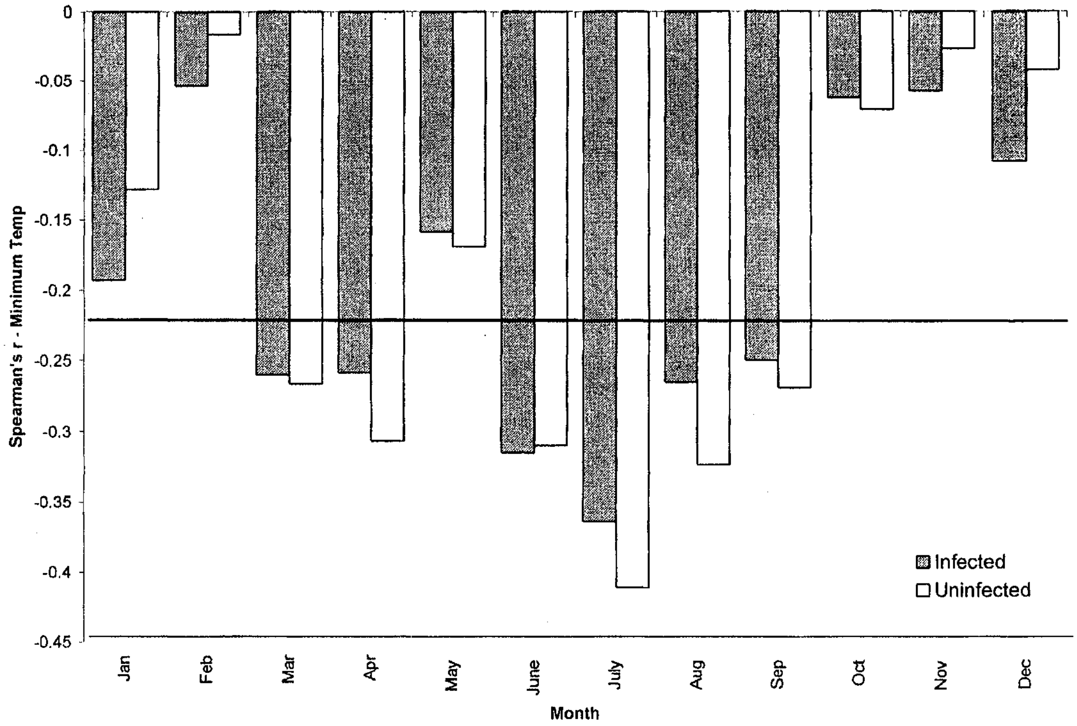

Figure 6.5: Spearman's correlation coefficients between standardized chronology index value for each year and minimum monthly temperature. The horizontal line indicates the 95% confidence interval; therefore all correlations below that line are significant ($p<0.05$).

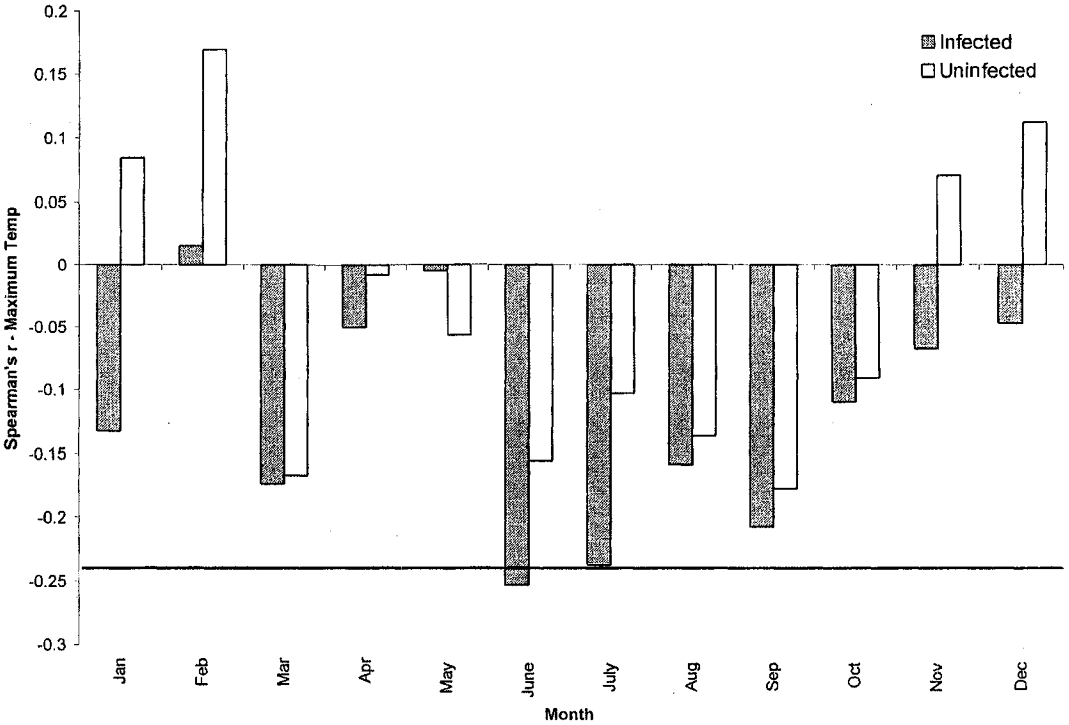

Figure 6.6: Spearman's correlation coefficients between standardized chronology index value for each year and maximum monthly temperature. The horizontal line indicates the 95% confidence interval; therefore all correlations below that line are significant ($p<0.05$).

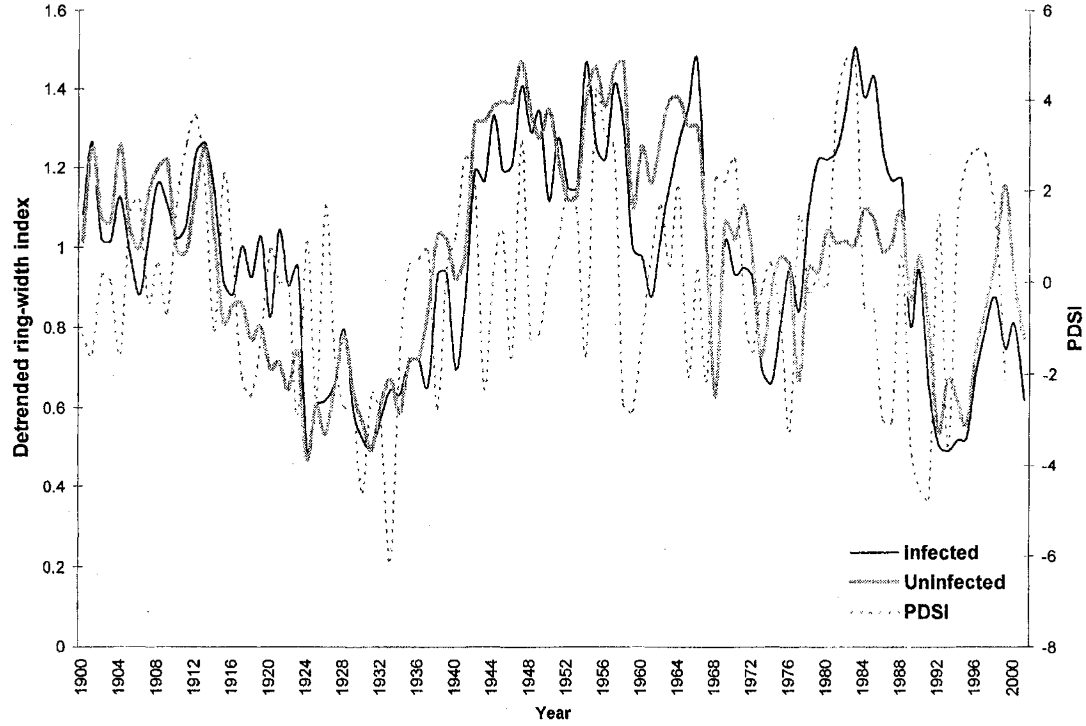

Figure 6.7: Detrended infected and uninfected chronologies and Palmer Drought Severity Index (PDSI) from 1900-2001. During times of high soil moisture supply (positive PDSI), infected trees grow more rapidly than uninfected trees; conversely, infected trees grow less rapidly than uninfected when moisture supply is low (negative PDSI). Infected trees do not appear to have an advantage over uninfected trees and both grow poorly when the PDSI is very low.

PART V

OVERALL CONCLUSIONS

CHAPTER 7

CONCLUSIONS AND RECOMMENDATIONS FOR FUTURE RESEARCH

The primary objective of my research is to quantify the structural and functional differences between forest stands with and without dwarf mistletoe. Mistletoe infection alters host tree growth and reproduction. I expect these changes to individual trees to exert influence on larger scales, mainly by altering fuel composition and fire behavior in infected stands. I also anticipate that mistletoe infection alters the relationships between host trees and climate variation, which could alter structure and function of forests at the landscape scale. My goal is to contribute to our understanding of the complex ecological relationships among mistletoe and host tree growth, broom development, fire susceptibility and behavior, and climate variation. My results support four of my original hypotheses and refute one (Fig. 7.1).

Fuel Composition

My investigation of fuel composition reveals that mistletoe infection increases fine fuel biomass in mature ponderosa pine stands, but the influence of mistletoe is complex and often indirect. Dwarf mistletoe infection results in higher fuel accumulations, but only for a subset of fuel types and the results differ between study sites. Crater Lake exhibited a positive correlation between infection level and accumulations of fine fuels (litter, 1-, 10-, and 100-hour). Mistletoe explains a significant amount of the variation in fuel composition at Crater Lake, but the relative dominance of white fir is a stronger explanatory variable. Infected plots at Lava Cast Forest also have higher accumulations of fine fuels, with ponderosa pine dominance and stand age explaining more of the variation in fuel composition than mistletoe infection. I cannot attribute how much of each fuel type is a direct result of mistletoe infection, however, my results indicate that fuel accumulation models would benefit from including infection level as a parameter.

My research shows that fuel composition is highly variable within and among my study sites. Consequently, the traditional stand variables I measured (mistletoe abundance, stand density and age, time since last fire), explain little of the variance in fuel accumulation. These results suggest the contribution of mistletoe to fuel loads cannot be elucidated by the singular contribution of these variables. Also, the large spatial and temporal variability of forest fuels is difficult to capture using traditional field sampling protocols. Alternatively, these traditional stand variables fail to capture some key explanatory variables or combination of variables that predict fuel accumulation.

Mistletoe appears to increase fine fuels on the forest floor, but my results from Crater Lake do not support previous research concerning the contribution of mistletoe to vertical fuel distribution. I measured height to the point where limbs attach to the main stem of the tree and found no difference between brooms and healthy branches. This sampling procedure provides a clear measurement of relative limb heights and limb age but introduces sampling bias regarding the distribution of canopy fuels. Brooms often have a rounded morphology that would make their maximum distance from the ground less than healthy branches. Similar attachment heights indicate brooms are not necessarily older as previously reported (Weir 1916, Koonce and Roth 1985, Harrington and Hawksworth 1990).

Broom longevity

Aging dwarf mistletoe brooms through the application of dendroecological techniques provided accurate but imprecise results. My results show that it is possible to estimate broom ages, but crossdating was either difficult or unsuccessful because of the large number of rings and irregular growth of broom samples. Core samples yielded a wide range in ring counts among the four increment cores removed from each broom and incremental growth displayed strong asymmetry with numerous false and missing rings. Estimated broom ages ranged from 64 – 350 years and host tree ages ranged from 91 – 452 years. Samples from younger brooms and host trees are easier to crossdate but less useful for assessing long-term ecological consequences of mistletoe infection.

Flammability and Mortality

Mistletoe increases fine fuel loads and may lead to lower live crowns, but infection appears to have little influence on prescribed fire behavior and flammability of infected tissue. Fuel composition was similar among the uninfected and infected plots at Crater Lake before and after the prescribed fire treatment. Fire behavior was similar in uninfected and infected plots, but infected plots tended to burn hotter and for less time with temperatures statistically related to fine fuels (duff and litter). Chamber burn experiments revealed that moderate intensity fires consume larger proportions of tissue in brooms than in comparable uninfected branches, but the majority of biomass lost during burns appears to consist of needles.

The Crater Lake plots suffered relatively high mortality rates (35%) following prescribed fire treatments and mistletoe appears to influence postfire mortality of mature ponderosa pine. Mortality among all trees did not differ between infected and uninfected plots, but the majority of mature sample trees that were killed or severely damaged during prescribed fire treatments were infected (5 of 7 trees). It is difficult to assign a specific cause of death. The dead and damaged trees experienced greater stem char and show evidence of post-fire beetle attack, indicating that mistletoe may interact with other mortality agents. Long-term monitoring of tree mortality and regeneration at the study site may increase our understanding of the effects of mistletoe infection, both direct and indirect.

Additional fuel composition and fire behavior data are needed from other mature stands of infected ponderosa pine, particularly from those rare communities where disturbance regimes are relatively natural. Future research also will need to address the difficulties in assessing the mistletoe infection history of mature host trees. More accurate estimates of infection histories will allow researchers to investigate interactions between mistletoe and other disturbance agents such as fire, and assess the role of mistletoe in the successional pathways of host stands.

Climate Response

I investigated host trees to determine how infection influences individual host tree growth in response to climate variation, which may explain how mistletoe ultimately alters fuel accumulation. Mature ponderosa pine trees infected with dwarf mistletoe are more responsive to climate variation, as demonstrated in higher mean sensitivities and stronger correlations with moisture availability. Infected trees grow faster than uninfected individuals during years with high moisture availability and slower in years with low moisture. Major wildfire years tend to occur during droughts that follow warm and wet periods, which allow for rapid growth of fine fuels. Host trees could be benefiting from infection when moisture is not limiting growth, resulting in the addition of needle biomass that contributes to fine fuel accumulation when the climate shifts to a dry period.

It is unclear if the climate response of other mistletoe-host combinations follows the same pattern or if younger infected ponderosa pine trees respond to climate in the same way as my old-growth sample. Additional information about the influence of mistletoe infection on host response to moisture and temperature variation would help us generate more accurate models of the effects of climate change on vegetation in western North America.

Conclusions

It is difficult to assess the historical role of mistletoe on fire behavior because of a lack of reliable methods to quantify infection histories for a given tree or stand or identify surface fire frequency. Low intensity surface fires consume fine fuels without leaving scars on residual trees or resulting in regeneration pulses that can be dated. Methods exist for identifying the timing and spatial extent of punctuated disturbance events, such as fire, insect outbreak, or wind throw, but chronic disturbances such as dwarf mistletoe infection are more difficult to assess within an historical context.

This research fills a gap in quantitative research on the role of dwarf mistletoe in community ecology. My findings contribute to our understanding of the interactions between two disturbance agents that shape the structure and function of ponderosa pine communities in central Oregon. While my conclusions are constrained by a limited data set resulting from inadequate areas of infected old-growth ponderosa pine in the Pacific Northwest, problems obtaining accurate fuel loads at an appropriate scale, and the difficult logistics involved with implementing prescribed fire treatments, it is clear that the effects of mistletoe span multiple spatial and temporal scales. My results indicate that dwarf mistletoe infection has a significant, but minimal and largely unpredictable influence on the fire ecology of old-growth ponderosa pine stands. My results challenge the largely qualitative and unsubstantiated view that dwarf mistletoe exacerbates fire hazard and intensity and highlight the need for more research to quantify the link between fire behavior and mistletoe infection.

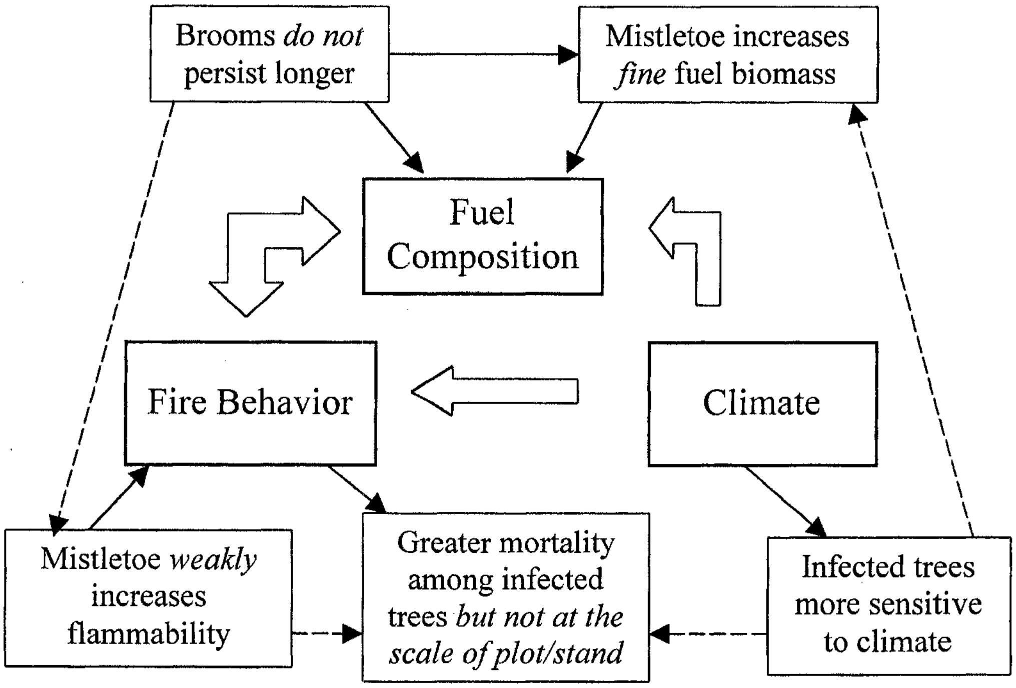

Figure 7.1: Conceptual diagram of the relationships among my five hypotheses and the results of my research. *Italics* represent changes to the original hypotheses as stated in Chapter 1, and dashed lines represent potential relationships revealed by the study results.

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