

THESIS

COMPLEX INTERACTIONS BETWEEN DWARF MISTLETOE, FUEL LOADING, AND FIRE IN
THE LODGEPOLE PINE DOMINATED FORESTS OF CENTRAL COLORADO

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ABSTRACT

COMPLEX INTERACTIONS BETWEEN DWARF MISTLETOE, FUEL LOADING, AND FIRE IN THE LODGEPOLE PINE DOMINATED FORESTS OF CENTRAL COLORADO

Lodgepole pine dwarf mistletoe (*Arceuthobium americanum* Nutt. ex Engelm) is an obligate hemiparasite that infects lodgepole pine (*Pinus contorta* Dougl. Ex. Loud) throughout the large majority of lodgepole pine's range. Lodgepole pine dwarf mistletoe increases mortality rates, alters tree biomass distributions, and slows overall tree growth, which results in substantial losses to stand productivity and wood quality. In lodgepole pine dominated forests, dwarf mistletoe and wildfire are fundamental disturbances that may interact with each other in complex ways. This interaction is bidirectional as wildfire can either positively or negatively affect post-fire dwarf mistletoe populations, and pre-fire dwarf mistletoe populations may influence wildfire severity. Though it has long been assumed that dwarf mistletoe increases potential wildfire severity in lodgepole pine forests through modifications to the fuels complex, empirical data to support this conclusion is lacking. The overall goal of this project was to enhance the understanding of both sides of the fire-dwarf mistletoe interaction through a combination of long-term post-fire data, forest measurements, and simulation of dwarf mistletoe impacts and intensification.

Chapter one provides background into dwarf mistletoe biology and pathology, and reviews the existing literature on interactions between fire and dwarf mistletoe. The second chapter documents the results of research into the influence of dwarf mistletoe infestation level on stand structure and fuel parameters that influence potential fire

behavior. To evaluate the relationship between infestation severity and stand structure and forest fuels plots were randomly located within stands containing a range of dwarf mistletoe infestation severities. Of primary interest were impacts to canopy base height and the loading of fuels both on the forest floor and in the canopy. Chapter three is a case study documenting the impact of three prescribed crown fires on dwarf mistletoe populations thirty years post-fire. These fires burned across a range of mortality levels allowing for a detailed evaluation of the influence of fire severity on dwarf mistletoe populations. This chapter combines field measurements with forest growth and yield simulations from the United States Forest Service's Forest Vegetation Simulator to understand longer-term impacts to both the dwarf mistletoe population and stand productivity.

Field data from randomly located plots indicate that dwarf mistletoe may have conflicting impacts on parameters influencing crown fire potential and wildfire severity. This finding suggests that the impact of dwarf mistletoe infestation on potential wildfire severity may not conform to the positive linear relationship assumed by many forest pathologists. Infestation level was found to have a strong positive relationship with the loading of surface fuels of all sizes, and was negatively related to canopy base height, and calculated canopy fuel load and canopy bulk density. Impacts to stand structure include significant reductions to live basal area and average tree size, and significant increases to the density and basal area of standing dead trees. The results from the long-term post-fire data set provide experimental evidence showing that fire severity negatively influences future dwarf mistletoe populations, and that long-term population reductions are possible without complete stand replacement. Over multiple fire cycles, feedbacks between fire and

dwarf mistletoe may enhance heterogeneity in burn patterns, infestation severity, and stand structures across the landscape.

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1. LODGEPOLE PINE DWARF MISTLEOTE: BIOLOGY, PATHOLOGY, AND INTERACTIONS WITH WILDFIRE

1.1 INTRODUCTION

Lodgepole pine (*Pinus contorta* Dougl. Ex. Loud) is widespread throughout the Rocky Mountain and Pacific Coast regions covering approximately 65 million acres in the United States and Canada (Lotan and Critchfield 1990). The species is divided into four geographically distinct varieties which hybridize where their ranges overlap (Wheeler and Guries 1982), however this study will be focused only on the inland variety known as Rocky Mountain lodgepole pine (*Pinus contorta* var. *latifolia*) whose range extends from southern Colorado up through the Rocky mountains and into British Columbia and Alberta (Figure 1; Lotan and Critchfield 1990). Within these widespread lodgepole pine dominated forests, wildfire is a fundamental disturbance influencing forest structure, stand dynamics, and landscape scale processes (Romme 1982, Lotan et al. 1985, Agee 1996). Lodgepole pine has generally been associated with high severity, stand replacing fires as it produces serotinous cones, regenerates prolifically following fire and, in many areas, exists as a mosaic of single age, fire initiated stands across the landscape (Romme 1982, Lotan et al. 1985). On more xeric sites, lodgepole pine can form self-replacing communities (Peet 1981), and can exist as part of a low to mixed severity fire regime with frequent surface fires resulting in persistent, multi-aged stands (Arno 1980, Stuart et al. 1989, Barrett et al. 1991, Amoroso et al. 2011, Heyerdahl et al. 2014). It is also important to note that even within fire perimeters typically labeled as ‘high severity’, there is a large amount of heterogeneity in fire effects that will increase diversity in stand structures and ages across the landscape (Turner et al. 1994). In the absence of subsequent stand-replacing fire

events, lodgepole pine is typically replaced by more shade tolerant species including Englemann spruce (*Picea engelmannii* Parry ex Engelman), subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.), and by Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) depending on the elevation and moisture conditions (Peet 1981, Lotan et al. 1985, Sibold et al. 2007).

Wildland fuel conditions are an important control of fire spread and behavior and in recent years there has been a large emphasis on understanding disturbance interactions and the influence of various forest disturbances on wildland fuels. For example, there has been much concern with regard to the impacts of epidemic populations of mountain pine beetle (*Dendroctonus ponderosae*) on forest trajectories (Sibold et al. 2007, Diskin et al. 2011, Pelz and Smith 2012), wildland fuel complexes (Page and Jenkins 2007, Klutsch et al. 2009, Pelz et al. 2015), and potential wildfire behavior (Simard et al. 2011, Hoffman et al. 2012, Jenkins et al. 2012, Schoennagel et al. 2012) within the lodgepole pine dominated forest of the Central Rockies. While mountain pine beetle mortality is an undeniably important disturbance in these forests, another significantly important disturbance agent that has received relatively little study into its interactions with fire, fuel complexes, and forest structure is lodgepole pine dwarf mistletoe (*Arceuthobium americanum* Nutt. ex Engelm, hereafter LPDM).

LPDM is the most damaging pathogen affecting all varieties of lodgepole pine and is present in 40-50% of stands throughout the vast majority of the tree's expansive range (Bolsinger 1978, Drummond 1982, Hawksworth and Dooley 1984, Kipfmüller and Baker 1998; Figure 1). LPDM is an obligate hemiparasite that derives its required energy and nutrients from the host (Hull and Leonard 1964a, Hull and Leonard 1964b), causing reductions in growth rate, seed production, and wood quality, as well as alterations to

individual-tree biomass distribution (Hawksworth and Dooley 1984, Wanner and Tinnin 1989, Hawksworth and Wiens 1996). Impacts to individual trees result in both direct and indirect impacts to stand structure and function as well as wildlife habitat quality (Hawksworth and Wiens 1996). It has often been suggested that dwarf mistletoes (*Arceuthobium spp.*) will enhance potential fire behavior as a result of increases in surface woody debris and vertical fuel continuity, however quantitative data across a range of infestation severities is lacking (Alexander and Hawksworth 1975, Lotan et al. 1985, Conklin and Armstrong 2001). In addition to dwarf mistletoes potentially influencing fire behavior, fires have the ability to alter dwarf mistletoe populations (Baranyay 1970). Observational studies have shown that fire history can be useful in predicting landscape scale patterns of LPDM infestation and suggest that the interaction between LPDM and fire plays an extremely important role in the ecology of the lodgepole pine forest type (Kipfmueller and Baker 1998).

The goal of this project was to increase our understanding of the LPDM-fire relationship by evaluating both the impact of LPDM infestation on fuels and overall forest structure and the impact of fire severity on LPDM populations. This was accomplished through a combination of long-term data, forest measurements, and simulations of LPDM impacts and intensification.

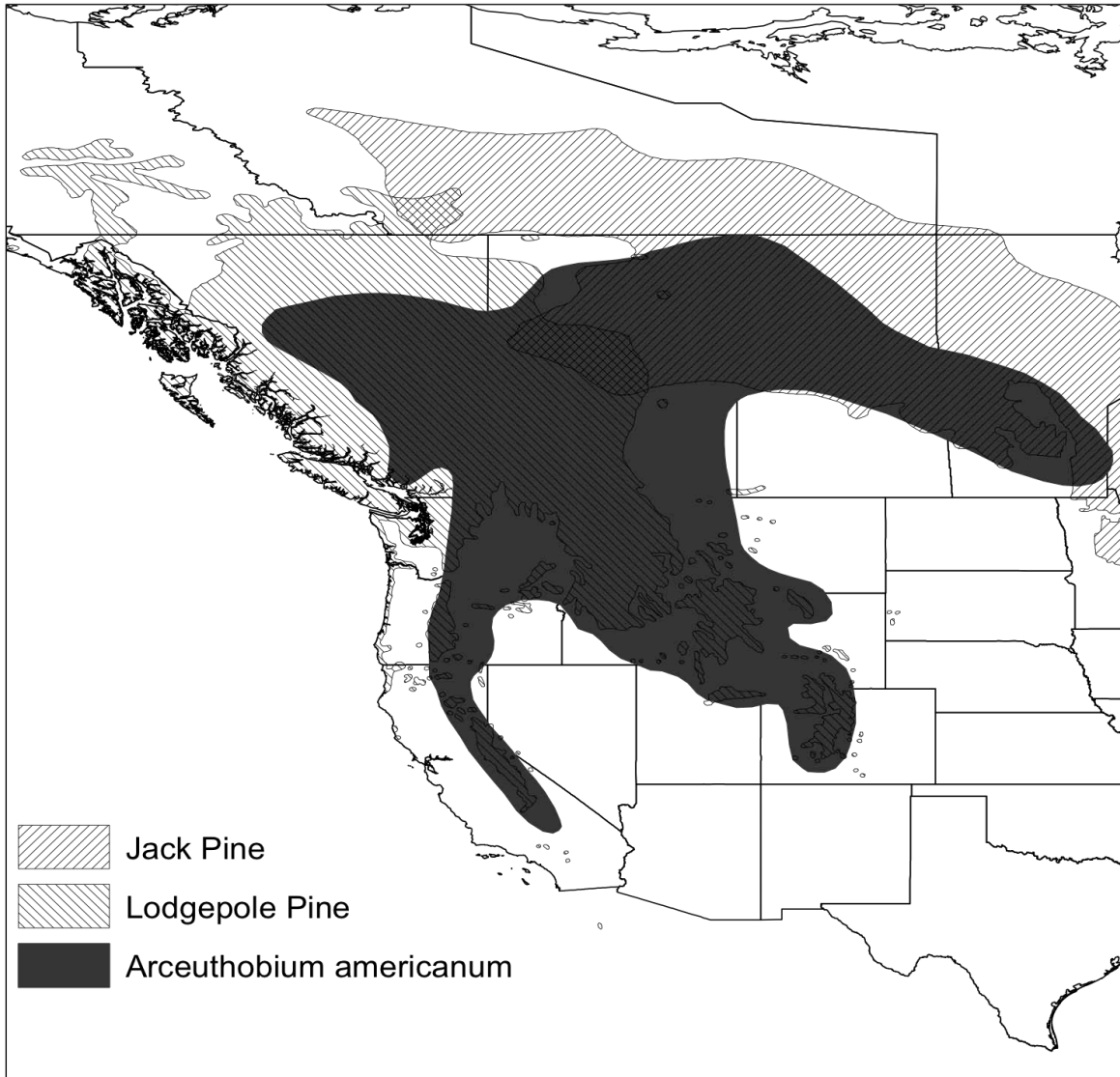


Figure 1. Range map showing the extent of lodgepole pine, jack pine, and lodgepole pine dwarf mistletoe in the Western United states (Lodgepole pine and jack pine ranges from Little 1971, lodgepole pine dwarf mistletoe range redrawn from Hawksworth and Weins 1996).

1.2 DWARF MISTLETOE BIOLOGY

LPDM is a hemiparasitic, dioecious flowering plant that occurs throughout much of the range of lodgepole pine. However, it is not present at the upper latitudinal and elevational limits of lodgepole pine due to extremely low temperatures, which kill LPDM

fruits prior to maturation and seed dispersal (Hawksworth 1956, Smith and Waas 1979, Hawksworth and Wiens 1996; Figure 1). Other dwarf mistletoes (*Arceuthobium spp.*) share this temperature limitation with a recent study in western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) forests infected with hemlock dwarf mistletoe (*Arceuthobium tsugense* (Rosend.) G.N. Jones) identifying a strong climatic limitation to the spread of *A. tsugense* within the range of the host tree (Barrett et al. 2012). This shared climatic limitation suggests that a warming climate may allow dwarf mistletoes to expand into areas previously limited by cold temperatures, however a major limitation to this potential range expansion is dwarf mistletoe's long life cycle and short seed dispersal distance.

Dwarf mistletoes disperse their seeds through the hydrostatic, explosive discharge of viscous seeds from fruits that ripen in the fall (Hawksworth and Wiens 1996). It was recently demonstrated that LPDM induces this explosive discharge via thermogenesis, implying that seed dispersal is triggered as a result of endogenous heat production within the fruit (DeBruyn et al. 2015), rather than solely through passive increases to internal water pressure due to external forces such as atmospheric temperature as previously believed (Hinds et al. 1963). These discharged seeds are covered in a viscous coating (viscin) that allows them to adhere to the needles of a susceptible host and are expelled at nearly 25 m s^{-1} , enabling them to travel up to 10 to 15 meters (Hinds et al. 1963). Though this explosive discharge can expel seeds reasonably far, average horizontal spread rates through stands are slow as the crowns of the host tree and those immediately adjacent to it intercept the vast majority of discharged seeds (Hawksworth and Wiens 1996). In addition, dwarf mistletoes have a long life cycle, requiring an average of 3-5 years from germination to seed dispersal, limiting the rate at which they can spread (Hawksworth and Wiens

1996). Reported horizontal spread rates in even-aged stands are 0.5m per year for open stands and 0.4m per year for closed stands (Hawksworth and Johnson 1989). Rates of spread are generally faster in uneven-aged stands as expelled seeds are less likely to intercept an adjacent tree crown allowing them to travel further before landing on a susceptible tree in the understory (Parmeter 1978). Due to this slow average rate of spread dwarf mistletoes are often aggregated at the scale of individual trees and small patches of trees (Reich et al. 1991, Shaw et al. 2005, Swanson et al. 2006). This aggregated pattern of infestation is also apparent at the landscape scale (Kipfmüller and Baker 1998). Though long-range transport by birds and small mammals has been documented, it seems to be a fairly rare occurrence (Hulder 1979, Punter and Gilbert 1989, Nichols et al. 1991). This is in contrast to true mistletoes, which do not have an explosive mechanism for seed dispersal and are instead wholly reliant on birds to disperse their seeds (Reid et al. 1995).

Once a seed lands on a host needle, rain and gravity will cause the seed to slide to the base of the needle where the seed's viscous coating (viscin) will dry, firmly adhering it to the needle. The seed overwinters on the needle and germination occurs the following spring. It will then penetrate the host branch with parasitic hyphae or cortical strands, which grow both longitudinally and circumferentially through the inner bark. From these cortical strands dwarf mistletoe's endophytic system penetrates the cambium with "sinkers" that grow radially into the branch and are successively embedded within each year's radial branch growth. These "sinkers" extract water, carbon, and nutrients from both the phloem and xylem of the host tree. The infection will progress within the host tissue, but symptoms are generally not apparent for 2 to 5 years after initial infection (Hawksworth and Wiens 1996). The first symptom of infection is the swelling of host tissue

prior to the emergence of the only external sign of infection: the male and female shoots. Flowering and pollination occurs between April and June, with fruit development and maturation occurring over the subsequent 16 months leading to fruit ripening and seed dispersal in August and September (Hawksworth and Wiens 1996).

Swelling usually occurs on infected branches, but infections close to or within the bole can cause stem swelling that significantly reduces wood quality and can result in girdling of the tree (Hawksworth and Wiens 1996). In addition to branch swelling, which can occur as a result of either systemic or localized (non-systemic) infections, systemic infections typically result in the formation of dense, abnormal branches commonly known as witches' brooms (Tinnin 1982). Systemic infections occur when the dwarf mistletoe endophytic system elongates along with the host plant's primary growth (acropetal spread) resulting in infection within the entire branch structure distal to the initial infection site. The resulting witches' brooms are comprised of extreme shoot elongation and branching, are often extremely resinous, and are especially common on for the *P. contorta* – *A. americanum* (LPDM) host-parasite combination (Hawksworth and Wiens 1996).

Dwarf mistletoes are entirely reliant on the host tree to survive and reproduce, but are classified as a hemiparasites as they are capable of some level of photosynthetic activity (Hull and Leonard 1964a, 1964b). In terms of water relations, foliage from branches infected with *A. campylopdum* have reduced water use efficiency (Sala et al. 2001), and other work has found that *A. tsugense* plants have far higher transpiration rates than host needles (Tocher et al. 1984). Taken together these findings suggest that infected trees will be more susceptible to drought stress due to disproportionate water use by both dense

witches' brooms and the dwarf mistletoe plants themselves. This is further supported by work that shows that LPDM maintains these high transpiration rates during periods of water stress, allowing the parasite to extract water and dissolved nutrients from the host regardless of dry conditions (Mark and Reid 1971). Reports of mortality of infected trees have also suggested that dwarf mistletoe caused mortality is more prevalent on drier sites than wetter ones (Hawksworth and Hinds 1964).

1.3 IMPACTS OF DWARF MISTLETOE

1.3.1 Impacts to individual trees

Individual trees infected with dwarf mistletoe suffer decreased rates of radial and height growth, reduced cone production, losses to wood quality, and increased mortality rates (Wanner and Tinnin 1989, Hawksworth and Wiens 1996). Rates of mortality are particularly high for young trees that become infected, with one study on young ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) infected with *A. campylopodum* reporting 50% mortality after 12 years (Roth 1971). Studies on stands of mature lodgepole pine showed that the ten-year mortality rate was 8% higher for highly infected trees (Dwarf mistletoe rating = 6; Hawksworth 1977) than uninfected trees (Hawksworth et al. 1995).

A primary impact of LPDM on lodgepole pine trees is the formation of the previously discussed witches' brooms as a result of systemic branch infections (Hawksworth and Wiens 1996). Witches' brooms are comprised of dense branching, are often extremely resinous, and may be retained lower on the stem than would be typical for the self-pruning lodgepole pine (Wicker and Leaphart 1976, Godfree et al. 2002). They significantly alter

tree architecture and biomass distribution by diverting biomass accumulation from diameter and height growth to infected branches (Wanner and Tinnin 1986, Godfree et al. 2002). This abnormal growth pattern alters the ratio of bole to branch mass with one study on LPDM induced witches' brooms reporting a ratio of 3.8:1 in lightly infected individuals compared to 1.6:1 in highly infected trees (Wanner and Tinnin 1986). This altered biomass distribution is partly responsible for losses seen in wood volume development, and may have implications for the risk of torching if infected trees are subjected to fire (Alexander and Hawksworth 1975, Tinnin et al. 1982). Witches' brooms also create more heterogeneous canopies and provide unique structures that are important to a variety of wildlife taxa (Tinnin et al. 1982, Mathiasen 1996, Parks et al. 1999, Marshall et al. 2003, Garnett et al. 2006).

Dwarf mistletoe may also alter individual tree defenses, which has important implications for tree resistance to other pathogens and insects (Hawksworth and Wiens 1996). In particular, dwarf mistletoe infection has been associated with increased susceptibility to bark beetle mortality (*Ips pini*, Kenaley et al. 2006, 2008; *Dendroctonus ponderosae*, Johnson et al. 1976, McCambridge et al. 1982). A recent study in jack pine (*Pinus banksiana*) suggests that this relationship is highly complex and needs further research as dwarf mistletoe infections alter the survival of both *D. ponderosae* larva as well as the survival of wood-boring beetles (Coleoptera: Curculionidae) that compete with *D. ponderosae* (Klutsch et al. 2016). It has also been suggested by Agne et al. (2014) that increases to stand structural heterogeneity associated with dwarf mistletoe infestation may increase the resilience of infested stands to epidemic outbreaks of *D. ponderosae*.

Understanding the complex interactions between bark beetles and dwarf mistletoes has

important implications for both stand trajectories (Agne et al. 2014) and surface fuel accumulations (Kenaley et al. 2006, Klutsch et al. 2014) and merits further research.

1.3.2 Impacts to stands

At the stand level, dwarf mistletoe associated impacts to rates of growth and mortality result in reduced live basal area, canopy volume, and height of dominant trees (Godfree et al. 2002, 2003a), and increased densities of snags, seedlings, and proportion of trees in the suppressed canopy class (Bennetts et al. 1996, Hoffman et al. 2007, Agne et al. 2014). In general, infestation by LPDM has been associated with substantial increases to the density of live trees that is often primarily driven by increases to the number of trees in smaller size classes (Hawksworth and Hinds 1964, Tinnin 1984, Wanner and Tinnin 1989, Godfree et al. 2003a). One study in Oregon suggests that highly infested stands may have increased densities due to alterations to the regeneration environment resulting from reduced resource use by large trees, increased light availability at the forest floor, and increased microsite availability due to a greater quantity of downed branches (Wanner and Tinnin 1989).

These indirect effects on stand structure generally result in stands that are more vertically heterogeneous with larger number of age classes present (Hawksworth and Johnson 1989, Hawksworth and Wiens 1996). Dwarf mistletoes also increase heterogeneity through the formation of infestation centers around infected trees from which the parasite expands outward into the rest of the stand (Shaw et al. 2005, Swanson et al. 2006). These infestation centers cause the distribution of infected trees within a stand to be highly aggregated (Reich et al. 1991). This spatial pattern may result in small patches

of mortality within an otherwise unaffected stand, however, as the infection centers expand they will begin to coalesce eventually resulting in a completely infected stand. The distribution of dwarf mistletoe infestations is also patchy at the landscape scale with infestation patterns of LPDM largely being driving by fire history (Kipfmüller and Baker 1998).

1.3.3 Impacts to surface fuels

Another potential impact of dwarf mistletoe infestation is increasing surface woody debris mass. While dwarf mistletoe has also long been assumed to increase the amount of woody debris on the forest floor (e.g. Weir 1916, Brown 1975, Alexander and Hawksworth 1975), published quantitative data on the impacts of LPDM in lodgepole pine dominated systems is lacking. Some data is available from research on infection by either *A. vaginatum* or *A. campylopodum* in ponderosa pine dominated systems in Arizona (Hoffman et al. 2007) and Oregon (Koonce and Roth 1985, Stanton and Hadley 2010). This work has shown that increased stand level infestation severity results in significantly increased surface woody debris in finer fuel classes, < 7.62 cm (Koonce and Roth 1985, Hoffman et al. 2007, Stanton and Hadley 2010). However, the results from these studies varied with regards to the relationship between dwarf mistletoe infestation severity and the loading of coarse dead down and dead woody fuel (> 7.62cm diameter). Hoffman et al. (2007) found a positive relationship between coarse fuel and infestation severity, Koonce and Roth (1985) reported a negative relationship, and Stanton and Hadley (2010) found no relationship between dwarf mistletoe infestation severity and coarse fuel loads. These conflicting findings may be the result of differences between these study areas including stand age,

management history, the proportion of ponderosa pine basal area, and the region in which they were conducted. More research across a range on infestation severities and host-parasite combinations is needed to better understand the relationship between dwarf mistletoes and surface fuel complexes.

Characterizing the effects of dwarf mistletoe on fuel (otherwise known as woody debris) accumulation is critical not only because woody debris on the forest floor drives fire behavior (Rothermel 1972), but because it influences nutrient cycling (Harmon et al. 1986), increases microbial activity (Busse 1994), is an important global carbon pool (Turner et al 1995, Woodall et al. 2013), and provides habitat for a variety of organisms including small mammals, invertebrates, fungi, and plants (Harmon et al. 1986, Loeb 1999, Butts and McComb 2000, Bull et al. 1997). Coarse woody debris (>7.62 cm), both standing and downed, is particularly important ecologically as it provides irreplaceable structural features essential for nesting, forage, and shelter for a wide range of species (Harmon et al. 1986, Bull et al. 1997, Bull 2002). As the ecological importance of woody debris has become increasingly recognized over the past several decades (Harmon et al. 1986, Woodall et al. 2013) a need exists to better understand the interaction between dwarf mistletoe and woody debris dynamics in the lodgepole pine dominated forests that cover some 26 million hectares in North America (Lotan and Critchfield 1990).

1.3.4 Impacts to canopy fuels

Dwarf mistletoes have also been associated with alterations to the loading of available canopy fuels through impacts to the amount and vertical distribution of these fuels (e.g. Weir 1916, Brown 1975, Wicker and Leaphart 1976, Koonce and Roth 1985,

Godfree et al. 2002). These proposed alterations may be the result of both direct impacts due to the formation of witches' brooms in tree crowns (e.g. increased crown length, increased crown biomass; Koonce and Roth 1985, Wanner and Tinnin 1986, Harrington and Hawksworth 1990, Godfree et al. 2002) and indirect impacts to stand structure (e.g. increased densities of small trees in the understory; Tinnin 1984, Wanner and Tinnin 1989, Godfree et al. 2003a). Some quantitative work has shown that infected trees have reduced crown base height (Koonce and Roth 1985) and increased canopy biomass (Wanner and Tinnin 1986), and that infested stands have more biomass in the lower canopy (Koonce and Roth 1985, Godfree et al. 2002).

However, the implications of these findings for potential fire behavior are complex as increases to crown biomass occur primarily in larger diameter branch wood (>7.62 cm) and fuels of this size are not typically thought to contribute to crown fire initiation and spread (Scott and Reinhardt 2002). It is also not clear whether these impacts will increase the stand level canopy fuel loading as small trees hold less crown biomass (Brown 1978) and infested stands tend to have smaller trees (Wanner and Tinnin 1989, Agne et al. 2014). In addition, increases to the total crown biomass of individual trees due to witches' broom formation may be offset by reductions to crown biomass in other infested trees in the stand due to the reduced mass observed in leaves and twigs distal to infections and the substantial levels of crown dieback often seen in infected trees (Broshot et al. 1978, Tinnin and Knutson 1980, Meinzer et al. 2004, Mathiasen et al. 2008). Overall, more research is needed to understand how dwarf mistletoe influences the length of individual tree crowns, the accumulation and distribution of biomass within these crowns, and how changes to both individual trees and stand structure alter stand level canopy fuel loads. It will also be

important to test for differences between host-parasite combinations, as there are substantial differences in tree responses and witches' broom formation depending on the particular host-parasite species combination (Tinnin 1982).

1.3.5 Ecological impacts

While these tree and stand level impacts negatively influence timber volume production, dwarf mistletoes provide many positive habitat benefits for a host of wildlife species. Dwarf mistletoe plants provide direct benefits as food for insects, birds, and small and large mammals, which consume the plant tissue and fruits (Hawksworth and Wiens 1996). Indirect benefits result from structural impacts associated with dwarf mistletoe infection (witches' brooms, snags) that can provide ideal nesting and foraging sites for birds (Bennetts et al 1996, Bull et al. 1997, Hedwall and Mathiasen 2006, Ganey et al. 2013) and small mammals (Parks et al. 1999, Tinnin and Forbes 1999, Garnett et al. 2006, Hedwall and Mathiasen 2006, Hedwall et al. 2006). As discussed above, alterations to surface woody debris mass also provides benefits for wildlife, particularly small mammals. Additionally, stand opening as a result of tree mortality may have benefits to large mammals including mule deer and elk (Bennetts et al. 1991, Hawksworth and Wiens 1996). Some researchers have suggested that mistletoes are a keystone species as their effects on ecosystem structure and function are disproportionate to their biomass (Watson 2001, Press and Phoenix 2005, Mathiasen et al. 2008).

1.4 WILDFIRE AND DWARF MISTLETOE INTERACTIONS

Fire is an important disturbance agent in all Western forest types commonly affected by dwarf mistletoe and due to the obligate nature of the parasite, when an infected tree is killed by fire the associated dwarf mistletoe plants will also be killed. For this reason, wildfire is considered the largest natural factor influencing the density and distribution of dwarf mistletoe populations in the Western United States (Baranyay 1970, Wicker and Leaphart 1976, Alexander and Hawksworth 1975). Several studies have shown that fire frequency and time since fire are important predictors of dwarf mistletoe infestation intensities (Zimmerman and Laven 1984, Kipfmüller and Baker 1998). The impact of fire on dwarf mistletoe populations can be either positive or negative depending on the context and severity of the fire (Baranyay 1970, Alexander and Hawksworth 1975, Conklin 2000). For example, when a fire burns at high severity and kills all infected overstory trees it will have a sanitizing effect on the stand with the only possibility of infection coming from either long range seed transport via animal vectors or the slow progressive spread from infested peripheral stands (Alexander and Hawksworth 1975, Hawksworth and Wiens 1996). Alternatively, fires that burn at lower severities, allowing some infected trees to survive, may result in a more highly infested future stand as the remaining infected trees will rain seeds down onto any regeneration, thereby resulting in extremely high rates of infection (Hawksworth and Wiens 1996). Fires may also promote dwarf mistletoe at the landscape scale by increasing the prevalence of susceptible, early seral host species that regenerate well following fire, such as lodgepole pine (Alexander and Hawksworth 1975).

Based on this understanding of the relationship between fire and dwarf mistletoe populations, researchers have long suggested the use of prescribed fires to reduce dwarf mistletoe infestation severities or regenerate new stands free from infection (Weir 1916, Alexander and Hawksworth 1975, Zimmerman and Laven 1990). More recently attempts have been made to utilize surface fires in infested ponderosa pine stands to scorch infections in lower crowns, thereby reducing stand level infestation severities (Koonce and Roth 1980, Harrington and Hawksworth 1990, Conklin and Armstrong 2001, Conklin and Geils 2008). Scorch pruning is particularly effective because trees tend to have larger numbers of dwarf mistletoe plants in the lower crown, and therefore scorching of the lower crown will remove a disproportionately large amount of dwarf mistletoe from the stand (Conklin and Armstrong 2001, Baker and Guyon 2010). In addition, infected trees are killed more readily than uninfected ones as they are more likely to torch due to the presence of witches' brooms low on the bole and are more susceptible to fire mortality as a result of dwarf mistletoe induced stress (Conklin and Geils 2008). While these studies into prescribed fire effects report short-term reductions in infestation severity (Koonce and Roth 1980, Harrington and Hawksworth 1990, Conklin and Armstrong 2001, Conklin and Geils 2008), they do not provide data on the effect of prescribed fires on infestation severity across longer time scales, which is imperative to understand the true effect of fire on dwarf mistletoe populations. Additionally, nearly all documented uses of prescribed fire to reduce dwarf mistletoe populations were prescribed surface fires in ponderosa pine dominated forests, with very little experimental work occurring on the influence of crown fires. With a growing push from forest ecologists to restore natural fire regimes and reduce stand and landscape scale fuel loadings, it will be important to better understand the

influence of all types of fire on dwarf mistletoe populations in both the short and long terms.

In addition to fires influencing dwarf mistletoe populations, it has also long been thought that dwarf mistletoe populations have the ability to alter fire behavior by increasing the chance of individual tree torching and crown fire initiation in heavily impacted stands (Alexander and Hawksworth 1975, Brown 1975, Lotan et al. 1985). The proposed mechanism for this increase is two-fold. First, it has been suggested that highly infested stands will have increased surface fuel loading due to enhanced rates of mortality and breakage of infected branches (Brown 1975). Second, it is thought that infected trees have lower crown base heights due to the retention of witches' brooms lower on the bole than would be typical for healthy branches (Wicker and Leaphart 1976, Godfree et al. 2002). While surface fuel loading and canopy base height are two key variables in predicting crown fire risk (along with fuel moisture and wind speed), more quantitative data is needed to fully understand dwarf mistletoe's impacts to these important fuel complexes and the implications of such changes for potential fire behavior.

Though there are no published studies that link dwarf mistletoe infestation to surface fuel loadings in lodgepole pine dominated forests, there has been some work, discussed above, in ponderosa pine systems. In terms of dwarf mistletoe impacts to tree crowns, some research has suggested that witches' brooms in the lower crown result in reduced crown base height (Godfree et al. 2002), and that the amount of foliage and fuel close to the forest floor has a positive relationship with dwarf mistletoe infestation intensity (Koonce and Roth 1985, Godfree et al. 2003b). It is, however, unclear whether these effects are the direct result of dwarf mistletoe infection or whether they are a result

of the structural impacts that infestation has on stands (e.g. reductions to density of dominate trees, altered light regimes). More quantitative data on the impacts of dwarf mistletoe infestations to these important fuel complexes are needed to evaluate potential impacts to fire behavior.

1.5 PROJECT GOALS

The overall goal of this project was to gain a better understanding of the mechanisms driving interactions between LPDM populations and wildfire in lodgepole pine dominated ecosystems. This interaction is bidirectional as fire severity can effect post-fire LPDM populations, and pre-fire LPDM populations may influence fire severity. To evaluate the influence of fire severity on future LPDM populations, three prescribed crown fires were resampled 30 years post-fire. Based on these data and growth simulations using the United States Forest Service's Forest Vegetation Simulator, the influence of fire severity on LPDM populations through time was evaluated. These simulations were also used to evaluate long-term impacts to stand growth and development. In order to test the potential impact of LPDM infestation on stand structure and the fuels complex, pure lodgepole pine stands infested by LPDM were sampled. Of primary interest was the relationship between dwarf mistletoe infestation severity and surface and canopy fuel loads as these parameters are primary drivers of potential fire behavior. By combining these two lines of inquiry a more complete understanding of interrelationships between wildfire and dwarf mistletoe can be achieved.

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2. IMPACTS OF LODGEPOLE PINE DWARF MISTLETOE (*ARCEUTHOBIMUM AMERICANUM*) INFESTATION OF STAND STRUCTURE AND FUEL LOAD IN LODGEPOLE PINE DOMINATED FORESTS IN CENTRAL COLORADO

2.1 INTRODUCTION

Parasitic plants, though often overlooked in community ecology theory, can have ecological effects vastly disproportionate to their relative biomass (Press and Phoenix 2005). Parasitic plants directly affect host physiology and in turn alter community biomass, structure and composition, as well as disturbance regimes (Press and Phoenix 2005, Parker et al. 2006). Dwarf mistletoes (*Arceuthobium spp.*) are a group of obligate hemiparasites that infect trees in the Pinaceae and Cupressaceae families, including many important conifer species in Western North America. While dwarf mistletoes affect a number of North American conifers, one important host-parasite combination is that of lodgepole pine (*Pinus contorta* Dougl. Ex. Loud) and lodgepole pine dwarf mistletoe (*Arceuthobium americanum*; hereafter LPDM). LPDM is estimated to be present in 40 to 60% of stands across the expansive range of lodgepole pine (Bolsinger 1978, Drummond 1982, Hawksworth and Wiens 1996, Kipfmüller and Baker 1998). Although dwarf mistletoes are considered a pest in many western forests, these species may also act as keystone resources due to direct benefits as a wildlife food source, as well as structural effects which alter community level patterns and processes (Hawksworth and Wiens 1996, Watson 2001).

Dwarf mistletoes impact forest structure and ecosystem function through direct effects on individual trees, which suffer reduced growth and increased mortality (Hawksworth and Hinds 1964, Wanner and Tinnin 1989, Hawksworth and Wiens 1996).

Infected trees may also develop systemic infections that cause abnormal branch structures, known as witches' brooms, which are comprised of extremely dense branching (Tinnin et al. 1982). These brooms result in alterations to the distribution of plant biomass by diverting plant resources from diameter and height growth to broom development and maintenance (Wanner and Tinnin 1986). At larger scales direct impacts to individual trees result in reduced productivity and biomass, increased snag densities, and altered stand structure (Wanner and Tinnin 1989, Hawksworth and Wiens 1996, Hoffman et al. 2007). Changes in stand structure in turn alter the habitat for wildlife, often resulting in increased biodiversity, and act upon the interactions among various disturbance agents (e.g. fire and dwarf mistletoe interactions, dwarf mistletoe and mountain pine beetle interactions, mountain pine beetle fire interactions) (Alexander and Hawksworth 1975, Hawksworth and Wiens 1996, Parker et al. 2006, Hicke et al. 2012, Agne et al. 2014, Hoffman et al. 2015, Klustch et al. 2016). Though a large body of work has been conducted into the impacts of dwarf mistletoes on the productivity of individual trees and timber stands (e.g. Weir 1916, Hawksworth and Hinds 1964, Baranyay and Safranyik 1970, Johnson et al. 1981, Drummond 1982, Mathiasen et al. 1986, Mathiasen et al. 1990), less research exists into their influence on community structure and interactions with other disturbance agents.

A number of disturbance agents can impact forest structure, stand dynamics, and landscape scale processes within lodgepole pine dominated forests (Lotan et al. 1985, Lotan and Critchfield 1990). Although wildland fires are often thought to be the most important disturbance in this forest type, the interactions between dwarf mistletoe and fire may play an important role in these ecosystems (Lotan et al. 1985). Wildland fire directly influences dwarf mistletoe populations through mortality of infected hosts and the

subsequent alterations to stand structure and composition (Baranyay 1970, Wicker and Leaphart 1976). However, the direction and magnitude of this effect is directly dependent upon the severity of host mortality (Baranyay 1970, Wicker and Leaphart 1976). For example dwarf mistletoe populations can increase following a fire when large infected trees survive and quickly infect susceptible trees in the post-fire cohort (Baranyay 1970, Alexander and Hawksworth 1975, Wicker and Leaphart 1976).

Conversely, dwarf mistletoes may alter potential fire behavior and fire regimes as they can alter the magnitude, trend, and direction of fuel dynamics via three primary mechanisms; 1) alterations to the amount and distribution of biomass in individual trees, 2) alterations to stand development, and 3) increased rates of mortality (Alexander and Hawksworth 1975, Brown 1975, Wicker and Leaphart 1976, Wanner and Tinnin 1986). Dwarf mistletoe infestation impacts the amount and vertical distribution of available canopy fuels directly through increased mortality and the formation of witches' brooms, and indirectly through alterations to stand development including increased levels of regeneration and suppressed trees (Wanner and Tinnin 1986, Wanner and Tinnin 1989). In addition to altering the amount and distribution of canopy fuels, dwarf mistletoe infested stands are thought to have greater surface fuel loading compared to uninfested stands due to increased mortality rates of infected trees and the breakage of witches' brooms which redistribute canopy fuels to the surface fuel layer (Wicker and Leaphart 1976). However, the relationship among infected trees, dwarf mistletoe induced mortality, and fuel accumulation can be complex (Stanton and Hadley 2010). Several previous studies in ponderosa pine dominated forests have suggested that the magnitude of effects vary as a function of dwarf mistletoe severity and by fuel component and size (Koonce and Roth

1985, Hoffman et al. 2007, Stanton and Hadley 2010). The significance and magnitude of effects across a range of host-parasite combinations and site factors, including stand densities and physical environments, has not been well studied, and it is unknown if the magnitude and trend in effects between dwarf mistletoe severity and fuel loading are generalizable across all conditions and host-parasite combinations.

Understanding fuel conditions through space and time has important implications to fire managers, as it is the only component of the wildfire behavior humans can manipulate and directly impacts all aspects of fire behavior and effects (Keane 2013, Keane 2016). Just as landscape ecologists think of forested ecosystems as a shifting mosaic of patches characterized by differences in age, structure, disturbance history, and species composition, wildland fuel ecologists must also view the landscape as a heterogeneous mosaic of fuel conditions that are dynamic and changing through time. These mosaics of fuels impact the pattern, severity, and effects of a particular fire event, and their dynamics through time are an important bottom-up control of fire regimes (Whitlock et al. 2010, Keane 2016). As LPDM is an extremely important disturbance agent within the extensive lodgepole pine dominated ecosystems of North America, it is necessary to characterize its effect on local fuel conditions in order to better understand its role in landscape scale fuel dynamics.

The objectives of this study were to characterize the effect of LPDM severity on stand structure and fuel loading within lodgepole pine forests in central Colorado. More specifically we asked the following questions: (1) How does increasing LPDM infestation severity alter stand structure and snag density? (2) How does LPDM infestation severity relate to canopy fuel load, canopy bulk density, and canopy base height? (3) Does LPDM

infestation impact total surface woody debris, and are the impacts constant across surface fuel size classes?

2.2 METHODS

2.2.1 Study Area

This research was completed on the western flank of the Sawatch Range in the Gunnison National Forest's Upper Taylor River Basin (38°52'10" N, 106°32'30" W). The underlying geology of the Taylor River Basin is comprised of Precambrian granites and gneisses, which have been overlaid by sandy, well-drained glacial till (Johnson et al. 2001). The area has a typical high-elevation, continental climate with mean July temperatures of 14.1°C, mean January temperatures of -12.2°C, and an average of 46.4 cm of annual precipitation that has a slight peak during the late summer (WRCC, Monthly Tabular Data 2016).

Vegetation types in the basin follow a characteristic elevation sequence with sagebrush (*Artemisia tridentate* Nutt.) occurring at lower elevations (2800-3000m), moving into forested land dominated by rocky mountain lodgepole pine (*Pinus contorta* var. *latifolia*) at mid elevations (2900-3200m), before transitioning into Engelmann spruce (*Picea engelmannii* Parry ex Engelmann) - Subalpine fir (*Abies lasiocarpa* Hook. Nutt) forests, which extend to the alpine tree line at around 3400m (Johnson et al. 2001). The lodgepole pine dominated forests within the basin were established following stand replacing fire events in the middle to late 1800's and are similar to the fire initiated, monotypic, even-aged lodgepole pine forests found across the Southern and Central

Rockies (Parker and Parker 1994). There have been no documented outbreaks of mountain pine beetle (*Dendroctonus ponderosae* Hopkins) in the basin during the past century (Parker and Parker 1994, Colorado State Forest Service 2015).

2.2.2 Field Measurements

Sampling was completed within lodgepole pine dominated forests occurring on the generally west facing, shallow slopes of the western flank of the Sawatch Range to control for abiotic variables including soil type, slope, and aspect. A preliminary survey of the project area was conducted to locate lodgepole pine stands that originated between 1850 and 1880, contained a range of dwarf mistletoe infestation severities, and showed no signs of other natural disturbances or recent management. These selection criteria were intended to limit as many sources of variability as possible in order to isolate the effect of dwarf mistletoe infestation on stand structure and fuel loadings.

In total, fifty-five plots were sampled within three 15 to 30 hectare sites that matched our selection criteria. Plots were randomly located within each site by first walking a random azimuth and distance from the site edge. Subsequent plots were located by walking a random azimuth and distance from the previous plot center and could not be within 30 meters of an existing plot edge. At each site at least four 20 m by 20 m overstory plots were sampled in each of four dwarf mistletoe infestation severity classes based on the plot dwarf mistletoe rating (DMR). Each live tree (taller than 1.37m) was assigned a DMR rating using Hawksworth six-point system (Hawksworth 1977) and the plot level DMR rating was assigned by averaging the ratings for all live trees in the plot. The four severity classes were non-infested (DMR = 0-.2), lightly infested (DMR = 0.2-2), moderately infested

(DMR = 2.1-4), and highly infested (DMR = 4.1-6). This approach was meant to ensure that sampling occurred across the full continuum of infestation levels, however it was imperfect and at one site only three plots were sampled in the high severity class. Overall a total of 15 mistletoe free plots, 15 low severity plots, 13 medium severity plots, and 12 high severity plots were sampled.

Within each 20 m by 20 m overstory plot the species, diameter at breast height (DBH), crown base height, tree height, and DMR were recorded for all trees at least 1.37m tall. Crown base height was measured as the height to the bottom of continuous live crown. In the center of each overstory plot a 40.96m² subplot (1/100th acre) was placed to quantify regeneration. In this subplot the number, species, and presence or absence of dwarf mistletoe infection was recorded for all trees less than 1.37m tall.

Loading of woody surface fuels less than 7.62 cm in diameter (fine fuels) was determined using the Photoload method for visually estimating fuel loading within five 1m² photoload plots randomly located within the 20 m by 20 m overstory plot (Keane and Dickinson 2007). In this method the loadings within each time-lag fuel class (1-hr: 0.0 - 0.6 cm, 10-hr: 0.6 - 2.5 cm, 100-hr: 2.5 - 7.6 cm; Bradshaw et al. 1983) are estimated individually. Litter and duff depths were measured at two opposite corners of each photoload plot. In order to reduce bias and increase the accuracy of visually estimated fuel loadings, a 20 percent double sampling approach was implemented based upon the methods suggested by Tinkham et al. (2016). At each overstory plot, one of the photoload plots was randomly selected for destructive sampling. All fuels within the randomly selected photoload plot were sorted by time-lag size class (1-hr, 10-hr, 100-hr). If a fuel particle extended outside of the plot it was cut at the plot edge and sorted accordingly. Fuel

samples were brought back to the lab and dried at 70°C for 48 hours before being weighed to determine the true dry mass (ASTM International 2007). The destructive sample mass was regressed on the visually estimated mass to create a linear regression model, which was subsequently used to correct all ocular estimates of fuel loading.

Surface fuels greater than 7.62 cm in diameter (1000-hr fuels) were recorded by measuring the length, both end diameters and decay class (sound or rotten) of all coarse woody debris in the plot. If a log extended outside of the plot, the log was considered to end the plot edge and diameter at the plot edge was recorded. Coarse woody fuel mass was determined using a two-step process. First, coarse woody fuel volume was calculated from field measurements of each log using the equation for the volume of a frustum of a cone:

$$\text{Volume} = \frac{\pi * l}{3} (R^2 + R * r + r^2) \quad (1)$$

In equation 1, l is the log length, R is the large end radius, and r is the small end radius (all units in meters). Fuel mass was then calculated by multiplying the total volume by the species-specific densities for lodgepole pine (.378 g/cm³ sound and .164 g/cm³ rotten) reported in Harmon et al. (2008). As it was not possible to reliably identify the species of all logs and overstory trees were overwhelming lodgepole pine, it was assumed that all coarse woody debris was lodgepole pine.

Canopy fuel load and bulk density were calculated following methods used by the Fire and Fuels Extension to the Forest Vegetation Simulation (FFE-FVS; Rebaun et al. 2010). Crown biomass was calculated for every tree taller than breast height using allometric equations developed by Brown (1978) that relate DBH to crown biomass. Following the methods used by FFE-FVS only available canopy biomass (mass of all live foliage plus ½ of branchwood < .64 cm in diameter) was included in the calculation of canopy fuel load and

bulk density. The calculated available canopy biomass was then equally distributed into 0.3m thick canopy layers throughout the length of the live crown. These individual tree fuel distributions were then summed with all trees in a given plot to determine the total mass in each canopy layer for the plot. Plot canopy fuel load (CFL) is equal to the sum of the biomass in each canopy layer divided by the plot area. Plot level canopy bulk density (CBD) was calculated by finding the maximum of the 4-meter running mean bulk density from these plot level canopy layers. This method, and similar ones, are commonly used to calculate CFL and CBD for fire behavior simulations, but they are problematic as fuels are not equally distributed throughout tree crowns in reality, and relationships between diameter and biomass vary widely depending on species, canopy position, stand density, site productivity, and region (Ex et al. 2015, Ex et al. 2016).

2.2.3 Data analysis

To determine the effect of LPDM severity on stand structure and fuel loading a linear mixed modeling approach was used. Site was incorporated as a random effect in all models and plot level DMR, stand density (live trees ha⁻¹), and their interaction were considered as potential covariates. Live trees ha⁻¹ may have a large independent effect on stand structure and fuel loadings and therefore its inclusion as a covariate is necessary to identify the importance of dwarf mistletoe alone. No relationship was detected between DMR and live trees per hectare allowing its inclusion as a potential covariate without issues of collinearity.

Model selection was completed using Bayesian information criteria (BIC) to select the best model for each of our response variables. In cases where the selected model did

not include DMR it was forced into the model, as the influence of dwarf mistletoe was the primary question in this study. All selected models included live trees ha^{-1} as a covariate excepting those predicating surface woody fuels, canopy base height (CBH), and average crown ratio (Table 1, Table 2). An interaction term (DMR times live trees ha^{-1}) was selected in a single model predicting the number of dead trees ha^{-1} (Table 1). In addition to BIC, model fit was evaluated using the marginal and conditional pseudo- R^2 values following methods outlined by Nakagawa and Schielzeth (2013). Marginal R^2 values represent the amount of variability explained by the fixed effects in the model, while conditional R^2 values capture the variability explained by both the fixed and random effects. Cases where the conditional R^2 is much larger than the marginal R^2 signify greater inter-site variability for the particular response variable.

In order to satisfy model assumptions of homoscedasticity and normality some response variables were transformed. Snag density, 100-hr fuel loading, and 1000-hr fuel loading were square root transformed and duff depth, 1-hr fuel loading, 10-hr fuel loading, total fuel loading were logarithmically transformed. Diagnostic plots were visually evaluated to ensure model assumptions were met for both the full model and the model ultimately selected. Model significance was determined using a likelihood ratio test where the selected model was compared with the intercept only model. Individual parameter significance was determined by calculating the Wald chi-squared test statistic for each parameter coefficient. P-values smaller than 0.05 were considered highly significant, but due to concerns over the validity of p-values in general (Wasserstein and Lazar 2016) and when using mixed models in particular (Bolker et al. 2009), effect size (as reflected by the standardized regression coefficient) was also considered when discussing the ecological

importance of a particular predictor variable. Effect size analysis is a useful tool as it allows for the comparison of the relative importance of a particular predictor variable between different models and studies (Schielzeth 2010).

All response and predictor data were z-transformed prior to model development, resulting in calculated parameter coefficients that are standardized regression coefficients. Standardized parameter coefficients are similar in interpretation to correlation coefficients and can only take on a value between -1 and 1. The sign represents the direction of the relationship and the absolute value represents the strength of the relationship while holding all other parameters constant. These standardized regression coefficients are used in this study as a measure of relative effect size (Schielzeth 2010). Unstandardized and back-transformed regression coefficients are also reported to allow for easy interpretation on the scale of the original data.

All analyses were completed using the program R version 3.2.3 (R Core Team 2015). Linear mixed models were created using the lme4 package (Bates et al. 2015), and pseudo- R^2 values were calculated following the methods of Nakagawa and Schielzeth (2013) as implemented in the piecewiseSEM package (Lefcheck 2015).

2.3 RESULTS

2.3.1 Stand structure

In total, 55 plots were sampled and 2,329 live trees and 824 dead trees were measured. Of these live trees all were lodgepole pine with the exception of just 11 Engelmann spruce. At the plot level, live tree densities ranged from 525 to 1800 trees per

hectare (mean = 1051 ± 349 SD), live basal area ranged from 10.5 to 47.7 m²/ha (mean = 29.7 ± 8.2 SD), and average live tree DBH ranged from 8.4 to 26.3 cm (mean = 17.3 ± 4.0 SD). Plot level dead tree densities ranged from 0 to 1100 trees per hectare (mean = 369.5 ± 296.9 SD), dead basal area ranged from 0 to 9.9 m²/ha (mean = 3.9 ± 2.8 SD), and average dead tree DBH ranged from 1.5 to 22.2 cm (mean = 11.1 ± 2.3 SD).

There were strong negative relationships between plot DMR and mean DBH ($\beta = -0.4$, $p < 0.001$, Table 1), mean tree height ($\beta = -0.33$, $p < 0.01$, Table 1), stand density index (SDI; $\beta = -0.37$, $p < 0.001$, Table 1), and live basal area ($\beta = -0.43$, $p < 0.001$; Table 1, Figure 2b). Of these live tree variables the strongest effects were on DBH and live basal area (Figure 3). Negative impacts to SDI and tree height were slightly weaker (Figure 3), but are still significant (Table 1). There was, however, no significant relationship detected between plot DMR and the density of live trees ($p = 0.5$, Figure 2a, Table 1), or the density of seedlings ($p=1$, Table 1). Given that live basal area and SDI are based on the number and size of trees it is clear that the primary effect of LPDM on is through the reduction in size of trees and not the reduction of density.

Both the number of dead trees ha⁻¹ ($\beta = 0.46$, $p < 0.001$; Table 1, Figure 2c) and the basal area of dead trees ($\beta = 0.62$, $p < 0.001$; Table 1, Figure 2d) were positively related to plot DMR. However, the model for the total number of dead trees per hectare identified a significant negative interaction between plot DMR and live trees ha⁻¹ ($\beta = -0.21$, $p = 0.03$; Table 1). This suggests that although both DMR and live tree density have a positive effect

Table 1. Results of linear mixed models to evaluate the relative effect of lodgepole pine dwarf mistletoe on measures of stand structure. Parameter coefficients and regression statistics for the only selected linear mixed models are reported. Potential parameters included plot level dwarf mistletoe rating (DMR), live trees per hectare, and their interaction. Standardized beta coefficients (β) show the relative effect size. Unstandardized parameter coefficients (b) and intercept (α) are also reported. Values in parenthesis are the standard error of the coefficient.

Response and Predictor(s)	Regression Coefficients			Model Statistics			
	β	b	p-value	α	Marginal R ²	Conditional R ²	p-value
Live Trees (live trees ha⁻¹)							
DMR	0.07(0.13)	14(25)	0.6	1020(95)	0.005	0.108	0.6
Stand Density Index							
DMR	-0.37(0.09)	-35(9)	< 0.001	439(68)	0.36	0.5	< 0.001
Live Trees ha ⁻¹	0.49(0.10)	0.3(0.05)	< 0.001				
Dead Trees (dead trees ha⁻¹)							
DMR	0.46(0.10)	148(52)	< 0.001	-353(140)	0.51	0.52	< 0.001
Live Trees ha ⁻¹	0.47(0.10)	0.6(0.13)	< 0.001				
DMR * Live Trees ha ⁻¹	-0.21(0.10)	-0.07(0.05)	0.03				
Live Basal Area (m² ha⁻¹)							
DMR	-0.43(0.10)	-1.9(0.43)	< 0.001	24.3(3.5)	0.29	0.51	< 0.001
Live Trees ha ⁻¹	0.37(0.10)	0.009(0.002)	< 0.01				
Dead Basal Area (m² ha⁻¹)							
DMR	0.62(0.10)	0.9(0.15)	< 0.001	0.02(1)	0.44	0.48	< 0.001
Live Trees ha ⁻¹	0.24(0.10)	0.002(0.0008)	0.02				
Live Tree dbh (cm)							
DMR	-0.4(0.10)	-0.9(0.21)	< 0.001	26.2(1.5)	0.49	0.57	< 0.001
Live Trees ha ⁻¹	-0.6(0.10)	-0.007(0.001)	< 0.001				
Seedlings (seedling ha⁻¹)							
DMR	0.01(0.14)	16(279)	1	6833(1687)	0.07	0.07	0.1
Live Trees ha ⁻¹	-0.27(0.14)	-2.9(1.5)	0.04				
Tree Height (m)							
DMR	-0.33(0.12)	-0.6(0.19)	< 0.01	15.9(1.5)	0.18	0.4	0.001
Live Trees ha ⁻¹	-0.3(0.12)	-0.003(0.001)	0.01				
Live Crown Ratio							
DMR	0.14(0.13)	0.009(0.009)	0.3	7.5(0.9)	0.02	0.13	0.3

on snag density, the interaction is not strictly additive and the combination of high plot DMR ratings and high live tree densities result in fewer snags than would be expected if the two variables were additive. Effect size analysis suggests that snag density and snag basal area are the structural parameters most related to plot DMR (Figure 3).

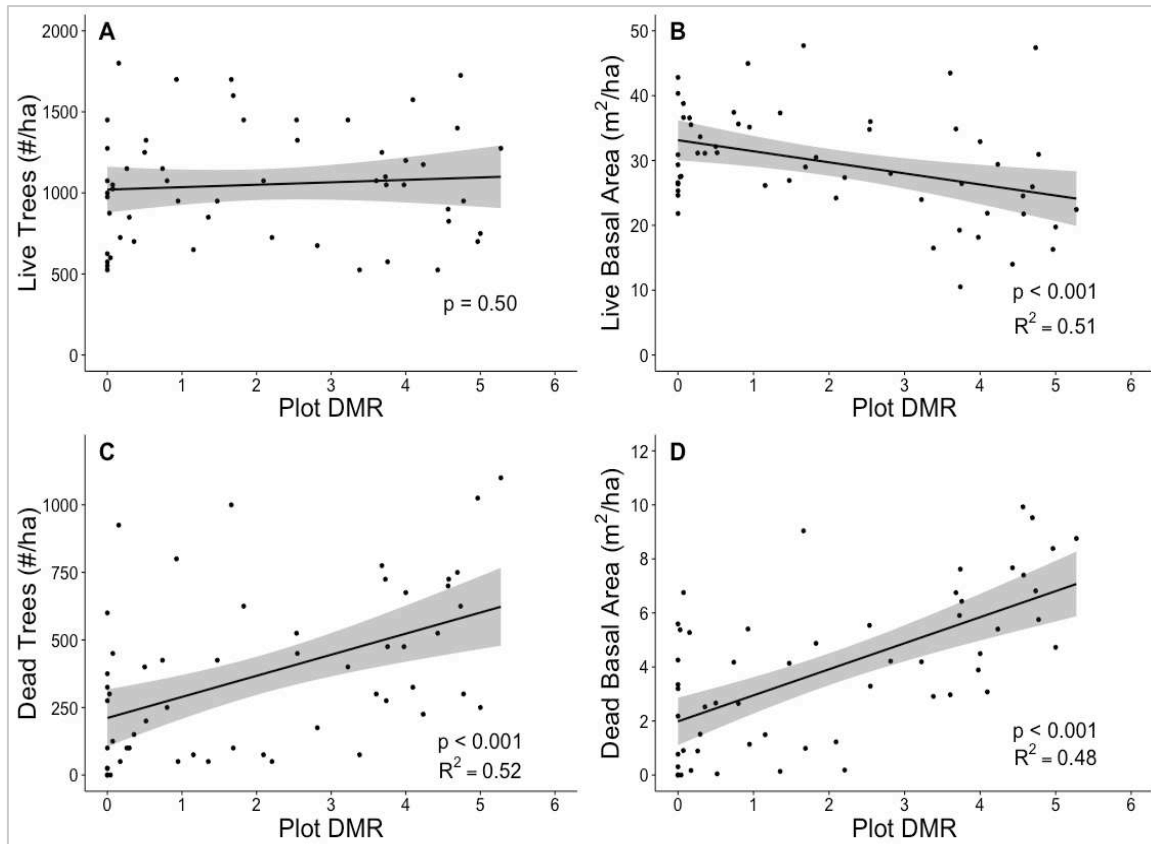


Figure 2. Simple linear regressions of the relationship between dwarf mistletoe rating (DMR) and live and dead tree variables. P-value are for the selected linear mixed models not the simple linear regressions plotted. Scatterplots of A) live trees ha^{-1} B) live basal area (m^2/ha) C) dead trees ha^{-1} D) dead basal area (m^2/ha). Shaded areas represent 95% confidence intervals.

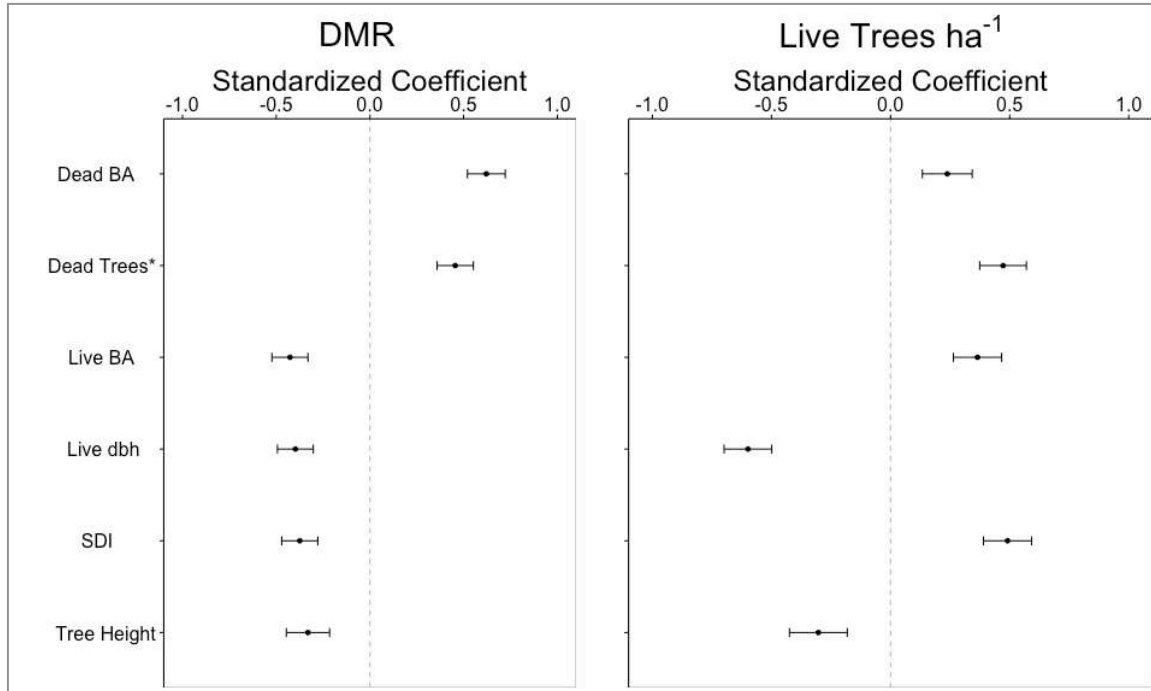


Figure 3. Standardized beta coefficients from the selected linear mixed models quantifying the effect of dwarf mistletoe rating (DMR) on dead basal area (Dead BA), dead trees ha⁻¹ (Dead Trees), live basal area (Live BA), live diameter breast height (Live dbh), stand density index (SDI), and tree height. Terms are ordered by DMR effect size. Error bars reflect standard error.

*The model for dead tree density also includes interaction between DMR and live trees ha⁻¹, which has a beta coefficient of -.21.

2.3.2 Canopy and Surface Fuel Loading

The results show that all canopy fuel metrics were negatively related to plot DMR. When the number of live trees ha⁻¹ is held constant, these data indicate a negative relationship between DMR and both the CFL and CBD (Table 2, Figure 4). These data also suggests a negative relationship between canopy base height (CBH) and plot DMR ($\beta = -0.28$, $p = 0.02$; Table 2, Figure 4). Beta coefficients indicate that plot DMR had the strongest effect on CFL, and while the effects on CBD and measured CBH were weaker they are still significant (Figure 4).

Table 2. Results of linear mixed models to evaluate the relative effect of lodgepole pine dwarf mistletoe on measures of the fuels complex. Parameter coefficients and regression statistics for the only selected linear mixed models are reported. Potential parameters including plot level dwarf mistletoe rating (DMR), live trees per hectare, and their interaction. Standardized beta coefficients (β) show the relative effect size. Unstandardized parameter coefficients (b) and intercept (α) are also reported. Values in parenthesis are the standard error of the coefficient.

Response and Predictor(s)	Parameter Coefficients			Model Statistics			
	β	b	p-value	α	Marginal R ²	Conditional R ²	p-value
Litter Depth (cm)							
DMR	-0.22(.12)	-0.1(0.07)	0.07	3.2(0.5)	0.13	0.24	0.01
Live Trees ha ⁻¹	0.32(.13)	0.0009(0.0004)	0.01				
Duff Depth (cm)							
DMR	0.14(.11)	0.2(0.13)	0.2	1(1)	0.09	0.33	< 0.001
Live Trees ha ⁻¹	0.26(.12)	0.002(0.0007)	0.03				
1-hr Fuel (kg m⁻¹)							
DMR	0.23(.12)	0.009(0.005)	0.05	0.11(0.02)	0.046	0.318	0.05
10-hr Fuel (kg m⁻¹)							
DMR	0.40(.12)	0.04(0.01)	0.001	0.24(0.04)	0.154	0.232	0.001
100-hr Fuel (kg m⁻¹)							
DMR	0.50(.12)	0.4(0.10)	< 0.001	0.23(0.28)	0.246	0.246	< 0.001
Fine Fuel (kg m⁻¹)							
DMR	0.52(.12)	0.4(0.11)	< 0.001	0.59(0.31)	0.264	0.264	< 0.001
1000-hr Fuel (kg m⁻¹)							
DMR	0.58(.11)	0.2(0.04)	< 0.001	0.20(0.14)	0.326	0.388	< 0.001
Total Fuel (kg m⁻¹)							
DMR	0.62(.11)	0.6(0.12)	< 0.001	0.78(0.33)	0.384	0.384	< 0.001
Canopy Base Height (m)							
DMR	-0.28(.12)	-0.4(0.17)	0.02	7.5(0.9)	0.07	0.27	0.02
Canopy Fuel Load (kg m⁻²)							
DMR	-0.38(.10)	-0.05(0.01)	< 0.001	0.64(0.1)	0.32	0.49	< 0.001
Live Trees ha ⁻¹	0.45(.10)	0.0004(0.000007)	< 0.001				
Canopy Bulk Density (kg m⁻³)							
DMR	-0.54(.12)	-0.004(0.001)	< 0.01	0.04(0.008)	0.27	0.27	< 0.01
Live Trees ha ⁻¹	0.42(.12)	0.0001(0.000006)	< 0.001				

Dead, down woody debris were positively related to plot DMR across all fuel size classes (Table 2, Figure 5). The number of live trees ha^{-1} was not a significant predictor of any size class of woody fuel (Table 2). Plot DMR had the largest effect on 100-hr fuels ($\beta = 0.5$, $p < 0.001$; Table 2, Figure 5). The model for total woody surface fuel loading predicts a 0.6 kg m^{-2} increase in woody fuel for each one-unit increase in plot DMR, which translates to a nearly 6-fold increase in fuel loading when moving from a plot with a DMR of zero to a plot with a DMR of 6. Though woody fuels were significantly increased, the results did not indicate a significant relationship between plot DMR and litter and duff depth. However, the relationship between plot DMR and litter depth has a p-value less than .1, which is evidence that a negative relationship may exist ($\beta = -0.22$, $p = 0.07$; Table 2).

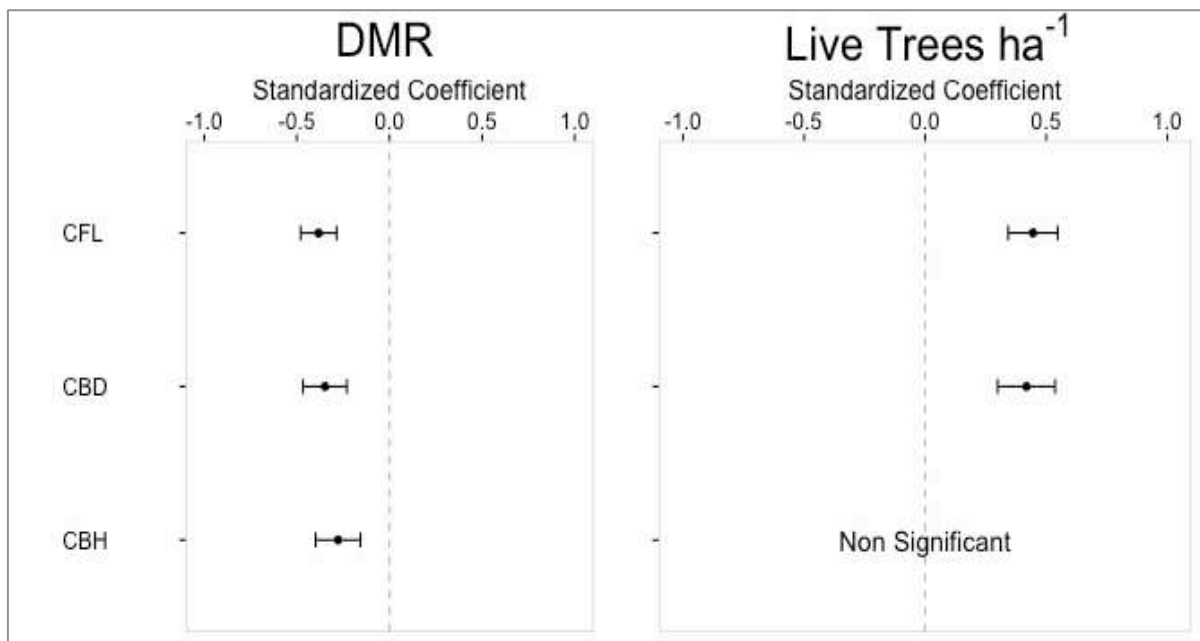


Figure 4. Standardized beta coefficients from the selected linear mixed models quantifying the effect of dwarf mistletoe rating (DMR) on canopy fuel load (CFL), canopy bulk density (CBD), and measured canopy base height (CBH). Terms are ordered by DMR effect size. Error bars reflect standard error.

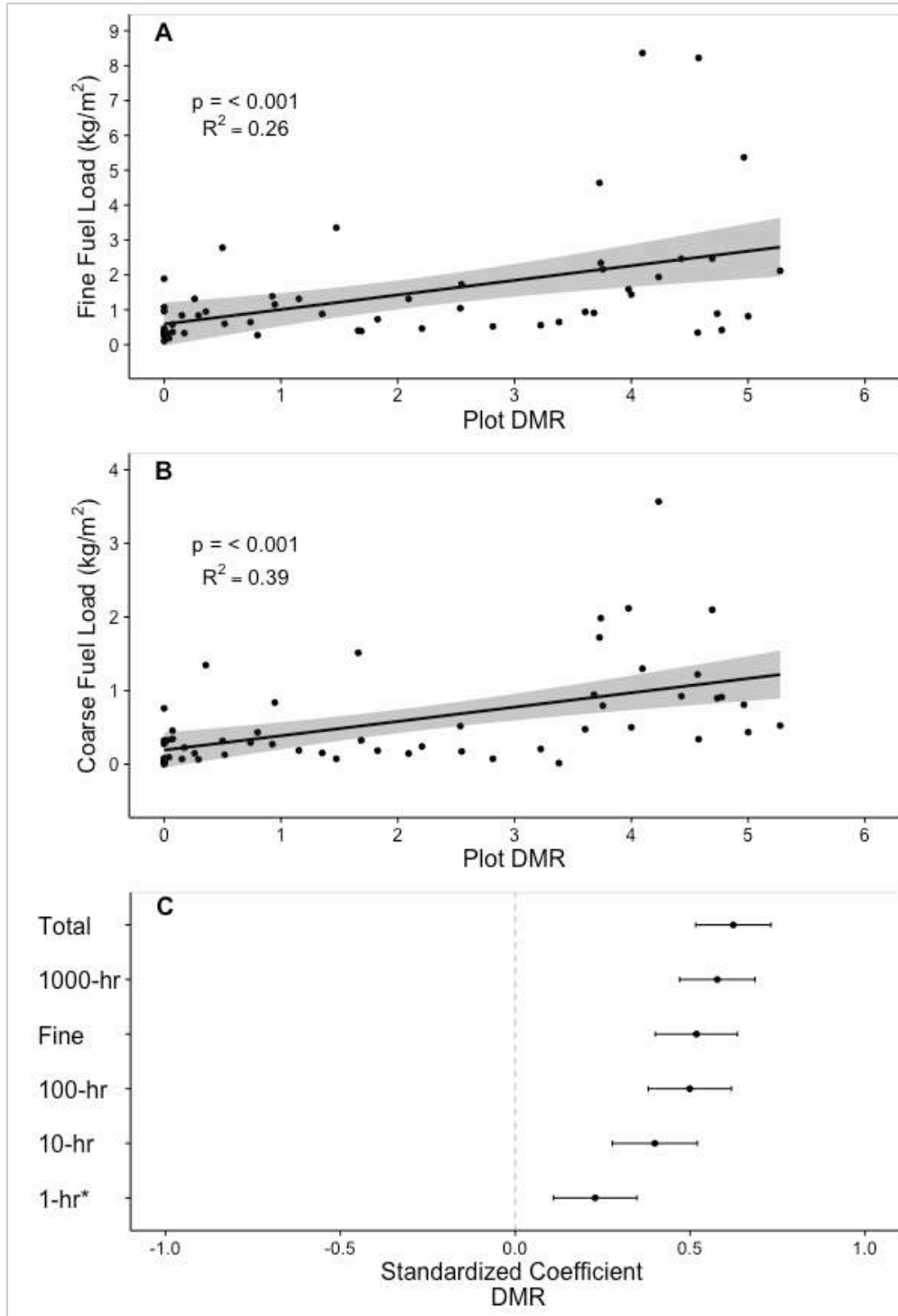


Figure 5. Plots showing the relationship between dwarf mistletoe rating (DMR) and surface fuel loads. A) Linear mixed model of DMR on back transformed fine fuel load (<7.62cm). Shaded areas represent 95% confidence interval. B) Linear mixed model of DMR on back transformed coarse fuel load (>7.62cm). Shaded areas represent 95% confidence interval. C) Standardized DMR beta coefficients for each woody surface fuel model.

2.4 DISCUSSION

These results indicate that the effect of LPDM on stand structure varies in both magnitude and direction across various metrics. They show a strong negative effect of LPDM infestation on stand level forest structure variables including the mean tree size, height, basal area, and SDI. These results are consistent with findings from several previous studies in both lodgepole pine communities and other host-parasite combinations from the western United States that indicate a negative effect on forest productivity in dwarf mistletoe infested stands (Weir 1916, Hawksworth 1961, Hawksworth and Hinds 1964, Baranyay and Safranyik 1970, Mathiasen et al. 1986, Wanner and Tinnin 1989, Hawksworth and Geils 1990, Mathiasen et al. 1990). The data also indicate that LPDM had a positive effect on the density of standing dead trees. These results are also consistent with previous research and are expected given the established relationship between dwarf mistletoe infection and tree mortality (Hawksworth and Hinds 1964, Wanner and Tinnin 1989). There was no effect of LPDM severity on live tree densities, which is inconsistent with several studies that have indicated a positive relationship between live tree density and LPDM (Hawksworth and Hinds 1964, Tinnin 1984, Wanner and Tinnin 1989, Godfree et al. 2003). These studies point to both increased numbers of suppressed trees and enhanced regeneration success as potential mechanisms driving these increases to overall live tree density. Differences between this studies results and previous studies suggest that other unaccounted for factors may be influencing the number and timing of regeneration including both top-down controls such as seasonal climatic regimes, differences in population level serotiny, and various disturbance regimes, as well as bottom-up controls such as site productivity and plant competition. Additional studies that investigate how

these top-down and bottom-up controls alter the relationship between LPDM and forest stand dynamics are needed. In addition to developing a more mechanistic understanding of the relationship between LPDM and forest structure, additional studies that link these changes to ecological processes should be undertaken. For example, dwarf mistletoes also impact fine scale canopy heterogeneity through the formation of witches' brooms. Several authors have suggested that these changes to fine-scale forest heterogeneity alter a variety of ecological processes including microhabitat for plants and wildlife, plant-atmospheric interactions, soil processes, and disturbance regimes (Hawksworth and Wiens 1996, Mathiasen 1996).

Previous researchers have suggested that alterations in stand structure due to LPDM directly influence fire behavior through alterations to the amount and distribution of canopy fuels (Brown 1975, Alexander and Hawksworth 1976, Koonce and Roth 1985, Hoffman et al. 2007). The results of this work indicate that LPDM infestation severity was negatively related to both the measured CBH and the calculated CFL and CBD. It has been hypothesized that dwarf mistletoe infestations will reduce CBH through two primary mechanisms. First, dwarf mistletoe infection may result in an increase in the crown ratio due to reduced pruning of lower infected branches (Koonce and Roth 1985, Harrington and Hawksworth 1990, Godfree et al. 2002). Secondly, CBH may be reduced due to increased densities of small trees in heavily infested stands (Godfree et al. 2002). Though the results confirm findings from other studies that have shown reduced CBH in stands impacted by LPDM, there was no significant relationship detected between LPDM and crown ratio demonstrating that LPDM is not directly lengthening tree crowns in our stands as has been suggested. Rather these results indicate that infested stands tend to have shorter trees with

proportionally lower crown base heights. This effect is the result of the reported impact of LPDM on stand productivity as indicated by the negative relationship between DMR and live basal area.

In addition to lower CBH, this work suggests that there is a negative relationship between LPDM infestation severity and the available CFL and CBD. These findings show consistent trends with data from both lodgepole pine dominated forests (Agne 2013) and ponderosa pine dominated forests infested with dwarf mistletoe (Hoffman et al. 2007). Although this research contributes to a growing body of literature that supports the notion that dwarf mistletoes alter the canopy fuel complex and in turn wildland fire behavior there remains a paucity of studies that have directly quantified these changes. Both Agne (2013) and Hoffman et al. (2007) have suggested that dwarf mistletoes reduce the potential for active crown fire spread while increasing the potential for passive crown fire. However, the models used in these studies did not explicitly account for the fine scale alterations in canopy structure associated with dwarf mistletoe nor the potential interactions among the fuels, atmosphere and fire that drive fire behavior (Hoffman et al. 2007, Parsons et al. 2011, Linn et al. 2013, Hoffman et al. 2015), and thus it is unknown how well they capture the true effects of dwarf mistletoe.

It is important to note that in this study, as well as Agne (2013) and Hoffman et al. (2007), canopy fuel loadings were calculated based on relationships between DBH and crown biomass (Brown 1978). However, these relationships were developed using healthy trees and it is unclear what impact dwarf mistletoe infestation have on the crown biomass, particularly on heavily infected trees containing a large number of witches' brooms. Trees containing extensive witches' brooms have increased ratios of branch biomass to bole

biomass (Wanner and Tinnin 1986) and leaf area to sapwood area (Sala et al. 2001). This suggests that highly infected trees may have greater proportion of available canopy fuel loading relative to an uninfected tree of the same diameter. However, increases in branch biomass are primarily occurring in the 100-hr canopy fuel class (Koonce and Roth 1985), which is not considered in most estimates of available CFL or CBD (Scott and Reinhardt 2002). Furthermore, potential increases in available CFL due to altered biomass distributions may be offset by both the reduced mass observed in leaves and twigs distal to infections and the substantial levels of crown dieback often seen in infected trees (Broshot et al. 1978, Meinzer et al. 2004, Mathiasen et al. 2008). Though it is possible that witches' broom formation may increase canopy biomass locally within individual trees, the Brown (1978) allometric relationships may tend to over predict stand level available CFL for the factors mentioned above. If true, this over prediction bias would make the effect sizes and observed negative relationships between canopy fuel parameters and plot DMR even larger than reported in this study.

Results also indicated that LPDM severity had a positive relationship with the total woody surface fuel load. Although there are no other estimates of the relationship between LPDM and woody surface fuel loads in lodgepole pine dominated forests, previous work in dwarf mistletoe infested ponderosa pine communities have also identified a positive relationship between dwarf mistletoe severity and total woody surface fuel load (Koonce and Roth 1985, Hoffman et al. 2007, Stanton and Hadley 2010). However, these studies have indicated that the effect of dwarf mistletoe on woody fuel load may be inconsistent across time-lag size classes. The data indicate a consistent positive effect of LPDM across all dead down woody time-lag size classes, but the magnitude of this effect varied with the

greatest effects occurring for larger size classes (100-hr and 1000-hr). Keane (2015) states that the accumulation of wildland fuels is due to a combination of disturbance (e.g. fire, wind, insect outbreaks, dwarf mistletoe), development (e.g. establishment, growth, and mortality of vegetation), deposition of fuel on the forest floor, and the rate of decomposition of deposited fuels. Characterizing and predicting how these processes vary through space and time is critical for understanding fire behavior and effects, as well as estimating changes in fire regimes, global carbon pools, local nutrient cycling, microbial activity, and wildlife and plant communities (Harmon et al. 1986, Busse 1994, Turner et al 1995, Bull et al. 1997, Loeb 1999, Butts and McComb 2000, Woodall et al. 2013, Keane 2016). While disturbances such as dwarf mistletoe directly influence the spatial and temporal mosaic of fuels through mortality, they also affect stand development through reduced productivity, which in turn alters both fuel deposition and decomposition. Further understanding of the relative impact of dwarf mistletoe on each of these processes could help improve fuel mapping efforts, which are critical for determining spatial fire hazard and risk, simulating fire growth, and understanding vegetation dynamics following disturbances such as fire (Keane 2013, Keane et al. 2015).

As suggested by Keane (2016) understanding the spatial and temporal variability in wildland fuels is perhaps the most important concept in fire management today, in part because this variability impacts a number of ecosystem processes including fire behavior and effects, population dynamics, and community structure (e.g. Thaxton and Platt 2006, Hiers et al. 2009, O'Brien et al. 2016, Vakili et al. 2016). Despite several long-held assumptions about the impact of LPDM on fuel dynamics this work is the first quantitative study that has evaluated the influence of LPDM on surface fuel accumulations in lodgepole

pine dominated forests. The findings of this study show that LPDM infestation severity is positively related to surface fuel load and negatively related to available canopy fuel. These findings generally agree with studies conducted in other geographic regions and host-parasite combinations, and support several hypothesized generalities regarding the effect of dwarf mistletoe on surface and canopy fuel loads. An important implication of this finding is that dwarf mistletoe infestation will increase the variability in forest structure and fuel loads across both stands and landscapes, as dwarf mistletoe is not evenly distributed across these scales (Reich et al. 1991, Kipfmüller and Baker 1998, Shaw et al. 2005). However, further research that characterizes the spatial and temporal effects of dwarf mistletoe on fuels at the landscape scale is needed. Characterizing variability in fuel loading is necessary as fine-scale fuel variability is extremely important to ecologically relevant fire effects (Thaxton and Platt 2006, Hiers et al. 2009), and landscape scale spatial and temporal variability of fuels may serve as a strong bottom-up control of fire regimes (Whitlock et al. 2010, Keane 2016). More research is needed that quantifies the implications of these alterations on potential fire behavior and effects, and fire regimes. Unfortunately, current operational fire behavior modeling tools are not capable of accounting for the fine scale heterogeneity in fuels that are associated with dwarf mistletoe infestations (Pimont et al. 2009, Parsons et al. 2011). However the recent development of newer physics based modeling tools (e.g. FIRETEC, Linn et al. 2002; WFDS, Mell et al. 2007) may hold promise to provide further insights into the potential effect of LPDM on fire behavior and effects.

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3. THE IMPACT OF VARYING FIRE SEVERITY ON THE LONG-TERM TRAJECTORY OF DWARF MISLTEOTE INFESTED LODGEPOLE PINE STANDS: A CASE STUDY

3.1 INTRODUCTION

Lodgepole pine dwarf mistletoe (*Arceuthobium americanum* Nutt. ex. Engelm; hereafter simply dwarf mistletoe) is an obligate hemiparasite that infects lodgepole pine (*Pinus contorta* Dougl. Ex. Loud) throughout the tree's expansive range (Hawksworth and Wiens 1996). Dwarf mistletoe reproduces through the explosive discharge of sticky seeds, allowing for maximum dispersal distances around 10 - 15m, however spread rates through dense stands are much slower, on the order of 0.4m per year (Hawksworth and Wiens 1996). The pathogenic effects of dwarf mistletoes on individual trees include reduced growth rates, seed production, and water use efficiency (Hawksworth 1961, Hawksworth and Hinds 1964, Wanner and Tinnin 1989, Sala et al. 2001, Meinzer et al. 2004), increased mortality rates and susceptibility to other insects and pathogens (Hawksworth and Wiens 1996), and altered distributions of tree biomass due to abnormal branch growth and the formation of witches; brooms (Wanner and Tinnin 1986). Stand scale impacts of dwarf mistletoe infestation include reduced live basal area, reduced density and height of dominant trees, and increased live crown ratio and snag density (Bennets et al. 1996, Godfree et al. 2002, 2003a, and 2003b). These impacts become more pronounced as stand level infestation severity increases, ultimately impacting both fiber production and ecosystem properties including wildlife habitat quality, surface woody debris loadings, and potential fire behavior (Alexander and Hawksworth 1975, Hawksworth and Johnson 1989, Hawksworth and Wiens 1996).

Wildfires are a fundamental disturbances in the lodgepole pine dominated forests of the Central and Southern Rockies, and have long been considered the only natural control of dwarf mistletoe populations (Baranyay 1970, Alexander and Hawksworth 1975). Wildfires are extremely important to dwarf mistletoe populations, as dwarf mistletoe is reliant on living trees for survival. If a fire burns at high severity and kills all infected overstory trees it will have a sanitizing effect on the stand with the only possibility of infection coming from either long range seed transport via animal vectors or the slow progressive spread from infested peripheral stands (Baranyay 1970, Alexander and Hawksworth 1975). Alternatively, a fire that burns at lower severity and allows some infected trees to survive may result in a highly infested future stand as the remaining infected trees will rain seeds down onto new regeneration, resulting in extremely high infection rates as the stand matures (Baranyay 1970, Alexander and Hawksworth 1975). This basic concept has been supported by landscape scale observations which suggest that time since fire is strongest predictor of dwarf mistletoe infection intensities in lodgepole pine dominated systems characterized by periodic high severity fire (Kipfmüller and Baker 1998). Other work in a lodgepole pine systems exposed to a more regular surface fire regime found a negative relationship between stand level dwarf mistletoe infection intensity and average fire frequency, implying that regular surface fires may serve to temper dwarf mistletoe populations in these systems (Zimmerman and Laven 1984).

This predicted and observed relationship between fire and dwarf mistletoe populations has lead to numerous suggestions, beginning in the early 20th century, that prescribed fire could be used to control mistletoe populations (e.g. Weir 1916, Baranyay and Smith 1972, Alexander and Hawksworth 1975, Zimmerman et al. 1990). In the past

several decades, prescribed surface fires have been used successfully in ponderosa pine communities to reduce infestation severity through both the scorching of infections low in the crown and the preferential mortality of infected trees (Koonce and Roth 1980, Harrington and Hawksworth 1990, Conklin and Armstrong 2001, Conklin and Geils 2008, Hessburg et al. 2008). To more fully understand the relationship between fire and *Arceuthobium spp.* long-term follow up is needed to determine how populations will respond over time, and more work is needed across a range on fire severities, particularly in higher severity fires. With the exception of Zimmerman et al. (1990) there has been no experimental work on the influence of crown fires in any forest type. The current study seeks to provide some much needed quantitative data that relates fire severity, measured as percent tree mortality, to both short and long term dwarf mistletoe populations.

To provide some much needed long-term data and to more fully characterize the relationship between dwarf mistletoe populations and fire, three of the prescribed fires described in Zimmerman et al. (1990) were resampled in the summer of 2015. The goal of this research was to answer the following questions: (1) How have the stands regenerated and recovered following fire? (2) What are the post-fire fuel dynamics across time-lag fuel classes? (3) What is the relationship between fire severity and dwarf mistletoe infestation severity thirty years post-fire? (4) What is the trajectory of these post-fire stands based on the United States Forest Service's Forest Vegetation Simulator and the Dwarf Mistletoe Impact Model?

3.2 METHODS

3.2.1 Study area and sampling design

In the fall of 1982 and the spring of 1983 five prescribed fires were set in highly infected stands of lodgepole pine in the Gunnison National Forest (38°52'10" N, 106°32'30" W) with the goal of controlling dwarf mistletoe populations and regenerating stands free from infection (Zimmerman et al. 1990). Prior to these fires, permanent plots were established within each burned area, and all trees within the plots were measured and tagged. All plots were resampled the summer following the fires. One fire was later salvage logged and was excluded from further study, and a second fire burned at rather low severity and could not be relocated in 2015. For this reason, only six permanent plots within the three remaining fires were resampled during the summer of 2015. The three fires surveyed all burned during September or October of 1982.

The six permanent plots were variable in size ranging from 375m² to 725m². Within the six plots the species, diameter at breast height (DBH), Hawksworth's 6-point dwarf mistletoe rating (DMR; Hawksworth 1977), crown base height, and tree height were recorded for all trees taller than breast height (>1.37 m). DBH was also recorded for all dead trees over breast height. All trees under breast height were counted and rated as either infected or uninfected.

Loading of woody surface fuels less than 7.62 cm in diameter (fine fuels) was determined using the Photoload method for visually estimating fuel loading within ten 1m² photoload plots randomly located within the permanent plots (Keane and Dickinson 2007). In this method the loadings within each time-lag fuel class (1-hr: 0.0 - 0.6 cm, 10-hr: 0.6 - 2.5 cm, 100-hr: 2.5 - 7.6 cm; Bradshaw et al. 1983) are estimated individually. Litter and

duff depths were measured at two opposite corners of each photoload plot. In order to reduce bias and increase the accuracy of visually estimated fuel loadings, a 20 percent double sampling approach was implemented based upon the methods suggested by Tinkham et al. (2016). At each permanent plot, two of the photoload plots was randomly selected for destructive sampling. All fuels within the randomly selected photoload plot were sorted by time-lag size class (1-hr, 10-hr, 100-hr). If a fuel particle extended outside of the plot it was cut at the plot edge and sorted accordingly. Fuel samples were brought back to the lab and dried at 70°C for 48 hours before being weighed to determine the true dry mass (ASTM International 2007). The destructive sample mass was regressed on the visually estimated mass to create a linear regression model, which was subsequently used to correct all ocular estimates of fuel loading.

Surface fuels greater than 7.62 cm in diameter (1000-hr fuels) were recorded by measuring the length, both end diameters and decay class (sound or rotten) of all coarse woody debris in the plot. If a log extended outside of the plot, the log was considered to end the plot edge and diameter at the plot edge was recorded. Coarse woody fuel mass was determined using a two-step process. First, coarse woody fuel volume was calculated from field measurements of each log using the equation for the volume of a frustum of a cone:

$$\text{Volume} = \frac{\pi * l}{3} (R^2 + R * r + r^2) \quad (1)$$

In equation 1, l is the log length, R is the large end radius, and r is the small end radius (all units in meters). Fuel mass was then calculated by multiplying the total volume by the species-specific densities for lodgepole pine (.378 g/cm³ sound and .164 g/cm³ rotten) reported in Harmon et al. (2008). As it was not possible to not reliably identify the species

of all logs and no other tree species were recorded on site, it was assumed that all coarse woody debris was lodgepole pine.

3.2.2 FVS modeling

In order to predict the long-term effects of these fires on dwarf mistletoe populations and stand growth the United States Forest Service's Forest Vegetation Simulator (FVS; Dixon 2002) coupled with the Dwarf Mistletoe Impact Modeling System (DMIM; Hawksworth et al. 1995) was used to simulate the trajectory of each post-fire stand. The FVS is a distance-independent, individual-tree growth model widely used in North America to support forest management decision-making. Using a standard ten-year cycle, forest growth was simulated for 200-year period starting from the 2015 stand conditions. Simulations were completed both with and without the DMIM enabled in order to compare the impacts of dwarf mistletoe infestation on growth and mortality with identical stands unaffected by the parasite.

The DMIM is comprised of four modules: 1) and 2) predict nonspatial spread and intensification, 3) predicts modifications to diameter growth, and 4) predicts mortality. The spread and intensification module uses logistic regressions to predict the probability of an individual tree either increasing or decreasing in DMR (Equations 2 and 3, respectively).

$$P_I = \frac{1}{1 + e^{-(-1.67226 + MD - 0.074720HG - 0.0012397TPA)}} * UIM \quad 2)$$

$$P_D = \frac{1}{1 + e^{-(-5.5978 + 0.013267HG - 0.00011505TPA + 0.098376DMR)}} * UIM \quad 3)$$

Where:

P_I = probability that the rating will increase

P_D = probability that the rating will decrease

DMR = current dwarf mistletoe rating

HG = height growth of the tree (feet per cycle)

TPA = density of the stand (trees per acre)

UIM = optional user entered multiplier

MD = mistletoe “dummy” variables with the following values

DMR	Coefficient
0	0
1	2.45047
2	2.30723
3	1.8809
4	2.11457
5	1.43293
6	0

These calculated probabilities for individual trees are compared with a number randomly drawn from a uniform distribution with a range of 0 to 1. If the calculated probability of increase is larger than the random number then the tree’s DMR is increased by one. If a separately drawn random number is greater than probability of decrease then the DMR of the tree is reduced by one. These same equations are used to predict spread and intensification for all impacted species, however modifications to diameter growth are

species dependent with individual adjustments for lodgepole pine, western larch, Douglas-fir, true fir, and ponderosa pine. This diameter adjustment works by simply reducing the FVS predicted diameter increment at the end of each model cycle by some factor based on the tree's DMR (Equation 4). The final module predicts the ten-year mortality rate using a linear regression based on DMR and DBH (Equation 5). The calculated mortality rate is multiplied by 1.2 if the tree has a DBH less than 9 inches. The calculated mortality based on this equation is then compared to the FVS calculation of mortality and the larger of the two values is used.

$$ADG = NDG * DGP * \frac{CL}{10} \quad 4)$$

Where:

ADG = altered diameter growth

NDG = normal diameter growth

CL = cycle length

DGP = dwarf mistletoe growth potential based on DMR (see adjustment values for lodgepole pine below)

DMR	0	1	2	3	4	5	6
10-year diameter growth potential (percent)	100	100	100	100	94	80	59

$$PM = (0.00112 + 0.0217DMR - 0.0017DMR^2) * UIM * 100 \quad 5)$$

Where:

PM = percent mortality due to mistletoe

DMR = dwarf mistletoe rating

UIM = optional user entered multiplier

3.2.3 Data analysis

Statistical analysis was completed using the R program for statistical computing version 3.2.3 and all functions utilized came from the base R package (R Core Team 2015). Current tree density and plot DMR (average DMR of all trees in the plot) were compared to pre-fire density and plot DMR using a simple paired t-test. Fuel loadings at each time step (pre-fire, post-fire, current) were compared using pairwise ANOVA contrasts with Bonferroni multiple testing adjustments. Fuels were separated by time-lag fuel classes and received a \log_{10} transformation prior to analysis in order to achieve homogeneity of variance. Simple linear regression models were created to test for significant relationships between pre-fire density and current density, as well as fire mortality and response variables including plot level DMR and coarse and total fuel loading.

3.3 RESULTS

3.3.1 Stand structure

Post fire tree establishment has been prolific, but variable, with current plot level tree densities ranging from 2,430 to 13,218 trees per hectare and average DBHs ranging from 4.1 cm to 5.4 cm with a mean of 4.6 cm (Table 3). Current densities are highly related to pre-fire tree density ($p < 0.001$, $R^2 = 0.962$, Figure 6), but are significantly denser than pre-fire conditions ($p = 0.022$). Average trees size is relatively small with average tree height ranging from 3.1 to 3.8 meters and average crown base height ranging from 1.1 to 2.2 meters.

Table 3. Stand structure and dwarf mistletoe infection levels pre-fire, post-fire, and thirty years post-fire. Lodgepole pine made up 100 percent of trees in all plots.

Plot	Fire Mortality	Time	DMR	Tree Density (trees/ha)	Mean Diameter (cm)	Seedling Density (trees/ha)	Height (m)	CBH (m)
17.1	62.1%	1982	4.36	800	10.7	1407	6.8	2.1
		1983	4.27	303	12.3	428	7.7	3.6
		2015	1.88	4359	4.4	1213.8	3.1	1.2
17.2	20.8%	1982	5.00	800	14.2	1540	8.8	3.4
		1983	4.98	634	15.4	1162	9.2	3.8
		2015	3.41	2430	4.5	6505.7	3.4	1.3
18.1	85.7%	1982	3.51	713	10.6	3767	10.6	5.0
		1983	4.29	102	18.1	596	14.5	9.1
		2015	0.13	4073	5.4	145.5	3.3	1.1
18.2	60.7%	1982	3.59	815	8.8	3083	6.1	1.4
		1983	3.41	320	8.5	873	6.1	1.9
		2015	2.29	3898	5.2	320.0	3.4	1.2
38.1	100.0%	1982	5.15	1655	9.8	2673	8.3	1.5
		1983	-	-	-	-	-	-
		2015	0.00	13218	4.2	254.5	3.8	2.2
38.2	77.4%	1982	5.45	1413	8.8	3520	8.8	3.2
		1983	5.33	320	13.7	907	10.1	3.4
		2015	0.81	10960	4.1	1066.7	3.5	2.0

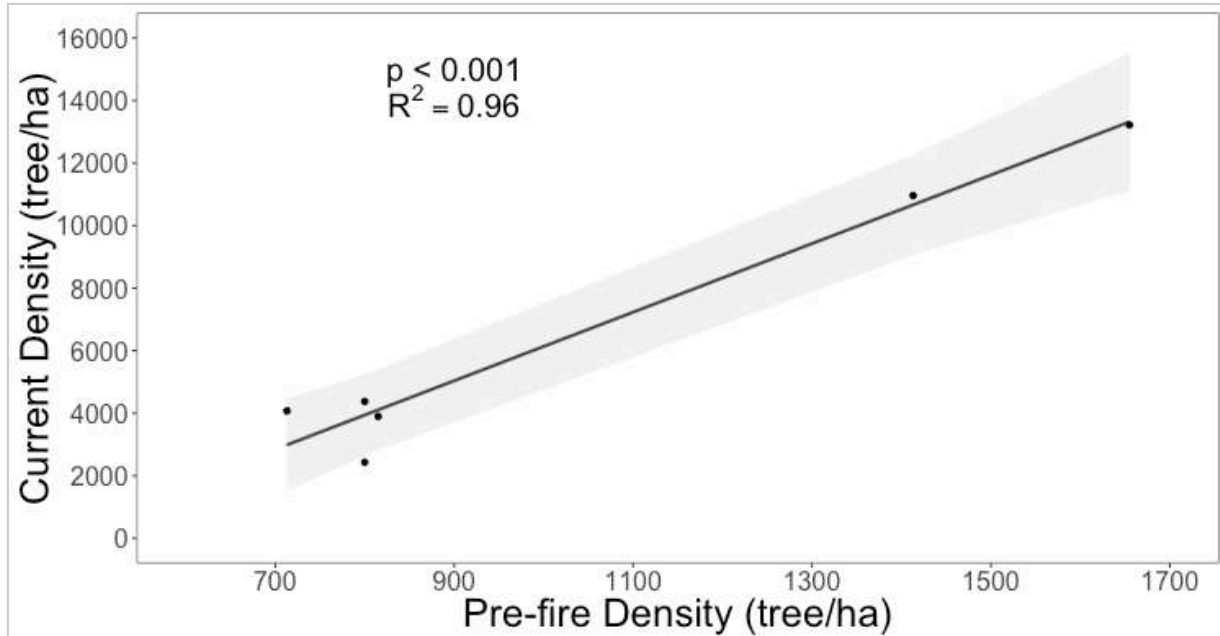


Figure 6. Simple linear regression of pre-fire tree density on current tree density. Shaded region represents the 95% confidence interval.

3.3.2 Surface fuel loading

As was reported in Zimmerman et al. (1990) on average the three fires consumed 61% of coarse woody debris (> 7.62cm) and 58% of fine woody debris (<7.62cm) (Figure 7). These reductions in fuel loadings were not sustained, as surface fuel loadings have doubled in the thirty-three years since the fires (Figure 7). This doubling in surface fuel was driven solely by a substantial increase in fine fuels (Bonferroni $p = 0.011$), as the loading of coarse fuels was unchanged (Bonferroni $p = 1$).

When current total surface fuel loading is compared to the pre-fire level there is no significant difference detected (Bonferroni $p = 1$). However, the proportion of fuel loading in each size class is different than the pre-fire conditions. There has been an increase in fine fuel loading from 1.85 kg/m² pre-fire to 4.41 kg/m² (Figure 7), however due to the small sample size and large variability between plots this difference was not statistically

significant (Bonferroni $p = 0.19$). The coarse fuel loading has not changed in the time since fire, and has remained significantly lower than pre-fire levels (Bonferroni $p = 0.008$).

Though coarse fuel loadings have not changed, they were strongly predicted by the number of trees killed by fire in each plot ($p < 0.001$, $R^2 = 0.956$; Figure S1).

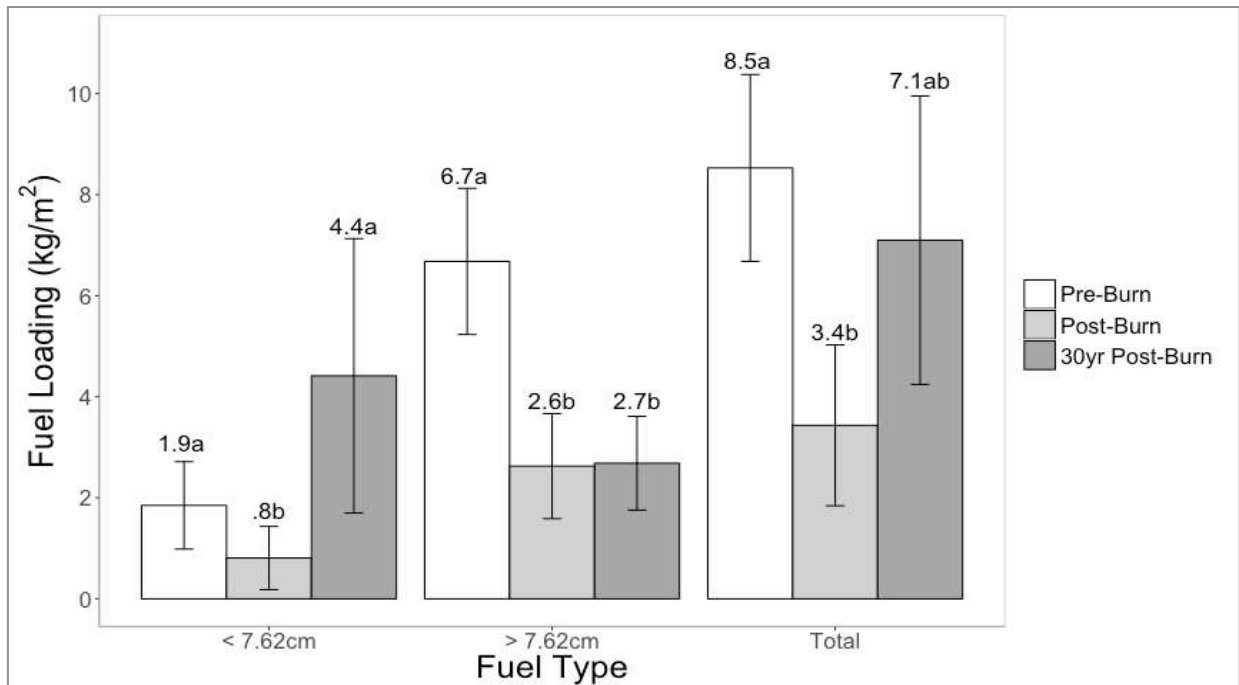


Figure 7. Surface fuel loading through time divided by fuel types. Letters represent significant differences between time periods within each fuel class. Error bars are +/- one standard deviation.

3.3.3 Dwarf mistletoe population

The immediate fire effects on DMR were some what mixed with the DMR for plots 17.1, 17.2, 18.2, and 38.2 relatively unchanged, the DMR for plot 18.1 increasing, and DMR dropping to zero for plot 38.1 due to complete mortality (Table 3). The true effect of the prescribed fires on plot level DMR can be seen clearly when considering the current DMRs, which are significantly lower than pre-fire levels ($p = 0.005$). While all DMRs were reduced,

of particular interest is the significant negative relationship between percent overstory mortality and current DMR ($p = 0.002$, $R^2 = 0.932$; Figure 8).

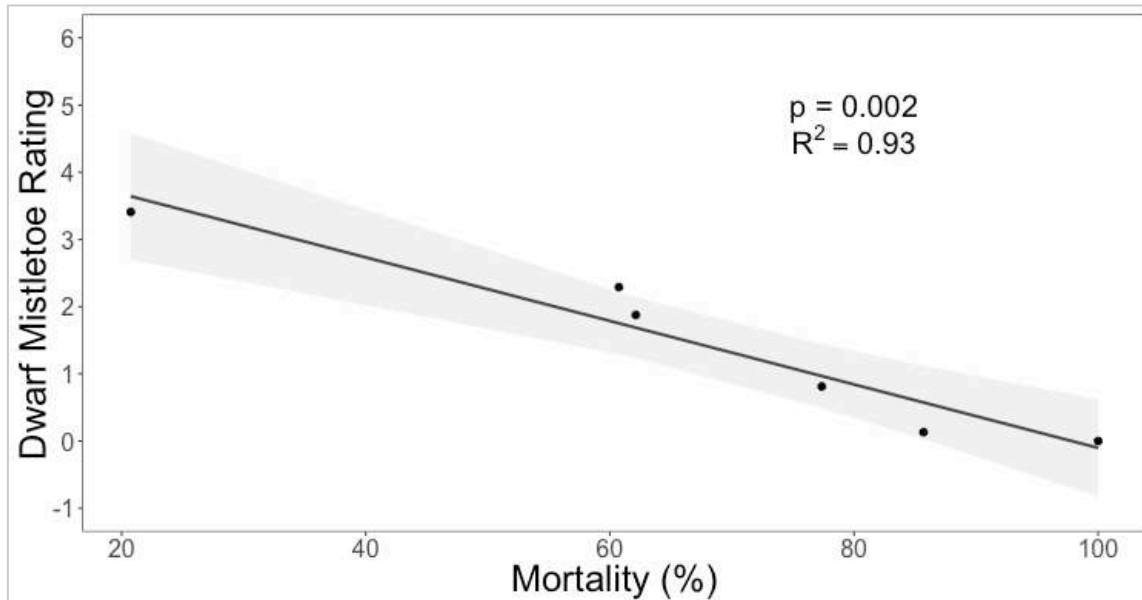


Figure 8. Relationship between fire severity (as measured by overstory mortality one year post-fire) and intensity of dwarf mistletoe infection thirty years post fire. Grey area represents the 95% confidence interval.

3.3.4 FVS Simulation

FVS simulations began in the current year (2015) and continued until 2215, representing a total of 233 years of growth since the prescribed fires in 1982. These simulations predict that stand 17 will return to its pre-fire dwarf mistletoe infestation level by approximately 110 years post fire (Figure 9), which is roughly the same age the stand was at the time of fire. By 2200 this stand reaches an extremely high DMR of 5.8, which is approximately 25% higher than pre-fire. The fire in stand 18 resulted in higher mortality levels than stand 17, and FVS simulations predict that stand level DMR will not return to pre-fire levels until the stand is ~170 years in age (Figure 9). Stand 38 sustained the highest severity burn, and showed persistent dwarf mistletoe reduction with levels

remaining below pre-fire levels for the entirety of the 200 year simulation, reaching a maximum stand level DMR of 2.95 by the year 2215 (44% reduction from pre-fire; Figure 9).

Stand growth was compared with and without dwarf mistletoe impacts to evaluate the relative impact of dwarf mistletoe on stand development, tree growth, and volume accretion (Figure 10). By the end of the 200-year simulation, dwarf mistletoe related growth impacts were substantial for stands 17 and 18 but were minor in stand 38. After 200 years, the simulations predicted basal area reductions of 60.6%, 24.8%, and 3.7% for stands 17, 18, and 38, respectively. The high levels of dwarf mistletoe in stand 17 resulted in stagnation and eventual basal area decline beginning around 2135. This stand was predicted to reach a maximum basal area of $30 \text{ m}^2 \text{ ha}^{-1}$ in 2135 before declining to $27 \text{ m}^2 \text{ ha}^{-1}$ by the end of the simulation. In stand 18, dwarf mistletoe related stagnation and decline did not begin until 2185, achieving a maximum basal area of $\sim 52 \text{ m}^2/\text{ha}$ in 2185 before beginning to decline. Stand 38 continued to accumulate basal area throughout the simulation reaching a maximum basal area of $65 \text{ m}^2/\text{ha}$, but appears to be approaching a maximum by the end of the simulation. Overall, the impacts to stand growth in stand 38 are relatively minimal; in fact basal area remains within 1 percent of the no dwarf mistletoe simulation for the first 100 years (133 years post-fire). It is self evident that these basal area reductions resulted in decreased production of total wood volume. The simulations predicted that by year 2215 dwarf mistletoe would reduce total wood volume by 61%, 27%, and 5% for stands 17, 18, and 38, respectively.

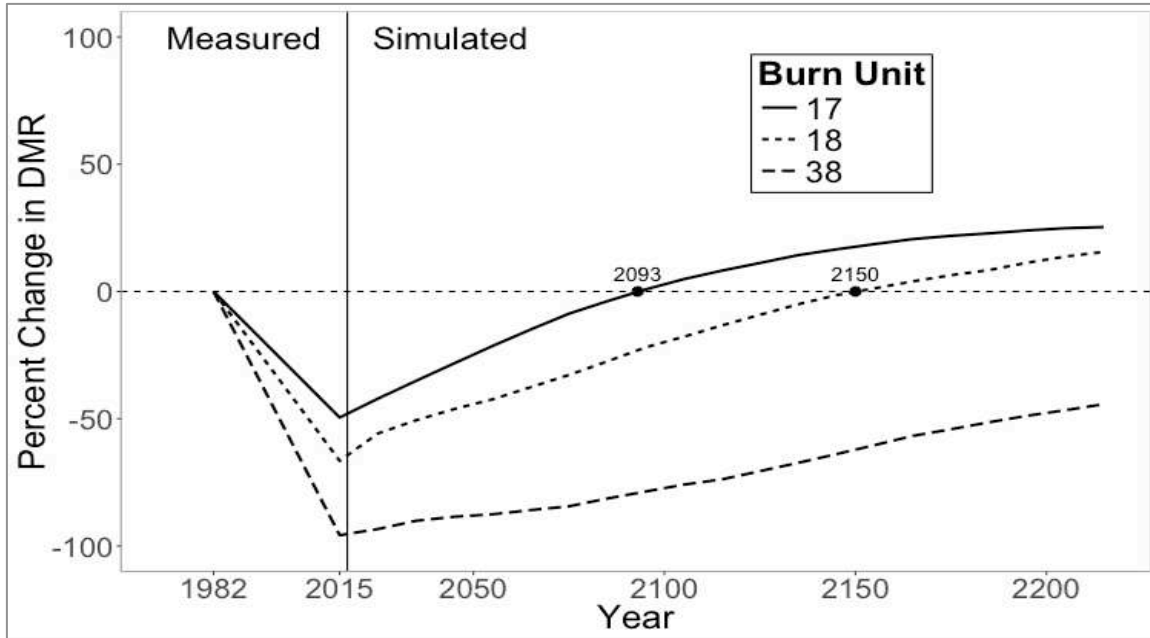


Figure 9. Stand level DMR ratings through time. Left of the vertical line are the pre-fire (1982) and current levels (2015) as measured in the field, and to the right are the simulated DMR levels from USFS FVS.

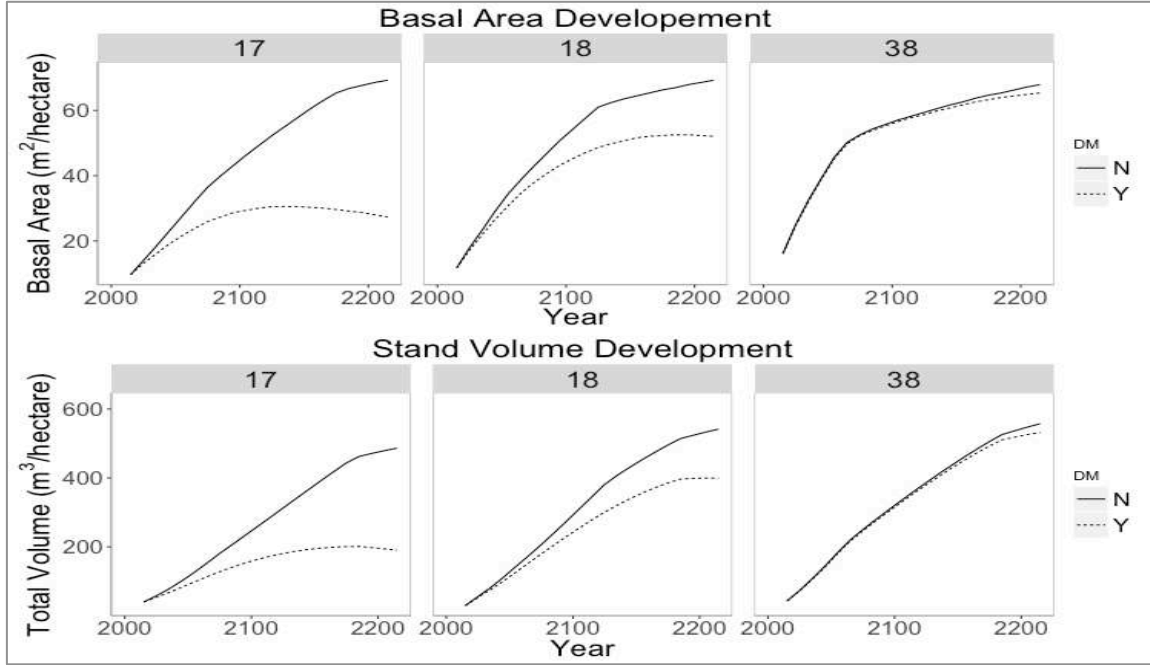


Figure 10. Plots showing the simulated effect of dwarf mistletoe on basal area and volume accumulation through time. These plots were derived from FVS simulation results with the dwarf mistletoe extension on (Y) and with it deactivated (N).

3.5 DISCUSSION

3.5.1 Post-fire Stand Structure

These results confirmed lodgepole pine's ability to regenerate prolifically following high severity fire, as the measured regeneration densities are extremely high, resulting in stands that are far denser than pre-fire conditions. The results also showed a positive relationship between pre-fire density and regeneration density, which would be expected for a species such as lodgepole pine that has a large canopy seed bank in the form of serotinous cones (Lotan et al. 1985). Other studies in post-fire lodgepole pine forests have shown a strong relationship between the amount of available seed in the canopy seed bank and the density of regeneration following a high severity fire event (Tinker et al. 1994, Schoennagel et al. 2003). The amount of seed in the canopy seed bank is related to factors including percent serotiny and live tree density. There were insufficient data for a detailed comparison of serotiny levels across stands, but pre-fire serotiny surveys indicate that percent serotiny was generally high (>85% of trees serotinous), suggesting that live tree density would be expected to provide a reasonable estimation of the available seed bank (Zimmerman 1990).

3.5.2 Surface Fuel Dynamics

The findings with regard to surface fuel loadings were somewhat unexpected, as the amount of coarse fuel has not changed in the thirty years since the fires. This lack of change in coarse woody debris is surprising, as significant inputs from falling fire-killed trees would be expected based upon both intuition and prevailing theories related to post-fire fuel dynamics (Keane 2015). Decomposition of coarse fuels left unconsumed by the fire

cannot explain this result, as decomposition of coarse fuels in this region is extremely slow with turnover times for lodgepole pine logs in the area of 580 years (Kueppers 2004). It is clear that there must have been inputs to surface fuels from fire-killed trees as very few fire-killed trees remain as standing snags. Additionally, the detected positive relationship between the number of trees killed by fire and current thousand-hour fuel loading supports that idea that there have been significant inputs from fire killed trees (Figure S1). While the unchanged coarse woody debris loading may be a true result, it is more likely that the mean loadings reported in the original surveys overestimated loadings due to the high error rates and bias associated with the Brown's transect sampling method that was utilized in the 1982 and 1983 measurements (Brown 1974), as compared to the complete coarse woody debris census conducted in 2015.

In contrast to coarse fuel, fine fuels have increased substantially and are currently higher than both pre and post-fire loadings. These results indicate that there is as much as twice the loading of fine fuels in comparison to pre-fire levels. This is important in the context of fire hazard, as fine fuels drive fire rate of spread and fireline intensity (Rothermel 1972). In addition to high fine fuel loads, these stands are currently very dense with average crown base heights between 1 and 2 meters. This combination of factors suggests there is substantial risk that a reburn of these areas would result in an active crown fire consuming all live trees. At this stage in development, this type of fire could be devastating to forest cover as young lodgepole pine typically do not possess serotinous cones (Schoennagel et. al 2003) and there are limited old trees remaining on site.

3.5.3 Current Dwarf Mistletoe Population

Overall, this case study supports the prevailing ideas related to the interaction between fire severity and dwarf mistletoe populations, while providing some insight into required mortality thresholds to achieve long-term dwarf mistletoe population reductions and improved stand productivity. With increased fire severity there is a very sharp decline in both the stand level DMR and the percent of trees infected by dwarf mistletoe (Figure 8, Figure S2). This result is not entirely surprising in light of the life cycle and obligate nature of dwarf mistletoe, but the study does serve as the first experimental test into the effects of prescribed crown fires on dwarf mistletoe populations and infestation intensity. These results confirm that prescribed stand replacing fire can be a viable method of regenerating a stand that is relatively free from dwarf mistletoe infection, assuming that adequate levels of mortality are achieved. The relationship between fire severity and DMR appears to be linear, however this linear relationship may break down at very low mortality levels. It is also important to note that there were no data points between 20.8% and 60.7% mortality, so it is unclear whether the relationship would remain linear across that severity range.

At lower overstory mortality levels (5%-15%) a fire may simply have the effect of thinning the stand without initiating a large pulse of regeneration. In these low mortality situations DMR levels may be temporarily reduced, but in the long-term, the overall dwarf mistletoe population will either be unaffected or increased. Research focused on dwarf mistletoe and prescribed surface fires in ponderosa pine and dry-mixed conifer forests have shown that infected trees suffer increased levels of crown scorch and mortality, which results in net reductions to the dwarf mistletoe population (Koonce and Roth 1980, Harrington and Hawksworth 1990, Conklin and Armstrong 2001). However, this control is

short lived and stands may return to pre-fire levels within 10 years (Conklin and Geils 2008). Though less common than in ponderosa pine/dry-mixed conifer, surface fires have been documented as part of the natural fire regime in many lodgepole pine dominated systems (Arno 1980, Barrett et al. 1991, Amoroso et al. 2011, Heyerdahl et al. 2014), including the present study site (Zimmerman and Laven 1984). It is unclear whether fire effects in these systems will follow patterns seen in the more open ponderosa pine/dry-mixed conifer forests. More research, both observational and experimental, is required to more fully understand how low severity fires (< 20 percent overstory mortality) in lodgepole pine dominated forests will influence short and long-term dwarf mistletoe population levels.

3.5.4 Dwarf mistletoe intensification and impacts to stand growth

Based on the FVS simulations of the overall dwarf mistletoe population, only burn 38 showed a substantial, long-term reduction in DMR with DMR levels remaining below pre-fire levels for the duration of the simulation. Stand 18 showed a small reduction in the overall population with DMR remaining below pre-fire levels for approximately 170 years. Though this represents a net reduction in the overall dwarf mistletoe population, stand 18 would still ultimately reach very high levels of infestation. Stand 17 saw no effect of fire on overall dwarf mistletoe populations as the DMR is predicted to return to pre-fire levels by the time that this stand reaches its age at the time of burning (~110 years). These results suggest that dwarf mistletoe populations will only be substantially reduced in high severity fire events (>85% mortality), though slightly lower mortality rates can result in net reductions to the dwarf mistletoe population.

It is important to note that a major limitation to the DMIM spread model is that fact that it is nonspatial. Dwarf mistletoe is capable of dispersing seeds up to 10 or 15 meters from an infected tree, however most seeds will land much closer to the host tree. As a result, the risk of infection or intensification is highly associated with the distance to other infected trees. The logistic regressions that predict the probability of DMR change were derived from a study in even-aged lodgepole pine stands that were thinned to a range of tree densities, therefore representing the simplest possible case (Dooling et al. 1986). More testing and evaluation is need to understand how well this model will predict spread in complex stands that contain high levels of vertical and horizontal heterogeneity of trees and/or an aggregated pattern of infected trees. With these limitations in mind, the relative differences in spread and intensification between stands in this study would be expected to be the same and therefore the simulated results are still valuable.

In terms of impacts to growth and productivity, FVS simulations revealed that only at the highest levels of overstory mortality were dwarf mistletoe populations reduced to levels that would not have strong negative impacts on the post-fire stand. The fires on stands 17 and 18 resulted in 41.5 and 73.2 percent overstory mortality, respectively, and it was clear that these mortality levels were not high enough to regenerate stands free from the damaging effects of dwarf mistletoe infection. However, in stand 38 the mortality rate was 88.7% and FVS simulations predict that basal area losses due to dwarf mistletoe infestation will be minimal. This result suggests that fires in highly infected lodgepole pine stands need to kill about 85% of overstory trees to achieve sustained reductions to the dwarf mistletoe population and create stands whose growth and development will not be significantly impacted by dwarf mistletoe.

As previously discussed, studies examining dwarf mistletoe populations at large scales have shown that time since fire is the single largest predictor of infection severity, and both the empirical and modeled results from this study confirm the mechanism behind these findings (dwarf mistletoe spread from fire surviving trees). These results also provide some insight into the mortality rates needed to achieve sustained, long-term reductions in the overall dwarf mistletoe population. While these findings support the claim made by many researchers that 100 percent overstory mortality is required for complete mistletoe sanitation (e.g. Baranyay and Smith 1972, Alexander and Hawksworth 1975), they also suggests that partial overstory mortality can reduce populations for ecologically and economically significant periods of time.

3.6 MANAGEMENT IMPLICATIONS

The original goal of these prescribed burns was to evaluate whether or not prescribed crown fire could be an economically viable method of destroying heavily infected precommercial stands in order to regenerate an uninfected stand for timber production. The implementation costs discussed in Zimmerman et al. (1990) suggest that prescribed fire may be a cheaper alternative than simply clear-felling a stand with no commercial value, and the results of this study have shown that fire can regenerate uninfested or lightly infested stands if adequate mortality is achieved. In the event of inadequate overstory mortality, mechanical girdling of surviving trees immediately post-fire could be used to prevent them from infecting new regeneration. Though this combination of fire and post-fire girdling may be a cheaper alternative to precommercial clear-felling, it would be challenging to implement in most cases given the difficulty, both

operationally and politically, of igniting prescribed fires under the fuel and weather conditions required to achieve high severity crown fire. In addition, the cost per unit area for these prescribed fires was very low due to extremely limited personnel and equipment on-site. Current public awareness and concern over the potential for prescribed fires to escape would likely result in the need to utilize a greater number of resources to achieve the same result as the fires implemented in 1982 by Zimmerman et al. (1990) (Quinn-Davidson and Varner 2012, Ryan et al. 2013).

3.7 CONCLUSION

Overall this study showed that prescribed fire is a viable method of initiating new stands of lodgepole pine free from the damaging effects of dwarf mistletoe infestation, but these results also have implications for understanding how natural wildfires influence dwarf mistletoe populations across the landscape. Kipfmueller and Baker (1998) conducted a landscape analysis of dwarf mistletoe populations and wildfire history within the Medicine Bow National Forest and reported that dwarf mistletoe infestation severity generally increased with time since fire, but variability was quite high. They indicated that this variability was the result of the survival of infected trees, but they made no attempt to control for the severity of a particular fire, rather plots were categorized by the presence of absence of tree that survived the previous fire event. They report a patchy distribution of infection centers across the landscape, which were associated with plots containing trees that survived the most recent fire event. As wildfires in lodgepole pine forests often burn in patchy, heterogeneous patterns (Turner et al. 1994), it is important to consider the percent wildfire mortality achieved at a particular location in order to fully predict how the dwarf

mistletoe population will respond to a specific wildfire event. Results from this study suggest a negative linear relationship between fire severity and future dwarf mistletoe infestation severity and could be used to predict the impact to the dwarf mistletoe population as a result of a wildfire passing through a highly infested area.

Another important implication of these results is that increased heterogeneity of fire effects will result in increased heterogeneity of dwarf mistletoe populations across the landscape, thereby creating a complex mosaic of infestation severities which is dictated by landscape patterns of wildfire severity and pre-fire dwarf mistletoe. Furthermore, if dwarf mistletoe infestations alter wildfire behavior and effects there may be feedback loops across multiple fire cycles. For example, if dwarf mistletoe increases fire severity, then multiple fire cycles will tend to reduce the severity of a particular infestation center or even completely eliminate it. In contrast, if dwarf mistletoe infestation reduces fire severity or increases the heterogeneity in fire effects, then multiple fire cycles will tend to amplify a particular infestation center. As lodgepole pine forests are not generally considered to be fuel limited, wildfire severities are largely controlled by local weather conditions at the time of burning (Turner et al. 1994, Bessie and Johnson 1995, Buechling and Baker 2004), and it is therefore unlikely that responses across multiple fire cycles will be as consistent and predictable as suggest by these simplified examples. With that said, the results of this study do provide a clearer picture of the mechanisms by which dwarf mistletoe populations are controlled at landscape scales and further explain the highly variable, patchy nature of dwarf mistletoe infestation within this forest type.

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APPENDIX

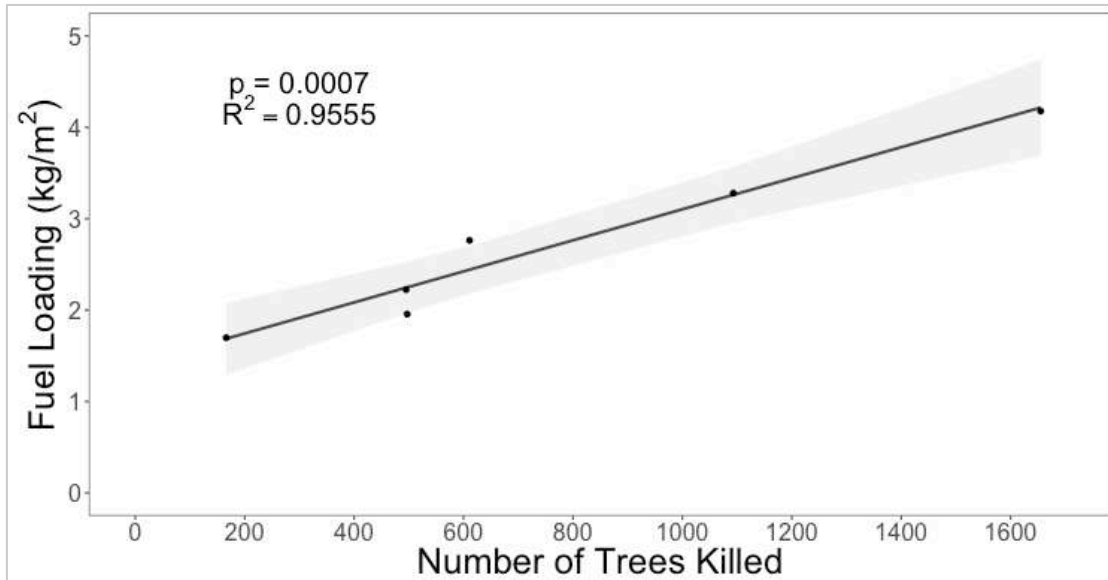


Figure S1. Simple linear regression of number of trees killed per hectare on current loading of thousand hour fuels. Shaded region represents the 95% confidence interval.

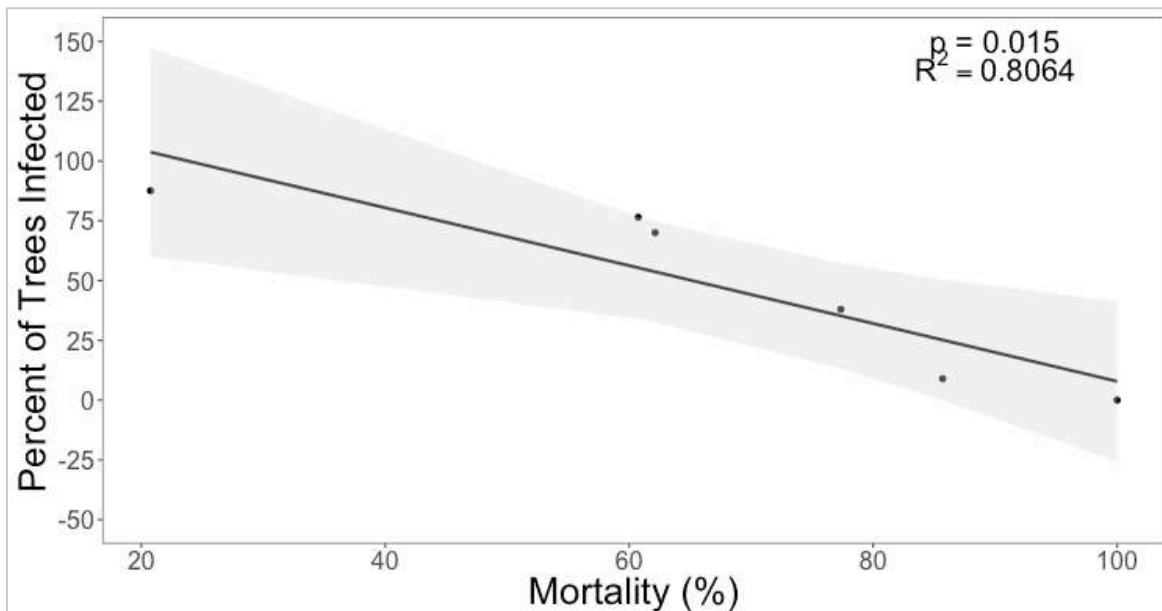


Figure S2. Simple linear regression of fire mortality on percent of trees currently infected with dwarf mistletoe. Shaded region represents the 95% confidence interval.