

AN ABSTRACT OF THE THESIS OF

Michelle C. Agne for the degree of Master of Science in Sustainable Forest Management
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Title: Influence of Dwarf Mistletoe (*Arceuthobium americanum*) on Stand Structure,
Canopy Fuels, and Fire Behavior in Lodgepole Pine (*Pinus contorta*) Forests 21-28 Years
Post-Mountain Pine Beetle (*Dendroctonus ponderosae*) Epidemic in Central Oregon

Abstract approved:

David C. Shaw

Lodgepole pine (*Pinus contorta*) forests are widely distributed throughout western North America. However, the lodgepole pine forests of central Oregon are ecologically unique to the region, with a mixed severity fire regime, low cone serotiny, and their occasional presence as a climax species. Most of the research conducted regarding the stand structure and disturbance regimes of lodgepole pine has occurred in the intermountain west. Research findings from other geographical locations may not be applicable to central Oregon lodgepole pine forests, given their distinctive ecological attributes.

Lodgepole pine forests are subject to three widespread disturbance regimes: mountain pine beetle, dwarf mistletoe, and fire. Although much is known about each of these disturbances in lodgepole pine, little is known about their interactive effects. These disturbances occur pervasively in lodgepole pine and are known to co-occur on the landscape, so their effects must be investigated and interpreted simultaneously. This thesis describes the combined influences of dwarf mistletoe and mountain pine beetle on stand structure, canopy fuels, and fire behavior in central Oregon lodgepole pine forests.

We randomly selected and sampled 39 0.075-hectare plots within 13 stands in the Deschutes National Forest in central Oregon. The plots varied from 0 to 4 in average dwarf mistletoe rating (DMR) and all had experienced a mountain pine beetle mortality event 21 to 28 years prior to sampling. In Chapter 2, we compared stand density, stand basal area, canopy volume, proportion of the stand in dominant/codominant, intermediate, and suppressed cohorts, and average height and average diameter of each cohort, across the range of DMR. We found strong evidence of a decrease in canopy volume, suppressed cohort height, and dominant cohort diameter with increasing DMR. There was strong evidence that as DMR increases, proportion of the stand in the dominant/codominant cohort decreases, while proportion of the stand in the suppressed cohort increases. Structural differences associated with dwarf mistletoe create heterogeneity in this forest type and may have a large impact on the productivity, resistance, and resilience of these stands. These findings show that it is imperative to

incorporate dwarf mistletoe effects when studying stand productivity and ecosystem recovery processes.

In Chapter 3, we compared canopy base height, the fuel parameter that drives passive crown fire, and canopy bulk density, the fuel parameter that drives active crown fire, over the range of DMR to determine the effect of dwarf mistletoe on canopy fuels. We then used BehavePlus to model passive crown fire and active crown fire in our plots. We found strong evidence of a decrease in canopy base height with increasing DMR. There was suggestive evidence of decrease in canopy bulk density with increasing DMR, after accounting for stand density. The results of the fire behavior modeling suggest that at low to moderate wind speeds, likelihood of passive crown fire increases with increased DMR. However, under more extreme weather (wind speeds >20 mph), the effect of dwarf mistletoe on passive crown fire potential was not shown to be important. The potential for active crown fire was extremely low in our plots, regardless of DMR. These findings show that dwarf mistletoe is having a significant effect on the potential for passive crown fire in lodgepole pine forests 21 to 28 years post-mountain pine beetle epidemic, and should be considered in future research regarding post-mountain pine beetle fuels and fire behavior.

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

Michelle C. Agne, Author

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Chapter 1: General Introduction

Lodgepole pine (*Pinus contorta*) forests are widely distributed throughout western North America (Lotan and Critchfield 1990). However, the lodgepole pine forests of central Oregon are ecologically unique to the region. Distinctive from other areas with the forest type, two varieties of the species are thought to intersect in central Oregon: *Pinus contorta* var. *murrayana* (Sierra lodgepole pine) and *Pinus contorta* var. *latifolia* (Rocky Mountain lodgepole pine) (Lotan and Critchfield 1990). Although Sierra lodgepole pine is the dominant variety represented in these forests, Rocky Mountain lodgepole pine can be found as well, distinguishing these forests from lodgepole pine in other regions.

Central Oregon lodgepole pine is often found in nearly pure stands as an edaphic or topoedaphic climax species (Simpson 2007), while in the intermountain west it is commonly seral and succeeds to another species (Amman 1977, Diskin et al 2011). Lodgepole pine forests in the intermountain west experience a high severity, stand replacement fire regime, leading to establishment of single-aged lodgepole pine stands following the release of seed from serotinous cones (Lotan et al 1985). The fire regime in central Oregon lodgepole pine is mixed severity and cone serotiny is infrequent, leading to variability of structural complexity within and among stands (Stuart et al 1989), and to variable future fire potential (Agee 1993). There is a considerable body of research regarding the stand structure (Parker 1986, Stuart et al 1989, Parker and Parker 1994) and disturbance regimes of lodgepole pine forests (Lotan et al 1985, Wanner and

Tinnin 1989, Godfree et al 2002a, b, Page and Jenkins 2007a, Sibold et al 2007, Collins et al 2011, Kayes and Tinker 2012, Pelz and Smith 2012). However, much of the research regarding lodgepole pine has occurred in the intermountain west, and the research findings may not be applicable to central Oregon lodgepole pine forests, given their distinctive ecological attributes.

Forest stand structure influences many aspects of forests, such as biodiversity (Hooper et al 2005, McIntosh et al 2013), wildlife niches (Garnett et al 2006, Hedwall and Mathiasen 2006), hydrologic processes (Varhola et al 2010), stand productivity (Ishii et al 2004, Mainwaring and Maguire 2004), and ecosystem resistance and resilience to disturbances (Asterup et al 2008, Diskin et al 2011). Closely related to stand structure are fuels loadings and arrangement, which are key drivers of fire behavior (Reinhardt et al 2006). An increased understanding of insect and pathogen interactions will be extremely important for understanding future ecosystems and fire regimes (Parker et al 2006) because there is a large impact from these types of forest disturbances on stand structure, fuels loadings, and potential fire behavior. Characterization of fuels loadings associated with various forest types, age classes, and structures is essential to obtain accurate information regarding fire hazard (Sandberg et al 2001). It is necessary to examine the entire disturbance ecology of an ecosystem simultaneously when determining its health and functionality because of the potential importance of interactive effects of multiple disturbances (Gara et al 1985, Parker et al 2006, Derosé and Long 2009, Metz et al 2011).

Lodgepole pine dwarf mistletoe (*Arceuthobium americanum* Nutt. Ex Engelm.), is a widespread pathogen of lodgepole pine, occurring throughout the range of its host (Johnson and Hawksworth 1981). Dwarf mistletoe is an obligate hemiparasite which obtains the majority of its carbohydrates and other nutrients from its host (Hull and Leonard 1964a, Hull and Leonard 1964b), leading to host growth loss, lowered vigor, and higher susceptibility to mortality at high infection severities (Hawksworth and Hinds 1964, Baranyay and Safranyik 1970, Johnson and Hawksworth 1981). In addition to growth loss, moderate to severe infection by dwarf mistletoe often induces host deformities due to the formation of structures called witches brooms, which concentrate biomass in infected branches, often low in the crown of the tree, and act as nutrient sinks (Tinnin et al 1982, Hawksworth and Dooling 1984, Godfree et al 2002a, Mathiasen et al 2008). Severely infected trees have greater vertical fuel continuity than uninfested trees, potentially leading to a greater probability of torching (Brown 1975, Wicker and Leaphart 1976, Conklin and Geils 2007). The individual structure of crowns has been shown to be significantly impacted via this mechanism (Hawksworth 1961, Godfree et al 2002a), but less work has been done surrounding the impacts of dwarf mistletoe on overall structure at the stand scale (Parmeter 1978, Mathiasen 1996, Godfree et al 2003).

The role that mountain pine beetle (*Dendroctonus ponderosae* Hopkins) epidemics may play in altering fuels and potential fire behavior (Hicke et al 2012), as well as the ecosystem recovery trajectories of post-epidemic lodgepole pine stands (Collins et al 2011, Kayes and Tinker 2012, Pelz and Smith 2012) has received great

research attention in recent years. Although this bark beetle is native to lodgepole pine forests, at epidemic levels it has the ability to cause mortality to large percentages of mature trees over expansive areas (Amman 1977). This has a large impact on stand structure, leaving residual smaller diameter trees and advance regeneration in the understory (Roe and Amman 1970). Previous studies have found variable effects of mountain pine beetle epidemics on canopy fuels loadings and fire behavior. Findings are largely dependent on the time since beetle epidemic (Simard et al 2011), and may be dependent on geographical location.

Dwarf mistletoe and mountain pine beetle occur pervasively in lodgepole pine forests and they are likely interacting in the environment. A random sample of 212 lodgepole pine dominated plots in central Oregon 2-31 years post-mountain pine beetle indicated that 72% of post-mountain pine beetle lodgepole pine stands in the area had some level of dwarf mistletoe infection (T.J. Woolley et al, Oregon State University, unpublished data). Although these disturbances frequently occur together on the landscape and both influence stand structure, fuels and fire behavior, no study has attempted to quantify their interactive impacts on stand structure, fuels loadings, or fire behavior. Not only is it important to investigate the cumulative impacts of these two widespread disturbances, but given the high frequency with which they each occur on the landscape, it is nearly impossible to accurately identify the impacts of one without accounting for the other.

The objective of this project was to describe effects of dwarf mistletoe infection in unmanaged central Oregon lodgepole pine stands over a range of dwarf mistletoe severities while controlling for the effect of the previous mountain pine beetle epidemic 21 to 28 years prior to measurement. The specific research questions I addressed were:

- 1) How does the overall stand structure of lodgepole pine forests 21-28 years post-mountain pine beetle change with varying levels of dwarf mistletoe severity?;
- 2) How do canopy fuels in lodgepole pine forests 21-28 years post-mountain pine beetle change with varying levels of dwarf mistletoe severity?;
- 3) Do differences in canopy fuels over the range of dwarf mistletoe severity result in changes in modeled crown fire behavior?

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Chapter 2: Effects of Dwarf Mistletoe (*Arceuthobium americanum*) on Stand Structure of Lodgepole Pine (*Pinus contorta*) Forests 21-28 Years Post-Mountain Pine Beetle (*Dendroctonus ponderosae*) Mortality Event in Central Oregon

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Abstract

Forest stand structure is a determinant of many forest processes, such as the maintenance of biodiversity, wildlife niche creation, hydrologic processes, stand productivity, and ecosystem resistance and resilience. Many individual disturbances have been shown to impact forest stand structure, but synergistic effects of multiple disturbances are not well understood in many ecosystems. Lodgepole pine (*Pinus contorta*) is widely distributed throughout North America and is subject to mountain pine beetle (*Dendroctonus ponderosae*) and dwarf mistletoe (*Arceuthobium americanum*) throughout its range. Although each of these disturbances has been well studied, few studies have incorporated both disturbance effects simultaneously although they occur together frequently on the landscape. We randomly selected and sampled 39 0.075-hectare plots within 13 stands in the Deschutes National Forest in central Oregon. The plots varied from 0 to 4 in average dwarf mistletoe rating (DMR) and all experienced a mountain pine beetle mortality event 21 to 28 years prior to sampling. We compared stand density, stand basal area, canopy volume, proportion of the stand in dominant/codominant, intermediate, and suppressed cohorts, and average height and average diameter of each cohort, across the range of DMR. We found strong evidence of a decrease in canopy volume ($p = 0.0146$), suppressed cohort height ($p = 0.0061$), and dominant cohort diameter ($p = 0.0074$) with increasing DMR. There was strong evidence that as DMR increases, proportion of the stand in the dominant/codominant cohort decreases ($p = 0.0095$) while proportion of the stand in the suppressed cohort increases (p

= 0.0016). Structural differences associated with dwarf mistletoe create heterogeneity in this forest type and may have a significant influence on the productivity, resistance, and resilience of these stands. Our findings show that it is imperative to incorporate dwarf mistletoe when studying stand productivity and ecosystem recovery processes because of its large influence on stand structure.

Introduction

Forest stand structure is a determinant of many processes within forests, such as the maintenance of biodiversity (Hooper et al 2005, McIntosh et al 2013), wildlife niche creation (Garnett et al 2006, Hedwall and Mathiasen 2006), hydrologic processes (Varhola et al 2010), stand productivity (Ishii et al 2004, Mainwaring and Maguire 2004), and ecosystem resistance and resilience to disturbances (Waring and Pitman 1985, Asterup et al 2008, Diskin et al 2011). Heterogeneity of stand structure is closely associated with the diversity of understory vegetation conditions (Van Pelt and Franklin 2000), differentiation of soil microorganism communities (McIntosh et al 2013), and diversification of wildlife habitat (Hooper et al 2005). Vertically and horizontally diversified forest stands have been shown to have higher overall stand productivity (Ishii et al 2004) and support higher volumes of biomass in both the understory and overstory than stands with uniform structure (Van Pelt and Franklin 2000). Typically, stands with high structural diversity are more resistant and resilient to both native and invasive disturbances than are stands with low structural diversity (Millar et al 2007).

Disturbances are known to influence the development of stand structure, forest communities, and landscape patterns (Dobson and Crawley 1994, Clark 1991, Turner et al 1989), and considerably impact processes such as gap dynamics and succession (Spies and Franklin 1989, Veblen et al 1991). As knowledge of individual disturbances has increased, the importance of understanding interactions of multiple disturbances within an ecosystem has gained recognition (Bigler et al 2005, Turner 2005, Kulakowski and

Veblen 2007, D'Amato et al 2011, Simard et al 2011). Concern for synergistic disturbance interactions (compound disturbances) necessitates that multiple disturbance effects are accounted for simultaneously in ecosystems, as summing their individual effects may not represent their combined effects (Paine et al 1998). Complex interactions surrounding disturbance dynamics on the landscape have begun to be quantified, but many uncertainties remain (Turner 2010). Understanding these relationships will be imperative for managing stands into the future (Dale et al 1998).

Lodgepole pine (*Pinus contorta*) forests are widely distributed throughout western North America (Lotan and Critchfield 1990). There is a considerable body of research regarding their stand structure (Parker 1986, Stuart et al 1989, Parker and Parker 1994) and the manner in which disturbances interact with stand structure (Lotan et al 1985, Wanner and Tinnin 1989, Godfree et al 2002a, 2002b, Sibold et al 2007, Collins et al 2011, Kayes and Tinker 2012, Pelz and Smith 2012). However, much of the research regarding lodgepole pine stand structure has occurred in the intermountain west. The lodgepole pine forests of central Oregon are ecologically unique to the region. Distinctive from other areas across the forest type, two varieties of the species are thought to intersect in central Oregon: *Pinus contorta* var. *murrayana* (Sierra lodgepole pine) and *Pinus contorta* var. *latifolia* (Rocky Mountain lodgepole pine) (Lotan and Critchfield 1990). Although Sierra lodgepole pine is the dominant variety represented in these forests, Rocky Mountain lodgepole pine can be found as well, distinguishing these forests from lodgepole pine in other regions.

Central Oregon lodgepole pine is often found in nearly pure stands as an edaphic or topoedaphic climax species (Simpson 2007), while in the intermountain west it is commonly seral and succeeds to another species (Amman 1977, Diskin et al 2011). Lodgepole pine forests in the intermountain west experience a high severity, stand replacement fire regime, leading to establishment of single-aged lodgepole pine stands following the release of seed from serotinous cones (Lotan et al 1985). The fire regime in central Oregon lodgepole pine is mixed severity and cone serotiny is infrequent, leading to variability of structural complexity within and among stands (Stuart et al 1989), and to variable future fire potential (Agee 1993). The ecological differences in lodgepole pine forests suggest that geographically specific work is needed to understand how disturbances influence stand structure in this forest type.

Lodgepole pine dwarf mistletoe (*Arceuthobium americanum* Nutt. Ex Engelm.), is a widespread pathogen of lodgepole pine, occurring throughout the range of its host (Johnson and Hawksworth 1981). Dwarf mistletoe is an obligate hemiparasite which obtains the majority of its carbohydrates and other nutrients from its host (Hull and Leonard 1964a, Hull and Leonard 1964b), leading to host growth loss, lowered vigor, and higher susceptibility to mortality when trees are severely infested (Hawksworth and Hinds 1964, Baranyay and Safranyik 1970, Johnson and Hawksworth 1981). In addition to growth loss, moderate to severe infection by dwarf mistletoe often induces host deformities due to the formation of structures called witches brooms, which concentrate biomass in infected branches and act as nutrient sinks (Hawksworth and Dooling 1984,

Mathiasen et al 2008). The individual structure of crowns is significantly impacted via this mechanism (Hawksworth 1961, Godfree et al 2002a), but less work has been done surrounding the impacts of dwarf mistletoe on overall structure at the stand scale (Parmeter, 1978, Mathiasen 1996, Godfree et al 2003).

Dwarf mistletoe impacts many aspects of stand structure in lodgepole pine forests. Stand density has been shown to increase five-fold between uninfested and severely infested stands (Wanner and Tinnin 1989). The increase in stand density is attributed to a shift in tree size distribution to smaller size classes, with increased densities of suppressed trees and decreased densities of dominant trees in stands with high levels of dwarf mistletoe as compared with stands without dwarf mistletoe (Wanner 1986, Wanner and Tinnin 1989, Godfree et al 2002a). Similarly, densities of saplings have been observed to increase fifteen-fold between uninfected and severely infected lodgepole pine stands (Godfree et al 2002b). Decreases in average diameter within size classes, particularly in larger size classes, have also been observed with increased DMR (Hawksworth and Hinds 1964, Baranyay and Safranyik 1970, Wanner and Tinnin 1989). Significant decreases in average height of dominant trees have been frequently observed (Weir 1916, Hawksworth and Hinds 1964, Baranyay and Safranyik 1970), although Wanner and Tinnin (1989) found no significant difference in average height of dominant trees among infection levels.

Stand structure of lodgepole pine forests is also known to be severely impacted by mountain pine beetle (*Dendroctonus ponderosae* Hopkins) mortality events. Although this bark beetle is native to lodgepole pine forests, at epidemic levels it has the ability to cause mortality to large percentages of mature trees over expansive areas (Amman 1977). This imitates the effect of thinning from above, leaving residual smaller diameter trees and advance regeneration in the understory (Roe and Amman 1970). The effect of mountain pine beetle on stand structure is highly dependent upon the time since beetle (TSB) as post-epidemic stand structure goes through rapid and drastic changes through time (Mitchell and Priesler 1998, Simard et al 2011).

The effect of mountain pine beetle on stand density is highly dependent on TSB. Stand density is greatly decreased immediately post-epidemic and declined by 50 - 62% as compared with pre-epidemic stands during a recent epidemic in Colorado (Diskin et al 2011, Klutsch et al 2009). However, by 20 to 30 years TSB, stand density has been shown to recover to pre-epidemic conditions in some cases (Pelz and Smith 2012), and may surpass the density of stands which have not been recently attacked (Sibold et al 2007). Similarly, stand basal area is immediately reduced by about 63 - 70% post-epidemic (Diskin et al 2011, Klutsch et al 2009), but reaches about 60% of pre-epidemic basal area by 25-30 years TSB (Pelz and Smith 2012) and is predicted to recover fully by 80 years TSB in some cases (Collins et al 2011).

Tree size distribution is immediately skewed toward the small size classes post-epidemic with the removal of large trees, decreasing overall stand height and average DBH (Amman 1977, Klutsch et al 2009). Regeneration density increased seven-fold between pre-epidemic conditions and 25 to 30 years TSB in lodgepole pine stands in Colorado (Pelz and Smith 2012). However, even immediately post-epidemic, lodgepole pine advance regeneration has been measured at relatively high densities from, 970 to 1200 stems/ha (Collins et al 2011, Kayes and Tinker 2012).

The effects of dwarf mistletoe on stand structure from central Oregon reflect the same effects reported for bark beetles, but previous research (Wanner 1986, Wanner and Tinnin 1989, Godfree et al 2002a, Godfree et al 2002b) did not take into account time since the previous mountain pine beetle mortality event in their studies. Although the manner in which dwarf mistletoe and mountain pine beetle disturbances influence stand structure is fairly well-understood, their interaction has not been investigated. A random sample of 212 lodgepole pine dominated plots in central Oregon 2-31 years post-mountain pine beetle indicated that 72% of post-mountain pine beetle lodgepole pine stands in the area had some level of dwarf mistletoe infection (T.J. Woolley et al, Oregon State University, unpublished data). 53% of the total plots had light to moderate dwarf mistletoe infection while 19% of the plots had severe dwarf mistletoe infection. The two disturbances co-occur with high frequency, so the response of stand structure to both mountain pine beetle and dwarf mistletoe at various severity levels must be considered simultaneously to understand what is occurring on the landscape.

To address this interaction, we asked: “How does stand structure of lodgepole pine forests 21-28 years post-mountain pine beetle mortality event change with varying levels of dwarf mistletoe infection?” We identified several important metrics for assessment of stand structure: stand density, stand basal area, canopy volume, proportion of live trees in dominant/codominant, intermediate, and suppressed cohorts, average height and DBH of trees within cohorts, regeneration density and regeneration infection intensity. Each of these characteristics is affected by either dwarf mistletoe, mountain pine beetle, or both of these disturbance agents. However, the combined impacts of dwarf mistletoe and mountain pine beetle have not been investigated.

We hypothesized: 1) stand density increases with increasing dwarf mistletoe severity, 2) stand basal area and canopy volume decrease as dwarf mistletoe severity increases, 3) as dwarf mistletoe severity increases, larger proportions of the stands are represented by cohorts of small trees and smaller proportions of stands are represented by cohorts of large trees, 4) average height and diameter of all cohorts decreases as dwarf mistletoe severity increases, and 5) regeneration density increases with increasing dwarf mistletoe severity and there is a significant amount of regeneration infection in the understory of severely infected stands. Many of the canopy structural changes associated with dwarf mistletoe infestation occur as a result of witches’ brooms, so we also compared volume in brooms and dwarf mistletoe rating systems to ensure we were accurately capturing the effect of brooms on canopy structure.

Materials and Methods

Study Area

The study area for this research is located in central Oregon within the Deschutes National Forest. The Deschutes National Forest is located on the east side of the Cascade Mountains, covering an area of approximately 728,000 hectares (Figure 2.1). Sites were chosen within the edaphic and topoedaphic climax lodgepole pine zones according to the plant association guide for the area (Hopkins 1979, Volland 1988, Simpson 2007). In this area, the ecological site characteristics of the climax lodgepole pine type are relatively uniform, characterized by pumice soils and flat to gently rolling topography which often results in cold air drainage to these areas (Franklin and Dyrness 1973). The lodgepole pine zone is located between 1,200 and 1,525 meters elevation with mean annual temperatures ranging from 4.3 to 5.8° C and mean annual precipitation ranging from 38 to 89 cm depending upon the specific plant association (Simpson 2007). The Wickiup Dam climate station (the most representative climate station for the study area) showed average daily temperatures ranging from -2.2° C in January to 18.3° C in July (Western Regional Climate Center 2013).

Measured sites were restricted to areas 21-28 years post mountain pine beetle epidemic to control for the effect of mountain pine beetle on stand structure. The year of initiation of each mountain pine beetle mortality event was determined using Aerial Detection Survey (ADS) data (USDA Forest Service 2012). Areas with known past management or recent fire were excluded from sampling. Typically, the stands were

characterized by large amounts of coarse wood, few standing snags, dense lodgepole pine regeneration, and an overstory comprised of lodgepole pine too small to support a mountain pine beetle brood at the time of the epidemic that subsequently released after the removal of the previous overstory.

A minimum of 70% of live trees at each site measured were lodgepole pine. Other tree species found at the sites varied with elevation in the study area. Ponderosa pine (*Pinus ponderosa*) was present at lower elevations, while white fir (*Abies concolor*), grand fir (*Abies grandis*), mountain hemlock (*Tsuga mertensiana*), and whitebark pine (*Pinus albicaulis*) were located at higher elevations. Engelmann spruce (*Picea engelmanni*) and western white pine (*Pinus monticola*) were occasionally present within the study area as well. Common shrub species in the study area are *Purshia tridentata*, *Arctostaphylos nevadensis*, and *Ribes cereum*. Common herbaceous species found in the understory were *Acnatherum occidentale*, *Carex inops*, *Carex rossii*, *Elymus elemoides*, *Epilobium angustifolium*, *Fragaria virginiana*, and *Lupinus argenteus*.

Site Selection

Sites were selected based on a network of 119 plots randomly located within post-mountain pine beetle climax lodgepole pine in the Deschutes National Forest that were established during the summers of 2010 and 2011 (T.J. Woolley et al, unpublished data). The network of plots was designed using a spatially balanced random sampling design (Stevens and Olsen 2004) with the purpose of broadly characterizing change in stand structure across lodgepole pine forests after a mountain pine beetle mortality event in

central Oregon. However, individual stands were not intensively sampled. Therefore, stand polygons were drawn in ArcGIS 9.3 around the original plots (ESRI 2007) to more intensively sample the areas in which the original plots were located. Stand lines were drawn based on the presence of a climax lodgepole pine plant association, ADS data regarding the most recent mountain pine beetle epidemic, and GIS layers from the Deschutes National Forest regarding past management activities, to ensure that the stand polygons were ecologically consistent with the original plot.

Within each polygon, three GPS points were selected as beginning points for the plots using a spatially balanced random sampling design (Stevens and Olsen 2004), and an additional three points were selected as replacement points. A random azimuth used for plot orientation was chosen for each plot. If an azimuth led to plots within the stand intersecting, a second azimuth was randomly chosen such that the plots did not overlap. Upon arrival at the stand, each point was checked to ensure that the associated plot was dominated by lodgepole pine, had past influence of mountain pine beetle (as indicated by the amount of coarse wood and snags in the area), and had no sign of past management or recent fire. If any of these criteria were not met for a given point, a randomly selected replacement GPS point within the stand was used in its place. If undesirable site characteristics were found at four or more of the randomly selected points, the stand was determined to be inappropriate for sampling.

Plot Layout and Sampling Protocol

During the summer of 2012, a total of thirteen stands were sampled within the study area, with three 75 m x 10 m (0.075 ha) belt transects randomly located and oriented within each stand (Appendix, Figure 1.1), for a total of 39 plots (Appendix, Table 1.1). This layout was chosen in order to obtain spatially explicit canopy data following the methods of Van Pelt and Nadkarni (2004). Upon establishment of the plot, UTM coordinates were taken at each end of the transect using a Trimble™ unit. From these points, slope and aspect of the transect were recorded.

Live trees were measured for several stand structure attributes within each plot. Species, vigor rating, crown class (dominant, codominant, intermediate, or suppressed), an X, Y coordinate, and diameter at breast height (DBH) were determined for each live tree (DBH \geq 5 cm). Tree height, height to crown base, and height to widest crown were measured to the nearest 0.1 meters. Tree height was defined as the distance from the base of the tree to the tree's highest live crown. Height to crown base was defined as the distance from the base of the tree to the tree's lowest live foliage. Height to widest crown was defined as the distance from the base of the tree to the tree's widest live crown as visually estimated by the laser operator. Crown width was measured for each tree by attaching a logger's tape to the tree bole, walking to the edge of each side of the live crown, and using a clinometer to determine precisely where the edge of the live crown fell. For snags DBH \geq 5 cm, similar measurements were taken within each plot. An X, Y coordinate, DBH, and height were taken following the same methods as live trees

discussed above. A decay class rating was assigned based on the five class method (Thomas, 1979) (Appendix, Table 1.2).

Two measures of dwarf mistletoe infestation severity were used to quantify the dwarf mistletoe on trees with $DBH \geq 5$ cm in each plot. Each live tree was given a rating using the Hawksworth Six-Class Dwarf Mistletoe Rating (DMR) System (Hawksworth 1977) (Appendix, Figure 1.2). This system is based upon a rating of the number of branches visibly infected by dwarf mistletoe within each third of the tree's live crown. Scores range from 0 (no visible infections) to 6 (50% or more of the branches in each third of the tree have visible infections). Brooms influence DMR estimations (Shaw et al 2000), so we observed crowns with binoculars and based DMR ratings on the presence of dwarf mistletoe plants themselves, rather than associated symptoms such as witches' brooms. We anticipate that our DMR estimations are accurate given visibility of crowns in this forest type.

The DMR system does not directly describe the amount of witches' brooming associated with the dwarf mistletoe infections, a potentially important determinant of canopy structure within lodgepole pine stands (Figure 2.2). A total broom volume (TBV) rating system adapted from the methods of Parker and Mathiasen (2004) was used to quantify the presence of witches' brooms within stands. Using this system, the crown was divided into thirds and each third was assigned a percentage of live crown in dwarf mistletoe-induced witches' brooms from 0 to 100. A total percent volume of live crown

volume in witches' brooms was then calculated by averaging the percentages from each third. For each of these systems, ratings of all lodgepole pine were averaged over the plot to obtain a plot-level DMR and TBV. Hereafter, DMR refers to dwarf mistletoe severity rating at the plot level, and TBV refers to total broom volume rating at the plot level, rather than the individual tree level.

To determine the amount of dwarf mistletoe infection in trees under 5 cm DBH (regeneration), four 4 m x 2 m (0.0008 ha) subplots were installed at regular intervals within each plot. Beginning at the 0 m mark on the transect, a subplot was installed at 24 meter intervals, extending two meters along the transect and two meters to each side of the transect. Within the subplot, saplings (trees under 5 cm DBH) were measured for height and rated for presence or absence of visible dwarf mistletoe infection. Due to the rarity of dwarf mistletoe infecting lodgepole pine saplings under one meter in height, only saplings over one meter in height were included in the sample. However, infected saplings under one meter in height were noted.

Stand Structure Metric Calculations

Stand density is defined as the total number of stems $DBH \geq 5.0$ cm/ha (Table 2.1). Stand basal area is defined as the sum of live tree basal area of lodgepole pine $DBH > 5.0$ cm (m^2/ha) using the formula: $3.142 * (DBH/200)^2$. Crown volume (m^3) measurements were calculated for live trees ($DBH \geq 5.0$ cm) using measurements of crown length, width, and height taken in the field. A crown form factor (CFF) was then applied to each volume to simulate the shape of a lodgepole pine crown (Coder, 2000).

The idealized crown shape “fat cone” (CFF: 0.2945) was used for dense stands (>1000 stems/ha), while the idealized crown shape “paraboloid” (CFF: 0.3927) was used for moderate and open stands (<1000 stems/ha). Individual crown volumes were summed over each plot to obtain total canopy volume (m³).

Cohorts were defined by tree crown class assigned in the field. Three cohorts were identified (Appendix, Table 1.3): dominant/codominant, intermediate, and suppressed. Our crown class system was such that very few trees were classified as “dominant,” and these trees were often not significantly larger than the trees were classified as “codominant.” This lack of distinction suggested that it was not appropriate to refer to dominant and codominant as separate cohorts. Hereafter, they will be grouped as a single cohort and referred to as “dominant.”

For each cohort, we calculated the proportion of total lodgepole pine (DBH \geq 5.0 cm) represented by that cohort (proportion in cohort), the average height of the cohort (cohort height), and the average DBH of the cohort (cohort diameter) (Table 2.2). We included only lodgepole pine in our cohorts because we were interested in the response of the cohorts to dwarf mistletoe infestation. Although ponderosa pine, whitebark pine, and Engelmann spruce are known occasional hosts of *A. americanum* (Hawksworth and Wiens 1996), we never observed infection of occasional hosts in our plots and consider them non-hosts for the purposes of this study.

Regeneration was defined as lodgepole pine saplings over one meter in height and less than 5 cm DBH. Regeneration density was determined by summing the lodgepole pine saplings over the four subplots within each plot and scaling up to stems per hectare. Regeneration infection intensity is defined as the proportion of total lodgepole pine saplings which were infected by dwarf mistletoe (Table 2.1).

Model Selection and Data Analysis

We used linear mixed models (LMMs) in which the response and predictor variables were continuous to describe the responses of stand structure parameters to DMR. Plots were nested within stands to account for potentially high levels of within-stand structural variability. Several covariates were identified as potentially influential in the responses of various aspects of stand structure to DMR. Stand density (live stems/ha), site productivity, and mountain pine beetle mortality were all determined to be potentially influential to stand structure, and could have the ability to mask an effect of DMR if not accounted for in the model. Because there are previous findings of a relationship between stand density and DMR (Wanner and Tinnin 1989), stand density could only be used as a covariate if there was no significant relationship between stand density and DMR in our data. Provided that this was found to be true, stand density would be accounted for as a continuous covariate. Plots were assigned to a site productivity category (low, moderate, or high) using plant association data (Hopkins 1979, Volland 1988) (Table 2.1). Plots were also assigned to a mountain pine beetle mortality category (low, moderate, or high) based upon total mortality (trees per acre)

mapped from ADS from 1979 to 2008 (Table 2.1). These covariates were assessed for multicollinearity with DMR prior to model fitting.

To ensure that our final fitted models adequately captured ecological relationships of interest while retaining maximum parsimony, we used Bayesian Information Criterion (BIC) to select the most appropriate model(s) from a set of candidate models (Appendix, Tables 1.5 – 1.16). Models were fitted using the maximum likelihood method for each response (Burnham and Anderson 2002). We chose to use BIC rather than other information criteria because it performs well when there are redundant explanatory variables in many of the candidate models (Ramsey and Schaffer 2013). A candidate model with the lowest BIC value (ΔBIC of 0) was considered to be the most appropriate model, however models with ΔBIC values of less than two were considered to perform equally well. In situations with more than one preferred model ($\Delta\text{BIC} < 2$), we chose to interpret the preferred model which included DMR as a predictor variable as the primary interest of this investigation is in the impact of dwarf mistletoe on stand structure. Model likelihoods, BIC weights, and evidence ratios were also calculated for each set of candidate models to further assess the weight of evidence for each model in the set (Burnham and Anderson 2002) (Appendix, Tables 1.5 – 1.16).

Assumptions of equal variance and normality were assessed for all candidate models using standard diagnostics prior to model selection (Ramsey and Schaffer 2013). We used a log-transformation on the response variables stand density, cohort diameter of

dominants, cohort diameter of intermediates, and cohort diameter of suppressed to correct for departures from the assumption of constant variance. Although it is customary to use logistic regression for proportion data, the proportion in cohort data was found to meet the assumptions of normality and homogeneous variance required for analysis using a linear mixed model. We used linear mixed models to model all of our response parameters to keep our analysis methods consistent. We refitted the preferred candidate using the residual maximum likelihood method to make our final inference.

Models with p-values below an α -level of 0.05 were interpreted to have strong evidence of a linear relationship. Models with $P < 0.10$ were interpreted to have suggestive but inconclusive evidence of a linear relationship to lower the probability of making a Type II error given our sample size and the inherent variability of this study area (Ramsey and Schafer 2013). We calculated marginal and conditional R^2 values as described as appropriate for description of goodness of fit for linear mixed models by Nakagawa and Schielzeth (2013). The marginal R^2 represents variance explained by fixed factors alone and conditional R^2 represents the variance explained by fixed and random factors. Both measures were calculated to fully understand the fit of these models. All analyses were performed using the program R, version 2.12.0 (R Development Core Team 2009).

Results

Dwarf Mistletoe Severity Metrics

A high Pearson correlation coefficient was found between total broom volume (TBV) and dwarf mistletoe rating (DMR) on a plot scale ($r = 0.901$) (Figure 2.3). TBV and DMR rating systems provide similar information in this study. We used DMR rather than TBV as the metric for describing dwarf mistletoe infestation in all following analyses because the DMR system is more widely used to describe dwarf mistletoe infection severity (Hawksworth and Wiens 1996).

Stand Attributes

For each of the responses of stand density, stand basal area, and log of canopy volume, BIC showed that a model including the single continuous predictor variable of DMR was preferred (Appendix, Tables 1.5-1.7). Although this model was selected for stand density, there was no evidence of a difference in stand density over the range of DMR ($F_{1,25} = 2.01$, $p = 0.1686$) (Table 2.3, Figure 2.4). This finding allowed us to consider stand density as a covariate in subsequent analyses. There was suggestive but inconclusive evidence that stand basal area decreased with increasing DMR ($F_{1,25} = 3.04$, $p = 0.094$) (Table 2.3). There was an estimated 0.12 m² decrease (95% CI: 0.25 m² decrease, 0.02 m² increase) in mean stand basal area for each unit increase in DMR (Figure 2.4). There was strong evidence that the log of canopy volume decreased with increasing DMR in these stands ($F_{1,25} = 6.89$, $p = 0.0146$) (Table 2.3). There was an estimated 17.8% (95% CI: 4.1%, 29.4%) decrease in the median canopy volume for each unit increase in DMR (Figure 2.4).

Cohort Attributes

The proportion of the stand in the dominant cohort and the proportion of the stand in the suppressed cohort used DMR as their only predictor in the BIC preferred models (Appendix, Tables 1.8 – 1.9). There was strong evidence that the proportion of the stand in the dominant cohort decreased with DMR severity ($F_{1,25} = 7.893$, $p = 0.0095$) while the proportion of the stand in the suppressed cohort increased with DMR severity ($F_{1,25} = 12.56$, $p = 0.0016$) (Table 2.3). There was an estimated 5.5% (95% CI: 1.5%, 9.5%) decrease in the mean number of dominants and a 6.5% (95% CI: 2.7%, 10.2%) increase in the mean number of suppressed trees for each unit increase in DMR (Figure 2.5). The proportion of the stand in the intermediate cohort used stand density as its only predictor variable in the BIC preferred model (Table 2.3). However, there was no evidence of a significant relationship in the preferred model ($p = 0.1300$) (Appendix, Table 1.10), nor was there evidence of a significant relationship between the proportion of the stand in the intermediate cohort with DMR ($p = 0.6810$) (Figure 2.5).

Cohort height of intermediates and cohort height of suppressed trees were both best predicted by DMR alone (Appendix, Tables 1.11 – 1.12), while the preferred model for cohort height of dominants included both DMR and stand density as predictors (Appendix, Table 1.13). There was suggestive but inconclusive evidence that cohort height of dominants decreased with DMR after accounting for stand density (Table 2.3). There was an estimated 0.48 meter decrease (95% CI: 1.13 meter decrease, 0.18 meter increase) in mean cohort height with each unit increase in DMR ($F_{1,24} = 4.257$, $p = 0.0501$) (Figure 2.6). The relationship of cohort height of intermediates to DMR was also

inconclusive ($F_{1,25} = 4.24$, $p = 0.0501$) (Table 2.3). There was an estimated 0.66 (95% CI: 0, 1.33) meter decrease in the mean cohort height of intermediate lodgepole pine for each unit increase in DMR (Figure 2.6). However, there was strong evidence of an effect of DMR on cohort height of suppressed trees ($F_{1,25} = 8.975$, $p = 0.0061$) (Table 2.3). There was an estimated 0.45 (95% CI: 0.14, 0.76) meter decrease in the mean cohort height of suppressed trees for each unit increase in DMR (Figure 2.6).

Conversely, there was no evidence of an effect of DMR on the log of cohort diameter of suppressed trees ($F_{1,25} = 0.419$, $p = 0.5235$) (Table 2.3, Figure 2.7). Although other models were equally preferred by BIC, no significant relationships were found within the set of candidate models (Appendix, Table 1.14). However, the BIC preferred model (Appendix, Table 1.15) showed there was strong evidence of an effect of DMR on the log of cohort diameter of dominants after accounting for stand density ($F_{1,24} = 8.563$, $p = 0.0074$) (Table 2.3). There was an estimated 4.2% (95% CI: 0.3%, 8.0%) decrease in the median cohort diameter of dominants for each unit increase in DMR after accounting for stand density (Figure 2.7). The BIC indicated log cohort diameter of intermediate trees was best explained by stand density alone ($F_{1,25} = 16.212$, $p = 0.0005$) (Table 2.3, Figure 2.7), with no evidence of a significant effect of DMR (Appendix, Table 1.16).

Regeneration Attributes

Results of the analysis of the regeneration data indicated that our sampling may have been insufficient to answer our original research question regarding the association between regeneration density and DMR. Of particular concern was the complete absence

of regeneration from 6 of our 39 total plots (Table 2.1). We do not have confidence that those absences are representative of our plots and suspect that in some areas our subplots may have been too small to accurately capture the density of regeneration. We chose not to perform statistical analyses on this data for this reason. However, we assessed the data for general patterns to determine whether these relationships would be valuable to further investigate in future studies. The trend in our data suggests that the relationship is non-linear. There are overall higher levels of regeneration in plots with light to moderate dwarf mistletoe ($DMR < 2$), with lower densities found in plots without dwarf mistletoe and heavy dwarf mistletoe ($DMR > 2$) (Figure 2.8). While this result is inconclusive given our dataset, the trend suggests that there is an effect of DMR on regeneration density in this study area.

We were also interested in identifying the level of dwarf mistletoe infection of the regeneration as compared with the overstory DMR. In 10% of the plots, 100% of sampled regeneration was infected with dwarf mistletoe (Figure 2.8). Between 7.5 and 100% of sampled regeneration was infected with dwarf mistletoe in plots with overstory $DMR > 2$ (Table 2.1). There was presence of infection in the regeneration in 95% of plots with overstory $DMR > 1$ (Figure 2.8). Within 45% of those plots, 50% or more of lodgepole pine regeneration was found to be infected (Table 2.1). Infected regeneration was not observed in plots with overstory $DMR < 1$ (Table 2.1). The Pearson correlation coefficient between overstory DMR and percent of regeneration infected with dwarf

mistletoe was fairly high ($r = 0.712$) although there was a large amount of variation in regeneration infection at high levels of overstory DMR (Figure 2.8).

Discussion

Effects of Dwarf Mistletoe on Stand Structure and Cohort Distribution

We found that in lodgepole pine stands 21-28 years TSB in central Oregon the proportion of the stand in the dominant (and codominant) cohort significantly decreased ($p = 0.0095$) with increased DMR. Conversely, the proportion of the stand in the suppressed cohort significantly increased ($p = 0.0016$) as DMR increased. Both findings are consistent with previous work (Hawksworth and Hinds 1964, Wanner and Tinnin 1989), but our findings are more broadly applicable due to our randomly selected plots and intensive sampling of stands in our study area. The shift in proportion of trees in each cohort can be attributed to overall decreased growth of hosts as stands become increasingly infested with dwarf mistletoe (Hawksworth and Wiens 1996). However, this shift associated with increased DMR was not reflected in the proportion of trees in the intermediate cohort ($p = 0.6810$). This may be attributed to an equivalent proportional shift of both the dominant cohort and the intermediate cohort to the next smallest size class, reflecting zero net change of the proportion of the stand in the intermediate cohort.

We further found that average height of the suppressed cohort ($p = 0.0061$) and average diameter of the dominant cohort ($p = 0.0074$) significantly decreased with increasing DMR. This is consistent with previous work (Hawksworth and Hinds 1964, Baranyay and Safranyik 1970, Wanner and Tinnin 1989), but our findings confirm that

this process is happening at a stand-scale across various levels of dwarf mistletoe severity. In addition to shifting the cohort distribution of trees within a stand, dwarf mistletoe decreases average tree size within cohorts. Dwarf mistletoe may be keeping trees in the suppressed cohort after a mountain pine beetle mortality event, as well as slowing height and diameter growth of trees within cohorts. Severe dwarf mistletoe infestation may subsequently slow ecosystem recovery as compared with that of uninfested stands. However, published studies of post-mountain pine beetle stand structure and ecosystem recovery have not accounted for dwarf mistletoe effects (Collins et al 2011, Diskin et al 2011, Kayes and Tinker 2012, Pelz and Smith 2012). Dwarf mistletoe is impacting stand development and must be incorporated to accurately project ecosystem recovery of stands after a mountain pine beetle epidemic.

We found that overall canopy volume decreased with increasing DMR in our study area ($p = 0.0146$). Canopy volume is a measure of site occupancy of trees in an area. Our results show that one of the pathogenic effects of dwarf mistletoe in lodgepole pine stands 21 to 28 years TSB is a reduction the site occupancy of tree crowns. Although Godfree et al (2002b) found that individual crown size was reduced in lodgepole pine stands with increased DMR, Godfree et al (2003) demonstrated that total canopy volume did not change with infection level. However, Godfree et al (2002b) also found that individual crown shape was significantly different among severity infection levels. We modeled crowns using measurements of crown width and length and applied two different idealized crown forms for all lodgepole pine. Crown dimensions were

measured, but it is likely that there is some error associated with the idealized crown forms applied to trees with high DMR. Future research on dwarf mistletoe effects on crowns and canopies should involve assessment of its effect on crown shape in addition to crown dimensions.

There was suggestive evidence ($p = 0.094$) that stand basal area decreases with increasing DMR, but within our study there was some uncertainty associated with our understanding of this relationship. The confidence interval around our estimated decrease in stand basal area (0.12 m^2) included zero, so the nature of the relationship is inconclusive. The relationship may be difficult to detect because of a high level of heterogeneity in the study area. Previous work in central Oregon lodgepole pine has found various results; Wanner and Tinnin (1989) found no relationship between stand basal area among dwarf mistletoe infection levels, while Godfree et al (2002a) found a significant reduction in stand basal area associated with increased dwarf mistletoe severity. The uncertainty associated with this relationship is likely a result of differences in mountain pine beetle legacy, as previous studies have not accounted for this factor. Although we found no effect of mountain pine beetle mortality density in any tested relationship, previous research (Klutsch et al 2009, Collins et al 2011, Diskin et al 2011, Pelz and Smith 2012) has shown that stand basal area changes drastically over time after a mountain pine beetle mortality event. Therefore, interpretation of the effect of dwarf mistletoe on stand basal area must be made within the context of the time since a mountain pine beetle epidemic.

There was no evidence that overall stand density varied with DMR ($p = 0.1686$), which is in disagreement with our original hypothesis and previous findings that overall stand density increases with increasing DMR. The disagreement between our study and previous studies (Wanner and Tinnin 1989, Godfree et al 2002b) may be related to the effect of the mountain pine beetle epidemic that occurred 21-28 years prior to sampling in our study area. We hypothesize that the epidemic occurred with variable severity within our study area unrelated to dwarf mistletoe severity, from which the ecosystem has not yet fully recovered to pre-epidemic conditions. This hypothesis is contrary to findings in Colorado regarding post-mountain pine beetle stand density recovery, which found stand density to fully recover by 20 to 30 years post-epidemic (Sibold et al 2007, Pelz and Smith 2012). However, central Oregon lodgepole pine forests are distinctive from lodgepole pine forests in the intermountain west and may behave differently due to their distinctive ecological attributes, such as their presence as a climax forest type (Franklin and Dyrness 1973), their mixed severity fire regime (Agee 1993), low cone serotiny (Simpson 2007), and their typical occurrence on extremely low productivity sites on the pumice plain (Gara et al 1985). Comparison of previous results with the findings of our study shows that the effects of dwarf mistletoe and mountain pine beetle on stand structural attributes may confound one another, so their effects must be interpreted simultaneously.

Previous work has also shown that at the individual-tree scale, the average height of dominant lodgepole was significantly decreased as DMR increased (Weir 1916,

Hawksworth and Hinds 1964, Baranyay and Safranyik 1970). However, this trend was suggestive but not conclusive in our research at the plot-scale for the dominant cohort ($p = 0.0501$) as well as the intermediate cohort ($p = 0.0501$). The disparity between our results and previous work is likely caused by a difference in scale. Individual tree height decreases with tree-level DMR. However, not all dominant or intermediate trees are infected even in plots with high plot-level DMR. *A. americanum* has not been shown to significantly impact height growth until tree-level infection is severe ($DMR \geq 4$) (Hawksworth and Wiens 1996). Trees which are not infected or are lightly infected by dwarf mistletoe in severely infested areas may be utilizing resources more efficiently due to weakened competition. If this were true, the overall effect of dwarf mistletoe on cohort height may be weakened or non-existent, as we saw in our data. Similarly, we found no relationship between DMR and suppressed cohort diameter. Diameter growth loss of lodgepole pine which have been infected by dwarf mistletoe does not typically occur until the host has a DMR of 4 or higher (Hawksworth and Wiens 1996). Given the long life cycle of dwarf mistletoe (about six years), it is likely that the trees in this cohort are mostly young and have not been infected for a long enough period of time to have experienced diameter growth loss as a result (Hawksworth and Hinds 1964).

Dwarf mistletoe presence on lodgepole pine regeneration was highly correlated ($r = 0.712$) with overstory DMR. This was expected and agrees with previous findings in post-mountain pine beetle lodgepole pine stands in British Columbia (Shore et al 1982). Although the infection level of regeneration was highly variable and these numbers may

be subject to undersampling bias, several of our plots had a 100% infection incidence in the understory. The high infection rate of saplings in some stands implies that dwarf mistletoe will continue to intensify in these stands as the stands mature. Trends of decreased canopy volume, cohort height and diameter, and proportion of trees in the dominant cohort are likely to continue and perhaps intensify as the severely infested stands mature. Stand development trajectories should be monitored in these stands as ecosystem recovery following a mountain pine beetle epidemic is likely to be further slowed when 100% of saplings are infected with dwarf mistletoe.

Potential Impacts of Structural Heterogeneity Associated with Dwarf Mistletoe

Dwarf mistletoe's influences on canopy volume, proportion of the stand in each cohort, and average diameter and height within cohorts show that the presence of dwarf mistletoe of various severities introduces structural heterogeneity to these forests. Although dwarf mistletoe is known to decrease vigor of individual trees (Hawksworth and Dooling 1984), heterogeneity of stand structure leads to higher overall landscape resistance and/or resilience to various disturbances in some systems (Asterup et al 2008, Turner, 2010, Diskin et al 2011). Diverse structure introduced by dwarf mistletoe may actually increase landscape resistance and resilience to disturbances, such as mountain pine beetle epidemics. To reach epidemic populations, mountain pine beetle need large, densely stocked lodgepole pine in which to lay their brood (Amman 1977). These conditions are more likely to be found in stands with low levels of dwarf mistletoe, given our results of increased proportion of the suppressed cohort, as well as decreased

diameter of the dominant cohort in stands with severe dwarf mistletoe. The variability of dwarf mistletoe severity in our study area suggests that stands in this area may be somewhat resistant to mountain pine beetle epidemics that remove mature lodgepole pine from the landscape over large geographical expanses, perhaps partially due to presence of dwarf mistletoe. Although each stand measured will undoubtedly continue to experience mountain pine beetle epidemics, the between-stand heterogeneity associated with dwarf mistletoe may decrease the occurrence of landscape-scale mortality events.

Light to moderate presence of dwarf mistletoe could also contribute to the resilience of these stands after mountain pine beetle epidemics due to increased regeneration density in stands where there was light to moderate dwarf mistletoe (DMR 0.1 – 2.0). Although we did not statistically test this relationship due to potential undersampling, our data suggest that lodgepole pine regeneration is highest at light to moderate dwarf mistletoe severity. Similarly, Godfree et al (2002b) found that densities of saplings have been observed to increase fifteen-fold between uninfected and severely infected lodgepole pine stands. It is thought that dwarf mistletoe brooms encourage the regeneration of lodgepole pine by providing sheltered conditions (Wanner and Tinnin 1989).

However, we found that in severely infested sites, regeneration density decreased as compared with lightly and moderately infested sites. We hypothesize that at higher levels of dwarf mistletoe severity, trees become less vigorous and more resource-stressed,

and produce fewer viable seeds and cones, leading to lowered regeneration densities. Previous work agrees with the hypothesis that individual lodgepole pine severely infested with dwarf mistletoe produce fewer seeds which are smaller in size, but found increased survival of first-year seedlings in severely infested stands (Wanner 1986). The study attributed increased survival of seedlings in severely infested stands to increased woody litter, which created more suitable seedbed conditions for seedling survival. In our study, all sites were characterized by large amounts of woody litter regardless of dwarf mistletoe severity because of the previous mountain pine beetle epidemic, and may explain the difference in our findings. Recent studies of regeneration of lodgepole pine post-mountain pine beetle epidemic have shown that regeneration density increases after a mortality event, but there is variability attributed to pre-epidemic species composition and site quality (Collins et al 2011, Kayes and Tinker 2012, Pelz and Smith 2012). We found that additional variability may be associated with DMR of the stand. The association between dwarf mistletoe and regeneration suggests that dwarf mistletoe be taken into account in future post-mountain pine beetle regeneration studies.

The relationship between decreased tree vigor associated with dwarf mistletoe infestation and mountain pine beetle susceptibility is poorly understood. Several studies have suggested that during the early phase of an epidemic, trees which have low vigor may be preferred by mountain pine beetle due to lowered defense capabilities (Smith et al 2011, Kulakowski and Jarvis 2013). Others have shown that more successful mountain pine beetle brood production occurs in trees with thick phloem (Roe and Amman 1970,

Amman 1972), which is related to strong tree vigor (Cole 1973). This has led to the hypothesis that dwarf mistletoe-infested trees are less susceptible to mountain pine beetle attack because they have thinner phloem than uninfested trees (Amman 1978, McGregor 1978, Stevens and Hawksworth 1984). However, the evidence that dwarf mistletoe infection decreases phloem thickness in lodgepole pine is inconclusive. Roe and Amman (1970) found that infected trees have significantly lower phloem thickness than uninfected trees, and concluded that there was a negative relationship between dwarf mistletoe infection and mountain pine beetle brood production. Conversely, Hawksworth et al (1983) found no relationship between dwarf mistletoe infection and phloem thickness in lodgepole pine. They further concluded that there was little relationship between dwarf mistletoe and mountain pine beetle host preference in lodgepole pine. The disagreement of these results indicates it is possible that the presence of dwarf mistletoe has some influence on individual trees' ability to support a mountain pine beetle brood, but further research is required to discern the nature of this relationship.

The effect of mountain pine beetle epidemics on overall stand-level dwarf mistletoe rating is another relationship that is not well understood. In this study, we did not have data for the stands we measured prior to the mountain pine beetle epidemic, so we cannot draw conclusions about this relationship specifically. However, it can be inferred given the nature of spread and intensification of dwarf mistletoe in forest stands that dwarf mistletoe was present within the measured stands prior to the mountain pine beetle epidemic 21 to 28 years prior. Dwarf mistletoe seed primarily disperses

explosively from the parent plant, and can move laterally a maximum of about 16 meters, but generally is intercepted within 4 meters of the dispersal origin (Hawksworth and Wiens 1996). Although thousands of seeds may be dispersed from a single severely infested tree, typically only 1-2 percent of seeds develop successful infections (Hawksworth and Wiens 1996). It takes about two years for successful infections to develop visible shoots and two additional years to produce flowers (Mathiasen 1996). The length of dwarf mistletoe's life cycle and the nature of its dispersal lead to a very slow rate of reinvasion of sanitized forests (30 – 60 cm/year) (Mathiasen 1996). Hawksworth and Hinds (1964) showed that in even-aged stands of lodgepole pine 15-60 years old, it took an average of 14 years to intensify stand level DMR by one unit.

Dwarf mistletoe's slow nature of colonization and intensification suggests that it would be unlikely that it has established in the stands since the previous mountain pine beetle epidemic, particularly in the heavily infested areas. While this suggests that mountain pine beetle does not completely sanitize stands of dwarf mistletoe, it is unknown whether overall stand level DMR is decreased or increased after an epidemic. A study of post-mountain pine beetle dwarf mistletoe infestation in British Columbia found a higher level of dwarf mistletoe in unattacked trees than in recently attacked trees, suggesting that mountain pine beetle may prefer uninfected trees to infected trees (Shore et al 1982). They hypothesize that dwarf mistletoe will intensify in stands post-mountain pine beetle epidemic, rather than decrease. However, further research regarding host

selection by mountain pine beetle and survival of attacked hosts is necessary to fully understand this relationship in lodgepole pine.

Conclusions

Dwarf mistletoe has a significant influence on stand structure in lodgepole pine forests. Increasing DMR in lodgepole pine stands leads to reduced canopy volume, greater representation of the suppressed cohort, reduced representation and average diameter of the dominant cohort, and reduced average height of the suppressed cohort. The mountain pine beetle influences many stand structural attributes, so it is important to interpret these effects within the context of the previous epidemic. Structural differences associated with dwarf mistletoe create heterogeneity in this forest type and may have a significant influence on the productivity, resistance, and resilience of these stands. Our findings show that it is imperative to incorporate dwarf mistletoe effects when studying stand productivity and ecosystem recovery processes in lodgepole pine forests. Dwarf mistletoe may be similarly influencing other forest types and should be investigated in other systems within the context of other disturbance regimes.

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Tables

Table 2.1. Characteristics of 39 plots within 13 stands of lodgepole pine in the Deschutes National Forest, Oregon. DMR represents dwarf mistletoe rating, Prod represents productivity, MPB represents mountain pine beetle, and Regen represents regeneration (trees over one meter in height and under 5 cm DBH).

Stand	Plot	DMR	Prod Class	MPB Mortality Class	Stand Density (stems/ha)	Basal Area (m ²)	Canopy Volume (m ³)	Regen Density (stems/ha)	Regen Infected (%)
CRL	1	2.78	L	L	1213	11.94	409.9	2812.5	44
	2	2.93	L	L	680	6.57	266.4	5312.5	35
	3	2.4	L	L	600	15.02	539.1	625	50
CRP	1	0	H	H	1120	21.29	1129.3	312.5	0
	2	1.02	H	H	880	16.55	1235.3	6562.5	57
	3	0	H	H	1107	23.87	608.0	0	0
CRP2	1	1.81	H	L	1107	14.58	337.0	10000	13
	2	2.45	H	L	893	14.99	313.9	2812.5	11
	3	2.94	H	L	1187	15.26	265.9	1875	100
CUL2	1	2.42	H	L	973	14.67	329.4	1875	50
	2	2.35	H	M	1040	11.08	252.3	2500	50
	3	2.38	H	H	827	7.70	316.7	6250	25
CUL6	1	3.98	M	H	987	12.78	696.9	625	100
	2	3.7	M	L	1000	10.67	431.7	4375	7
	3	2.59	M	L	1760	22.12	931.2	625	50
DES	1	0	M	M	600	19.91	1347.1	1250	0
	2	0	M	M	720	16.18	1216.4	0	0
	3	0	M	M	493	15.00	1422.8	625	0
EFR	1	0	L	M	600	18.94	764.4	312.5	0
	2	0	L	M	387	19.25	1185.0	0	0
	3	0	L	M	893	23.04	640.0	312.5	0
EFR3	1	0	L	H	613	16.00	917.3	0	0
	2	0	L	L	373	14.09	905.8	0	0
	3	0	L	M	2053	34.09	734.2	0	0
LDES	1	0.54	M	M	680	9.64	332.6	1875	0
	2	0	M	M	1053	21.78	1305.7	625	0
	3	0.73	M	M	1013	18.29	813.1	312.5	0
LVLK	1	1.11	H	H	880	7.70	282.4	8125	31
	2	2.09	H	H	1227	15.08	934.9	3750	33
	3	0	H	H	1093	7.84	341.3	10625	0
ODL	1	2.5	L	L	827	16.53	390.5	2500	13
	2	1.85	L	L	987	12.27	396.4	3437.5	0
	3	2.88	L	L	800	11.70	387.7	312.5	100
PAU	1	2.36	H	M	1733	21.87	602.3	1562.5	100
	2	2.38	H	H	2493	26.03	609.8	6250	60
	3	1.8	H	H	1560	23.48	664.9	4375	21
SNC	1	1.4	H	H	533	8.02	277.4	13437.5	2
	2	1.26	H	H	413	10.51	376.7	16250	4
	3	0.16	H	H	493	12.99	590.6	10937.5	0

Table 2.2. Cohort characteristics of 39 plots within 13 stands of lodgepole pine in the Deschutes National Forest, Oregon. DMR is dwarf mistletoe rating, Dom is dominant, Int is intermediate, and Sup is suppressed.

Stand	Plot	DMR	Proportion of Stand in Cohort			Cohort Height (m)			Cohort Diameter (cm)		
			Dom	Int	Sup	Dom	Int	Sup	Dom	Int	Sup
CRL	1	2.78	22	49	29	13.3	7.0	4.1	20.53	10.38	6.46
	2	2.93	9	24	67	17.2	9.2	3.9	22.5	14.21	7.28
	3	2.4	47	44	9	17.5	10.8	4.1	22.62	16.18	8.08
CRP	1	0	32	44	24	18.9	13.8	6.9	22.47	14	7.49
	2	1.02	32	34	34	20.3	11.7	6.2	24.78	13.13	8.2
	3	0	65	31	4	19.4	15.3	7.6	21.7	12.68	8.93
CRP2	1	1.81	20	28	52	19.6	8.6	4.6	29.67	10.77	7.02
	2	2.45	37	33	29	19.2	12.6	4.5	24.05	15.53	6.82
	3	2.94	27	30	43	17.3	8.6	4.0	21.79	12.07	6.9
CUL2	1	2.42	31	25	45	18.7	11.2	4.3	22.28	12.64	7.52
	2	2.35	26	31	43	15.5	8.3	4.1	18.31	11.66	6.93
	3	2.38	17	15	69	17.3	7.0	3.8	21.15	11.41	6.99
CUL6	1	3.98	22	39	39	15.9	11.1	5.3	21.02	13.32	8.27
	2	3.7	21	32	47	14.3	8.0	4.2	18.9	12.53	8.02
	3	2.59	36	33	31	15.7	10.7	5.2	18.79	11.04	7.34
DES	1	0	48	26	26	19.1	13.2	7.5	27.65	16.09	13.17
	2	0	32	21	47	17.8	12.8	5.6	27.16	15.97	8.39
	3	0	48	33	18	16.8	9.3	5.5	30.57	13.09	8.05
EFR	1	0	44	36	20	16.8	11.1	6.5	26.69	15.62	8.87
	2	0	59	28	14	18.8	12.4	5.8	37.07	16.98	10.53
	3	0	46	37	16	15.7	11.7	6.4	23.1	15.06	9.24
EFR3	1	0	52	33	15	15.0	11.0	6.0	22.87	14.65	7.56
	2	0	68	25	7	17.8	13.4	5.5	26.62	16.6	6.95
	3	0	40	39	21	15.7	11.7	6.3	20.15	12.48	7.36
LDES	1	0.54	21	42	37	18.8	8.3	4.8	24.53	12.99	7.87
	2	0	23	52	25	20.2	12.2	6.1	26.54	13.4	6.47
	3	0.73	24	39	37	17.1	11.8	5.5	24.15	14.29	8.03
LVLK	1	1.11	5	38	57	20.1	6.7	3.8	25.73	11.64	7.01
	2	2.09	27	42	31	13.6	7.6	4.4	18.57	11.16	7.02
	3	0	16	41	43	13.5	6.6	4.2	17.73	9.26	6.51
ODL	1	2.5	52	23	25	18.1	13.4	7.1	24.43	16.2	9.73
	2	1.85	14	23	64	18.4	8.3	4.1	24.31	15.08	8.49
	3	2.88	22	28	50	16.1	9.3	3.7	21.45	13.33	8.42
PAU	1	2.36	29	31	40	14.2	8.7	4.6	21.26	12.16	7.35
	2	2.38	27	31	42	12.4	7.8	4.2	18.62	11.04	6.97
	3	1.8	27	29	43	14.8	7.9	4.0	25.77	12.48	7.36
SNC	1	1.4	30	23	48	19.2	11.3	4.2	21.36	12.58	6.51
	2	1.26	42	39	19	21.9	9.9	4.1	23.43	12.93	6.18
	3	0.16	46	19	35	21.4	8.6	4.1	24	14.3	7.16

Table 2.3. BIC preferred linear mixed models of stand characteristics. Models of stand density (SD), stand basal area (SBA), canopy volume (CV), proportion of trees in dominant (PD), intermediate (PI), and suppressed (PS) cohorts, cohort height of dominant (CHD), intermediate (CHI), and suppressed (CHS) cohorts, and cohort diameter of dominant (CDD), intermediate (CDI), and suppressed (CDS) cohorts, with parameter estimates and standard errors. DMR represents dwarf mistletoe rating. Also included are BIC values from respective BIC calculations, goodness of fit (marginal and conditional r^2 values), and p values where $p < 0.01$ indicates strong evidence of a relationship (**), $p < 0.05$ indicates some evidence of a relationship (*), and $p < 0.1$ indicates suggestive but inconclusive evidence of a relationship (.).

Response variable	Model with parameter estimates (SE)	BIC	Marginal r^2	Conditional r^2	p value
Stand density	Log(SD) = 6.652 (0.128) + 0.094 * DMR (0.066)	-31.95	0.07	0.39	0.1686
Stand basal area	SBA = 1.355 (0.130) - 0.117 * DMR (0.067)	53.52	0.1	0.41	0.0940 .
Canopy volume	Log(CV) = 6.615 (0.146) - 0.195 * DMR (0.074)	59.11	0.21	0.53	0.0146 *
Proportion dominant	PD = 40.69 (3.726) - 5.494 * DMR (1.956)	324.06	0.21	0.36	0.0095 **
Proportion intermediate	PI = 28.00 (3.424) - 0.005 * SD (0.003)	283.75	0.06	0.44	0.1300
Proportion suppressed	PS = 25.373 (3.422) + 6.477 * DMR (1.828)	329.81	0.25	0.25	0.0016 **
Cohort height of dominants	CHD = 20.19 (0.881) - 0.476 * DMR (0.317) - 0.002 * SD (0.001)	175.34	0.31	0.56	0.0501 .
Cohort height of intermediates	CHI = 11.154 (0.620) - 0.663 * DMR (0.322)	179.23	0.13	0.37	0.0501 .
Cohort height of suppressed	CHS = 5.676 (0.295) - 0.450 * DMR (0.150)	113.39	0.26	0.57	0.0061 **
Cohort diameter of dominants	Log(CDD) = 3.37 (0.055) - 0.0428 * DMR (0.020) - 0.0002 * SD (0.00004)	-39.51	0.42	0.59	0.0074 **
Cohort diameter of intermediates	Log(CDI) = 2.76 (0.050) - 0.0002 * SD (0.00004)	-44.62	0.3	0.56	0.0005 **
Cohort diameter of suppressed	Log(CDS) = 2.06 (0.048) - 0.015 * DMR (0.024)	-33.95	0.02	0.47	0.5235

Figures

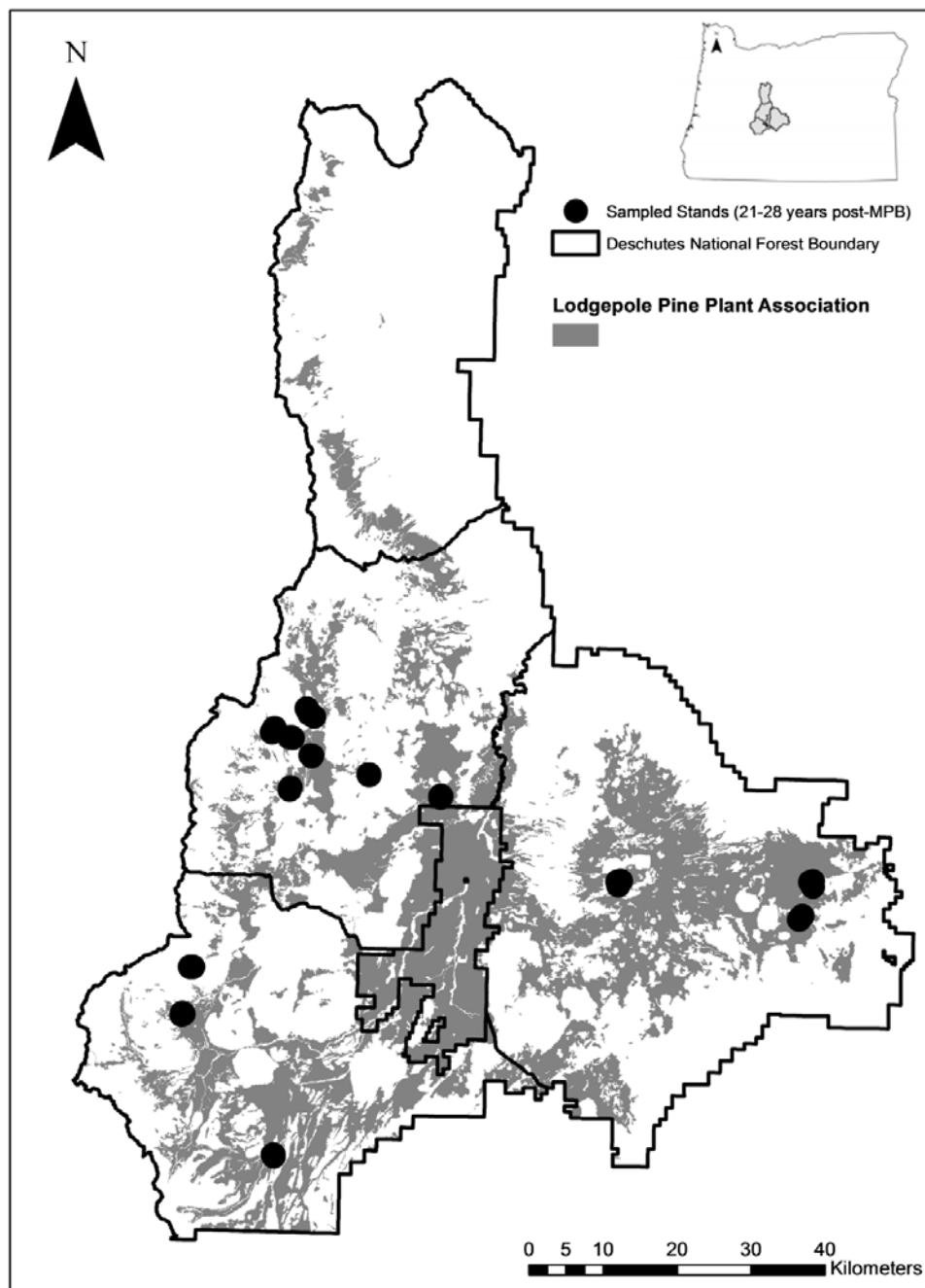


Figure 2.1. Study area map. Deschutes National Forest, Oregon boundary with sampled stands and lodgepole pine plant associations.

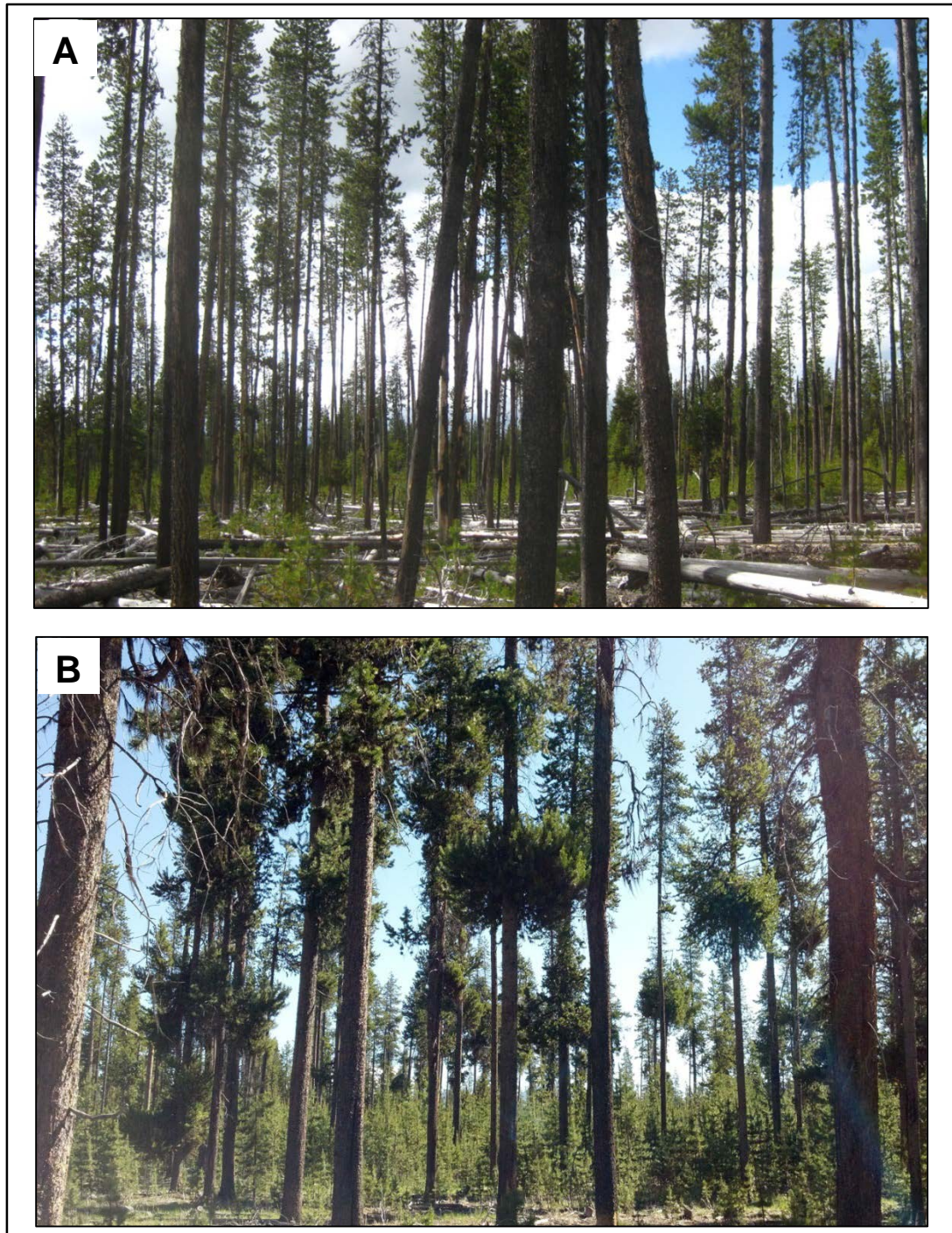


Figure 2.2. Forest structures of lodgepole pine stands 21-28 years after a mountain pine beetle mortality event. Pictured are stands A) without dwarf mistletoe and B) with severe dwarf mistletoe infestation and high levels of witches' brooming.

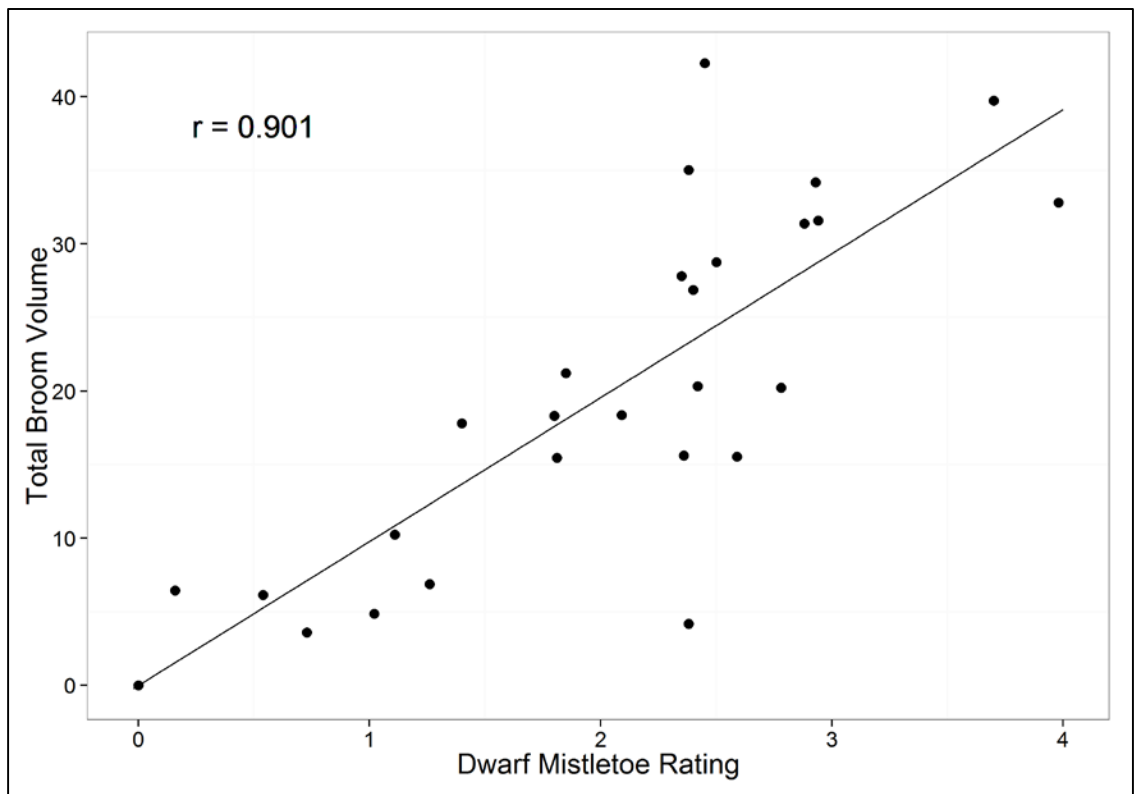


Figure 2.3. Scatterplot of dwarf mistletoe rating vs. total broom volume.

Figure 2.4. Linear mixed models of stand attributes on dwarf mistletoe rating. Scatterplots of linear mixed models of A) stand density (stems/ha), B) stand basal area (m^2/ha), and C) backtransformed log of canopy volume (m^3) on dwarf mistletoe rating (DMR) with 95% confidence intervals. All models are BIC preferred.

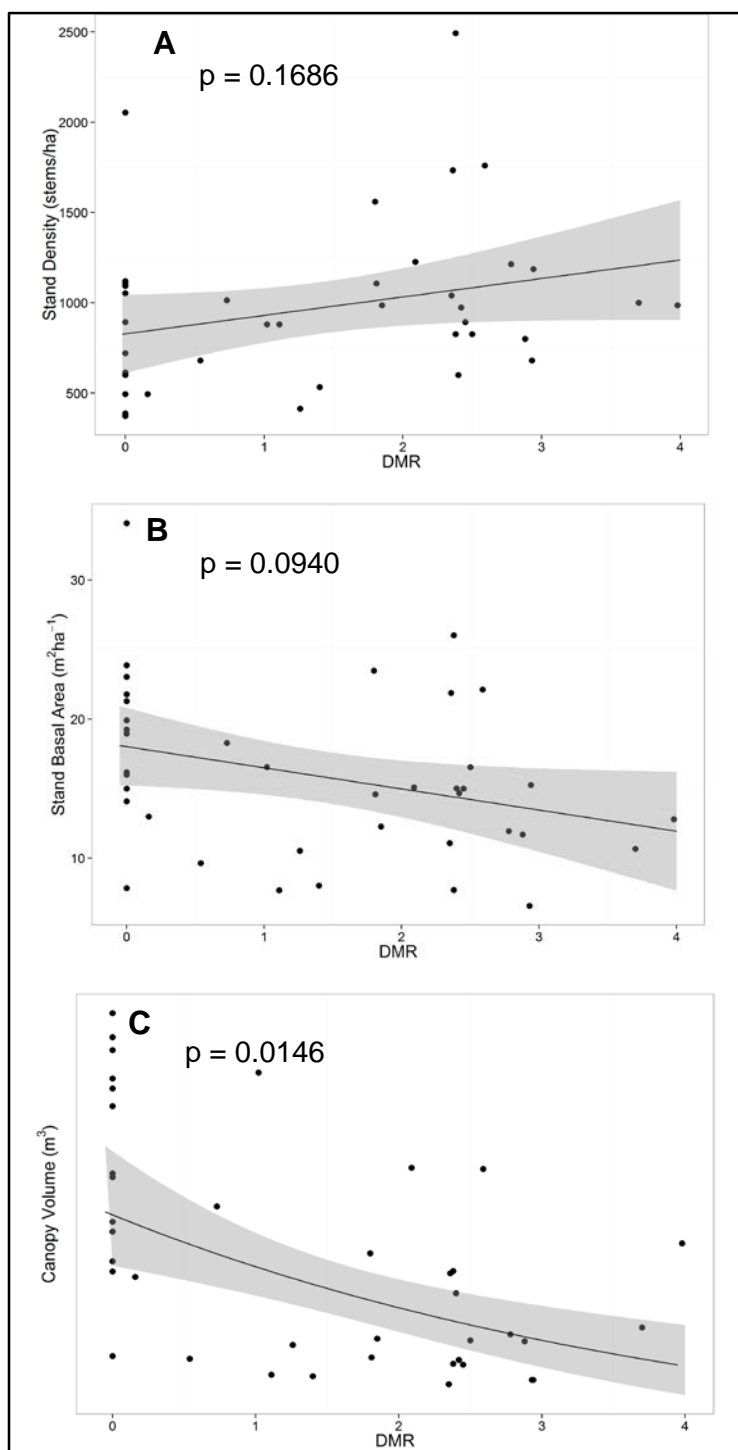


Figure 2.4.

Figure 2.5. Linear mixed models of proportion of lodgepole pine in cohorts on dwarf mistletoe rating. Scatterplots of linear mixed models of A) dominant cohort, B) intermediate cohort, and C) suppressed cohort on dwarf mistletoe rating (DMR) with 95% confidence intervals.

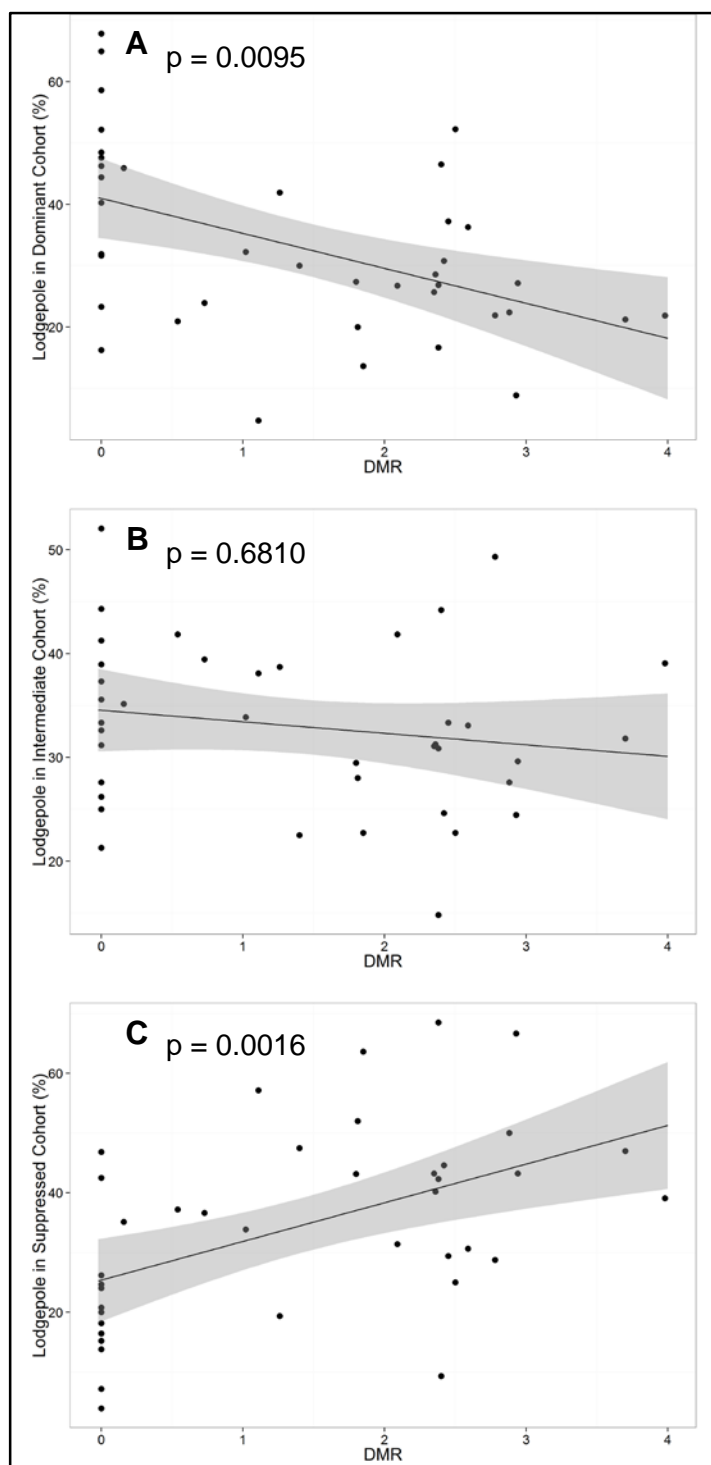


Figure 2.5.

Figure 2.6. Linear mixed models of cohort height on dwarf mistletoe rating. Scatterplots of linear mixed models of A) cohort height of dominant lodgepole pine (m) with stand density fixed at its mean, B) cohort height of intermediate lodgepole pine (m), and C) cohort height of suppressed lodgepole pine (m) on dwarf mistletoe rating (DMR) with 95% confidence intervals.

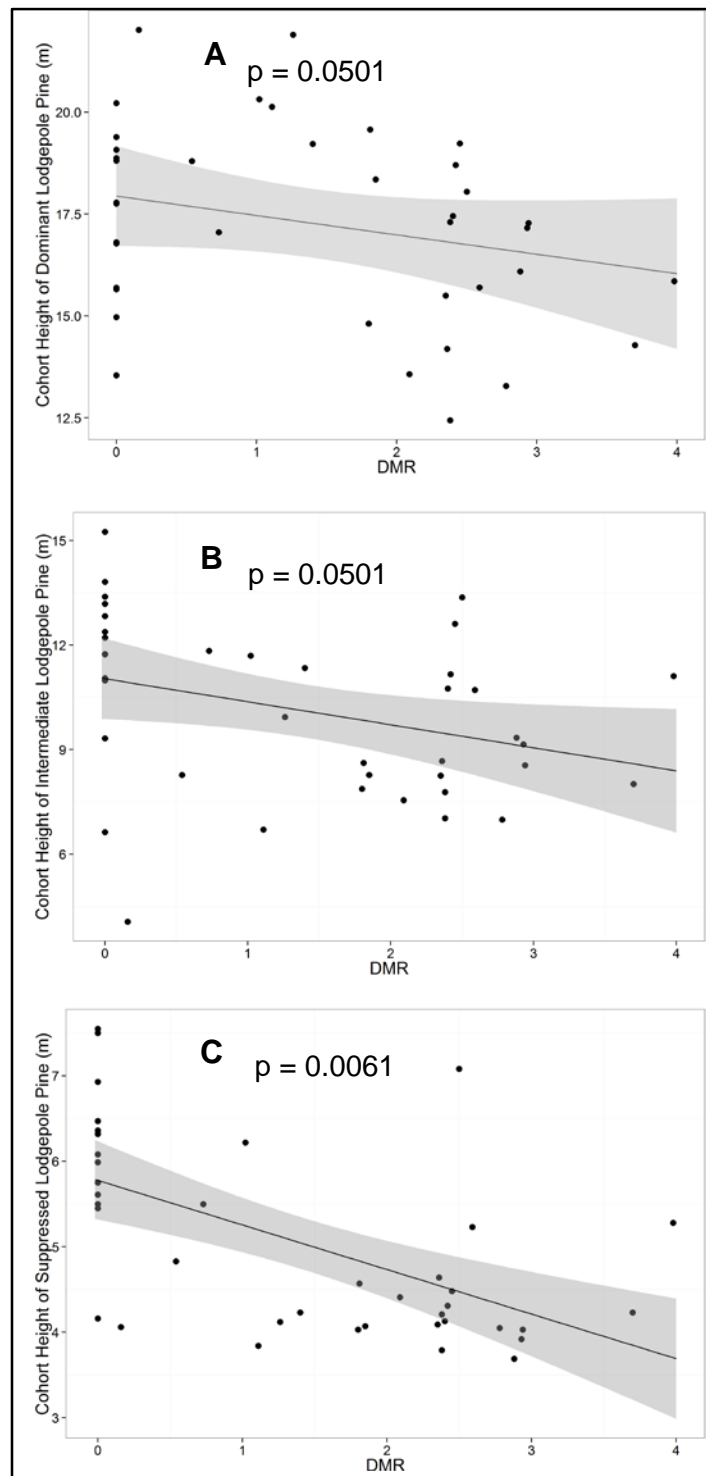


Figure 2.6.

Figure 2.7. Linear mixed models of log of cohort diameter on BIC preferred explanatory variables. Scatterplots of backtransformed linear mixed models of A) log of cohort diameter of dominant lodgepole pine (cm) on dwarf mistletoe rating (DMR) with stand density fixed at its mean, B) log of cohort diameter of intermediate lodgepole pine (cm) on stand density and C) log of cohort diameter of suppressed lodgepole pine on DMR with 95% confidence intervals. All models are BIC preferred.

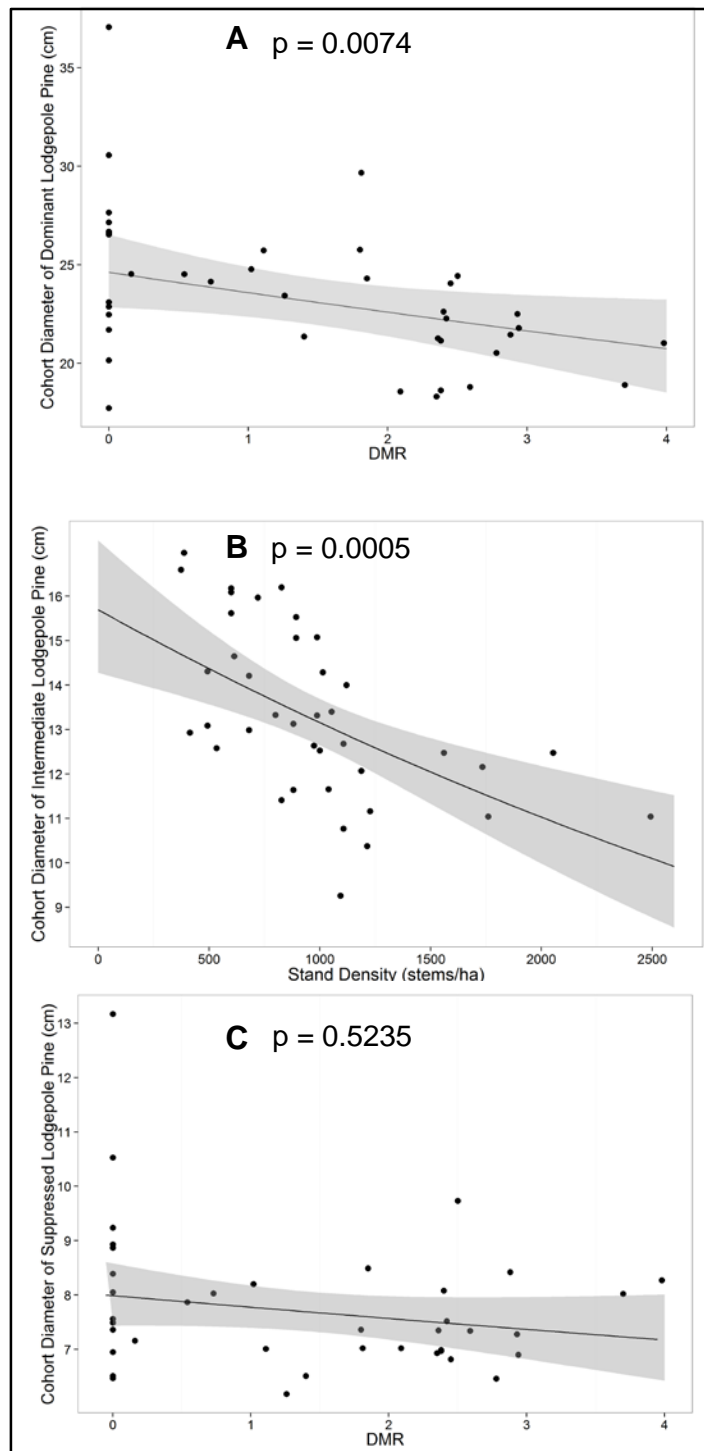


Figure 2.7.

Figure 2.8. Scatterplots of regeneration attributes versus dwarf mistletoe rating. Scatterplots of dwarf mistletoe rating (DMR) vs. A) lodgepole pine regeneration (> 1 meter in height) density (stems/ha), and B) percent lodgepole pine regeneration (> 1 meter in height) infected by dwarf mistletoe.

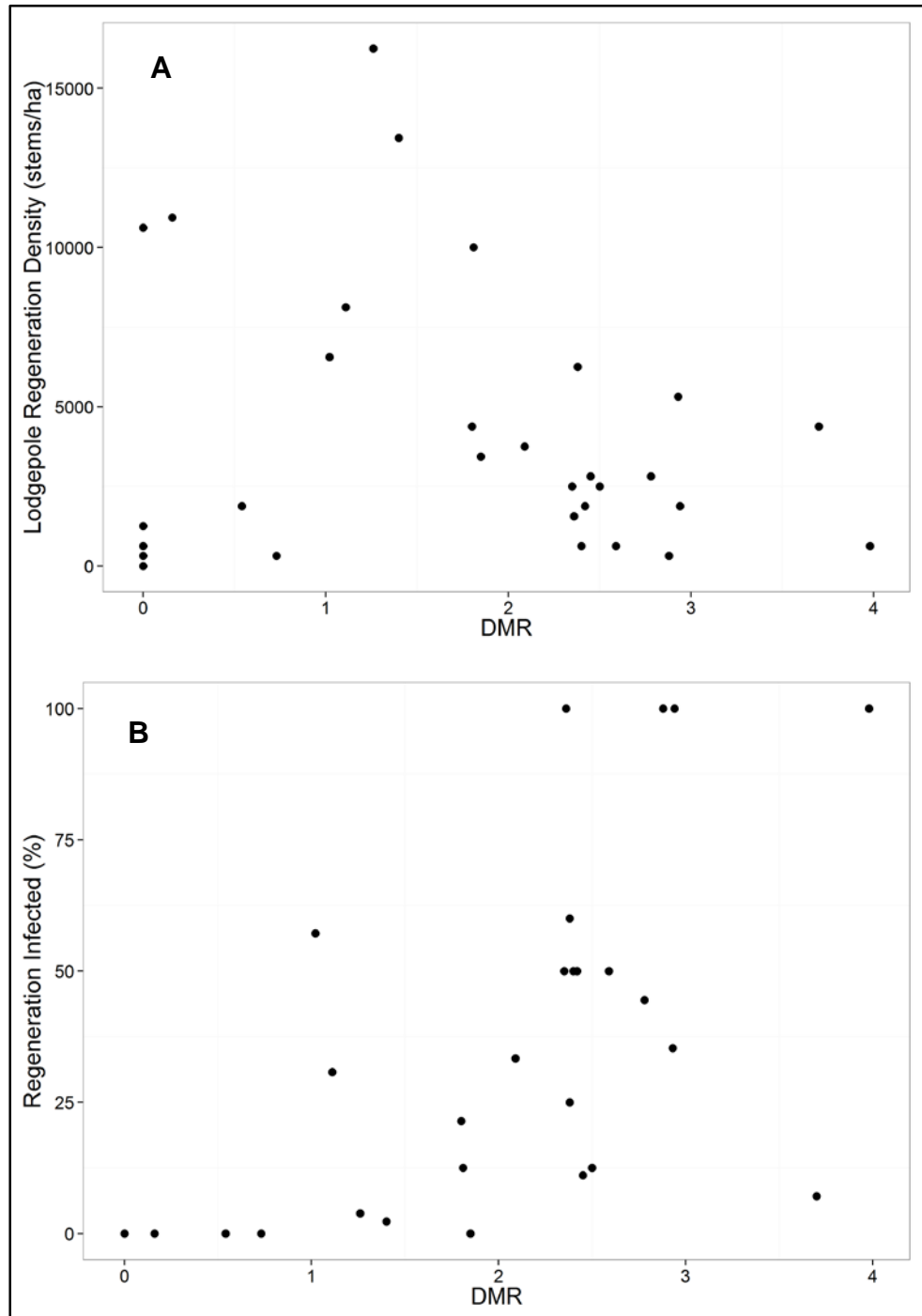


Figure 2.8.

Chapter 3: Dwarf Mistletoe Influence on Fuels And Modeled Fire Behavior in Lodgepole Pine Forests 21-28 Years After a Mountain Pine Beetle Epidemic in Central Oregon

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Prepared for submission to *Fire Ecology*

Abstract

Central Oregon lodgepole pine forests have a unique fire regime distinctive from that of Rocky Mountain lodgepole pine in the intermountain west. In central Oregon, lodgepole pine forests are typically seral and experience a mixed severity fire regime, leading to different ecological properties than those of Rocky Mountain lodgepole pine forests. The ecological differences in lodgepole pine forests of various locations must be taken into account when examining fuels and fire behavior, a topic of much recent research in this forest type. Interest in the effects of other forest disturbances and their interactions on fuels and fire behavior has grown rapidly in recent years. Two disturbance agents are known to influence fuels and fire behavior in lodgepole pine forests: mountain pine beetle and dwarf mistletoe. These disturbance agents co-occur pervasively throughout this forest type. However, their effects have not been examined simultaneously, nor have they been examined in central Oregon lodgepole pine. To understand the effect of dwarf mistletoe and mountain pine beetle on fuels and fire behavior, we randomly selected and sampled 39 0.075-hectare plots within 13 stands in the Deschutes National Forest in central Oregon. The plots varied from 0 to 4 in average dwarf mistletoe rating (DMR) and all experienced a mountain pine beetle mortality event 21 to 28 years prior to sampling. We compared canopy base height and canopy bulk density over the range of DMR to determine the effect of dwarf mistletoe on canopy fuels. We then used BehavePlus to model transition to crown fire and active crown fire in our plots. We found strong evidence of a decrease in canopy base height with

increasing DMR ($p = 0.0025$). There was suggestive evidence of decrease in canopy bulk density with increasing DMR, after accounting for stand density ($p = 0.078$). The results of the fire behavior modeling suggest that at low to moderate wind speeds, likelihood of torching increases with increased DMR. However, under more extreme weather (wind speeds >20 mph), the effect of dwarf mistletoe on torching potential was not shown to be important. The potential for active crown fire was extremely low in our plots, regardless of DMR. Our findings show that dwarf mistletoe is having a significant effect on the potential for torching in lodgepole pine forests 21 to 28 years post-mountain pine beetle epidemic, and should be considered in future research regarding post-mountain pine beetle fuels and fire behavior.

Introduction

Central Oregon lodgepole pine forests have a unique fire regime distinctive from that of Rocky Mountain lodgepole pine in the intermountain west. In central Oregon, two varieties of lodgepole pine intersect, *Pinus contorta* var. *murrayana* (Sierra lodgepole pine) and *Pinus contorta* var. *latifolia* (Rocky Mountain lodgepole pine), while only Rocky Mountain lodgepole pine is found in the intermountain west (Lotan and Critchfield 1990). Central Oregon lodgepole pine is typically found in nearly pure stands as an edaphic or topoedaphic climax species (Simpson 2007), while in the intermountain west it is generally seral and succeeds to another species (Amman 1977, Diskin et al 2011). Lodgepole pine in the intermountain west have serotinous cones and experience a high severity, stand replacement fire regime, generally leading to establishment of single-aged lodgepole pine stands post-fire (Lotan et al 1985).

However, in central Oregon lodgepole pine, cone serotiny is low and the fire regime is mixed severity, leading to variability of structural complexity within and among stands (Stuart et al 1989), and to variable fire potential (Agee 1993). The fire return interval of these forests is estimated to be 60 to 80 years, but fire-free intervals of 350 years have been documented (Agee 1993). Low intensity surface fires along log corridors have been documented in this type (Agee 1981, Gara et al 1985), and although stand replacement fires have been noted (Stuart 1983, Agee 1993), it is thought that these

forests are often fuel-limited due to low productivity (Gara et al 1985) and require strong winds to carry a crown fire (Agee 1993).

An increased understanding of insect and pathogen interactions with fire will be extremely important for understanding future ecosystems and fire regimes (Parker et al 2006) because there can be a large impact from these other forest disturbances on fuels loadings and potential fire behavior. Characterization of fuels loadings associated with various forest types, age classes, and structures is essential to obtain accurate information regarding fire hazard (Sandberg et al 2001). It is necessary to examine the entire disturbance ecology of an ecosystem simultaneously when determining its health and functionality because of the potential importance of interactive effects of multiple disturbances (Gara et al 1985, Parker et al 2006, Deroose and Long 2009, Metz et al 2011).

Mountain pine beetle (*Dendroctonus ponderosae* Hopkins) is a bark beetle native throughout the range of lodgepole pine, which has caused mortality on millions of acres of forest in western North America within the past several decades (Raffa et al 2008). Densely stocked stands of lodgepole pine > 16 cm DBH are particularly susceptible to mountain pine beetle epidemics (Gibson et al 2009). Lodgepole pine dwarf mistletoe (*Arceuthobium americanum* Nutt. Ex Engelm.) is also an important disturbance agent in these forests. Dwarf mistletoes (*Arceuthobium* spp.) are hemiparasitic plants which infect many species of North American conifers, leading to host deformities, growth loss, and higher susceptibility to mortality (Hawksworth and Wiens 1996). Lodgepole pine

dwarf mistletoe is the main dwarf mistletoe species of concern for lodgepole pine and has the largest geographical range of the North American dwarf mistletoes, occurring throughout the range of its primary host (Hawksworth and Wiens 1996).

Both dwarf mistletoe and mountain pine beetle have an influence on canopy fuels loadings in western US forests because they affect the two most important fuel load components used by resource managers to determine crown fire potential: canopy base height and canopy bulk density. Canopy base height is defined as the height at which a surface fire can be propagated into the forest canopy, and is the main canopy fuel parameter driving passive crown fire, or torching. Canopy bulk density is a measure of the mass of available canopy fuel per unit of canopy volume that drives active crown fire (Reinhardt et al 2006). It has been shown that severe dwarf mistletoe infection lowers individual crown base height of its hosts (Tinnin et al 1982, Koonce and Roth 1985, Godfree et al 2002a) and mountain pine beetle epidemics cause immediate decreases in canopy bulk density (Klutsch et al 2011, Simard et al 2011). In central Oregon lodgepole pine, Godfree et al (2002a) found that severely infected trees have crown bases approximately 37% lower than uninfected trees. Koonce and Roth (1985) found that average height to crown base in Oregon ponderosa pine was 21% of tree height for infected trees as compared with 38% of tree height for uninfected trees. However, Hoffman et al (2007) found no difference in canopy base height at the stand scale between uninfested and infested ponderosa pine stands, indicating that this process may

vary among spatial scales in ponderosa pine. Similarly, they observed no difference in stand-scale canopy bulk density among dwarf mistletoe severity classes in ponderosa pine.

Dwarf mistletoe may increase the potential for passive crown fire (torching) as a result of associated changes in canopy fuels. Witches' brooms, a common symptom of severe dwarf mistletoe infection, have been found to concentrate biomass low in the crowns of infested trees (Tinnin et al 1982, Godfree et al 2002a), leading to greater vertical fuel continuity in infected trees, and potentially leading to a greater probability of torching (Brown 1975, Wicker and Leaphart 1976, Conklin and Geils 2007). Witches' brooms are also believed to act as traps for fine fuels such as dead needles or fine branches, leading to compact arrangements of highly flammable fine fuels in infested trees (Alexander and Hawksworth 1975, Brown 1975). In addition, witches' brooms are more resinous than uninfected branches and are therefore may be more flammable (Alexander and Hawksworth 1975), which could lead to an increased probability of passive crown fire. However, witches' brooms act as nutrient sinks which have higher metabolic demands than dwarf mistletoe plants themselves (Hawksworth and Wiens 1996), which leads to overall decreased canopy volume (Chapter 2). This also likely leads to decreased canopy bulk density, and decreased active crown fire potential.

Several previous studies in ponderosa pine (*Pinus ponderosa*) forests have demonstrated that dwarf mistletoe influences fire behavior (Hoffman et al 2007,

Harrington and Hawksworth 1990, Stanton 2009). Crown scorch increased with increasing dwarf mistletoe infection in severely infested ponderosa pine stand in Grand Canyon National Park, which was attributed to low crowns and flammable witches' brooms (Harrington and Hawksworth 1990). Hoffman et al (2007) found that the wind speed required to carry a surface fire to the crown was lower in severely infested stands than in uninfested stands. Conversely, little difference in fuel load and branch flammability was found between infested and uninfested sites at Crater Lake National Park (Stanton 2009), indicating that there may be complexity to the fire ecology of dwarf mistletoe in ponderosa pine that is not yet understood. Although there has been some work done to quantify this relationship in ponderosa pine, there is little information available regarding the impacts of dwarf mistletoe on fire behavior in lodgepole pine. Turner et al (1999) found that crown fire was more likely to occur in stands with moderate to severe mistletoe infestation in a study of the 1988 Yellowstone fires, indicating that the relationship between dwarf mistletoe and fire may be similar in lodgepole pine to that in ponderosa pine. However, additional investigation using data from additional fires or fire behavior modeling is necessary to further support this finding.

The role that mountain pine beetle epidemics may play in altering fuels and potential fire behavior both immediately post-epidemic and for many decades thereafter has been a primary focus of research in recent years (Hicke et al 2012). Several studies

have examined fire risk following historical mountain pine beetle outbreaks to attempt to understand this relationship. Lynch et al (2006) found that areas that had experienced an epidemic 13-16 years previously were 11% more likely to burn in the 1988 Yellowstone fires than unaffected areas, while areas attacked 5-8 years prior were not more likely to burn. Other work in Colorado and Wyoming found no increase in high severity fire 5-15 years following mountain pine beetle epidemics, and the fire regime in Rocky Mountain lodgepole pine forests is rather driven by drought (Kulakowski and Jarvis 2011).

Previous studies have found variable effects of mountain pine beetle epidemics on canopy fuels loadings. Page and Jenkins (2007a) found both in stands with recent and older attacks, there were decreases in canopy base height, canopy bulk density, and overall available canopy fuels. Klutsch et al (2011) found that canopy base height increased and canopy bulk density decreased in plots currently experiencing an epidemic as compared with unattacked stands. Simard et al (2011) found no significant difference in canopy base height between unattacked stands and those 1-5 years post-epidemic. They also found a decrease in canopy bulk density of 53% in the same stands. In stands 10-40 years post-epidemic, they found a significant decrease in canopy base height as compared with unattacked stands.

Many studies have been conducted using fire behavior modeling techniques and post-mountain pine beetle epidemic fuels loading data to simulate fire behavior. Stands in Colorado which had experienced an epidemic 7 years prior to measurement were

predicted to be less susceptible to both active and passive crown fire (Klutsch et al 2011). In Idaho and Utah, stands 5 years post-epidemic were more susceptible to passive crown fire, but less susceptible to active crown fire than unattacked stands (Page and Jenkins 2007b). In Colorado and Wyoming, Schoennagel et al (2012) found that both passive and active crown fire were more likely to occur at lower wind speeds in stands of all stages (1-30 years) post-mountain pine beetle epidemic than in unattacked stands. However, in the same geographical area, Simard et al (2011) found that probability of crown fire in stands 1-5 years post-epidemic was lower than in unattacked stands, while stands 10-40 years post-epidemic were more likely to experience passive but not active crown fire. Although there is uncertainty and disagreement regarding the relationship of mountain pine beetle-caused mortality to fuels and fire behavior, Hicke et al (2012) discuss that this disagreement is considerably decreased when comparisons are limited to studies within a single TSB class. They note that disagreement is also decreased when studies which used modeled or observed fire behavior data are compared separately.

Dwarf mistletoe and mountain pine beetle occur pervasively in lodgepole pine forests and they are likely interacting in the environment. A random sample of 212 lodgepole pine dominated plots in central Oregon 2-31 years post-mountain pine beetle indicated that 72% of post-mountain pine beetle lodgepole pine stands in the area had some level of dwarf mistletoe infection (T.J. Woolley et al, Oregon State University, unpublished data). 53% of the total plots had light to moderate dwarf mistletoe infection

while 19% of the plots had severe dwarf mistletoe infection. Additionally, severity of dwarf mistletoe infection of the stand was not found to be related to the time since beetle in the sampled plots. Although these disturbances frequently occur together on the landscape and are both thought to separately influence fuels and fire behavior, no study has attempted to quantify their interactive effects on fuels or fire behavior. Not only is it important to investigate the cumulative effects of these two widespread disturbances, but given the high frequency with which they each occur on the landscape, it is nearly impossible to identify the impacts of one without accounting for the other.

The purpose of this study is 1) to describe the impacts of dwarf mistletoe infection on the major fuel parameters governing crown fire behavior, canopy base height and canopy bulk density, and 2) to contrast predicted crown fire behavior amongst levels of dwarf mistletoe infection, in unmanaged central Oregon lodgepole pine stands 21-28 years after a mountain pine beetle epidemic (TSB). It is typical for a mountain pine beetle epidemic to kill most lodgepole pine over 16 cm DBH (Gibson et al 2009), so it is not possible to assess the impact of any other disturbance on the canopy fuels structure of lodgepole pine forests without accounting for the effect this insect has had.

We hypothesize that average canopy base height will decrease with increasing average dwarf mistletoe infection at the plot scale, following the mechanism by which individual crown base height is influenced by dwarf mistletoe. We hypothesize that average canopy bulk density will decrease with increasing average dwarf mistletoe

infection at the plot scale, as a result of overall growth loss caused by dwarf mistletoe.

We further hypothesize that with increasing average dwarf mistletoe infection, plots will be more likely to experience passive crown fire due to lower canopy base height and less likely to experience active crown fire due to lower canopy bulk density under all weather and surface fuel scenarios.

Materials and Methods

Study Area

The study area was located in central Oregon in the Deschutes National Forest. The Deschutes National Forest is located on the east side of the Cascade Mountains, covering an area of approximately 728,000 hectares (Figure 3.1). Sites were chosen within the edaphic and topoedaphic climax lodgepole pine zones according to the plant association guide for the area (Hopkins 1979, Volland 1988, Simpson 2007). In this area, the ecological site characteristics of the climax lodgepole pine type are relatively uniform, characterized by pumice soils and flat to gently rolling topography which often results in cold air drainage (Franklin and Dyrness 1973). The lodgepole pine zone is located between 1,200 and 1,525 meters elevation with mean annual temperatures ranging from 4.3 to 5.8° C and mean annual precipitation ranging from 38 to 89 cm depending upon the specific plant association (Simpson 2007). The Wickiup Dam climate station (the most representative climate station for the study area) showed average daily temperatures ranging from -2.2° C in January to 18.3° C in July (Western Regional Climate Center 2013).

Measured sites were restricted to areas 21-28 years TSB, to control for the effect of mountain pine beetle on canopy fuels structure. Aerial Detection Survey (ADS) data (USDA Forest Service 2012) was used to determine TSB. Areas with known past management or recent fire were excluded from sampling. Typically, the stands were characterized by large amounts of coarse wood, few standing snags, dense lodgepole pine regeneration, and an overstory comprised of lodgepole pine too small to support a mountain pine beetle brood at the time of epidemic, which subsequently released after the death of the previous overstory.

A minimum of 70% of the mature trees at each site measured were lodgepole pine. Other tree species found at the sites varied with elevation in the study area. Ponderosa pine (*Pinus ponderosa*) was present at lower elevations, while white fir (*Abies concolor*), grand fir (*Abies grandis*), mountain hemlock (*Tsuga mertensiana*), and whitebark pine (*Pinus albicaulis*) were located at higher elevations. Engelmann spruce (*Picea engelmanni*) and western white pine (*Pinus monticola*) were occasionally present within the study area as well. Common shrub species in the study area were *Purshia tridentata*, *Arctostaphylos nevadensis*, and *Ribes cereum*. Common herbaceous species found in the understory were *Acnatherum occidentale*, *Carex inops*, *Carex rossii*, *Elymus elemoides*, *Epilobium angustifolium*, *Frageria virginiana*, and *Lupinus argenteus*.

Site Selection

Sites were selected based on a network of 119 plots randomly located within post-mountain pine beetle climax lodgepole pine in the Deschutes National Forest that were established during the summers of 2010 and 2011 (T.J. Woolley et al, unpublished data). The network of plots was designed using a spatially balanced random sampling design (Stevens and Olsen 2004) with the purpose of broadly characterizing change in fuels across lodgepole pine forests after a mountain pine beetle mortality event in central Oregon. However, individual stands were not intensively sampled in that study.

The stands used for this study were characterized as polygons and drawn around the original plots using ArcGIS 9.3 (ESRI 2007). To ensure that the stand polygons were ecologically consistent with the original plot, stand lines were drawn based on the presence of a climax lodgepole pine plant association, ADS data indicating a consistent year beginning the site's most recent mountain pine beetle epidemic, and GIS layers from the Deschutes National Forest regarding past management activities. Within each polygon, three GPS points were randomly selected as beginning points for the plots, and an additional three points were selected as replacement points.

A random azimuth used for plot orientation was chosen for each plot. If an azimuth led to plots within the stand intersecting, a second azimuth was randomly chosen such that the plots did not overlap. Upon arrival at the stand, each point was checked to ensure that the associated plot was dominated by lodgepole pine, had past influence of mountain pine beetle, and had no sign of past management or recent fire. If any of these

criteria were not met for a given point, a randomly selected replacement GPS point within the stand was used in its place. If undesirable site characteristics were found at four or more of the randomly selected points, the stand was determined to be inappropriate for sampling.

Plot Layout and Sampling Protocol

A total of thirteen stands were sampled within the study area during the summer of 2012, with three 75 m x 10 m (0.075 ha) belt transects randomly located and oriented within each stand following the methods of Van Pelt and Nadkarni (2004). Upon establishment of the plot, UTM coordinates were taken at each end of the transect using a Trimble™ unit. From these points, slope and aspect of the transect were recorded.

Live trees (DBH \geq 5 cm) were measured for several canopy structure attributes within each plot. Species, vigor rating, crown class, DBH, and an X, Y coordinate were determined for each live tree. Tree height and height to crown base were measured to the nearest 0.1 meter. Tree height was defined as the distance from the base of the tree to the tree's highest live crown. Height to crown base was defined as the distance from the base of the tree to the tree's lowest live foliage. Crown width was measured for each tree by attaching a logger's tape to the tree bole, walking to the edge of each side of the live crown, and using a clinometer to determine precisely where the edge of the live crown fell. Height and DBH were measured for snags DBH \geq 5 cm following the same methods

as live trees discussed above. A decay class rating was assigned based on the five class method (Thomas 1979) (Appendix, Table 1.2).

Two measures of dwarf mistletoe infection severity were used to quantify the dwarf mistletoe on trees with $DBH \geq 5$ cm within each plot. First, each tree was given a rating using the Hawksworth Six-Class Dwarf Mistletoe Rating (DMR) System (Hawksworth 1977) (Appendix, Figure 1.2). This system is based upon a rating of the number of branches visibly infected by dwarf mistletoe in each third of the tree's live crown. Scores range from 0 (no visible infections) to 6 (50% or more of the branches in each third of the tree have visible infections). However, this rating system does not directly describe the amount of witches' brooming associated with the dwarf mistletoe infections, a potentially important determinant of canopy fuels structure within lodgepole pine stands.

A total broom volume (TBV) system, adapted from the methods of Parker and Mathiasen (2004), was used to quantify the presence of witches' brooms within stands. Using this system, the crown was divided into thirds and each third was assigned a percentage of live crown volume in dwarf mistletoe-induced witches' brooms from 0 to 100. A total percent volume of live crown in witches' brooms was then calculated by averaging the percentages from each third. For each of these systems, ratings of all mature lodgepole pine were averaged over the plot to obtain a plot-level DMR and TBV.

Hereafter, DMR and TBV refer to dwarf mistletoe severity rating and broom volume rating, respectively, at the plot level rather than the individual tree level.

Fuel Computations

Canopy bulk density and canopy base height were calculated using the program FuelCalc v.0.52. This program defines canopy bulk density as the maximum of the 5 meter running mean of available canopy fuel load within a plot (Reinhardt et al. 2006). Available canopy fuel load is calculated as a proportion of total canopy weight, calculated for lodgepole pine using Brown's (1978) equation:

$$wt = \exp [0.1224 + 1.8820 * \log (\text{Diam})]$$

where wt is canopy weight (kg/m^2) and Diam is diameter at breast height (cm). Canopy base height is defined as the lowest point at which the 5 meter running mean of the canopy bulk density exceeds $0.012 \text{ kg}/\text{m}^3$ (Reinhardt et al. 2006). All live trees with $\text{DBH} \geq 5 \text{ cm}$ in the plot were used to calculate these values.

Model Selection and Data Analysis

We used linear mixed models (LMMs) in which the response and predictor variables were continuous to describe the responses of fuel parameters to DMR. Plots were nested within stands to account for potentially high levels of within-stand variability. Several covariates were identified as potentially influential in the responses of canopy base height and canopy bulk density to DMR. Stand density (live stems/ha),

site productivity, and mountain pine beetle mortality were all determined to be potentially influential to canopy base height and canopy bulk density, and could have the ability to mask an effect of DMR if not accounted for in the model. Plots were assigned to a site productivity category (low, moderate, or high) using plant association data for the area (Simpson 2007) (Table 3.1). Plots were assigned to a mountain pine beetle mortality category (low, moderate, or high) based upon total mortality (trees per acre) mapped from ADS from 1979 to 2008 (Table 3.1). These covariates were assessed for multicollinearity with DMR prior to model fitting.

We used Bayesian Information Criterion (BIC) to select the most appropriate model(s) from a set of 18 candidate models fitted using the maximum likelihood method for each response variable (Burnham and Anderson 2002). We used an information criterion for model selection to ensure that our final fitted models adequately captured these ecological relationships while retaining maximum parsimony. We chose to use BIC rather than other information criteria because it performs well when there are redundant explanatory variables in many of the candidate models (Ramsey and Schaffer 2013). A candidate model with the lowest BIC value (ΔBIC of 0) was considered to be the most appropriate model, however models with ΔBIC values < 2 were considered to perform equally well. Model likelihoods, BIC weights, and evidence ratios were also calculated for each set of candidate models to further assess the weight of evidence for each model in the set (Burnham and Anderson 2002) (Appendix, Tables 1.17 – 1.18).

Assumptions of equal variance and normality were assessed for all candidate models prior to model selection using standard diagnostics (Ramsey and Schafer 2013). We used a log-transformation on the response variables (canopy base height and canopy bulk density) to correct for departures from homoscedasticity. Final inference was made using the preferred candidate model refitted using the residual maximum likelihood method. Models with p-values below an α -level of 0.05 were interpreted to have strong evidence of a linear relationship. To lower the probability of making a Type II error given our sample size and the inherent variability of this study area, models with $P < 0.10$ were interpreted to have suggestive but inconclusive evidence of a linear relationship (Ramsey and Schafer 2013). We calculated marginal and conditional R^2 values as described as appropriate for description of goodness of fit for linear mixed models by Nakagawa and Schielzeth (2013). The marginal R^2 represents variance explained by fixed factors alone and conditional R^2 represents the variance explained by fixed and random factors. Both measures were calculated to fully understand the fit of these models. All analyses were performed using the program R, version 2.12.0 (R Development Core Team 2009).

Fire Behavior Modeling

BehavePlus 5.0.5 was used to calculate the potential for both passive (torching) and active (crowning) crown fire under two surface fuel scenarios and three weather scenarios (Andrews 2008). We did not measure surface fuels, but rather used surface fuel

inputs (fuel bed depth, 1 hour, 10 hour, 100 hour, live herbaceous, and live woody fuel loads) calculated using the 50th and 75th percentile values from plots 15 – 25 years TSB from the original plot network established in 2010 and 2011 (T.J. Woolley et al unpublished, data) (Table 3.2). Although our research used stands that were 21 - 28 years TSB, these time periods represent similar stages in the chronosequence of ecosystem recovery post-mountain pine beetle epidemic.

Two fuel moisture scenarios were applied to the surface fuels for modeling purposes. Moderate and extreme fuel moisture scenarios were adapted from a fire weather and fuels conditions analysis from central Oregon based on 1990-2011 weather records from May 1 to October 31 (L. Hollingsworth, US Forest Service, personal communication) (Table 3.3). Nine 20-foot wind speeds divided into three groupings (hereafter, wind scenarios) were used to simulate various fire weather scenarios. The 20-foot wind speed (hereafter, wind speed) is the wind speed measured 20 feet above the forest canopy, the US standard for measuring open wind speed (Schroder and Buck 1970). The low wind scenario used wind speeds of 3, 5, and 7 miles per hour, the moderate wind scenario used wind speeds of 11, 13, and 15 miles per hour, and the extreme wind scenario used wind speeds of 21, 23, and 25 miles per hour. To account for some of the variability associated with fire weather and fuels, there were a total of six model runs used for each wind scenario (using each combination of fuel moisture

scenario and wind speed). Each wind scenario was then modeled using both the 50th and 75th percentiles of surface fuel loads.

Prediction of torching (passive crown fire) is performed by interpreting the transition ratio within the BehavePlus modeling system. The transition ratio is defined as the fireline intensity of the given fuel scenario under the fire conditions specified, divided by the critical surface fireline intensity for that fuel scenario (Andrews 2008). Fireline intensity is determined by Rothermel's (1972) reaction intensity (I_R):

$$I_B = I_R * t_r * r$$

where I_B is fireline intensity (kW/m), I_R is reaction intensity (kW/m²), t_r is the flame-front residence time (s), and r is the rate of fire spread (m/s) (Alexander 1982). Critical surface fireline intensity is determined by the following equation from Van Wagner's (1977) crown fire initiation model:

$$I_0 = (0.01 * CBH * (460 + 25.9 * FMC))^{1.5}$$

where I_0 is the critical surface fireline intensity for combustion of the crown (kw/m), CBH is canopy base height (m), and FMC is foliar moisture content (%) (Cruz and Alexander 2010). A transition ratio value of 1 or greater indicates that transition to crown fire is predicted to occur. Although the threshold at which the transition ratio results in a predicted crown fire is 1, values near 1 may indicate greater uncertainty

regarding transition to crown fire than values much higher or lower than 1 (Andrews 2008).

Similarly, prediction of crowning (active crown fire) is performed by interpreting the active ratio. The active ratio is defined as the crown fire rate of spread of the given fuel scenario under the fire conditions specified, divided by the critical crown fire rate of spread for the given fuel scenario (Andrews 2008). Crown fire rate of spread is estimated using Rothermel's (1991) crown fire rate of spread model and critical crown fire rate of spread is given by Van Wagner's (1977) model:

$$R_0 = S_0/d$$

where R_0 is the critical spread rate to achieve crown spread (m/s), S_0 is the limiting mass flow rate ($\text{kg/m}^2\text{s}$), and d is canopy bulk density (kg/m^3). An active ratio value of 1 or greater indicates that active crown fire is predicted to occur. Although the threshold at which the active ratio results in a predicted crown fire is 1, values near 1 may indicate greater uncertainty regarding active crown fire than values much higher or lower than 1 (Andrews 2008).

Results

Fuel Parameters

The BIC preferred canopy base height model contained the single continuous predictor variable of DMR (BIC = 101.7) (Appendix, Table 1.17). There was no

evidence that stand density, mountain pine beetle mortality level, or site productivity were significant predictors of canopy base height 21-28 years TSB. There was strong evidence that the slope of the linear relationship between the log of canopy base height and DMR at the plot scale was different from zero ($F_{1,25} = 11.25$, $p = 0.0025$, marginal $r^2 = 0.30$, conditional $r^2 = 0.60$) (Table 3.4). There was an estimated 35.2% (95% CI: 15.4%, 50.4%) decrease in the median canopy base height for each unit increase in DMR (Figure 3.2).

Two canopy bulk density models of the set of 18 candidate models were equally preferred ($\Delta\text{BICs} = 0, 0.56$). One of the preferred models (hereafter referred to as model 1) included the continuous predictor variables of DMR and stand density ($\text{BIC} = 23.74$), while the other model (hereafter referred to as model 2) included those variables in addition to the categorical predictor variable of productivity ($\text{BIC} = 24.30$) (Appendix, Table 1.18). There was no evidence that mountain pine beetle mortality level was a significant predictor of canopy bulk density 21-28 years TSB. Interpreting model 1, there was suggestive evidence that the slope of the linear relationship between the log of canopy bulk density and DMR was different from zero after accounting for stand density ($F_{1,24} = 3.376$, $p = 0.078$, marginal $r^2 = 0.57$, conditional $r^2 = 0.66$) (Table 3.4). There was an estimated 12.8% (95% CI: 4.9%, 19.8%) decrease in the median canopy bulk density for each unit increase in DMR after accounting for stand density (Figure 3.3).

Model 2 also showed suggestive evidence that the slope of the linear relationship between the log of canopy bulk density and DMR was different from zero after accounting for stand density and productivity ($F_{1,24} = 3.822$, $p = 0.0623$, marginal $r^2 = 0.62$, conditional $r^2 = 0.66$) (Table 3.4). There was an estimated 12.5% (95% CI: 5.6%, 18.9%) decrease in the median canopy bulk density for each unit increase in DMR after accounting for stand density and productivity. Because the effect sizes of model 1 and model 2 were nearly identical, we will hereafter use model 1 for discussion of this relationship due to its lower BIC value.

Fire Behavior Modeling

Plots without dwarf mistletoe ($DMR = 0$) had low susceptibility to torching under the low wind scenario (Figure 3.4). 8% of model runs using DMR 0 plots transitioned to crown fire under the 50th percentile of surface fuels while an average of 19% of plots transitioned to crown fire under the 75th percentile of surface fuels (Table 3.5). These plots' susceptibility to torching increased with increasing wind speed and surface fuels. Under the moderate wind scenario, these plots were highly susceptible to changes in surface fuel loading (Figure 3.5). On average, 38% and 83% of model runs using DMR 0 plots were predicted to transition to crown fire using the 50th and 75th percentiles of surface fuels, respectively (Table 3.5). There was high susceptibility to torching in these plots under the extreme wind scenario, regardless of surface fuel loading (Figure 3.6).

Averages of 90% and 97% of the model runs using DMR 0 plots were predicted to torch under 50th and 75th percentiles of surface fuels, respectively (Table 3.5)

Plots with light to moderate dwarf mistletoe ($DMR = 0.1 - 2$) had moderate susceptibility to torching under the low wind scenario (Figure 3.4). Using the 50th and 75th percentiles of surface fuels, an average of 37% and 52% of the model runs using plots with DMR between 0.1 and 2 transitioned to crown fire, respectively (Table 3.5). Increased wind speed led to a small increase in torching in these plots (Figure 3.5). Averages of 65% and 70% of the model runs using these plots transitioned to crown fire under the 50th and 75th percentiles of surface fuels and the moderate wind scenario (Table 3.5). Little change in the instance of predicted crown fire occurred under the extreme wind scenario (Figure 3.6). An average of 70% of the model runs using these plots were predicted to experience torching under both surface fuel loadings (Table 3.5).

Plots with moderate to severe dwarf mistletoe ($DMR > 2$) were more susceptible to torching under the low wind scenario than were plots with lower instances of dwarf mistletoe (Figure 3.4). Averages of 69% and 87% of the model runs using plots with $DMR > 2$ transitioned to crown fire under the 50th and 75th percentiles of surface fuels, respectively (Table 3.5). Under increased wind speeds and increased surface fuels, torching was predicted to occur in nearly all of these plots (Figure 3.5). An average of 94% and 99% of the model runs using these plots were predicted to transition to crown fire under the moderate wind scenario and the 50th and 75th percentiles of surface fuels,

respectively (Table 3.5). Under the extreme wind scenario, 100% of the model runs using plots with $DMR > 2$ were predicted to transition to crown fire under both surface fuel loads (Table 3.5). Increased DMR was not shown to be strongly associated with increased probability of torching under the extreme wind scenario as it was under the low and moderate wind scenarios (Figure 3.6).

None of the plots of any DMR category were predicted to carry an active crown fire under the low or moderate wind scenarios using either the moderate or high surface fuel loads. An average of 5% and 6% of model runs of DMR 0 plots were predicted to carry an active crown fire under the extreme wind scenario and the moderate and high surface fuel loads, respectively (Figure 3.7). None of the model runs of $DMR > 0$ plots were predicted to carry a crown fire under the extreme wind scenario (Figure 3.7). These results indicate that there is no evidence that DMR level is associated with a difference in active crown fire behavior in these stands because the probability of active crown fire is extremely low in this forest type regardless of DMR.

Discussion

Effects of Dwarf Mistletoe on Fuel Parameters

Our results indicate strong statistical evidence for a negative linear relationship between the natural logarithm of canopy base height and DMR ($p = 0.0025$). This finding supports the hypothesis that increased DMR is associated with a lower canopy base height in post-mountain pine beetle epidemic lodgepole pine stands (21-28 years

TSB) in central Oregon over a large range of DMR. The magnitude of the decrease in canopy base height associated with each unit of decrease in DMR (35%) indicates a significant change in vertical fuel arrangement associated with dwarf mistletoe infestation. This is consistent with previous findings on the relationship between dwarf mistletoe and individual tree crown base height (Koonce and Roth 1985, Godfree et al 2002), but our findings are more broadly based as stands were randomly selected and accounted for the previous mountain pine beetle epidemic. Dwarf mistletoe clearly alters the vertical fuels arrangement of post-mountain pine beetle lodgepole pine stands and should be taken into account in future mountain pine beetle and fuels studies.

The relatively high conditional r^2 value (0.60) compared with the marginal r^2 value (0.30) for this model indicates that the within-stand variability of canopy base height among plots was high. Measurement of a single 0.075 ha plot per stand would not be adequate to characterize these highly heterogeneous stands. Although the conditional r^2 value of this model indicates relatively high precision of the regression equation in ecological terms, additional variability around the regression line may be attributed to the inherent variability in the structure of lodgepole pine forests two to three decades after a mountain pine beetle epidemic (Pelz and Smith 2012).

Our hypothesis that increased DMR is associated with a lower canopy bulk density in post-mountain pine beetle epidemic lodgepole pine stands (21-28 years TSB) in central Oregon over a large range of severity of dwarf mistletoe infestation was

supported. We found a weakly negative relationship between canopy bulk density and DMR in this ecosystem. There is suggestive statistical evidence for a negative linear relationship between the natural logarithm of canopy bulk density and DMR, after accounting for stand density ($p = 0.078$). The magnitude of the decrease in canopy bulk density associated with each unit of decrease in DMR (12.5%) indicates that there is a small effect of dwarf mistletoe on overall canopy bulk density. Hoffman et al (2007) found a similar trend between DMR and canopy bulk density in ponderosa pine although their results were not statistically significant. No other studies have specifically investigated the influence of dwarf mistletoes on canopy bulk density.

Although there was some evidence of a negative relationship between dwarf mistletoe infection and canopy bulk density at the plot scale, the nature of this relationship at the tree or branch scale is unknown. Measurements of canopy volume show that the relationship between dwarf mistletoe infection and canopy volume is similar to the relationship between dwarf mistletoe infection and canopy bulk density (Chapter 2). However, crown mass was not directly measured, necessitating the use of modeled numbers for canopy bulk density. The mass equation used in FuelCalc to calculate canopy bulk density is based on a generic allometric equation for lodgepole pine which does not take into account dwarf mistletoe effects on foliage and twig mass (Brown 1978, Reinhardt et al 2006). This parasite forms witches brooms that distort tree growth and redistribute nutrients within the tree (Hawksworth and Wiens 1996), so we do

not know if it is reasonable to assume that this allometric equation accurately reflects the mass of trees with witches' brooms. Although there has been little research on the effects of dwarf mistletoe on canopy bulk density, several studies have addressed the question of its effect on lodgepole pine foliage mass. Decreases in foliage mass of 50 to 60 percent have been observed in infected versus uninfected lodgepole pine trees (Broshot et al 1986, Littely et al 2008).

The decrease in canopy bulk density found in this analysis leads to a lower probability that these stands will carry an active crown fire. This may be attributed to the fuel limitation of these forests due to low productivity as proposed by Gara et al (1985). However, further examination of the effect of dwarf mistletoe on canopy bulk density at the branch scale is required to fully understand the implications of dwarf mistletoe infection on stand-level canopy bulk density. Overall, previous research shows that there is some evidence that mass of total foliage decreases rather than increases in trees infected by dwarf mistletoe. Canopy volume in our stands showed a decreasing trend with increasing dwarf mistletoe infection (Chapter 2), contrary to previous work in central Oregon lodgepole pine, which found no difference in canopy volume among stands with various levels of dwarf mistletoe infection (Godfree et al 2003). Given these trends there is no evidence to expect that we are under-predicting canopy bulk density at the plot level in severely infected stands due to uncertainty about tree or branch-level canopy bulk density in dwarf mistletoe infected trees.

A potential mechanism for the decrease of canopy bulk density with increased DMR is that the diversion of nutrients away from uninfected parts of the host decreases total canopy bulk density much more than the stimulation of biomass in witches' brooms increases it. Witches' brooms are known to act as nutrient sinks and dwarf mistletoe has extremely high metabolic demands, often starving uninfected areas of the host of carbohydrates and minerals (Hull and Leonard 1964a, Hull and Leonard 1964b, Mathiasen 1996, Mathiasen et al 2008). The weak evidence to support this relationship shown in our results may indicate that canopy bulk density is not strongly associated with dwarf mistletoe infestation on the stand scale at which we are examining it. Alternatively, it may indicate that at this time post-mountain pine beetle epidemic, the magnitude of the effect of the beetle has on canopy bulk density has obscured the effect of dwarf mistletoe.

We investigated several structural factors that might have confounding effects within our stands to understand the effect of dwarf mistletoe infection on fuel parameters. Although we controlled for the effect of mountain pine beetle by sampling from a single stage of post-mountain pine beetle stands, epidemics are known to have variable intensity, causing varying amounts of mature tree mortality. This is associated with a variety of stand structure attributes, such as average DBH, stand species composition, and stand density (Amman 1977, Hawkins et al 2012). Variable intensity of mountain pine beetle epidemics has been shown to be associated with variable magnitude of

regeneration of the stand establishing post-epidemic (Stuart et al 1989) and therefore may have an impact on canopy fuel loads. Site productivity also varies greatly throughout central Oregon lodgepole pine forests, with average site indices ranging from 37 to 89 (Simpson 2007). Site productivity is known to influence stand structure in lodgepole pine forests, which could have potential impacts on canopy base height and canopy bulk density (Parker 1986). Stand density, which was not shown to be associated with productivity or dwarf mistletoe rating in our data (Chapter 2), also has known impacts on the crown base height of individual trees and foliage density due to impacts on light availability (Chen et al 1996, Gary 1978, Godfree et al 2002).

We accounted for each of these potentially confounding factors in our models to ensure the effects on fuels we observed were associated with dwarf mistletoe infection and to ensure that we could detect an effect of dwarf mistletoe infection if there truly was one. However, only the addition of the predictor stand density to the canopy bulk density model improved our understanding of these relationships. Within this system, productivity and mountain pine beetle mortality density do not significantly impact the relationship between dwarf mistletoe rating and either canopy fuel parameter. The insignificance of these variables in our models may be attributed to the TSB of several decades. The time the stand has had to recover may mean the mortality density of the previous epidemic is no longer playing a large role in differentiating stand structure.

Effects of Dwarf Mistletoe on Fire Behavior

The results of the fire behavior modeling suggest that at low to moderate wind speeds, likelihood of torching increases with increased DMR. This is consistent with our hypothesis, with previous work on dwarf mistletoe in ponderosa pine using fire behavior models (Hoffman et al 2007), and with ground-based observations during wildfires (Brown 1975, Wicker and Leaphart 1976). However, under more extreme weather (wind speeds >20 mph), the effect of dwarf mistletoe on torching potential was not shown to be important. This is consistent with previous work which has shown that under extreme weather conditions, the effects of fuel loading and fuel arrangement become less important to fire behavior and the effect of weather becomes its main driver (Turner and Romme 1994, Bessie and Johnson 1995).

The likelihood of active crown fire in central Oregon lodgepole pine dominated forests 21-28 years post-mountain pine beetle epidemic is extremely low in stands at all levels of DMR. This is not consistent with our original hypothesis that likelihood of active crown fire would decrease with DMR, as active crown fire was shown to be unrelated to DMR in this system. Although there was suggestive evidence that canopy bulk density, the key fuel parameter driving active crown fire behavior, was negatively related to DMR, the decrease in canopy bulk density was not shown to be relevant to active fire behavior. The range of canopy bulk density values recorded for the plots in this study area was very low overall, ranging from 0.02 to 0.12 kg/m³. This suggests that

the magnitude of the effect of DMR on canopy bulk density was not large enough to have a significant influence on active crown fire behavior.

Investigation of dwarf mistletoe's influence on foliar moisture should be conducted to enhance understanding of dwarf mistletoe's influence on canopy fuels' flammability. Van Wagner's (1977) model uses three attributes to predict crown fire behavior: canopy base height, canopy bulk density, and foliar moisture content. We did not measure foliar moisture content, but used data observed in a fire weather and fuels analysis for central Oregon (L. Hollingsworth, personal communication). Dwarf mistletoes must obtain all of their water requirements from their host, leading to potentially varied water relations in infected trees as opposed to uninfected trees (Hawksworth and Wiens 1996, Meinzer et al 2004, Logan et al 2013). Water conductance in the dwarf mistletoe was found to be 2 to 5 times higher than in the host under drought conditions in infected lodgepole pine in central Oregon (Kirkpatrick 1989). Additionally, witches' brooms are thought to cause greater water loss than dwarf mistletoe plants themselves potentially further decreasing foliar moisture in witches' brooms (Hawksworth and Wiens 1996). It is likely that foliar moisture content varies with both severity of dwarf mistletoe infection and percent of the crown in brooms, so we may be underpredicting the flammability of severely infected stands in our models.

The uncertainty surrounding predictions of crown fire using operational fire modeling systems indicates there is a possibility that the models we used under-predicted

active crown fire potential in these stands. Operational fire modeling systems, such as BehavePlus, have limitations, especially for use in crown fire prediction. Many studies have demonstrated that fire models consistently under-predict the occurrence of both passive and active crown fire (Agee and Lolley 2006, Hall and Burke 2006, Page and Jenkins 2007b, Schoennagel et al 2012). Cruz and Alexander (2010) discuss this issue extensively in their review paper and suggest several sources of under-prediction bias in crown fire modeling systems. Sources of bias are related to inappropriate linkages of surface fire and crown fire initiation models in operational fire modeling systems as well as use of surface and crown fire rate of spread models which have inherent under-prediction biases for many of the forest types to which they are applied.

The limitation on prediction of active crown fire is of particular importance to this study, given the very low levels of crowning predicted in our data, even under the extreme weather scenario. However, the low values of canopy bulk density (exceeding 0.1 kg/m^3 in just one plot), indicate that the infrequent prediction of active crown fire may be accurate. If this is true, the legacy of the mountain pine beetle epidemic may be playing a large role in this relationship. These stands generally had recovered to high densities of mature trees by 21 to 28 years post-epidemic, averaging 971 stems/ha and ranging from 373 to 2493 stems/ha. However, the low levels of canopy bulk density in these stands may be attributed to the removal of the overstory canopy.

Previous findings regarding stand recovery to pre-epidemic conditions are inconsistent, so the nature of the relationship between canopy bulk density and mountain pine beetle is uncertain. In Colorado, high growth rates of advance regeneration were observed 8 years after the onset of a mountain pine beetle epidemic, but growth simulations using observed data suggested that the stands would not recover to pre-epidemic stand basal area and stand density conditions for at least 80 years (Collins et al 2011). This suggests that the stands in our study will not recover to pre-epidemic conditions for several decades. However, a study of a historical outbreak in Colorado showed a recovery to 91% of pre-epidemic stand basal area and 93% of pre-epidemic total overstory tree density 30 years post-epidemic (Pelz and Smith 2012). In British Columbia, 9 years after the onset of an epidemic, density of mature stems (> 4 meters in height) varied with stand age class at the time of beetle attack, but stands of all age classes were generally found to be well-stocked (>900 mature stems/ha) (Hawkins et al 2012). Growth simulations of well-stocked stands showed recovery to merchantable volumes (150 m³/ha) within 30 years. These studies suggest that the stands in our study may have recovered to pre-epidemic stand conditions at the time of measurement, if central Oregon lodgepole pine forests behave in the same manner as those of the intermountain west. However, it is likely that central Oregon lodgepole pine stands recover differently than stands in other regions due to their distinctive ecological features. Additional studies which incorporate dwarf mistletoe and mountain pine beetle effects

are required to fully address the question of active crown fire potential in lodgepole pine forests.

Fire Ecology of Dwarf Mistletoe in Lodgepole Pine

The fire regime of central Oregon lodgepole pine forests is characterized by mixed severity, variable intensity fires with fire-free periods of variable length (Agee 1993). This system is dominated by low productivity, fuel-limited stands which may serve as crown fire breaks (Gara et al 1985). The fire regime of central Oregon lodgepole pine is distinctive from that of seral Rocky Mountain lodgepole pine forests, which typically experience high severity, stand replacement fires (Lotan et al 1985). While the fire regime of Rocky Mountain lodgepole pine generates single-aged, structurally uniform stands (Lotan et al 1985), the variability of the fire regime of central Oregon lodgepole pine gives rise to higher levels of structural complexity (Stuart et al 1989). Additional complexity of stand structure is introduced through the variable presence of dwarf mistletoe in these stands and the potential that recurring mountain pine beetle epidemics have occurred (Chapter 2). Our results show that dwarf mistletoe is significantly influencing fuels in central Oregon lodgepole pine by lowering canopy base height at the stand scale and increasing the probability of torching, particularly under moderate fire weather. Dwarf mistletoe contributes to heterogeneous fuels and fire behavior across this landscape, further perpetuating the heterogeneity of future forest stands.

Conclusions

This study indicates the necessity to include the characterization of fuels associated with dwarf mistletoe infestation when examining fuels and fire behavior in post-mountain pine beetle epidemic lodgepole pine stands in central Oregon. Both mountain pine beetle and dwarf mistletoe have been shown to have impacts on fuels and fire behavior (Hicke et al 2012, Jenkins et al 2012, Shaw et al 2004). However, few fuels and fire behavior studies which take both disturbances into account have been conducted previously and their interactive effects were unknown. These findings agree with many other studies which have stressed the importance of simultaneously interpreting multiple interactive disturbance impacts within ecosystems (Bigler et al 2005, Deroose and Long 2009, Metz et al 2011). Given the current predictions for an increase in high severity fires in western North America under future climate conditions, it will be important for managers to have accurate information regarding fire potential associated with other widespread forest disturbances (IPCC 2007, Flannigan et al 2009). To do this accurately, it will be imperative that the whole suite of disturbance agents is considered when assessing fuels and overall ecosystem functionality.

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Tables

Table 3.1. Characteristics of 39 plots within 13 stands of lodgepole pine in central Oregon. DMR is dwarf mistletoe rating, CBH is canopy base height, CBD is canopy

Stand	Plot	DMR	CBH (m)	CBD (kg/m ³)	Productivity Class	MPB Mortality (trees/ha)	MPB Mortality Class	Stand Density (stem/ha)
CRL	1	2.78	1.22	0.0407	L	25	L	1213
	2	2.93	2.14	0.0172	L	25	L	680
	3	2.4	5.49	0.0353	L	25	L	600
CRP	1	0	6.1	0.0558	H	68	H	1120
	2	1.02	3.05	0.0382	H	68	H	880
	3	0	10.06	0.0769	H	68	H	1107
CRP2	1	1.81	1.53	0.0297	H	21	L	1107
	2	2.45	1.83	0.0393	H	22	L	893
	3	2.94	1.83	0.028	H	14	L	1187
CUL2	1	2.42	1.22	0.0313	H	34	L	973
	2	2.35	2.14	0.0263	H	53	M	1040
	3	2.38	0.31	0.0262	H	90	H	827
CUL6	1	3.98	0.31	0.0386	M	85	H	987
	2	3.7	1.22	0.0293	M	29	L	1000
	3	2.59	3.05	0.0647	M	29	L	1760
DES	1	0	6.41	0.0406	M	45	M	600
	2	0	5.49	0.0403	M	57	M	720
	3	0	3.05	0.0272	M	45	M	493
EFR	1	0	3.97	0.0427	L	41	M	600
	2	0	4.88	0.0361	L	41	M	387
	3	0	4.27	0.0686	L	41	M	893
EFR3	1	0	3.97	0.0446	L	74	H	613
	2	0	5.49	0.0325	L	33	L	373
	3	0	3.36	0.1174	L	50	M	2053
LDES	1	0.54	3.05	0.0173	M	44	M	680
	2	0	4.88	0.0433	M	44	M	1053
	3	0.73	4.27	0.0435	M	44	M	1013
LVLK	1	1.11	1.53	0.0276	H	88	H	880
	2	2.09	1.22	0.046	H	88	H	1227
	3	0	1.22	0.0347	H	72	H	1093
ODL	1	2.5	0.31	0.0588	L	20	L	827
	2	1.85	0.31	0.0455	L	28	L	987
	3	2.88	2.44	0.0247	L	29	L	800
PAU	1	2.36	1.83	0.0643	H	36	M	1733
	2	2.38	1.53	0.077	H	76	H	2493
	3	1.8	1.22	0.0525	H	85	H	1560
SNC	1	1.4	13.42	0.0234	H	69	H	533
	2	1.26	14.94	0.0271	H	69	H	413
	3	0.16	14.33	0.0298	H	70	H	493

bulk density, and MPB is mountain pine beetle.

Table 3.2. 50th and 75th percentiles of surface fuel loadings of plots. Values are from plots 15-25 years TSB from the original plot network established in 2010 and 2011 (T.J. Woolley et al, unpublished data).

Surface Fuel Loading	50th percentile surface fuels	75th percentile surface fuels
1-hr Fuels (Mg/ha)	5.59	8.12
10-hr Fuels (Mg/ha)	2.92	4.27
100-hr Fuels (Mg/ha)	7.29	10.53
Live Herbaceous Fuels (Mg/ha)	0.06	0.18
Live Woody Fuels (Mg/ha)	2.25	3.71
Fuel Bed Depth (m)	0.47	0.60

Table 3.3. Fuel moisture conditions for surface fuels under moderate and extreme weather conditions. Values were adapted from personal communication with LaWen Hollingsworth.

Fuel Moisture (%)	Extreme scenario	Moderate scenario
1-hr	2	4
10-hr	3	5
100-hr	7	9
Live Herbaceous	50	70
Live Woody	80	90
Foliar	100	100

Table 3.4. BIC preferred linear mixed models of canopy fuel parameters. Statistical models for canopy base height (CBH) and canopy bulk density (CBD) on dwarf mistletoe rating (DMR) with parameter estimates and standard errors in parentheses. SD is stand density, PL is low productivity and PM is moderate productivity. Also included are BIC values from respective BIC calculations, goodness of fit (marginal and conditional r^2 values), and p values where $p < 0.01$ indicates strong evidence of a relationship (**), $p < 0.05$ indicates some evidence of a relationship (*), and $p < 0.1$ indicates suggestive but inconclusive evidence of a relationship (.).

Model with parameter estimates (SE)	BIC	Marginal r^2	Conditional r^2	p value
Log (CBH) = 1.522 (0.255) – 0.434 * DMR (0.129)	101.7	0.30	0.60	0.0025 **
Log (CBD) = -3.747 (0.117) – 0.137 * DMR (0.041) + 0.0007 * SD (0.0001)	23.74	0.57	0.66	0.078 .
Log (CBD) = -3.88 (0.128) – 0.135 * DMR (0.036) + 0.0007 * SD (0.0001) + 0.254 * PL (0.107) + 0.042 * PM (0.115)	24.3	0.62	0.66	0.0623 .

Table 3.5. Percent torching of plots by dwarf mistletoe rating. Average percentage and (range of percentages) of plots that experienced torching under each combination of wind scenario and surface fuel loading by plot-level average DMR.

DMR	Wind scenario	Percent Torching	
		50 th Percentile Surface Fuels	75 th Percentile Surface Fuels
0	low	8	19 (8 – 46)
0.1 – 2.0	low	37 (20-40)	52 (40 – 70)
> 2.0	low	69 (44 – 88)	87 (69 – 94)
0	moderate	38 (15 – 62)	83 (62 – 92)
0.1 – 2.0	moderate	65 (60 – 70)	70
> 2.0	moderate	94	99 (94 – 100)
0	extreme	90 (77 – 92)	97 (92 – 100)
0.1 – 2.0	extreme	70	70
> 2.0	extreme	100	100

Figures

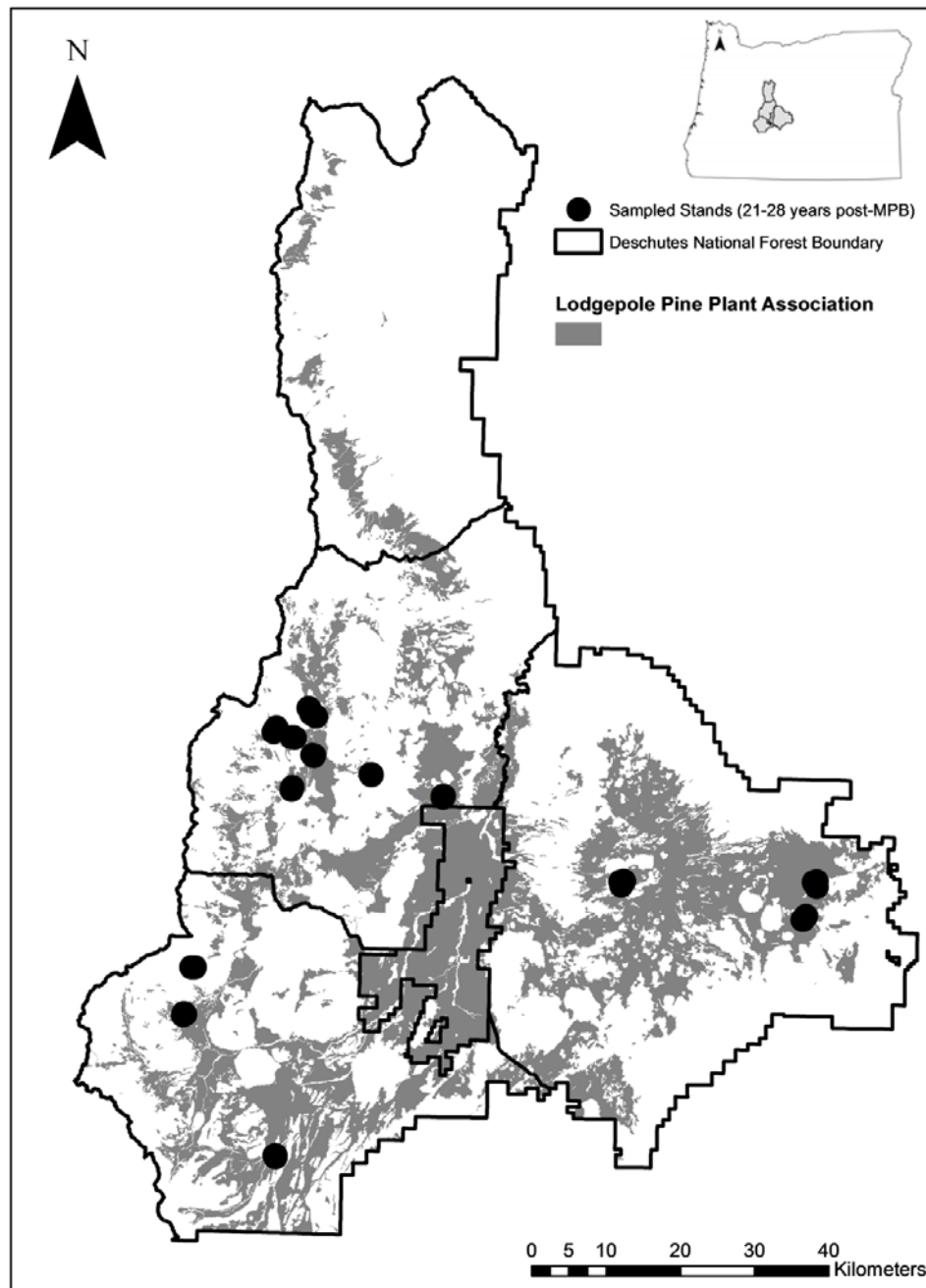


Figure 3.1. Study area map. Deschutes National Forest, Oregon boundary with sampled stands and lodgepole pine plant associations.

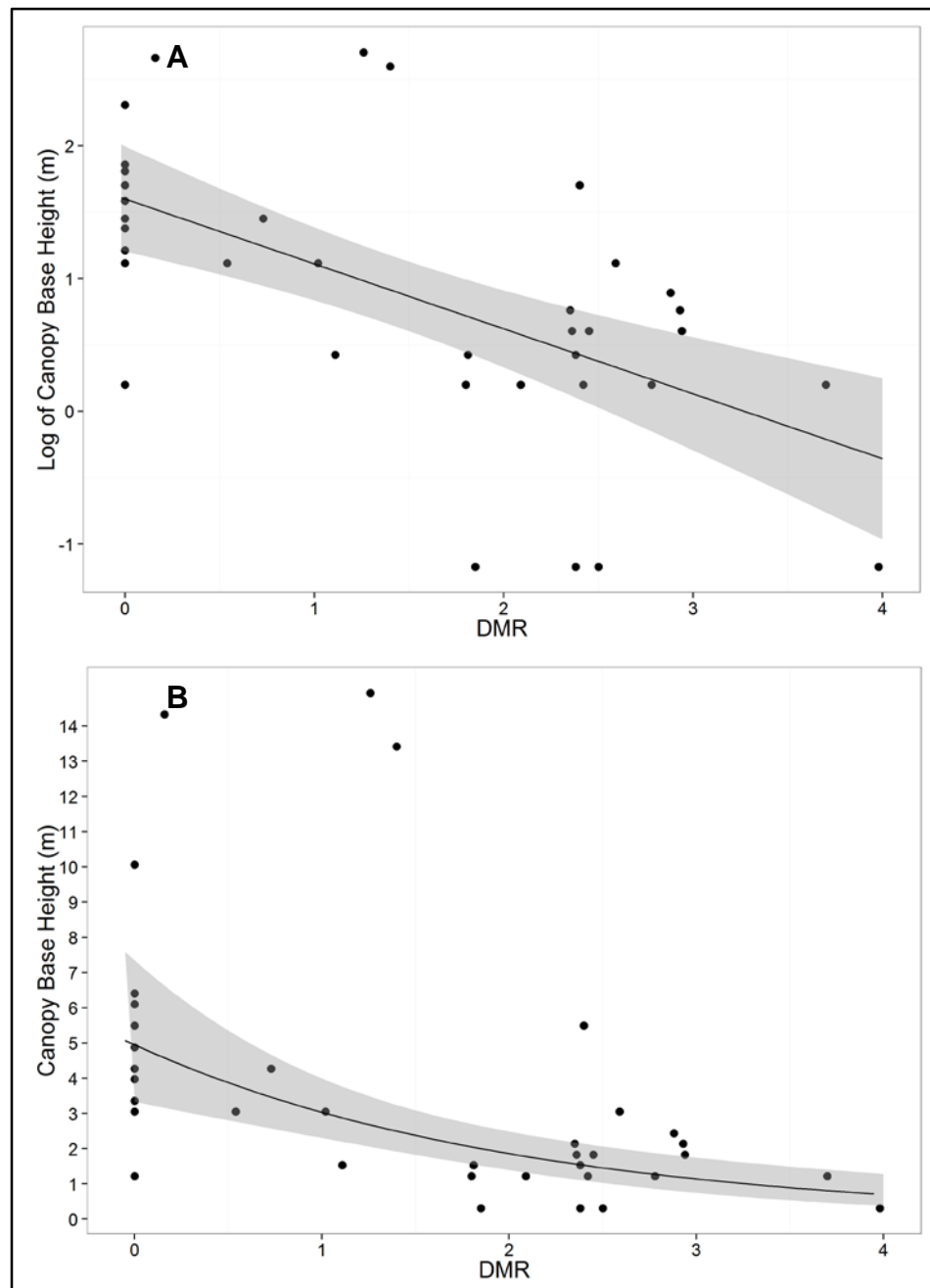


Figure 3.2. Linear mixed model of the log of canopy base height. Scatterplots of linear mixed models of A) the log of canopy base height (m) and B) the backtransformed log of canopy base height (m) (on the original scale) on dwarf mistletoe rating (DMR) with 95% confidence intervals. Marginal $r^2 = 0.30$, conditional $r^2 = 0.60$. Regression equation with (standard errors): $\text{Log}(\text{CBH}) = 1.522 (0.255) - 0.434 * \text{DMR} (0.129)$

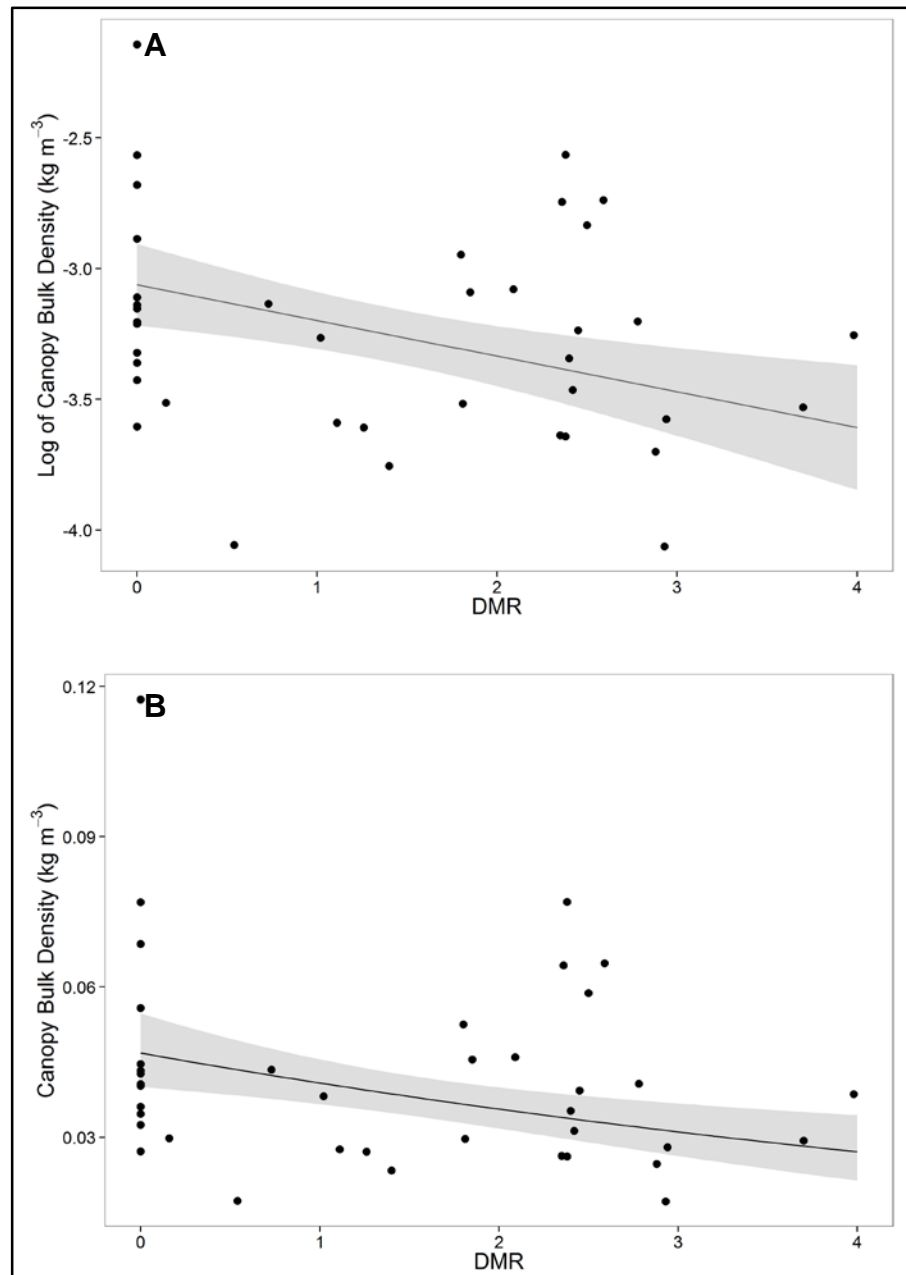


Figure 3.3. Linear mixed model of the log of canopy bulk density. Scatterplots of linear mixed models of A) the log of canopy bulk density (kg/m^3) and B) the backtransformed log of canopy bulk density (kg/m^3) (on the original scale), holding stand density constant, on dwarf mistletoe rating (DMR) with 95% confidence intervals. Marginal $r^2 = 0.57$, conditional $r^2 = 0.66$. Regression equation with (standard errors): $\text{Log}(\text{CBD}) = -3.747 (0.117) - 0.137 * \text{DMR} (0.041) + 0.0007 * \text{SD} (0.0001)$.

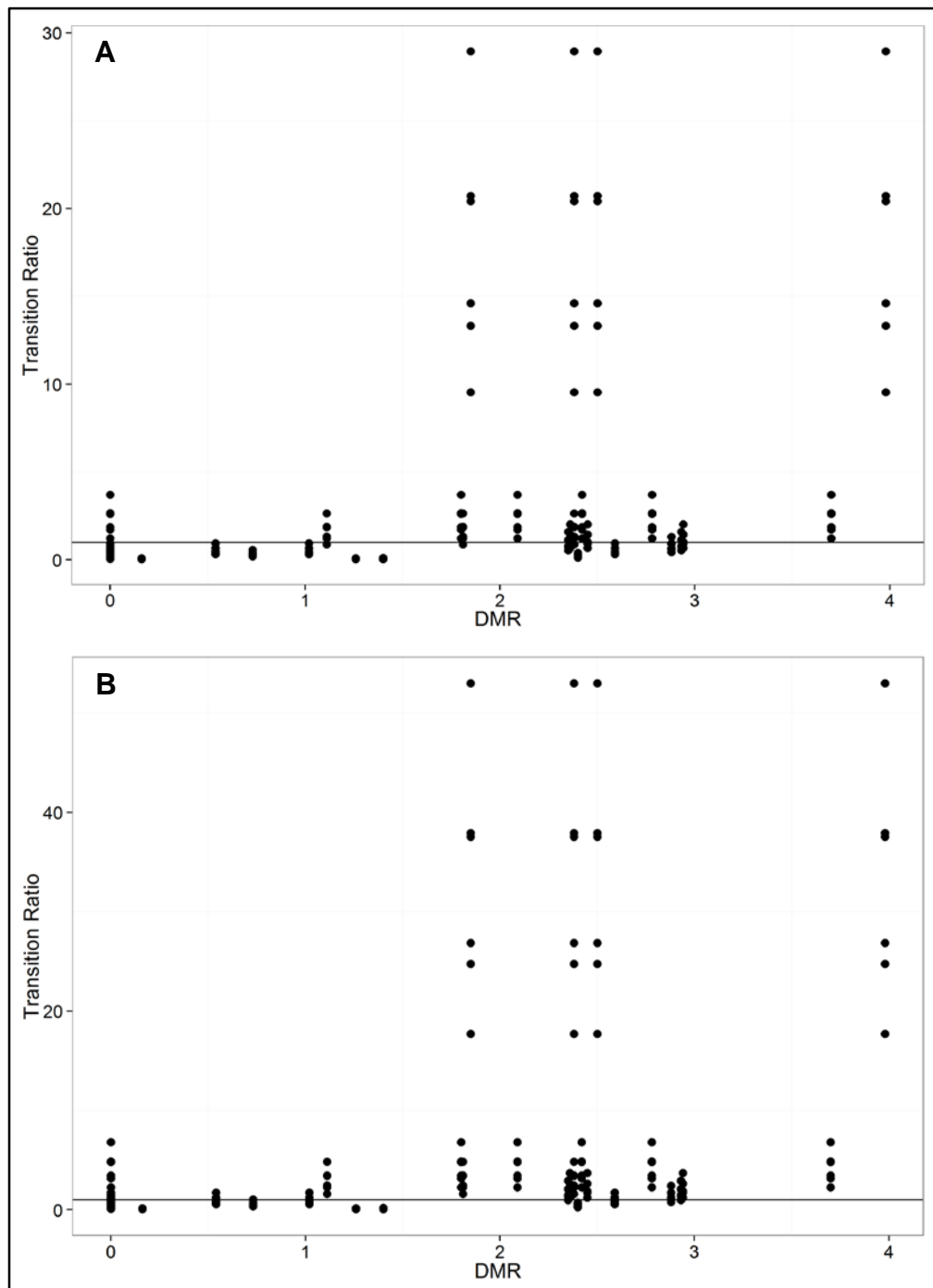


Figure 3.4. Scatterplots of predicted transition to crown fire by DMR under the low wind scenario. Transition ratios by DMR under the A) 50th, and B) 75th percentiles of surface fuels. Points above horizontal line at 1 are predicted to transition to crown fire.

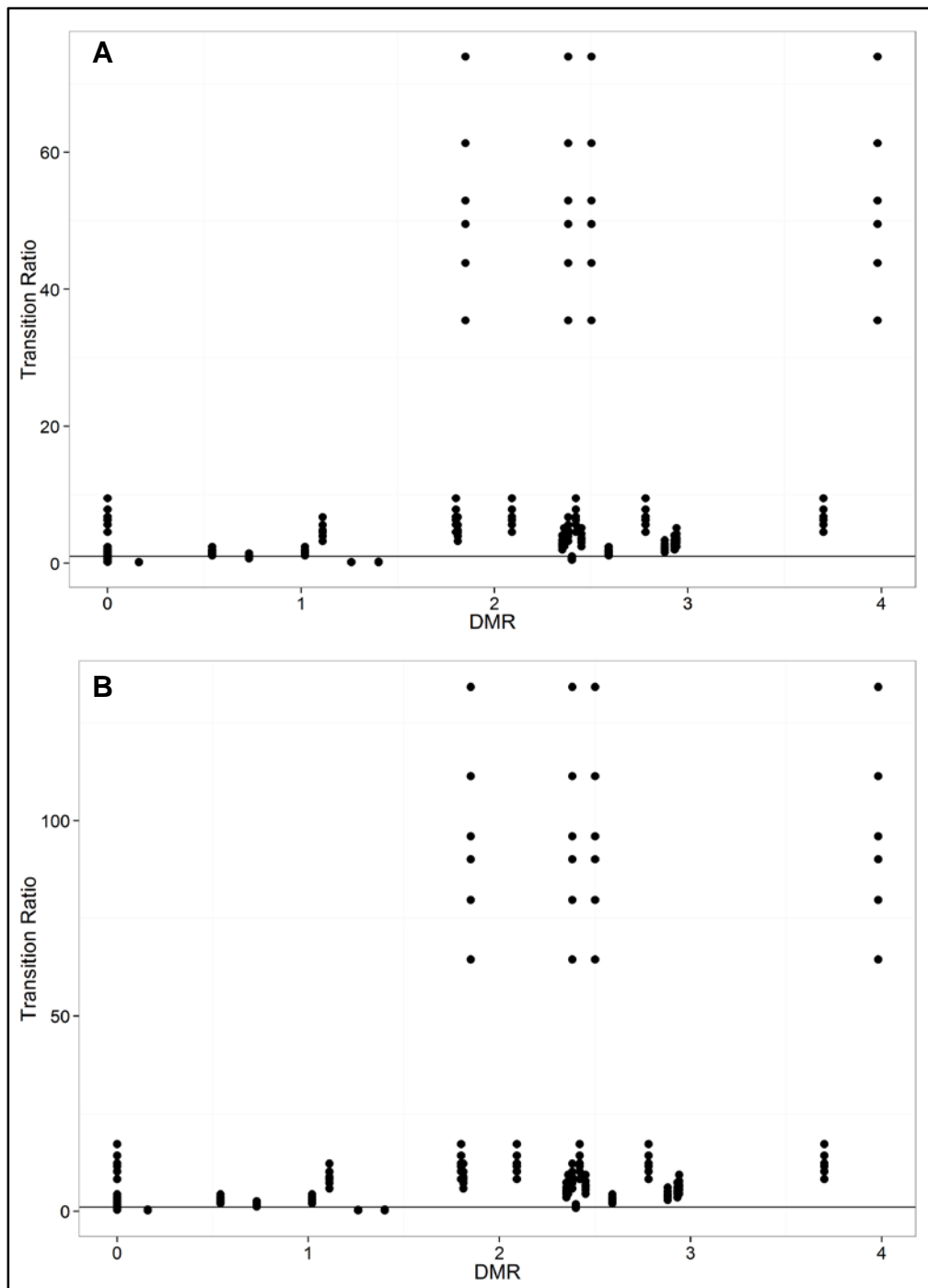


Figure 3.5. Scatterplots of predicted transition to crown fire by DMR under the moderate wind scenario. Transition ratios by DMR under the A) 50th, and B) 75th percentiles of surface fuels. Points above horizontal line at 1 are predicted to transition to crown fire.

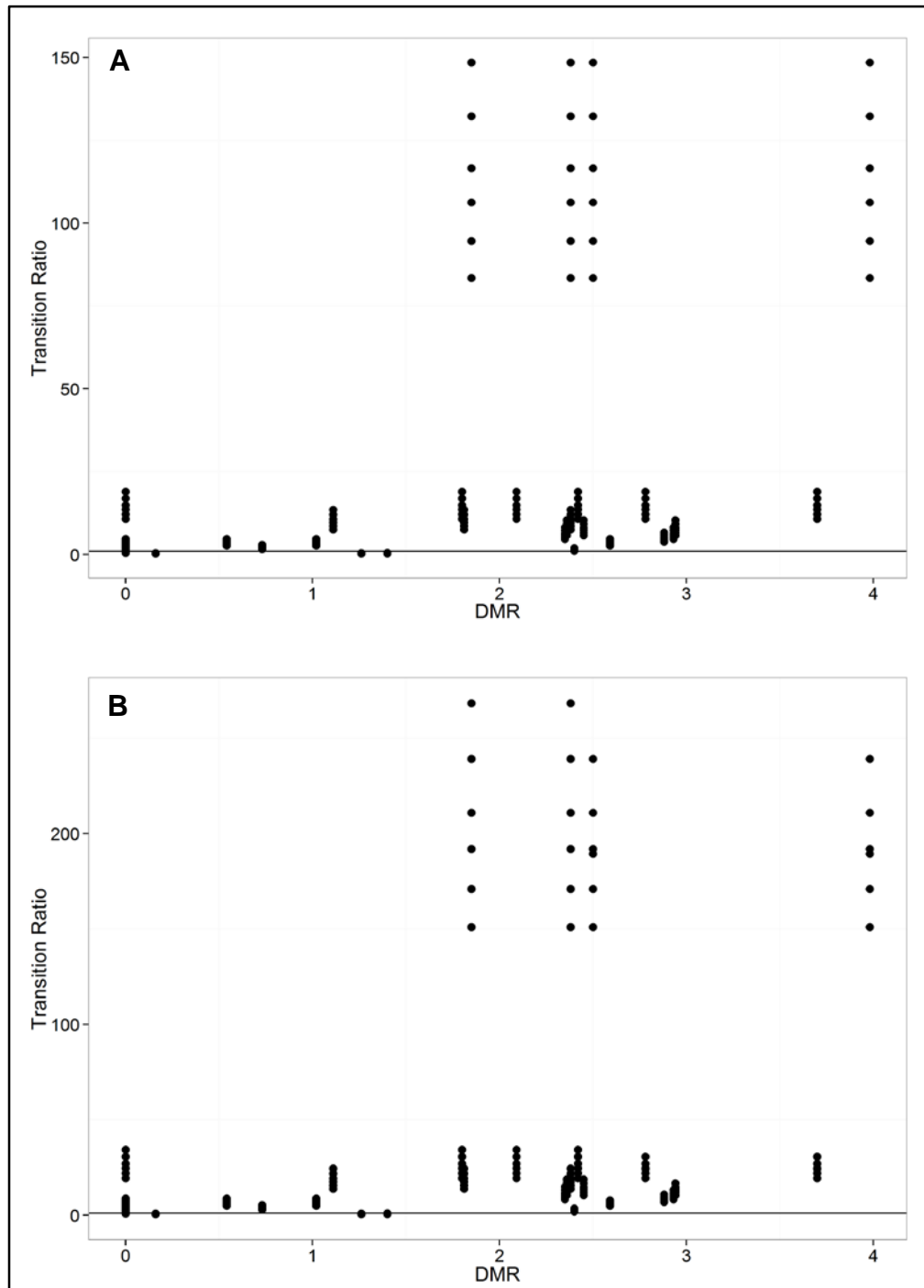


Figure 3.6. Scatterplots of predicted transition to crown fire by DMR under the extreme wind scenario. Transition ratios by DMR under the A) 50th, and B) 75th percentiles of surface fuels. Points above horizontal line at 1 are predicted to transition to crown fire.

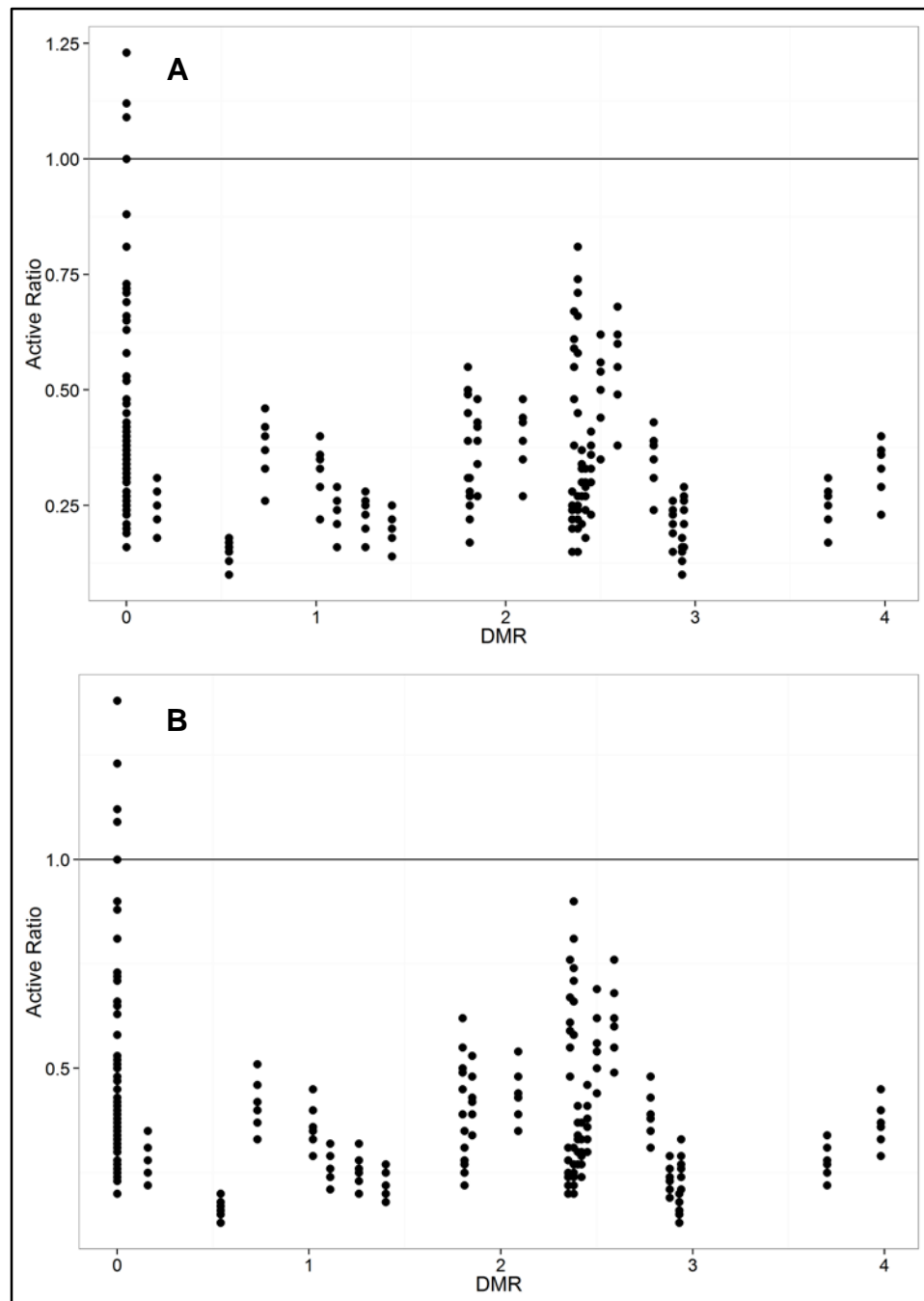


Figure 3.7. Scatterplots of predicted active crown fire by DMR. Active ratio by DMR under the extreme wind scenario and A) moderate surface fuel load B) high surface fuel load. Points above horizontal line at 1 are predicted to carry active crown fire.

Chapter 4: General Conclusions

Dwarf mistletoe has a significant influence on stand structure in central Oregon lodgepole pine forests 21 – 28 years after a mountain pine beetle epidemic (Chapter 2). Increasing DMR in lodgepole pine stands leads to reduced canopy volume, greater representation of the suppressed cohort, reduced representation and average diameter of the dominant cohort, and reduced average height of the suppressed cohort at the stand scale. The mountain pine beetle influences many stand structural attributes, so it is important to interpret these effects within the context of the previous epidemic. Structural differences associated with dwarf mistletoe create heterogeneity in this forest type and may have a significant influence on the productivity and resistance and resilience of these stands to future disturbances. Our findings show that it is imperative to incorporate both dwarf mistletoe and mountain pine beetle effects when studying stand productivity and ecosystem recovery processes in lodgepole pine forests, as particular attributes such as canopy volume and the proportion of stand in each cohort vary over the range of dwarf mistletoe ratings for a given period of time since beetle. Dwarf mistletoe may be similarly influencing other forest types and should be investigated in other systems within the context of other disturbance regimes.

Dwarf mistletoe significantly influences canopy fuels and potential crown fire in central Oregon lodgepole pine stands 21 – 28 years after a mountain pine beetle epidemic (Chapter 3). In these forests, dwarf mistletoe significantly lowers canopy base height at

the stand scale and increases the probability of torching, particularly under moderate fire weather. There was suggestive evidence that dwarf mistletoe also lowers canopy bulk density at the stand scale, although uncertainty remains regarding this relationship at the individual-branch scale. The likelihood of active crown fire in central Oregon lodgepole pine dominated forests 21-28 years post-mountain pine beetle epidemic is extremely low in stands at all levels of DMR. This indicates that while dwarf mistletoe is having an effect on the probability of torching, it has no effect on the probability of active crown fire. Dwarf mistletoe contributes to heterogeneous fuels and fire behavior across this landscape, which may further perpetuate the heterogeneity of future forest stands.

Dwarf mistletoe's influences on stand structure (Chapter 2) may have additional implications for fuels and fire behavior in forests after a mountain pine beetle epidemic. The decrease in canopy volume associated with increased dwarf mistletoe has a large effect on the calculation of canopy bulk density. This indicates that the negative relationship between modeled canopy bulk density and dwarf mistletoe (Chapter 3) may be more strongly negative when dwarf mistletoe effects are included in the calculation of canopy bulk density. Furthermore, the presence of higher densities of regeneration and greater representation of the suppressed cohort with increased dwarf mistletoe (Chapter 2) likely results in more frequent presence of ladder fuels in these stands. This may lead to an even greater probability of torching in stands with severe dwarf mistletoe than we

predicted taking into account the change in canopy base height of the overstory alone (Chapter 3).

These findings support the concept that interacting disturbances must be examined simultaneously when attempting to characterize their effects on an ecosystem. Disturbance effects also must be interpreted at the appropriate spatial scale, as processes occurring at the individual-tree scale may or may not occur in the same manner at a stand or landscape scale. Finally, geographically specific work regarding disturbance effects on stand structure, fire potential, and ecosystem functioning should be conducted for forest types which are not ecologically consistent throughout their range.

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Appendix

Tables

Table 1.1. Plot locations for 39 plots sampled in the Deschutes National Forest during the summer 2012. GPS coordinates provided for each end of transects are reported in UTM.

Stand	Plot	Date Sampled	Easting (0 m)	Northing (0 m)	Easting (75 m)	Northing (75 m)
CRL	1	8/21/2012	582777	4820232	582846	4820222
	2	8/23/2012	582796	4820548	582859	4820575
	3	8/23/2012	582996	4820409	583066	4820416
CRP	1	6/25/2012	596218	4851266	596266	4851333
	2	6/27/2012	596327	4851514	596372	4851569
	3	6/27/2012	596215	4851222	596220	4851155
CRP2	1	7/18/2012	606907	4853611	606950	4853661
	2	7/18/2012	606865	4853612	606802	4853648
	3	7/19/2012	606872	4853547	606942	4853557
CUL2	1	7/11/2012	593854	4859463	593921	4859495
	2	7/11/2012	593955	4859181	593881	4859191
	3	8/22/2012	593536	4858851	593609	4858849
CUL6	1	7/10/2012	595992	4858228	596036	4858284
	2	7/9/2012	596365	4858190	596444	4858201
	3	7/9/2012	596310	4858278	596253	4858330
DES	1	6/13/2012	616618	4851072	616659	4851138
	2	6/18/2012	616691	4850868	616621	4850895
	3	6/18/2012	616763	4851136	616839	4851136
EFR	1	7/17/2012	667098	4841202	667031	4841178
	2	7/17/2012	667003	4841299	666949	4841351
	3	7/17/2012	667331	4841469	667272	4841425
EFR3	1	7/12/2012	665659	4836181	665728	4836204
	2	7/16/2012	666081	4836692	666150	4836682
	3	7/16/2012	666122	4836343	666193	4836342
LDES	1	8/20/2012	595913	4801544	595923	4801619
	2	8/29/2012	595867	4801776	595917	4801829
	3	8/29/2012	595796	4801767	595840	4801831
LVLK	1	7/4/2012	598559	4861559	598530	4861631
	2	8/27/2012	599125	4861229	599188	4861190
	3	8/28/2012	598111	4862305	598191	4862293
ODL	1	6/19/2012	584091	4826802	584058	4826740
	2	6/19/2012	583762	4826714	583835	4826709
	3	6/21/2012	583692	4826804	583760	4826768
PAU	1	7/2/2012	641092	4839924	641097	4839852
	2	7/1/2012	641399	4840588	641428	4840516
	3	7/3/2012	640929	4840448	641000	4840440
SNC	1	8/7/2012	598950	4855963	598884	4855995
	2	8/8/2012	599033	4855931	599107	4855932
	3	8/8/2012	599054	4855889	599088	4855824

Table 1.2. Snag decay class codes and descriptions based on five class system. Descriptions are adapted from Thomas (1979).

Code	Bark	Heartwood Decay	Sapwood Decay	Limbs	Top Breakage	Bole Form
1	Intact	Minor	None to incipient	Mostly present	May be present	Intact
2	50% loose or missing	None to advanced	None to incipient	Small limbs missing	May be present	Intact
3	75% missing	Incipient to advanced	None to 25%	Few remain	Approx. 1/3	Mostly intact
4	> 75% missing	Advanced	> 25%	Absent	Approx. 1/3 to 1/2	Losing form, soft
5	100% missing	Advanced to crumbly	> 50%	Absent	> 1/2	Form mostly lost

Table 1.3. Crown class system used for classification of live trees.

Class	Definition
Dominant	Trees with crown extending above the general level of the crown cover and receiving full light from above and partly from the sides. These trees are taller than the average trees in the stand and their crowns are well developed, but they could be somewhat crowded on the sides. Also, these are trees whose crowns have received full light from above and from all sides during early development and most of their life. Their crown form or shape appears to be free of influence from neighboring trees.
Codominant	Trees with crowns at the general level of the crown canopy. Crowns receive full light from above, but little direct sunlight penetrates their sides. Usually they have medium-sized crowns and are somewhat crowded from the sides. In stagnated stands, co-dominant trees have small-sized crowns and are crowded on the sides.
Intermediate	Trees that are shorter than dominants and codominants, but their crowns extend into the canopy of codominant and dominant trees. They receive little direct light from above and none from the sides. As a result, intermediates usually have small crowns and are very crowded from the sides.
Suppressed	Trees with crowns entirely below the general level of the crown canopy that receive no direct sunlight either from above or the sides.

Table 1.4. Table of codes used to describe covariates in BIC candidate models. Codes are used in Tables 1.5 – 1.18.

Code	Description
B_x	Linear coefficient for the effect of the following covariate, where $x = 1, 2, 3 \dots 11$
DMR_{ij}	Dwarf mistletoe rating of the i th plot within the j th stand
SD_{ij}	Stand density of the i th plot within the j th stand
$PROD.L_{ij}$	Indicator that is 1 when the productivity of the i th plot within the j th stand is low and 0 otherwise
$PROD.M_{ij}$	Indicator that is 1 when the productivity of the i th plot within the j th stand is moderate and 0 otherwise
$MPBMORT.L_{ij}$	Indicator that is 1 when the mountain pine beetle mortality associated with the previous epidemic of the i th plot within the j th stand is low and 0 otherwise
$MPBMORT.M_{ij}$	Indicator that is 1 when the mountain pine beetle mortality associated with the previous epidemic of the i th plot within the j th stand is moderate and 0 otherwise
$SD*DMR_{ij}$	Interactive term for stand density and dwarf mistletoe rating of the i th plot within the j th stand
$PROD.L*DMR_{ij}$	Interactive term for productivity and dwarf mistletoe rating of the i th plot within the j th stand that is 1 when productivity is low and 0 otherwise
$PROD.M*DMR_{ij}$	Interactive term for productivity and dwarf mistletoe rating of the i th plot within the j th stand that is 1 when productivity is moderate and 0 otherwise
$MPBMORT.L*DMR_{ij}$	Interactive term for mountain pine beetle mortality associated with the previous epidemic and dwarf mistletoe rating of the i th plot within the j th stand that is 1 when mortality is low and 0 otherwise
$MPBMORT.M*DMR_{ij}$	Interactive term for mountain pine beetle mortality associated with the previous epidemic and dwarf mistletoe rating of the i th plot within the j th stand that is 1 when mortality is moderate and 0 otherwise

Table 1.5. BIC table for log of stand density model. $\text{Log}(SD)_{ij}$ represents the natural logarithm of the stand density of the i th plot within the j th stand, β_0 is the mean of the natural logarithm of stand density when all additional β 's = 0, b_j is the random error for the j th stand, $\mathbf{b}_j \sim N(0, \sigma_b^2)$ and \mathbf{b}_j and $\mathbf{b}_{j'}$ are independent, ε_{ij} is the random error from the natural logarithm of the stand density measurements i th plot replicate within the j th stand, $\varepsilon_{ij} \sim N(0, \sigma^2)$ and ε_{ij} and $\varepsilon_{i'j'}$ are independent.

Model	df	BIC	Δ BIC	L (gi x)	BIC weight	Evidence ratio
$\text{Log}(SD)_{ij} = \beta_0 + b_j + \beta_1 \text{DMR}_{ij} + \varepsilon_{ij}$	4	52.58	0	1	0.01	1
$\text{Log}(SD)_{ij} = \beta_0 + b_j + \beta_1 \text{PROD.L}_{ij} + \beta_2 \text{PROD.M}_{ij} + \varepsilon_{ij}$	5	56.43	3.85	0.15	1.93E-03	6.85
$\text{Log}(SD)_{ij} = \beta_0 + b_j + \beta_1 \text{MPBMORT.L}_{ij} + \beta_2 \text{MPBMORT.M}_{ij} + \varepsilon_{ij}$	5	57.63	5.05	0.08	1.06E-03	12.49
$\text{Log}(SD)_{ij} = \beta_0 + b_j + \beta_1 \text{DMR}_{ij} + \beta_2 \text{PROD.L}_{ij} + \beta_3 \text{PROD.M}_{ij} + \varepsilon_{ij}$	6	57.95	5.37	0.07	9.01E-04	14.69
$\text{Log}(SD)_{ij} = \beta_0 + b_j + \beta_1 \text{DMR}_{ij} + \beta_2 \text{MPBMORT.L}_{ij} + \beta_3 \text{MPBMORT.M}_{ij} + \varepsilon_{ij}$	6	58.16	5.57	0.06	8.15E-04	16.24
$\text{Log}(SD)_{ij} = \beta_0 + b_j + \beta_1 \text{DMR}_{ij} + \beta_2 \text{MPBMORT.L}_{ij} + \beta_3 \text{MPBMORT.M}_{ij} + \beta_4 \text{PROD.L}_{ij} + \beta_5 \text{PROD.L}_{ij} + \varepsilon_{ij}$	8	63.17	10.59	0.01	6.63E-05	199.47
$\text{Log}(SD)_{ij} = \beta_0 + b_j + \beta_1 \text{DMR}_{ij} + \beta_2 \text{MPBMORT.L}_{ij} + \beta_3 \text{MPBMORT.M}_{ij} + \beta_4 \text{DMR} * \text{MPBMORT.L}_{ij} + \beta_5 \text{DMR} * \text{MPBMORT.M}_{ij} + \varepsilon_{ij}$	8	63.59	11.01	4.06E-03	5.37E-05	246.23
$\text{Log}(SD)_{ij} = \beta_0 + b_j + \beta_1 \text{DMR}_{ij} + \beta_2 \text{PROD.L}_{ij} + \beta_3 \text{PROD.M}_{ij} + \beta_4 \text{DMR} * \text{PROD.L}_{ij} + \beta_5 \text{DMR} * \text{PROD.M}_{ij} + \varepsilon_{ij}$	8	65.14	12.56	1.87E-03	2.48E-05	534.48
$\text{Log}(SD)_{ij} = \beta_0 + b_j + \beta_1 \text{DMR}_{ij} + \beta_2 \text{MPBMORT.L}_{ij} + \beta_3 \text{MPBMORT.M}_{ij} + \beta_4 \text{PROD.L}_{ij} + \beta_5 \text{PROD.M}_{ij} + \beta_6 \text{PROD.L} * \text{DMR}_{ij} + \beta_7 \text{PROD.M} * \text{DMR}_{ij} + \beta_8 \text{MPBMORT.L} * \text{DMR}_{ij} + \beta_9 \text{MPBMORT.M} * \text{DMR}_{ij} + \varepsilon_{ij}$	12	74.14	21.56	2.09E-05	2.76E-07	47945.39

Table 1.6. BIC table for stand basal area model. $Log(SD)_{ij}$ represents the stand basal area of the i th plot within the j th stand, β_0 is the mean of stand basal area when all additional β 's = 0, b_j is the random error for the j th stand, $\mathbf{b}_j \sim N(0, \sigma_b^2)$ and \mathbf{b}_j and $\mathbf{b}_{j'}$ are independent, ε_{ij} is the random error from stand basal area measurements i th plot replicate within the j th stand, $\varepsilon_{ij} \sim N(0, \sigma^2)$ and ε_{ij} and $\varepsilon_{i'j'}$ are independent.

Model	df	BIC	Δ BIC	L (gi x)	BIC weight	Evidence ratio
$SBA_{ij} = \beta_0 + b_j + \beta_1 DMR_{ij} + \varepsilon_{ij}$	4	53.52	0	1	0.01	1
$SBA_{ij} = \beta_0 + b_j + \beta_1 MPBMORT.L_{ij} + \beta_2 MPBMORT.M_{ij} + \varepsilon_{ij}$	5	55.32	1.80	0.41	5.82E-03	2.46
$SBA_{ij} = \beta_0 + b_j + \beta_1 DMR_{ij} + \beta_2 MPBMORT.L_{ij} + \beta_3 MPBMORT.M_{ij} + \varepsilon_{ij}$	6	57.88	4.36	0.11	1.62E-03	8.86
$SBA_{ij} = \beta_0 + b_j + \beta_1 PROD.L_{ij} + \beta_2 PROD.M_{ij} + \varepsilon_{ij}$	5	60.06	6.54	0.04	5.46E-04	26.25
$SBA_{ij} = \beta_0 + b_j + \beta_1 DMR_{ij} + \beta_2 PROD.L_{ij} + \beta_3 PROD.M_{ij} + \varepsilon_{ij}$	6	60.69	7.17	0.03	3.98E-04	36.01
$SBA_{ij} = \beta_0 + b_j + \beta_1 DMR_{ij} + \beta_2 MPBMORT.L_{ij} + \beta_3 MPBMORT.M_{ij} + \beta_4 DMR * MPBMORT.L_{ij} + \beta_5 DMR * MPBMORT.M_{ij} + \varepsilon_{ij}$	8	61.64	8.12	0.02	2.47E-04	58.07
$SBA_{ij} = \beta_0 + b_j + \beta_1 DMR_{ij} + \beta_2 MPBMORT.L_{ij} + \beta_3 MPBMORT.M_{ij} + \beta_4 PROD.L_{ij} + \beta_5 PROD.M_{ij} + \varepsilon_{ij}$	8	64.83	11.31	3.50E-03	5.02E-05	285.32
$SBA_{ij} = \beta_0 + b_j + \beta_1 DMR_{ij} + \beta_2 PROD.L_{ij} + \beta_3 PROD.M_{ij} + \beta_4 DMR * PROD.L_{ij} + \beta_5 DMR * PROD.M_{ij} + \varepsilon_{ij}$	8	64.99	11.46	3.24E-03	4.65E-05	308.51
$SBA_{ij} = \beta_0 + b_j + \beta_1 DMR_{ij} + \beta_2 MPBMORT.L_{ij} + \beta_3 MPBMORT.M_{ij} + \beta_4 PROD.L_{ij} + \beta_5 PROD.M_{ij} + \beta_6 PROD.L * DMR_{ij} + \beta_7 PROD.M * DMR_{ij} + \beta_8 MPBMORT.L * DMR_{ij} + \beta_9 MPBMORT.M * DMR_{ij} + \varepsilon_{ij}$	12	72.54	19.02	7.42E-05	1.06E-06	13472.60

Table 1.7. BIC table for log of canopy volume model. $\text{Log}(CV)_{ij}$ represents the natural logarithm of the canopy volume of the i th plot within the j th stand, β_0 is the mean of the natural logarithm of canopy volume when all additional β 's = 0, b_j is the random error for the j th stand, $\mathbf{b}_j \sim N(0, \sigma_b^2)$ and \mathbf{b}_j and $\mathbf{b}_{j'}$ are independent, ε_{ij} is the random error from the natural logarithm of the canopy volume measurements i th plot replicate within the j th stand, $\varepsilon_{ij} \sim N(0, \sigma^2)$ and ε_{ij} and $\varepsilon_{i'j'}$ are independent.

Model	df	BIC	Δ BIC	L (gi x)	BIC weight	Evidence ratio
$\text{Log}(CV) = \beta_0 + b_j + \beta_1 \text{DMR}_{ij} + \varepsilon_{ij}$	4	59.11	0.00	1	7.95E-03	1
$\text{Log}(CV) = \beta_0 + b_j + \beta_1 \text{DMR}_{ij} + \beta_2 \text{PROD.L}_{ij} + \beta_3 \text{PROD.M}_{ij} + \varepsilon_{ij}$	6	59.53	0.41	0.814	6.47E-03	1.23
$\text{Log}(CV) = \beta_0 + b_j + \beta_1 \text{DMR}_{ij} + \beta_2 \text{SD}_{ij} + \beta_3 \text{PROD.L}_{ij} + \beta_4 \text{PROD.M}_{ij} + \varepsilon_{ij}$	7	60.67	1.56	0.459	3.65E-03	2.18
$\text{Log}(CV) = \beta_0 + b_j + \beta_1 \text{DMR}_{ij} + \beta_2 \text{SD}_{ij} + \varepsilon_{ij}$	5	62.30	3.19	0.203	1.61E-03	4.93
$\text{Log}(CV) = \beta_0 + b_j + \beta_1 \text{DMR}_{ij} + \beta_2 \text{SD}_{ij} + \beta_3 \text{DMR} * \text{SD}_{ij} + \varepsilon_{ij}$	6	62.45	3.34	0.188	1.50E-03	5.31
$\text{Log}(CV) = \beta_0 + b_j + \beta_1 \text{PROD.L}_{ij} + \beta_2 \text{PROD.M}_{ij} + \varepsilon_{ij}$	5	64.18	5.07	0.079	6.30E-04	12.62
$\text{Log}(CV) = \beta_0 + b_j + \beta_1 \text{DMR}_{ij} + \beta_2 \text{MPBMORT.L}_{ij} + \beta_3 \text{MPBMORT.M}_{ij} + \beta_4 \text{PROD.L}_{ij} + \beta_5 \text{PROD.L}_{ij} + \varepsilon_{ij}$	8	64.73	5.62	0.060	4.79E-04	16.59
$\text{Log}(CV) = \beta_0 + b_j + \beta_1 \text{SD}_{ij} + \varepsilon_{ij}$	4	64.83	5.71	0.058	4.57E-04	17.39
$\text{Log}(CV) = \beta_0 + b_j + \beta_1 \text{DMR}_{ij} + \beta_2 \text{MPBMORT.L}_{ij} + \beta_3 \text{MPBMORT.M}_{ij} + \beta_4 \text{PROD.L}_{ij} + \beta_5 \text{PROD.M}_{ij} + \beta_6 \text{SD}_{ij} + \varepsilon_{ij}$	9	65.24	6.12	0.047	3.72E-04	21.35
$\text{Log}(CV) = \beta_0 + b_j + \beta_1 \text{DMR}_{ij} + \beta_2 \text{PROD.L}_{ij} + \beta_3 \text{PROD.M}_{ij} + \beta_4 \text{DMR} * \text{PROD.L}_{ij} + \beta_5 \text{DMR} * \text{PROD.M}_{ij} + \varepsilon_{ij}$	8	65.59	6.48	0.039	3.12E-04	25.48

Table 1.7 (continued).

Model	df	BIC	ΔBIC	$\mathcal{L}(g_i x)$	BIC weight	Evidence ratio
$\text{Log}(CV) = \beta_0 + b_j + \beta_1 \text{DMR}_{ij} + \beta_2 \text{MPBMORT.L}_{ij} + \beta_3 \text{MPBMORT.M}_{ij} + \varepsilon_{ij}$	6	65.71	6.60	0.037	2.93E-04	27.10
$\text{Log}(CV) = \beta_0 + b_j + \beta_1 \text{MPBMORT.L}_{ij} + \beta_2 \text{MPBMORT.M}_{ij} + \varepsilon_{ij}$	5	66.47	7.36	0.025	2.00E-04	39.64
$\text{Log}(CV) = \beta_0 + b_j + \beta_1 \text{DMR}_{ij} + \beta_2 \text{SD}_{ij} + \beta_3 \text{PROD.L}_{ij} + \beta_4 \text{PROD.M}_{ij} + \beta_5 \text{SD} * \text{DMR}_{ij} + \beta_6 \text{PROD.L} * \text{DMR}_{ij} + \beta_7 \text{PROD.M} * \text{DMR}_{ij} + \varepsilon_{ij}$	10	66.59	7.48	0.024	1.89E-04	42.11
$\text{Log}(CV) = \beta_0 + b_j + \beta_1 \text{DMR}_{ij} + \beta_2 \text{MPBMORT.L}_{ij} + \beta_3 \text{MPBMORT.M}_{ij} + \beta_4 \text{DMR} * \text{MPBMORT.L}_{ij} + \beta_5 \text{DMR} * \text{MPBMORT.M}_{ij} + \varepsilon_{ij}$	8	68.40	9.28	9.65E-03	7.67E-05	103.65
$\text{Log}(CV) = \beta_0 + b_j + \beta_1 \text{DMR}_{ij} + \beta_2 \text{SD}_{ij} + \beta_3 \text{MPBMORT.L}_{ij} + \beta_4 \text{MPBMORT.M}_{ij} + \varepsilon_{ij}$	7	69.05	9.94	6.95E-03	5.52E-05	143.87
$\text{Log}(CV) = \beta_0 + b_j + \beta_1 \text{DMR}_{ij} + \beta_2 \text{SD}_{ij} + \beta_3 \text{MPBMORT.L}_{ij} + \beta_4 \text{MPBMORT.M}_{ij} + \beta_5 \text{SD} * \text{DMR}_{ij} + \beta_6 \text{MPBMORT.L} * \text{DMR}_{ij} + \beta_7 \text{MPBMORT.M} * \text{DMR}_{ij} + \varepsilon_{ij}$	10	70.11	11.00	4.09E-03	3.25E-05	244.79
$\text{Log}(CV) = \beta_0 + b_j + \beta_1 \text{DMR}_{ij} + \beta_2 \text{MPBMORT.L}_{ij} + \beta_3 \text{MPBMORT.M}_{ij} + \beta_4 \text{PROD.L}_{ij} + \beta_5 \text{PROD.M}_{ij} + \beta_6 \text{PROD.L} * \text{DMR}_{ij} + \beta_7 \text{PROD.M} * \text{DMR}_{ij} + \beta_8 \text{MPBMORT.L} * \text{DMR}_{ij} + \beta_9 \text{MPBMORT.M} * \text{DMR}_{ij} + \varepsilon_{ij}$	12	76.97	17.86	1.33E-04	1.05E-06	7539.68
$\text{Log}(CV) = \beta_0 + b_j + \beta_1 \text{DMR}_{ij} + \beta_2 \text{MPBMORT.L}_{ij} + \beta_3 \text{MPBMORT.M}_{ij} + \beta_4 \text{PROD.L}_{ij} + \beta_5 \text{PROD.M}_{ij} + \beta_6 \text{SD}_{ij} + \beta_7 \text{PROD.L} * \text{DMR}_{ij} + \beta_8 \text{PROD.M} * \text{DMR}_{ij} + \beta_9 \text{MPBMORT.L} * \text{DMR}_{ij} + \beta_{10} \text{MPBMORT.M} * \text{DMR}_{ij} + \beta_{11} \text{SD} * \text{DMR}_{ij} + \varepsilon_{ij}$	14	77.92	18.81	8.24E-05	6.55E-07	12138.95

Table 1.8. BIC table for the proportion of stand in the dominant cohort model. PD_{ij} represents the proportion of stand in the dominant cohort of the i th plot within the j th stand, β_0 is the mean of the proportion of stand in dominant cohort when all additional β 's = 0, b_j is the random error for the j th stand, $\mathbf{b}_j \sim N(0, \sigma_b^2)$ and \mathbf{b}_j and $\mathbf{b}_{j'}$ are independent, ε_{ij} is the random error from proportion of stand in dominant cohort measurements i th plot replicate within the j th stand, $\varepsilon_{ij} \sim N(0, \sigma^2)$ and ε_{ij} and $\varepsilon_{i'j'}$ are independent.

Model	df	BIC	Δ BIC	L (gi x)	BIC weight	Evidence ratio
$PD_{ij} = \beta_0 + b_j + \beta_1 DMR_{ij} + \varepsilon_{ij}$	4	324.06	0	1	6.05E-03	1
$PD_{ij} = \beta_0 + b_j + \beta_1 DMR_{ij} + \beta_2 SD_{ij} + \varepsilon_{ij}$	5	326.25	2.19	0.335	2.03E-03	2.98
$PD_{ij} = \beta_0 + b_j + \beta_1 DMR_{ij} + \beta_2 SD_{ij} + \beta_3 DMR * SD_{ij} + \varepsilon_{ij}$	6	327.26	3.19	0.203	1.23E-03	4.93
$PD_{i:} = \beta_0 + b_j + \beta_1 DMR_{i:} + \beta_2 PROD.L_{i:} + \beta_3 PROD.M_{i:} + \varepsilon_{i:}$	6	328.12	4.06	0.132	7.97E-04	7.60
$PD_{ij} = \beta_0 + b_j + \beta_1 SD_{ij} + \varepsilon_{ij}$	4	328.44	4.38	0.112	6.78E-04	8.93
$PD_{ij} = \beta_0 + b_j + \beta_1 DMR_{ij} + \beta_2 MPBMORT.L_{ij} + \beta_3 MPBMORT.M_{ij} + \varepsilon_{ij}$	6	328.82	4.75	0.093	5.62E-04	10.77
$PD_{ij} = \beta_0 + b_j + \beta_1 DMR_{ij} + \beta_2 SD_{ij} + \beta_3 PROD.L_{ij} + \beta_4 PROD.M_{ij} + \varepsilon_{ij}$	7	330.95	6.88	0.032	1.94E-04	31.24
$PD_{ij} = \beta_0 + b_j + \beta_1 DMR_{ij} + \beta_2 SD_{ij} + \beta_3 MPBMORT.L_{ij} + \beta_4 MPBMORT.M_{ij} + \varepsilon_{ij}$	7	331.64	7.57	0.023	1.37E-04	44.04
$PD_{ij} = \beta_0 + b_j + \beta_1 PROD.L_{ij} + \beta_2 PROD.M_{ij} + \varepsilon_{ij}$	5	332.37	8.30	0.016	9.54E-05	63.48
$PD_{ij} = \beta_0 + b_j + \beta_1 DMR_{ij} + \beta_2 PROD.L_{ij} + \beta_3 PROD.M_{ij} + \beta_4 DMR * PROD.L_{ij} + \beta_5 DMR * PROD.M_{ij} + \varepsilon_{ij}$	8	332.40	8.34	0.015	9.38E-05	64.57
$PD_{ij} = \beta_0 + b_j + \beta_1 MPBMORT.L_{ij} + \beta_2 MPBMORT.M_{ij} + \varepsilon_{ij}$	5	334.26	10.20	6.10E-03	3.69E-05	164.01

Table 1.8 (continued).

Model	df	BIC	ΔBIC	L (gi x)	BIC weight	Evidence ratio
$PD_{ij} = \beta_0 + b_j + \beta_1DMR_{ij} + \beta_2MPBMORT.L_{ij} + \beta_3MPBMORT.M_{ij} + \beta_4PROD.L_{ij} + \beta_5PROD.L_{ij} + \epsilon_{ij}$	8	334.52	10.46	5.36E-03	3.24E-05	186.71
$PD_{ij} = \beta_0 + b_j + \beta_1DMR_{ij} + \beta_2SD_{ij} + \beta_3PROD.L_{ij} + \beta_4PROD.M_{ij} + \beta_5SD*DMR_{ij} + \beta_6PROD.L*DMR_{ij} + \beta_7PROD.M*DMR_{ij} + \epsilon_{ij}$	10	334.84	10.78	4.56E-03	2.76E-05	219.09
$PD_{ij} = \beta_0 + b_j + \beta_1DMR_{ij} + \beta_2MPBMORT.L_{ij} + \beta_3MPBMORT.M_{ij} + \beta_4DMR*MPBMORT.L_{ij} + \beta_5DMR*MPBMORT.M_{ij} + \epsilon_{ij}$	8	335.08	11.01	4.06E-03	2.46E-05	246.27
$PD_{ij} = \beta_0 + b_j + \beta_1DMR_{ij} + \beta_2MPBMORT.L_{ij} + \beta_3MPBMORT.M_{ij} + \beta_4PROD.L_{ij} + \beta_5PROD.M_{ij} + \beta_6SD_{ij} + \epsilon_{ij}$	9	337.59	13.53	1.16E-03	7.00E-06	865.23
$PD_{ij} = \beta_0 + b_j + \beta_1DMR_{ij} + \beta_2SD_{ij} + \beta_3MPBMORT.L_{ij} + \beta_4MPBMORT.M_{ij} + \beta_5SD*DMR_{ij} + \beta_6MPBMORT.L*DMR_{ij} + \beta_7MPBMORT.M*DMR_{ij} + \epsilon_{ij}$	10	339.39	15.32	4.71E-04	2.85E-06	2124.74
$PD_{ij} = \beta_0 + b_j + \beta_1DMR_{ij} + \beta_2MPBMORT.L_{ij} + \beta_3MPBMORT.M_{ij} + \beta_4PROD.L_{ij} + \beta_5PROD.M_{ij} + \beta_6PROD.L*DMR_{ij} + \beta_7PROD.M*DMR_{ij} + \beta_8MPBMORT.L*DMR_{ij} + \beta_9MPBMORT.M*DMR_{ij} + \epsilon_{ij}$	12	344.47	20.41	3.70E-05	2.24E-07	27008.95
$PD_{ij} = \beta_0 + b_j + \beta_1DMR_{ij} + \beta_2MPBMORT.L_{ij} + \beta_3MPBMORT.M_{ij} + \beta_4PROD.L_{ij} + \beta_5PROD.M_{ij} + \beta_6SD_{ij} + \beta_7PROD.L*DMR_{ij} + \beta_8PROD.M*DMR_{ij} + \beta_9MPBMORT.L*DMR_{ij} + \beta_{10}MPBMORT.M*DMR_{ij} + \beta_{11}SD*DMR_{ij} + \epsilon_{ij}$	14	347.88	23.81	6.74E-06	4.08E-08	1.48E+05

Table 1.9. BIC table for the proportion of stand in the suppressed cohort model. PS_{ij} represents the proportion of stand in the suppressed cohort of the i th plot within the j th stand, β_0 is the mean of the proportion of stand in suppressed cohort when all additional β 's = 0, b_j is the random error for the j th stand, $\mathbf{b}_j \sim N(0, \sigma_b^2)$ and \mathbf{b}_j and $\mathbf{b}_{j'}$ are independent, ε_{ij} is the random error from proportion of stand in suppressed cohort measurements i th plot replicate within the j th stand, $\varepsilon_{ij} \sim N(0, \sigma^2)$ and ε_{ij} and $\varepsilon_{i'j'}$ are independent.

Model	df	BIC	Δ BIC	L (gi x)	BIC weight	Evidence ratio
$PS_{ij} = \beta_0 + b_j + \beta_1 DMR_{ij} + \varepsilon_{ij}$	4	329.81	0	1	4.91E-03	1
$PS_{ij} = \beta_0 + b_j + \beta_1 DMR_{ij} + \beta_2 SD_{ij} + \varepsilon_{ij}$	5	333.45	3.64	0.162	7.96E-04	6.17
$PS_{ij} = \beta_0 + b_j + \beta_1 DMR_{ij} + \beta_2 PROD.L_{ij} + \beta_3 PROD.M_{ij} + \varepsilon_{ij}$	6	333.79	3.97	0.137	6.73E-04	7.29
$PS_{ij} = \beta_0 + b_j + \beta_1 DMR_{ij} + \beta_2 MPBMORT.L_{ij} + \beta_3 MPBMORT.M_{ij} + \varepsilon_{ij}$	6	335.95	6.14	0.046	2.28E-04	21.53
$PS_{ij} = \beta_0 + b_j + \beta_1 DMR_{ij} + \beta_2 SD_{ij} + \beta_3 DMR*SD_{ij} + \varepsilon_{ij}$	6	336.62	6.80	0.033	1.64E-04	30.01
$PS_{ij} = \beta_0 + b_j + \beta_1 DMR_{ij} + \beta_2 SD_{ij} + \beta_3 PROD.L_{ij} + \beta_4 PROD.M_{ij} + \varepsilon_{ij}$	7	337.38	7.57	0.023	1.11E-04	44.04
$PS_{ij} = \beta_0 + b_j + \beta_1 DMR_{ij} + \beta_2 PROD.L_{ij} + \beta_3 PROD.M_{ij} + \beta_4 DMR*PROD.L_{ij} + \beta_5 DMR*PROD.M_{ij} + \varepsilon_{ij}$	8	338.33	8.52	0.014	6.93E-05	70.81
$PS_{ij} = \beta_0 + b_j + \beta_1 SD_{ij} + \varepsilon_{ij}$	4	338.84	9.03	0.011	5.38E-05	91.28
$PS_{ij} = \beta_0 + b_j + \beta_1 DMR_{ij} + \beta_2 SD_{ij} + \beta_3 MPBMORT.L_{ij} + \beta_4 MPBMORT.M_{ij} + \varepsilon_{ij}$	7	339.61	9.79	7.47E-03	3.66E-05	133.92
$PS_{ij} = \beta_0 + b_j + \beta_1 PROD.L_{ij} + \beta_2 PROD.M_{ij} + \varepsilon_{ij}$	5	340.52	10.71	4.73E-03	2.32E-05	211.63

Table 1.9 (continued).

Model	df	BIC	ΔBIC	L (gi x)	BIC weight	Evidence ratio
$PS_{ij} = \beta_0 + b_j + \beta_1DMR_{ij} + \beta_2MPBMORT.L_{ij} + \beta_3MPBMORT.M_{ij} + \beta_4PROD.L_{ij} + \beta_5PROD.L_{ij} + \epsilon_{ij}$	8	340.96	11.14	3.80E-03	1.87E-05	263.05
$PS_{ij} = \beta_0 + b_j + \beta_1MPBMORT.L_{ij} + \beta_2MPBMORT.M_{ij} + \epsilon_{ij}$	5	341.50	11.69	2.89E-03	1.42E-05	345.77
$PS_{ij} = \beta_0 + b_j + \beta_1DMR_{ij} + \beta_2MPBMORT.L_{ij} + \beta_3MPBMORT.M_{ij} + \beta_4DMR*MPBMORT.L_{ij} + \beta_5DMR*MPBMORT.M_{ij} + \epsilon_{ij}$	8	343.12	13.30	1.29E-03	6.34E-06	774.53
$PS_{ij} = \beta_0 + b_j + \beta_1DMR_{ij} + \beta_2MPBMORT.L_{ij} + \beta_3MPBMORT.M_{ij} + \beta_4PROD.L_{ij} + \beta_5PROD.M_{ij} + \beta_6SD_{ij} + \epsilon_{ij}$	9	344.50	14.68	6.48E-04	3.18E-06	1543.09
$PS_{ij} = \beta_0 + b_j + \beta_1DMR_{ij} + \beta_2SD_{ij} + \beta_3PROD.L_{ij} + \beta_4PROD.M_{ij} + \beta_5SD*DMR_{ij} + \beta_6PROD.L*DMR_{ij} + \beta_7PROD.M*DMR_{ij} + \epsilon_{ij}$	10	344.81	14.99	5.55E-04	2.72E-06	1801.68
$PS_{ij} = \beta_0 + b_j + \beta_1DMR_{ij} + \beta_2SD_{ij} + \beta_3MPBMORT.L_{ij} + \beta_4MPBMORT.M_{ij} + \beta_5SD*DMR_{ij} + \beta_6MPBMORT.L*DMR_{ij} + \beta_7MPBMORT.M*DMR_{ij} + \epsilon_{ij}$	10	349.89	20.08	4.36E-05	2.14E-07	22912.39
$PS_{ij} = \beta_0 + b_j + \beta_1DMR_{ij} + \beta_2MPBMORT.L_{ij} + \beta_3MPBMORT.M_{ij} + \beta_4PROD.L_{ij} + \beta_5PROD.M_{ij} + \beta_6PROD.L*DMR_{ij} + \beta_7PROD.M*DMR_{ij} + \beta_8MPBMORT.L*DMR_{ij} + \beta_9MPBMORT.M*DMR_{ij} + \epsilon_{ij}$	12	352.38	22.56	1.26E-05	6.19E-08	79343.83
$PS_{ij} = \beta_0 + b_j + \beta_1DMR_{ij} + \beta_2MPBMORT.L_{ij} + \beta_3MPBMORT.M_{ij} + \beta_4PROD.L_{ij} + \beta_5PROD.M_{ij} + \beta_6SD_{ij} + \beta_7PROD.L*DMR_{ij} + \beta_8PROD.M*DMR_{ij} + \beta_9MPBMORT.L*DMR_{ij} + \beta_{10}MPBMORT.M*DMR_{ij} + \beta_{11}SD*DMR_{ij} + \epsilon_{ij}$	14	358.95	29.13	4.72E-07	2.31E-09	2.12E+06

Table 1.10. BIC table for the proportion of stand in the intermediate cohort model. PI_{ij} represents the proportion of stand in the intermediate cohort of the i th plot within the j th stand, β_0 is the mean of the proportion of stand in intermediate cohort when all additional β 's = 0, b_j is the random error for the j th stand, $\mathbf{b}_j \sim N(0, \sigma_b^2)$ and \mathbf{b}_j and $\mathbf{b}_{j'}$ are independent, $\boldsymbol{\varepsilon}_{ij}$ is the random error from proportion of stand in intermediate cohort measurements i th plot replicate within the j th stand, $\boldsymbol{\varepsilon}_{ij} \sim N(0, \sigma^2)$ and $\boldsymbol{\varepsilon}_{ij}$ and $\boldsymbol{\varepsilon}_{i'j'}$ are independent.

Model	df	BIC	Δ BIC	L (gi x)	BIC weight	Evidence ratio
$PI_{ij} = \beta_0 + b_j + \beta_1 SD_{ij} + \varepsilon_{ij}$	4	283.75	0	1	4.74E-03	1
$PI_{ij} = \beta_0 + b_j + \beta_1 DMR_{ij} + \varepsilon_{ij}$	4	285.93	2.18	0.34	1.59E-03	2.98
$PI_{ij} = \beta_0 + b_j + \beta_1 DMR_{ij} + \beta_2 SD_{ij} + \varepsilon_{ij}$	5	286.86	3.12	0.21	9.98E-04	4.75
$PI_{ij} = \beta_0 + b_j + \beta_1 MPBMORT.L_{ij} + \beta_2 MPBMORT.M_{ij} + \varepsilon_{ij}$	5	287.50	3.75	0.15	7.28E-04	6.51
$PI_{ij} = \beta_0 + b_j + \beta_1 PROD.L_{ij} + \beta_2 PROD.M_{ij} + \varepsilon_{ij}$	5	288.92	5.17	0.08	3.58E-04	13.25
$PI_{ij} = \beta_0 + b_j + \beta_1 DMR_{ij} + \beta_2 SD_{ij} + \beta_3 DMR * SD_{ij} + \varepsilon_{ij}$	6	289.38	5.64	0.06	2.83E-04	16.74
$PI_{ij} = \beta_0 + b_j + \beta_1 DMR_{ij} + \beta_2 MPBMORT.L_{ij} + \beta_3 MPBMORT.M_{ij} + \varepsilon_{ij}$	6	291.07	7.33	0.03	1.22E-04	38.96
$PI_{ij} = \beta_0 + b_j + \beta_1 DMR_{ij} + \beta_2 PROD.L_{ij} + \beta_3 PROD.M_{ij} + \varepsilon_{ij}$	6	292.40	8.66	0.01	6.26E-05	75.78
$PI_{ij} = \beta_0 + b_j + \beta_1 DMR_{ij} + \beta_2 SD_{ij} + \beta_3 MPBMORT.L_{ij} + \beta_4 MPBMORT.M_{ij} + \varepsilon_{ij}$	7	292.71	8.96	0.01	5.38E-05	88.06
$PI_{ij} = \beta_0 + b_j + \beta_1 DMR_{ij} + \beta_2 SD_{ij} + \beta_3 PROD.L_{ij} + \beta_4 PROD.M_{ij} + \varepsilon_{ij}$	7	292.91	9.16	0.01	4.86E-05	97.60
$PI_{ij} = \beta_0 + b_j + \beta_1 DMR_{ij} + \beta_2 MPBMORT.L_{ij} + \beta_3 MPBMORT.M_{ij} + \beta_4 DMR * MPBMORT.L_{ij} + \beta_5 DMR * MPBMORT.M_{ij} + \varepsilon_{ij}$	8	297.86	14.11	8.63E-04	4.09E-06	1159.05
$PI_{ij} = \beta_0 + b_j + \beta_1 DMR_{ij} + \beta_2 MPBMORT.L_{ij} + \beta_3 MPBMORT.M_{ij} + \beta_4 PROD.L_{ij} + \beta_5 PROD.M_{ij} + \varepsilon_{ij}$	8	298.05	14.30	7.84E-04	3.72E-06	1275.392

Table 1.10 (continued).

Model	df	BIC	ΔBIC	L (gi x)	BIC weight	Evidence ratio
$PI_{ij} = \beta_0 + b_j + \beta_1 DMR_{ij} + \beta_2 MPBMORT.L_{ij} + \beta_3 MPBMORT.M_{ij} + \beta_4 PROD.L_{ij} + \beta_5 PROD.M_{ij} + \beta_6 SD_{ij} + \epsilon_{ij}$	9	299.14	15.39	4.55E-04	2.16E-06	2198.768
$PI_{ij} = \beta_0 + b_j + \beta_1 DMR_{ij} + \beta_2 PROD.L_{ij} + \beta_3 PROD.M_{ij} + \beta_4 DMR*PROD.L_{ij} + \beta_5 DMR*PROD.M_{ij} + \epsilon_{ij}$	8	299.48	15.73	3.84E-04	1.82E-06	2606.677
$PI_{ij} = \beta_0 + b_j + \beta_1 DMR_{ij} + \beta_2 SD_{ij} + \beta_3 PROD.L_{ij} + \beta_4 PROD.M_{ij} + \beta_5 SD*DMR_{ij} + \beta_6 PROD.L*DMR_{ij} + \beta_7 PROD.M*DMR_{ij} + \epsilon_{ij}$	10	302.22	18.47	9.76E-05	4.63E-07	10249.04
$PI_{ij} = \beta_0 + b_j + \beta_1 DMR_{ij} + \beta_2 SD_{ij} + \beta_3 MPBMORT.L_{ij} + \beta_4 MPBMORT.M_{ij} + \beta_5 SD*DMR_{ij} + \beta_6 MPBMORT.L*DMR_{ij} + \beta_7 MPBMORT.M*DMR_{ij} + \epsilon_{ij}$	10	302.79	19.04	7.32E-05	3.47E-07	13659.33
$PI_{ij} = \beta_0 + b_j + \beta_1 DMR_{ij} + \beta_2 MPBMORT.L_{ij} + \beta_3 MPBMORT.M_{ij} + \beta_4 PROD.L_{ij} + \beta_5 PROD.M_{ij} + \beta_6 PROD.L*DMR_{ij} + \beta_7 PROD.M*DMR_{ij} + \beta_8 MPBMORT.L*DMR_{ij} + \beta_9 MPBMORT.M*DMR_{ij} + \epsilon_{ij}$	12	311.63	27.88	8.84E-07	4.19E-09	1131673
$PI_{ij} = \beta_0 + b_j + \beta_1 DMR_{ij} + \beta_2 MPBMORT.L_{ij} + \beta_3 MPBMORT.M_{ij} + \beta_4 PROD.L_{ij} + \beta_5 PROD.M_{ij} + \beta_6 SD_{ij} + \beta_7 PROD.L*DMR_{ij} + \beta_8 PROD.M*DMR_{ij} + \beta_9 MPBMORT.L*DMR_{ij} + \beta_{10} MPBMORT.M*DMR_{ij} + \beta_{11} SD*DMR_{ij} + \epsilon_{ij}$	14	315.81	32.06	1.09E-07	5.18E-10	9150723

Table 1.11. BIC table for the cohort height of intermediates model. CHI_{ij} represents the cohort height of intermediates of the i th plot within the j th stand, β_0 is the mean of the cohort height of intermediates when all additional β 's = 0, b_j is the random error for the j th stand, $\mathbf{b}_j \sim N(0, \sigma_b^2)$ and \mathbf{b}_j and $\mathbf{b}_{j'}$ are independent, ϵ_{ij} is the random error from the cohort height of intermediates measurements i th plot replicate within the j th stand, $\epsilon_{ij} \sim N(0, \sigma^2)$ and ϵ_{ij} and $\epsilon_{i'j'}$ are independent.

Model	df	BIC	Δ BIC	L (gi x)	BIC weight	Evidence ratio
$CHI_{ij} = \beta_0 + b_j + \beta_1 DMR_{ij} + \epsilon_{ij}$	4	179.23	0	1	5.20E-03	1
$CHI_{ij} = \beta_0 + b_j + \beta_1 SD_{ij} + \epsilon_{ij}$	4	182.22	2.99	0.22	1.17E-03	4.45
$CHI_{ij} = \beta_0 + b_j + \beta_1 DMR_{ij} + \beta_2 SD_{ij} + \epsilon_{ij}$	5	182.29	3.06	0.22	1.13E-03	4.61
$CHI_{ij} = \beta_0 + b_j + \beta_1 DMR_{ij} + \beta_2 MPBMORT.L_{ij} + \beta_3 MPBMORT.M_{ij} + \epsilon_{ij}$	6	184.46	5.22	0.07	3.82E-04	13.62
$CHI_{ij} = \beta_0 + b_j + \beta_1 DMR_{ij} + \beta_2 PROD.L_{ij} + \beta_3 PROD.M_{ij} + \epsilon_{ij}$	6	184.65	5.41	0.07	3.47E-04	14.98
$CHI_{ij} = \beta_0 + b_j + \beta_1 DMR_{ij} + \beta_2 SD_{ij} + \beta_3 DMR*SD_{ij} + \epsilon_{ij}$	6	185.03	5.80	0.06	2.86E-04	18.16
$CHI_{ij} = \beta_0 + b_j + \beta_1 PROD.L_{ij} + \beta_2 PROD.M_{ij} + \epsilon_{ij}$	5	185.07	5.83	0.05	2.81E-04	18.49
$CHI_{ij} = \beta_0 + b_j + \beta_1 MPBMORT.L_{ij} + \beta_2 MPBMORT.M_{ij} + \epsilon_{ij}$	5	185.73	6.50	0.04	2.02E-04	25.76
$CHI_{ij} = \beta_0 + b_j + \beta_1 DMR_{ij} + \beta_2 SD_{ij} + \beta_3 MPBMORT.L_{ij} + \beta_4 MPBMORT.M_{ij} + \epsilon_{ij}$	7	187.74	8.50	0.01	7.41E-05	70.24
$CHI_{ij} = \beta_0 + b_j + \beta_1 DMR_{ij} + \beta_2 SD_{ij} + \beta_3 PROD.L_{ij} + \beta_4 PROD.M_{ij} + \epsilon_{ij}$	7	188.00	8.77	0.01	6.49E-05	80.14
$CHI_{ij} = \beta_0 + b_j + \beta_1 DMR_{ij} + \beta_2 MPBMORT.L_{ij} + \beta_3 MPBMORT.M_{ij} + \beta_4 DMR*MPBMORT.L_{ij} + \beta_5 DMR*MPBMORT.M_{ij} + \epsilon_{ij}$	8	190.38	11.15	3.80E-03	1.97E-05	263.49
$CHI_{ij} = \beta_0 + b_j + \beta_1 DMR_{ij} + \beta_2 MPBMORT.L_{ij} + \beta_3 MPBMORT.M_{ij} + \beta_4 PROD.L_{ij} + \beta_5 PROD.L_{ij} + \epsilon_{ij}$	8	190.79	11.55	3.10E-03	1.61E-05	322.51
$CHI_{ij} = \beta_0 + b_j + \beta_1 DMR_{ij} + \beta_2 PROD.L_{ij} + \beta_3 PROD.M_{ij} + \beta_4 DMR*PROD.L_{ij} + \beta_5 DMR*PROD.M_{ij} + \epsilon_{ij}$	8	191.69	12.46	1.97E-03	1.03E-05	507.53

Table 1.11 (continued).

Model	df	BIC	ΔBIC	L (gi x)	BIC weight	Evidence ratio
$CHI_{ij} = \beta_0 + b_j + \beta_1 DMR_{ij} + \beta_2 MPBMORT.L_{ij} + \beta_3 MPBMORT.M_{ij} + \beta_4 PROD.L_{ij} + \beta_5 PROD.M_{ij} + \beta_6 SD_{ij} + \varepsilon_{ij}$	9	194.27	15.04	5.43E-04	2.83E-06	1840.98
$CHI_{ij} = \beta_0 + b_j + \beta_1 DMR_{ij} + \beta_2 SD_{ij} + \beta_3 MPBMORT.L_{ij} + \beta_4 MPBMORT.M_{ij} + \beta_5 SD * DMR_{ij} + \beta_6 MPBMORT.L * DMR_{ij} + \beta_7 MPBMORT.M * DMR_{ij} + \varepsilon_{ij}$	10	196.11	16.87	2.17E-04	1.13E-06	4613.57
$CHI_{ij} = \beta_0 + b_j + \beta_1 DMR_{ij} + \beta_2 SD_{ij} + \beta_3 PROD.L_{ij} + \beta_4 PROD.M_{ij} + \beta_5 SD * DMR_{ij} + \beta_6 PROD.L * DMR_{ij} + \beta_7 PROD.M * DMR_{ij} + \varepsilon_{ij}$	10	197.53	18.29	1.06E-04	5.54E-07	9390.89
$CHI_{ij} = \beta_0 + b_j + \beta_1 DMR_{ij} + \beta_2 MPBMORT.L_{ij} + \beta_3 MPBMORT.M_{ij} + \beta_4 PROD.L_{ij} + \beta_5 PROD.M_{ij} + \beta_6 PROD.L * DMR_{ij} + \beta_7 PROD.M * DMR_{ij} + \beta_8 MPBMORT.L * DMR_{ij} + \beta_9 MPBMORT.M * DMR_{ij} + \varepsilon_{ij}$	12	203.78	24.55	4.67E-06	2.43E-08	214280.4
$CHI_{ij} = \beta_0 + b_j + \beta_1 DMR_{ij} + \beta_2 MPBMORT.L_{ij} + \beta_3 MPBMORT.M_{ij} + \beta_4 PROD.L_{ij} + \beta_5 PROD.M_{ij} + \beta_6 SD_{ij} + \beta_7 PROD.L * DMR_{ij} + \beta_8 PROD.M * DMR_{ij} + \beta_9 MPBMORT.L * DMR_{ij} + \beta_{10} MPBMORT.M * DMR_{ij} + \beta_{11} SD * DMR_{ij} + \varepsilon_{ij}$	14	209.45	30.22	2.75E-07	1.43E-09	3641783

Table 1.12. BIC table for the cohort height of suppressed model. CHS_{ij} represents the cohort height of suppressed of the i th plot within the j th stand, β_0 is the mean of the cohort height of suppressed when all additional β 's = 0, b_j is the random error for the j th stand, $\mathbf{b}_j \sim N(0, \sigma_b^2)$ and \mathbf{b}_j and $\mathbf{b}_{j'}$ are independent, ε_{ij} is the random error from the cohort height of suppressed measurements i th plot replicate within the j th stand, $\varepsilon_{ij} \sim N(0, \sigma^2)$ and ε_{ij} and $\varepsilon_{i'j'}$ are independent.

Model	df	BIC	Δ BIC	L (gi x)	BIC weight	Evidence ratio
$CHS_{ij} = \beta_0 + b_j + \beta_1 DMR_{ij} + \varepsilon_{ij}$	4	113.39	0	1	5.06E-03	1
$CHS_{ij} = \beta_0 + b_j + \beta_1 DMR_{ij} + \beta_2 SD_{ij} + \varepsilon_{ij}$	5	116.45	3.05	0.217	1.10E-03	4.61
$CHS_{ij} = \beta_0 + b_j + \beta_1 DMR_{ij} + \beta_2 PROD.L_{ij} + \beta_3 PROD.M_{ij} + \varepsilon_{ij}$	6	117.67	4.28	0.118	5.97E-04	8.48
$CHS_{ij} = \beta_0 + b_j + \beta_1 DMR_{ij} + \beta_2 MPBMORT.L_{ij} + \beta_3 MPBMORT.M_{ij} + \varepsilon_{ij}$	6	119.32	5.93	0.052	2.62E-04	19.36
$CHS_{ij} = \beta_0 + b_j + \beta_1 DMR_{ij} + \beta_2 SD_{ij} + \beta_3 DMR * SD_{ij} + \varepsilon_{ij}$	6	119.72	6.32	0.042	2.14E-04	23.61
$CHS_{ij} = \beta_0 + b_j + \beta_1 DMR_{ij} + \beta_2 SD_{ij} + \beta_3 PROD.L_{ij} + \beta_4 PROD.M_{ij} + \varepsilon_{ij}$	7	120.12	6.73	0.035	1.75E-04	28.92
$CHS_{ij} = \beta_0 + b_j + \beta_1 SD_{ij} + \varepsilon_{ij}$	4	120.29	6.90	0.032	1.61E-04	31.44
$CHS_{ij} = \beta_0 + b_j + \beta_1 MPBMORT.L_{ij} + \beta_2 MPBMORT.M_{ij} + \varepsilon_{ij}$	5	120.72	7.33	0.026	1.30E-04	39.05
$CHS_{ij} = \beta_0 + b_j + \beta_1 PROD.L_{ij} + \beta_2 PROD.M_{ij} + \varepsilon_{ij}$	5	122.12	8.73	0.013	6.45E-05	78.49
$CHS_{ij} = \beta_0 + b_j + \beta_1 DMR_{ij} + \beta_2 SD_{ij} + \beta_3 MPBMORT.L_{ij} + \beta_4 MPBMORT.M_{ij} + \varepsilon_{ij}$	7	122.64	9.24	9.84E-03	4.98E-05	101.62

Table 1.12 (continued).

Model	df	BIC	ΔBIC	L (gi x)	BIC weight	Evidence ratio
$CHS_{ij} = \beta_0 + b_j + \beta_1 DMR_{ij} + \beta_2 MPBMORT.L_{ij} + \beta_3 MPBMORT.M_{ij} + \beta_4 PROD.L_{ij} + \beta_5 PROD.L_{ij} + \epsilon_{ij}$	8	124.39	10.99	4.10E-03	2.08E-05	243.98
$CHS_{ij} = \beta_0 + b_j + \beta_1 DMR_{ij} + \beta_2 MPBMORT.L_{ij} + \beta_3 MPBMORT.M_{ij} + \beta_4 DMR*MPBMORT.L_{ij} + \beta_5 DMR*MPBMORT.M_{ij} + \epsilon_{ij}$	8	125.58	12.18	2.26E-03	1.14E-05	442.30
$CHS_{ij} = \beta_0 + b_j + \beta_1 DMR_{ij} + \beta_2 MPBMORT.L_{ij} + \beta_3 MPBMORT.M_{ij} + \beta_4 PROD.L_{ij} + \beta_5 PROD.M_{ij} + \beta_6 SD_{ij} + \epsilon_{ij}$	9	127.08	13.68	1.07E-03	5.41E-06	936.14
$CHS_{ij} = \beta_0 + b_j + \beta_1 DMR_{ij} + \beta_2 SD_{ij} + \beta_3 PROD.L_{ij} + \beta_4 PROD.M_{ij} + \beta_5 SD*DMR_{ij} + \beta_6 PROD.L*DMR_{ij} + \beta_7 PROD.M*DMR_{ij} + \epsilon_{ij}$	10	129.93	16.53	2.57E-04	1.30E-06	3891.92
$CHS_{ij} = \beta_0 + b_j + \beta_1 DMR_{ij} + \beta_2 SD_{ij} + \beta_3 MPBMORT.L_{ij} + \beta_4 MPBMORT.M_{ij} + \beta_5 SD*DMR_{ij} + \beta_6 MPBMORT.L*DMR_{ij} + \beta_7 MPBMORT.M*DMR_{ij} + \epsilon_{ij}$	10	132.50	19.11	7.09E-05	3.59E-07	14097.14
$CHS_{ij} = \beta_0 + b_j + \beta_1 DMR_{ij} + \beta_2 MPBMORT.L_{ij} + \beta_3 MPBMORT.M_{ij} + \beta_4 PROD.L_{ij} + \beta_5 PROD.M_{ij} + \beta_6 PROD.L*DMR_{ij} + \beta_7 PROD.M*DMR_{ij} + \beta_8 MPBMORT.L*DMR_{ij} + \beta_9 MPBMORT.M*DMR_{ij} + \epsilon_{ij}$	12	138.07	24.67	4.39E-06	2.22E-08	2.28E+05
$Y_{ij} = \beta_0 + b_j + \beta_1 DMR_{ij} + \beta_2 MPBMORT.L_{ij} + \beta_3 MPBMORT.M_{ij} + \beta_4 PROD.L_{ij} + \beta_5 PROD.M_{ij} + \beta_6 SD_{ij} + \beta_7 PROD.L*DMR_{ij} + \beta_8 PROD.M*DMR_{ij} + \beta_9 MPBMORT.L*DMR_{ij} + \beta_{10} MPBMORT.M*DMR_{ij} + \beta_{11} SD*DMR_{ij} + \epsilon_{ij}$	14	144.39	31.00	1.86E-07	9.40E-10	5.38E+06

Table 1.13. BIC table for the cohort height of dominants model. CHD_{ij} represents the cohort height of dominants of the i th plot within the j th stand, β_0 is the mean of the cohort height of dominants when all additional β 's = 0, b_j is the random error for the j th stand, $\mathbf{b}_j \sim N(0, \sigma_b^2)$ and \mathbf{b}_j and $\mathbf{b}_{j'}$ are independent, ε_{ij} is the random error from the cohort height of dominants measurements i th plot replicate within the j th stand, $\varepsilon_{ij} \sim N(0, \sigma^2)$ and ε_{ij} and $\varepsilon_{i'j'}$ are independent.

Model	df	BIC	Δ BIC	L (gi x)	BIC weight	Evidence ratio
$CHD_{ij} = \beta_0 + b_j + \beta_1 SD_{ij} + \varepsilon_{ij}$	4	173.99	0	1	4.67E-03	1
$CHD_{ij} = \beta_0 + b_j + \beta_1 DMR_{ij} + \beta_2 SD_{ij} + \varepsilon_{ij}$	5	175.34	1.36	0.507	2.37E-03	1.97
$CHD_{ij} = \beta_0 + b_j + \beta_1 DMR_{ij} + \beta_2 SD_{ij} + \beta_3 DMR * SD_{ij} + \varepsilon_{ij}$	6	177.69	3.71	0.157	7.32E-04	6.38
$CHD_{ij} = \beta_0 + b_j + \beta_1 DMR_{ij} + \beta_2 SD_{ij} + \beta_3 PROD.L_{ij} + \beta_4 PROD.M_{ij} + \varepsilon_{ij}$	7	177.86	3.88	0.144	6.72E-04	6.95
$CHD_{ij} = \beta_0 + b_j + \beta_1 DMR_{ij} + \varepsilon_{ij}$	4	181.24	7.25	0.027	1.24E-04	37.57
$CHD_{ij} = \beta_0 + b_j + \beta_1 DMR_{ij} + \beta_2 MPBMORT.L_{ij} + \beta_3 MPBMORT.M_{ij} + \beta_4 PROD.L_{ij} + \beta_5 PROD.M_{ij} + \beta_6 SD_{ij} + \varepsilon_{ij}$	9	181.35	7.36	0.025	1.18E-04	39.71
$CHD_{ij} = \beta_0 + b_j + \beta_1 DMR_{ij} + \beta_2 SD_{ij} + \beta_3 MPBMORT.L_{ij} + \beta_4 MPBMORT.M_{ij} + \varepsilon_{ij}$	7	181.60	7.61	0.022	1.04E-04	44.96
$CHD_{ij} = \beta_0 + b_j + \beta_1 DMR_{ij} + \beta_2 SD_{ij} + \beta_3 PROD.L_{ij} + \beta_4 PROD.M_{ij} + \beta_5 SD * DMR_{ij} + \beta_6 PROD.L * DMR_{ij} + \beta_7 PROD.M * DMR_{ij} + \varepsilon_{ij}$	10	185.61	11.62	2.99E-03	1.40E-05	334.39
$CHD_{ij} = \beta_0 + b_j + \beta_1 DMR_{ij} + \beta_2 MPBMORT.L_{ij} + \beta_3 MPBMORT.M_{ij} + \varepsilon_{ij}$	6	186.46	12.48	1.95E-03	9.13E-06	511.69

Table 1.13 (continued).

Model	df	BIC	ΔBIC	L (gi x)	BIC weight	Evidence ratio
$CHD_{ij} = \beta_0 + b_j + \beta_1DMR_{ij} + \beta_2PROD.L_{ij} + \beta_3PROD.M_{ij} + \epsilon_{ij}$	6	187.39	13.40	1.23E-03	5.74E-06	813.92
$CHD_{ij} = \beta_0 + b_j + \beta_1PROD.L_{ij} + \beta_2PROD.M_{ij} + \epsilon_{ij}$	5	187.48	13.49	1.18E-03	5.50E-06	849.34
$CHD_{ij} = \beta_0 + b_j + \beta_1MPBMORT.L_{ij} + \beta_2MPBMORT.M_{ij} + \epsilon_{ij}$	5	187.90	13.92	9.50E-04	4.44E-06	1052.47
$CHD_{ij} = \beta_0 + b_j + \beta_1DMR_{ij} + \beta_2SD_{ij} + \beta_3MPBMORT.L_{ij} + \beta_4MPBMORT.M_{ij} + \beta_5SD*DMR_{ij} + \beta_6MPBMORT.L*DMR_{ij} + \beta_7MPBMORT.M*DMR_{ij} + \epsilon_{ij}$	10	189.66	15.68	3.95E-04	1.84E-06	2534.19
$CHD_{ij} = \beta_0 + b_j + \beta_1DMR_{ij} + \beta_2MPBMORT.L_{ij} + \beta_3MPBMORT.M_{ij} + \beta_4PROD.L_{ij} + \beta_5PROD.L_{ij} + \epsilon_{ij}$	8	191.46	17.47	1.61E-04	7.52E-07	6215.49
$CHD_{ij} = \beta_0 + b_j + \beta_1DMR_{ij} + \beta_2MPBMORT.L_{ij} + \beta_3MPBMORT.M_{ij} + \beta_4DMR*MPBMORT.L_{ij} + \beta_5DMR*MPBMORT.M_{ij} + \epsilon_{ij}$	8	192.38	18.39	1.01E-04	4.74E-07	9853.35
$CHD_{ij} = \beta_0 + b_j + \beta_1DMR_{ij} + \beta_2MPBMORT.L_{ij} + \beta_3MPBMORT.M_{ij} + \beta_4PROD.L_{ij} + \beta_5PROD.M_{ij} + \beta_6SD_{ij} + \beta_7PROD.L*DMR_{ij} + \beta_8PROD.M*DMR_{ij} + \beta_9MPBMORT.L*DMR_{ij} + \beta_{10}MPBMORT.M*DMR_{ij} + \beta_{11}SD*DMR_{ij} + \epsilon_{ij}$	14	192.47	18.48	9.70E-05	4.53E-07	10306.37
$CHD_{ij} = \beta_0 + b_j + \beta_1DMR_{ij} + \beta_2PROD.L_{ij} + \beta_3PROD.M_{ij} + \beta_4DMR*PROD.L_{ij} + \beta_5DMR*PROD.M_{ij} + \epsilon_{ij}$	8	193.66	19.67	5.35E-05	2.50E-07	18675.16
$CHD_{ij} = \beta_0 + b_j + \beta_1DMR_{ij} + \beta_2MPBMORT.L_{ij} + \beta_3MPBMORT.M_{ij} + \beta_4PROD.L_{ij} + \beta_5PROD.M_{ij} + \beta_6PROD.L*DMR_{ij} + \beta_7PROD.M*DMR_{ij} + \beta_8MPBMORT.L*DMR_{ij} + \beta_9MPBMORT.M*DMR_{ij} + \epsilon_{ij}$	12	202.29	28.31	7.14E-07	3.33E-09	1.40E+06

Table 1.14. BIC table for log cohort diameter of suppressed model. $Log(CDS)_{ij}$ represents the natural logarithm of the cohort diameter of suppressed of the i th plot within the j th stand, β_0 is the mean of the natural logarithm of cohort diameter of suppressed when all additional β 's = 0, b_j is the random error for the j th stand, $\mathbf{b}_j \sim N(0, \sigma_b^2)$ and \mathbf{b}_j and $\mathbf{b}_{j'}$ are independent, ε_{ij} is the random error from the natural logarithm of the cohort diameter of suppressed measurements i th plot replicate within the j th stand, $\varepsilon_{ij} \sim N(0, \sigma^2)$ and ε_{ij} and $\varepsilon_{i'j'}$ are independent.

Model	df	BIC	Δ BIC	L (gi x)	BIC weight	Evidence ratio
$Log(CDS)_{ij} = \beta_0 + b_j + \beta_1 SD_{ij} + \varepsilon_{ij}$	4	-35.39	0	1	5.98E-03	1
$Log(CDS)_{ij} = \beta_0 + b_j + \beta_1 PROD.L_{ij} + \beta_2 PROD.M_{ij} + \varepsilon_{ij}$	5	-35.19	0.20	0.903	5.40E-03	1.11
$Log(CDS)_{ij} = \beta_0 + b_j + \beta_1 DMR_{ij} + \varepsilon_{ij}$	4	-33.95	1.44	0.486	2.91E-03	2.06
$Log(CDS)_{ij} = \beta_0 + b_j + \beta_1 DMR_{ij} + \beta_2 PROD.L_{ij} + \beta_3 PROD.M_{ij} + \varepsilon_{ij}$	6	-32.13	3.26	0.196	1.17E-03	5.11
$Log(CDS)_{ij} = \beta_0 + b_j + \beta_1 DMR_{ij} + \beta_2 SD_{ij} + \varepsilon_{ij}$	5	-32.04	3.35	0.187	1.12E-03	5.34
$Log(CDS)_{ij} = \beta_0 + b_j + \beta_1 MPBMORT.L_{ij} + \beta_2 MPBMORT.M_{ij} + \varepsilon_{ij}$	5	-31.86	3.54	0.171	1.02E-03	5.86
$Log(CDS)_{ij} = \beta_0 + b_j + \beta_1 DMR_{ij} + \beta_2 SD_{ij} + \beta_3 PROD.L_{ij} + \beta_4 PROD.M_{ij} + \varepsilon_{ij}$	7	-29.45	5.94	0.051	3.06E-04	19.52
$Log(CDS)_{ij} = \beta_0 + b_j + \beta_1 DMR_{ij} + \beta_2 SD_{ij} + \beta_3 DMR*SD_{ij} + \varepsilon_{ij}$	6	-28.42	6.97	0.031	1.83E-04	32.69
$Log(CDS)_{ij} = \beta_0 + b_j + \beta_1 DMR_{ij} + \beta_2 MPBMORT.L_{ij} + \beta_3 MPBMORT.M_{ij} + \varepsilon_{ij}$	6	-28.40	7.00	0.030	1.81E-04	33.05

Table 1.14 (continued).

Model	df	BIC	ΔBIC	L (gi x)	BIC weight	Evidence ratio
$\text{Log}(CDS)_{ij} = \beta_0 + b_j + \beta_1 DMR_{ij} + \beta_2 SD_{ij} + \beta_3 MPBMORT.L_{ij} + \beta_4 MPBMORT.M_{ij} + \varepsilon_{ij}$	7	-27.32	8.08	0.018	1.05E-04	56.74
$\text{Log}(CDS)_{ij} = \beta_0 + b_j + \beta_1 DMR_{ij} + \beta_2 MPBMORT.L_{ij} + \beta_3 MPBMORT.M_{ij} + \beta_4 PROD.L_{ij} + \beta_5 PROD.L_{ij} + \varepsilon_{ij}$	8	-25.60	9.80	7.46E-03	4.46E-05	134.05
$\text{Log}(CDS)_{ij} = \beta_0 + b_j + \beta_1 DMR_{ij} + \beta_2 PROD.L_{ij} + \beta_3 PROD.M_{ij} + \beta_4 DMR*PROD.L_{ij} + \beta_5 DMR*PROD.M_{ij} + \varepsilon_{ij}$	8	-24.89	10.50	5.25E-03	3.14E-05	190.62
$\text{Log}(CDS)_{ij} = \beta_0 + b_j + \beta_1 DMR_{ij} + \beta_2 MPBMORT.L_{ij} + \beta_3 MPBMORT.M_{ij} + \beta_4 PROD.L_{ij} + \beta_5 PROD.M_{ij} + \beta_6 SD_{ij} + \varepsilon_{ij}$	9	-23.41	11.98	2.50E-03	1.50E-05	399.57
$\text{Log}(CDS)_{ij} = \beta_0 + b_j + \beta_1 DMR_{ij} + \beta_2 MPBMORT.L_{ij} + \beta_3 MPBMORT.M_{ij} + \beta_4 DMR*MPBMORT.L_{ij} + \beta_5 DMR*MPBMORT.M_{ij} + \varepsilon_{ij}$	8	-23.31	12.09	2.38E-03	1.42E-05	420.98
$\text{Log}(CDS)_{ij} = \beta_0 + b_j + \beta_1 DMR_{ij} + \beta_2 SD_{ij} + \beta_3 MPBMORT.L_{ij} + \beta_4 MPBMORT.M_{ij} + \beta_5 SD*DMR_{ij} + \beta_6 MPBMORT.L*DMR_{ij} + \beta_7 MPBMORT.M*DMR_{ij} + \varepsilon_{ij}$	10	-19.57	15.82	3.66E-04	2.19E-06	2728.94
$\text{Log}(CDS)_{ij} = \beta_0 + b_j + \beta_1 DMR_{ij} + \beta_2 SD_{ij} + \beta_3 PROD.L_{ij} + \beta_4 PROD.M_{ij} + \beta_5 SD*DMR_{ij} + \beta_6 PROD.L*DMR_{ij} + \beta_7 PROD.M*DMR_{ij} + \varepsilon_{ij}$	10	-18.60	16.80	2.25E-04	1.35E-06	4440.24
$\text{Log}(CDS)_{ij} = \beta_0 + b_j + \beta_1 DMR_{ij} + \beta_2 MPBMORT.L_{ij} + \beta_3 MPBMORT.M_{ij} + \beta_4 PROD.L_{ij} + \beta_5 PROD.M_{ij} + \beta_6 PROD.L*DMR_{ij} + \beta_7 PROD.M*DMR_{ij} + \beta_8 MPBMORT.L*DMR_{ij} + \beta_9 MPBMORT.M*DMR_{ij} + \varepsilon_{ij}$	12	-12.05	23.34	8.53E-06	5.10E-08	1.17E+05
$\text{Log}(CDS)_{ij} = \beta_0 + b_j + \beta_1 DMR_{ij} + \beta_2 MPBMORT.L_{ij} + \beta_3 MPBMORT.M_{ij} + \beta_4 PROD.L_{ij} + \beta_5 PROD.M_{ij} + \beta_6 SD_{ij} + \beta_7 PROD.L*DMR_{ij} + \beta_8 PROD.M*DMR_{ij} + \beta_9 MPBMORT.L*DMR_{ij} + \beta_{10} MPBMORT.M*DMR_{ij} + \beta_{11} SD*DMR_{ij} + \varepsilon_{ij}$	14	-8.20	27.19	1.25E-06	7.45E-09	8.02E+05

Table 1.15. BIC table for log cohort diameter of dominants model. $\text{Log}(CDD)_{ij}$ represents the natural logarithm of the cohort diameter of dominants of the i th plot within the j th stand, β_0 is the mean of the natural logarithm of cohort diameter of dominants when all additional β 's = 0, b_j is the random error for the j th stand, $b_j \sim N(0, \sigma_b^2)$ and b_j and $b_{j'}$ are independent, ε_{ij} is the random error from the natural logarithm of the cohort diameter of dominants measurements i th plot replicate within the j th stand, $\varepsilon_{ij} \sim N(0, \sigma^2)$ and ε_{ij} and $\varepsilon_{i'j'}$ are independent.

Model	df	BIC	ΔBIC	L (gi x)	BIC weight	Evidence ratio
$\text{Log}(CDD)_{ij} = \beta_0 + b_j + \beta_1 DMR_{ij} + \beta_2 SD_{ij} + \varepsilon_{ij}$	5	-39.51	0	1	5.22E-03	1.00
$\text{Log}(CDD)_{ij} = \beta_0 + b_j + \beta_1 SD_{ij} + \varepsilon_{ij}$	4	-38.24	1.27	0.530	2.77E-03	1.89
$\text{Log}(CDD)_{ij} = \beta_0 + b_j + \beta_1 DMR_{ij} + \beta_2 SD_{ij} + \beta_3 DMR * SD_{ij} + \varepsilon_{ij}$	6	-37.23	2.27	0.321	1.67E-03	3.12
$\text{Log}(CDD)_{ij} = \beta_0 + b_j + \beta_1 DMR_{ij} + \beta_2 SD_{ij} + \beta_3 MPBMORT.L_{ij} + \beta_4 MPBMORT.M_{ij} + \varepsilon_{ij}$	7	-35.08	4.43	0.109	5.70E-04	9.16
$\text{Log}(CDD)_{ij} = \beta_0 + b_j + \beta_1 DMR_{ij} + \beta_2 SD_{ij} + \beta_3 MPBMORT.L_{ij} + \beta_4 MPBMORT.M_{ij} + \beta_5 SD * DMR_{ij} + \beta_6 MPBMORT.L * DMR_{ij} + \beta_7 MPBMORT.M * DMR_{ij} + \varepsilon_{ij}$	10	-33.69	5.82	0.055	2.85E-04	18.32
$\text{Log}(CDD)_{ij} = \beta_0 + b_j + \beta_1 DMR_{ij} + \beta_2 SD_{ij} + \beta_3 PROD.L_{ij} + \beta_4 PROD.M_{ij} + \varepsilon_{ij}$	7	-32.77	6.74	0.034	1.80E-04	29.01
$\text{Log}(CDD)_{ij} = \beta_0 + b_j + \beta_1 DMR_{ij} + \varepsilon_{ij}$	4	-31.95	7.55	0.023	1.19E-04	43.69
$\text{Log}(CDD)_{ij} = \beta_0 + b_j + \beta_1 DMR_{ij} + \beta_2 MPBMORT.L_{ij} + \beta_3 MPBMORT.M_{ij} + \varepsilon_{ij}$	6	-29.41	10.10	6.40E-03	3.34E-05	156.14
$\text{Log}(CDD)_{ij} = \beta_0 + b_j + \beta_1 DMR_{ij} + \beta_2 MPBMORT.L_{ij} + \beta_3 MPBMORT.M_{ij} + \beta_4 DMR * MPBMORT.L_{ij} + \beta_5 DMR * MPBMORT.M_{ij} + \varepsilon_{ij}$	8	-28.40	11.10	3.88E-03	2.03E-05	257.63
$\text{Log}(CDD)_{ij} = \beta_0 + b_j + \beta_1 DMR_{ij} + \beta_2 MPBMORT.L_{ij} + \beta_3 MPBMORT.M_{ij} + \beta_4 PROD.L_{ij} + \beta_5 PROD.M_{ij} + \beta_6 SD_{ij} + \varepsilon_{ij}$	9	-27.95	11.55	3.10E-03	1.62E-05	322.59
$\text{Log}(CDD)_{ij} = \beta_0 + b_j + \beta_1 DMR_{ij} + \beta_2 SD_{ij} + \beta_3 PROD.L_{ij} + \beta_4 PROD.M_{ij} + \beta_5 SD * DMR_{ij} + \beta_6 PROD.L * DMR_{ij} + \beta_7 PROD.M * DMR_{ij} + \varepsilon_{ij}$	10	-27.49	12.01	2.46E-03	1.28E-05	406.25

Table 1.15 (continued).

Model	df	BIC	ΔBIC	L (gi x)	BIC weight	Evidence ratio
$\text{Log}(CDD)_{ij} = \beta_0 + b_j + \beta_1 DMR_{ij} + \beta_2 PROD.L_{ij} + \beta_3 PROD.M_{ij} + \varepsilon_{ij}$	6	-26.59	12.92	1.56E-03	8.17E-06	639.11
$\text{Log}(CDD)_{ij} = \beta_0 + b_j + \beta_1 DMR_{ij} + \beta_2 MPBMORT.L_{ij} + \beta_3 MPBMORT.M_{ij} + \beta_4 PROD.L_{ij} + \beta_5 PROD.M_{ij} + \beta_6 SD_{ij} + \beta_7 PROD.L * DMR_{ij} + \beta_8 PROD.M * DMR_{ij} + \beta_9 MPBMORT.L * DMR_{ij} + \beta_{10} MPBMORT.M * DMR_{ij} + \beta_{11} SD * DMR_{ij} + \varepsilon_{ij}$	14	-24.26	15.25	4.89E-04	2.55E-06	2046.18
$\text{Log}(CDD)_{ij} = \beta_0 + b_j + \beta_1 MPBMORT.L_{ij} + \beta_2 MPBMORT.M_{ij} + \varepsilon_{ij}$	5	-23.48	16.03	3.31E-04	1.73E-06	3021.16
$\text{Log}(CDD)_{ij} = \beta_0 + b_j + \beta_1 DMR_{ij} + \beta_2 PROD.L_{ij} + \beta_3 PROD.M_{ij} + \beta_4 DMR * PROD.L_{ij} + \beta_5 DMR * PROD.M_{ij} + \varepsilon_{ij}$	8	-22.81	16.70	2.37E-04	1.24E-06	4224.97
$\text{Log}(CDD)_{ij} = \beta_0 + b_j + \beta_1 PROD.L_{ij} + \beta_2 PROD.M_{ij} + \varepsilon_{ij}$	5	-22.70	16.81	2.24E-04	1.17E-06	4468.87
$\text{Log}(CDD)_{ij} = \beta_0 + b_j + \beta_1 DMR_{ij} + \beta_2 MPBMORT.L_{ij} + \beta_3 MPBMORT.M_{ij} + \beta_4 PROD.L_{ij} + \beta_5 PROD.L_{ij} + \varepsilon_{ij}$	8	-22.20	17.31	1.75E-04	9.11E-07	5729.23
$\text{Log}(CDD)_{ij} = \beta_0 + b_j + \beta_1 DMR_{ij} + \beta_2 MPBMORT.L_{ij} + \beta_3 MPBMORT.M_{ij} + \beta_4 PROD.L_{ij} + \beta_5 PROD.M_{ij} + \beta_6 PROD.L * DMR_{ij} + \beta_7 PROD.M * DMR_{ij} + \beta_8 MPBMORT.L * DMR_{ij} + \beta_9 MPBMORT.M * DMR_{ij} + \varepsilon_{ij}$	12	-15.80	23.71	7.11E-06	3.71E-08	140723.61

Table 1.16. BIC table for log cohort diameter of intermediates model. $\text{Log}(CDI)_{ij}$ represents the natural logarithm of the cohort diameter of intermediates of the i th plot within the j th stand, β_0 is the mean of the natural logarithm of cohort diameter of intermediates when all additional β 's = 0, b_j is the random error for the j th stand, $\mathbf{b}_j \sim N(0, \sigma_b^2)$ and \mathbf{b}_j and $\mathbf{b}_{j'}$ are independent, ε_{ij} is the random error from the natural logarithm of the cohort diameter of intermediates measurements i th plot replicate within the j th stand, $\varepsilon_{ij} \sim N(0, \sigma^2)$ and ε_{ij} and $\varepsilon_{i'j'}$ are independent.

Model	df	BIC	Δ BIC	L (gi x)	BIC weight	Evidence ratio
$\text{Log}(CDI)_{ij} = \beta_0 + b_j + \beta_1 SD_{ij} + \varepsilon_{ij}$	4	-44.62	0	1	4.69E-03	1
$\text{Log}(CDI)_{ij} = \beta_0 + b_j + \beta_1 DMR_{ij} + \beta_2 SD_{ij} + \beta_3 PROD.L_{ij} + \beta_4 PROD.M_{ij} + \varepsilon_{ij}$	7	-42.60	2.02	0.36	1.71E-03	2.75
$\text{Log}(CDI)_{ij} = \beta_0 + b_j + \beta_1 DMR_{ij} + \beta_2 SD_{ij} + \varepsilon_{ij}$	5	-41.46	3.16	0.21	9.68E-04	4.85
$\text{Log}(CDI)_{ij} = \beta_0 + b_j + \beta_1 DMR_{ij} + \beta_2 SD_{ij} + \beta_3 MPBMORT.L_{ij} + \beta_4 MPBMORT.M_{ij} + \varepsilon_{ij}$	7	-38.06	6.56	0.04	1.76E-04	26.60
$\text{Log}(CDI)_{ij} = \beta_0 + b_j + \beta_1 DMR_{ij} + \beta_2 SD_{ij} + \beta_3 DMR*SD_{ij} + \varepsilon_{ij}$	6	-37.84	6.78	0.03	1.58E-04	29.64
$\text{Log}(CDI)_{ij} = \beta_0 + b_j + \beta_1 DMR_{ij} + \beta_2 MPBMORT.L_{ij} + \beta_3 MPBMORT.M_{ij} + \beta_4 PROD.L_{ij} + \beta_5 PROD.M_{ij} + \beta_6 SD_{ij} + \varepsilon_{ij}$	9	-36.40	8.22	0.02	7.69E-05	61.01
$\text{Log}(CDI)_{ij} = \beta_0 + b_j + \beta_1 DMR_{ij} + \beta_2 PROD.L_{ij} + \beta_3 PROD.M_{ij} + \varepsilon_{ij}$	6	-36.38	8.24	0.02	7.62E-05	61.55
$\text{Log}(CDI)_{ij} = \beta_0 + b_j + \beta_1 PROD.L_{ij} + \beta_2 PROD.M_{ij} + \varepsilon_{ij}$	5	-36.51	8.11	0.02	8.14E-05	57.64
$\text{Log}(CDI)_{ij} = \beta_0 + b_j + \beta_1 DMR_{ij} + \beta_2 SD_{ij} + \beta_3 PROD.L_{ij} + \beta_4 PROD.M_{ij} + \beta_5 SD*DMR_{ij} + \beta_6 PROD.L*DMR_{ij} + \beta_7 PROD.M*DMR_{ij} + \varepsilon_{ij}$	10	-34.03	10.59	0.01	2.35E-05	199.71
$\text{Log}(CDI)_{ij} = \beta_0 + b_j + \beta_1 DMR_{ij} + \varepsilon_{ij}$	4	-32.12	12.50	1.93E-03	9.08E-06	516.85
$\text{Log}(CDI)_{ij} = \beta_0 + b_j + \beta_1 DMR_{ij} + \beta_2 MPBMORT.L_{ij} + \beta_3 MPBMORT.M_{ij} + \beta_4 PROD.L_{ij} + \beta_5 PROD.L_{ij} + \varepsilon_{ij}$	8	-29.69	14.93	5.72E-04	2.68E-06	1748.68

Table 1.16 (continued).

Model	df	BIC	ΔBIC	L (gi x)	BIC weight	Evidence ratio
$\text{Log}(CDI)_{ij} = \beta_0 + b_j + \beta_1 DMR_{ij} + \beta_2 PROD.L_{ij} + \beta_3 PROD.M_{ij} + \beta_4 DMR*PROD.L_{ij} + \beta_5 DMR*PROD.M_{ij} + \varepsilon_{ij}$	8	-29.87	14.75	6.27E-04	2.94E-06	1594.68
$\text{Log}(CDI)_{ij} = \beta_0 + b_j + \beta_1 DMR_{ij} + \beta_2 SD_{ij} + \beta_3 MPBMORT.L_{ij} + \beta_4 MPBMORT.M_{ij} + \beta_5 SD*DMR_{ij} + \beta_6 MPBMORT.L*DMR_{ij} + \beta_7 MPBMORT.M*DMR_{ij} + \varepsilon_{ij}$	10	-29.86	14.76	6.23E-04	2.92E-06	1606.18
$\text{Log}(CDI)_{ij} = \beta_0 + b_j + \beta_1 DMR_{ij} + \beta_2 MPBMORT.L_{ij} + \beta_3 MPBMORT.M_{ij} + \varepsilon_{ij}$	6	-29.87	14.75	6.26E-04	2.94E-06	1597.55
$\text{Log}(CDI)_{ij} = \beta_0 + b_j + \beta_1 MPBMORT.L_{ij} + \beta_2 MPBMORT.M_{ij} + \varepsilon_{ij}$	5	-29.12	15.50	4.31E-04	2.02E-06	2319.72
$\text{Log}(CDI)_{ij} = \beta_0 + b_j + \beta_1 DMR_{ij} + \beta_2 MPBMORT.L_{ij} + \beta_3 MPBMORT.M_{ij} + \beta_4 DMR*MPBMORT.L_{ij} + \beta_5 DMR*MPBMORT.M_{ij} + \varepsilon_{ij}$	8	-25.31	19.31	6.40E-05	3.00E-07	15624.18
$\text{Log}(CDI)_{ij} = \beta_0 + b_j + \beta_1 DMR_{ij} + \beta_2 MPBMORT.L_{ij} + \beta_3 MPBMORT.M_{ij} + \beta_4 PROD.L_{ij} + \beta_5 PROD.M_{ij} + \beta_6 SD_{ij} + \beta_7 PROD.L*DMR_{ij} + \beta_8 PROD.M*DMR_{ij} + \beta_9 MPBMORT.L*DMR_{ij} + \beta_{10} MPBMORT.M*DMR_{ij} + \beta_{11} SD*DMR_{ij} + \varepsilon_{ij}$	14	-20.06	24.56	4.65E-06	2.18E-08	214963.8
$\text{Log}(CDI)_{ij} = \beta_0 + b_j + \beta_1 DMR_{ij} + \beta_2 MPBMORT.L_{ij} + \beta_3 MPBMORT.M_{ij} + \beta_4 PROD.L_{ij} + \beta_5 PROD.M_{ij} + \beta_6 PROD.L*DMR_{ij} + \beta_7 PROD.M*DMR_{ij} + \beta_8 MPBMORT.L*DMR_{ij} + \beta_9 MPBMORT.M*DMR_{ij} + \varepsilon_{ij}$	12	-16.24	28.38	6.88E-07	3.23E-09	1453616

Table 1.17. BIC table for log canopy base height model. $\text{Log}(CBH)_{ij}$ represents the natural logarithm of the canopy base height of the i th plot within the j th stand, β_0 is the mean of the natural logarithm of canopy base height when all additional β 's = 0, b_j is the random error for the j th stand, $\mathbf{b}_j \sim N(0, \sigma_b^2)$ and \mathbf{b}_j and $\mathbf{b}_{j'}$ are independent, ε_{ij} is the random error from the natural logarithm of the canopy base height measurements i th plot replicate within the j th stand, $\varepsilon_{ij} \sim N(0, \sigma^2)$ and ε_{ij} and $\varepsilon_{i'j'}$ are independent.

Model	df	BIC	Δ BIC	L (gi x)	BIC weight	Evidence ratio
$(\text{Log})CBH_{ij} = \beta_0 + b_j + \beta_1 DMR_{ij} + \varepsilon_{ij}$	4	101.74	0.00	1	4.80E-03	1
$(\text{Log})CBH_{ij} = \beta_0 + b_j + \beta_1 DMR_{ij} + \beta_2 SD_{ij} + \varepsilon_{ij}$	5	104.97	3.24	0.198	9.52E-04	5.04
$(\text{Log})CBH_{ij} = \beta_0 + b_j + \beta_1 DMR_{ij} + \beta_2 MPBMORT.L_{ij} + \beta_3 MPBMORT.M_{ij} + \varepsilon_{ij}$	6	107.30	5.56	0.062	2.98E-04	16.13
$(\text{Log})CBH_{ij} = \beta_0 + b_j + \beta_1 DMR_{ij} + \beta_2 SD_{ij} + \beta_3 DMR * SD_{ij} + \varepsilon_{ij}$	6	108.35	6.61	0.037	1.76E-04	27.24
$(\text{Log})CBH_{ij} = \beta_0 + b_j + \beta_1 DMR_{ij} + \beta_2 PROD.L_{ij} + \beta_3 PROD.M_{ij} + \varepsilon_{ij}$	6	108.72	6.98	0.030	1.46E-04	32.86
$(\text{Log})CBH_{ij} = \beta_0 + b_j + \beta_1 SD_{ij} + \varepsilon_{ij}$	4	110.38	8.64	0.013	6.38E-05	75.34
$(\text{Log})CBH_{ij} = \beta_0 + b_j + \beta_1 DMR_{ij} + \beta_2 SD_{ij} + \beta_3 MPBMORT.L_{ij} + \beta_4 MPBMORT.M_{ij} + \varepsilon_{ij}$	7	110.65	8.91	0.012	5.59E-05	85.95
$(\text{Log})CBH_{ij} = \beta_0 + b_j + \beta_1 MPBMORT.L_{ij} + \beta_2 MPBMORT.M_{ij} + \varepsilon_{ij}$	5	110.78	9.04	0.011	5.23E-05	91.87
$(\text{Log})CBH_{ij} = \beta_0 + b_j + \beta_1 DMR_{ij} + \beta_2 MPBMORT.L_{ij} + \beta_3 MPBMORT.M_{ij} + \beta_4 DMR * MPBMORT.L_{ij} + \beta_5 DMR * MPBMORT.M_{ij} + \varepsilon_{ij}$	8	111.06	9.32	9.44E-03	4.54E-05	105.89
$(\text{Log})CBH_{ij} = \beta_0 + b_j + \beta_1 DMR_{ij} + \beta_2 SD_{ij} + \beta_3 PROD.L_{ij} + \beta_4 PROD.M_{ij} + \varepsilon_{ij}$	7	111.75	10.02	6.68E-03	3.21E-05	149.61
$(\text{Log})CBH_{ij} = \beta_0 + b_j + \beta_1 DMR_{ij} + \beta_2 MPBMORT.L_{ij} + \beta_3 MPBMORT.M_{ij} + \beta_4 PROD.L_{ij} + \beta_5 PROD.L_{ij} + \varepsilon_{ij}$	8	113.09	11.35	3.43E-03	1.65E-05	291.19

Table 1.17 (continued).

Model	df	BIC	ΔBIC	L (gi x)	BIC weight	Evidence ratio
$(\text{Log})CBH_{ij} = \beta_0 + b_j + \beta_1\text{PROD.L}_{ij} + \beta_2\text{PROD.M}_{ij} + \varepsilon_{ij}$	5	114.28	12.55	1.89E-03	9.06E-06	530.18
$(\text{Log})CBH_{ij} = \beta_0 + b_j + \beta_1\text{DMR}_{ij} + \beta_2\text{PROD.L}_{ij} + \beta_3\text{PROD.M}_{ij} + \beta_4\text{DMR*PROD.L}_{ij} + \beta_5\text{DMR*PROD.M}_{ij} + \varepsilon_{ij}$	8	115.48	13.75	1.03E-03	4.97E-06	966.48
$(\text{Log})CBH_{ij} = \beta_0 + b_j + \beta_1\text{DMR}_{ij} + \beta_2\text{MPBMORT.L}_{ij} + \beta_3\text{MPBMORT.M}_{ij} + \beta_4\text{PROD.L}_{ij} + \beta_5\text{PROD.M}_{ij} + \beta_6\text{SD}_{ij} + \varepsilon_{ij}$	9	116.02	14.28	7.92E-04	3.80E-06	1262.81
$(\text{Log})CBH_{ij} = \beta_0 + b_j + \beta_1\text{DMR}_{ij} + \beta_2\text{SD}_{ij} + \beta_3\text{MPBMORT.L}_{ij} + \beta_4\text{MPBMORT.M}_{ij} + \beta_5\text{SD*DMR}_{ij} + \beta_6\text{MPBMORT.L*DMR}_{ij} + \beta_7\text{MPBMORT.M*DMR}_{ij} + \varepsilon_{ij}$	10	117.43	15.70	3.91E-04	1.88E-06	2560.68
$(\text{Log})CBH_{ij} = \beta_0 + b_j + \beta_1\text{DMR}_{ij} + \beta_2\text{SD}_{ij} + \beta_3\text{PROD.L}_{ij} + \beta_4\text{PROD.M}_{ij} + \beta_5\text{SD*DMR}_{ij} + \beta_6\text{PROD.L*DMR}_{ij} + \beta_7\text{PROD.M*DMR}_{ij} + \varepsilon_{ij}$	10	122.05	20.31	3.88E-05	1.86E-07	25776.45
$(\text{Log})CBH_{ij} = \beta_0 + b_j + \beta_1\text{DMR}_{ij} + \beta_2\text{MPBMORT.L}_{ij} + \beta_3\text{MPBMORT.M}_{ij} + \beta_4\text{PROD.L}_{ij} + \beta_5\text{PROD.M}_{ij} + \beta_6\text{PROD.L*DMR}_{ij} + \beta_7\text{PROD.M*DMR}_{ij} + \beta_8\text{MPBMORT.L*DMR}_{ij} + \beta_9\text{MPBMORT.M*DMR}_{ij} + \varepsilon_{ij}$	12	124.48	22.74	1.15E-05	5.55E-08	86582.24
$(\text{Log})CBH_{ij} = \beta_0 + b_j + \beta_1\text{DMR}_{ij} + \beta_2\text{MPBMORT.L}_{ij} + \beta_3\text{MPBMORT.M}_{ij} + \beta_4\text{PROD.L}_{ij} + \beta_5\text{PROD.M}_{ij} + \beta_6\text{SD}_{ij} + \beta_7\text{PROD.L*DMR}_{ij} + \beta_8\text{PROD.M*DMR}_{ij} + \beta_9\text{MPBMORT.L*DMR}_{ij} + \beta_{10}\text{MPBMORT.M*DMR}_{ij} + \beta_{11}\text{SD*DMR}_{ij} + \varepsilon_{ij}$	14	130.90	29.17	4.64E-07	2.23E-09	2155640.60

Table 1.18. BIC table for log canopy bulk density model. $\text{Log}(CBD)_{ij}$ represents the natural logarithm of the canopy bulk density of the i th plot within the j th stand, β_0 is the mean of the natural logarithm of canopy bulk density when all additional β 's = 0, b_j is the random error for the j th stand, $\mathbf{b}_j \sim N(0, \sigma_b^2)$ and \mathbf{b}_j and $\mathbf{b}_{j'}$ are independent, $\boldsymbol{\varepsilon}_{ij}$ is the random error from the natural logarithm of the canopy bulk density measurements i th plot replicate within the j th stand, $\boldsymbol{\varepsilon}_{ij} \sim N(0, \sigma^2)$ and $\boldsymbol{\varepsilon}_{ij}$ and $\boldsymbol{\varepsilon}_{i'j'}$ are independent.

Model	df	BIC	Δ BIC	L (gi x)	BIC weight	Evidence ratio
$\text{Log}(CBD)_{ij} = \beta_0 + b_j + \beta_1 \text{DMR}_{ij} + \beta_2 \text{SD}_{ij} + \boldsymbol{\varepsilon}_{ij}$	5	23.75	0.00	1	2.44E-03	1
$\text{Log}(CBD)_{ij} = \beta_0 + b_j + \beta_1 \text{DMR}_{ij} + \beta_2 \text{SD}_{ij} + \beta_3 \text{PROD.L}_{ij} + \beta_4 \text{PROD.M}_{ij} + \boldsymbol{\varepsilon}_{ij}$	7	24.30	0.56	0.756	1.84E-03	1.32
$\text{Log}(CBD)_{ij} = \beta_0 + b_j + \beta_1 \text{DMR}_{ij} + \beta_2 \text{SD}_{ij} + \beta_3 \text{DMR} * \text{SD}_{ij} + \boldsymbol{\varepsilon}_{ij}$	6	27.01	3.26	0.196	4.77E-04	5.11
$\text{Log}(CBD)_{ij} = \beta_0 + b_j + \beta_1 \text{SD}_{ij} + \boldsymbol{\varepsilon}_{ij}$	4	29.91	6.16	0.046	1.12E-04	21.78
$\text{Log}(CBD)_{ij} = \beta_0 + b_j + \beta_1 \text{DMR}_{ij} + \beta_2 \text{MPBMORT.L}_{ij} + \beta_3 \text{MPBMORT.M}_{ij} + \beta_4 \text{PROD.L}_{ij} + \beta_5 \text{PROD.M}_{ij} + \beta_6 \text{SD}_{ij} + \boldsymbol{\varepsilon}_{ij}$	9	30.47	6.73	0.035	8.43E-05	28.93
$\text{Log}(CBD)_{ij} = \beta_0 + b_j + \beta_1 \text{DMR}_{ij} + \beta_2 \text{SD}_{ij} + \beta_3 \text{MPBMORT.L}_{ij} + \beta_4 \text{MPBMORT.M}_{ij} + \boldsymbol{\varepsilon}_{ij}$	7	30.70	6.96	0.031	7.53E-05	32.39
$\text{Log}(CBD)_{ij} = \beta_0 + b_j + \beta_1 \text{DMR}_{ij} + \beta_2 \text{SD}_{ij} + \beta_3 \text{PROD.L}_{ij} + \beta_4 \text{PROD.M}_{ij} + \beta_5 \text{SD} * \text{DMR}_{ij} + \beta_6 \text{PROD.L} * \text{DMR}_{ij} + \beta_7 \text{PROD.M} * \text{DMR}_{ij} + \boldsymbol{\varepsilon}_{ij}$	10	31.10	7.36	0.025	6.16E-05	39.57
$\text{Log}(CBD)_{ij} = \beta_0 + b_j + \beta_1 \text{DMR}_{ij} + \beta_2 \text{SD}_{ij} + \beta_3 \text{MPBMORT.L}_{ij} + \beta_4 \text{MPBMORT.M}_{ij} + \beta_5 \text{SD} * \text{DMR}_{ij} + \beta_6 \text{MPBMORT.L} * \text{DMR}_{ij} + \beta_7 \text{MPBMORT.M} * \text{DMR}_{ij} + \boldsymbol{\varepsilon}_{ij}$	10	40.44	16.69	2.37E-04	5.78E-07	4214.78
$\text{Log}(CBD)_{ij} = \beta_0 + b_j + \beta_1 \text{DMR}_{ij} + \beta_2 \text{MPBMORT.L}_{ij} + \beta_3 \text{MPBMORT.M}_{ij} + \beta_4 \text{PROD.L}_{ij} + \beta_5 \text{PROD.M}_{ij} + \beta_6 \text{SD}_{ij} + \beta_7 \text{PROD.L} * \text{DMR}_{ij} + \beta_8 \text{PROD.M} * \text{DMR}_{ij} + \beta_9 \text{MPBMORT.L} * \text{DMR}_{ij} + \beta_{10} \text{MPBMORT.M} * \text{DMR}_{ij} + \beta_{11} \text{SD} * \text{DMR}_{ij} + \boldsymbol{\varepsilon}_{ij}$	14	45.49	21.75	1.90E-05	4.62E-08	52721.56
$\text{Log}(CBD)_{ij} = \beta_0 + b_j + \beta_1 \text{DMR}_{ij} + \boldsymbol{\varepsilon}_{ij}$	4	52.08	28.34	7.02E-07	1.71E-09	1.42E+06

Table 1.18 (continued).

Model	df	BIC	ΔBIC	L (gi x)	BIC weight	Evidence ratio
$\text{Log}(\text{CBD})_{ij} = \beta_0 + b_j + \beta_1 \text{MPBMORT.L}_{ij} + \beta_2 \text{MPBMORT.M}_{ij} + \varepsilon_{ij}$	5	55.76	32.01	1.12E-07	2.72E-10	8.95E+06
$\text{Log}(\text{CBD})_{ij} = \beta_0 + b_j + \beta_1 \text{PROD.L}_{ij} + \beta_2 \text{PROD.M}_{ij} + \varepsilon_{ij}$	5	56.75	33.00	6.82E-08	1.66E-10	1.47E+07
$\text{Log}(\text{CBD})_{ij} = \beta_0 + b_j + \beta_1 \text{DMR}_{ij} + \beta_2 \text{PROD.L}_{ij} + \beta_3 \text{PROD.M}_{ij} + \varepsilon_{ij}$	6	58.86	35.11	2.37E-08	5.78E-11	4.22E+07
$\text{Log}(\text{CBD})_{ij} = \beta_0 + b_j + \beta_1 \text{DMR}_{ij} + \beta_2 \text{MPBMORT.L}_{ij} + \beta_3 \text{MPBMORT.M}_{ij} + \varepsilon_{ij}$	6	58.94	35.20	2.27E-08	5.54E-11	4.40E+07
$\text{Log}(\text{CBD})_{ij} = \beta_0 + b_j + \beta_1 \text{DMR}_{ij} + \beta_2 \text{PROD.L}_{ij} + \beta_3 \text{PROD.M}_{ij} + \beta_4 \text{DMR} * \text{PROD.L}_{ij} + \beta_5 \text{DMR} * \text{PROD.M}_{ij} + \varepsilon_{ij}$	8	63.70	39.95	2.11E-09	5.14E-12	4.74E+08
$\text{Log}(\text{CBD})_{ij} = \beta_0 + b_j + \beta_1 \text{DMR}_{ij} + \beta_2 \text{MPBMORT.L}_{ij} + \beta_3 \text{MPBMORT.M}_{ij} + \beta_4 \text{PROD.L}_{ij} + \beta_5 \text{PROD.L}_{ij} + \varepsilon_{ij}$	8	65.15	41.41	1.02E-09	2.48E-12	9.81E+08
$\text{Log}(\text{CBD})_{ij} = \beta_0 + b_j + \beta_1 \text{DMR}_{ij} + \beta_2 \text{MPBMORT.L}_{ij} + \beta_3 \text{MPBMORT.M}_{ij} + \beta_4 \text{DMR} * \text{MPBMORT.L}_{ij} + \beta_5 \text{DMR} * \text{MPBMORT.M}_{ij} + \varepsilon_{ij}$	8	66.06	42.31	6.49E-10	1.58E-12	1.54E+09
$\text{Log}(\text{CBD})_{ij} = \beta_0 + b_j + \beta_1 \text{DMR}_{ij} + \beta_2 \text{MPBMORT.L}_{ij} + \beta_3 \text{MPBMORT.M}_{ij} + \beta_4 \text{PROD.L}_{ij} + \beta_5 \text{PROD.M}_{ij} + \beta_6 \text{PROD.L} * \text{DMR}_{ij} + \beta_7 \text{PROD.M} * \text{DMR}_{ij} + \beta_8 \text{MPBMORT.L} * \text{DMR}_{ij} + \beta_9 \text{MPBMORT.M} * \text{DMR}_{ij} + \varepsilon_{ij}$	12	77.23	53.48	2.43E-12	5.93E-15	4.11E+11

Figures

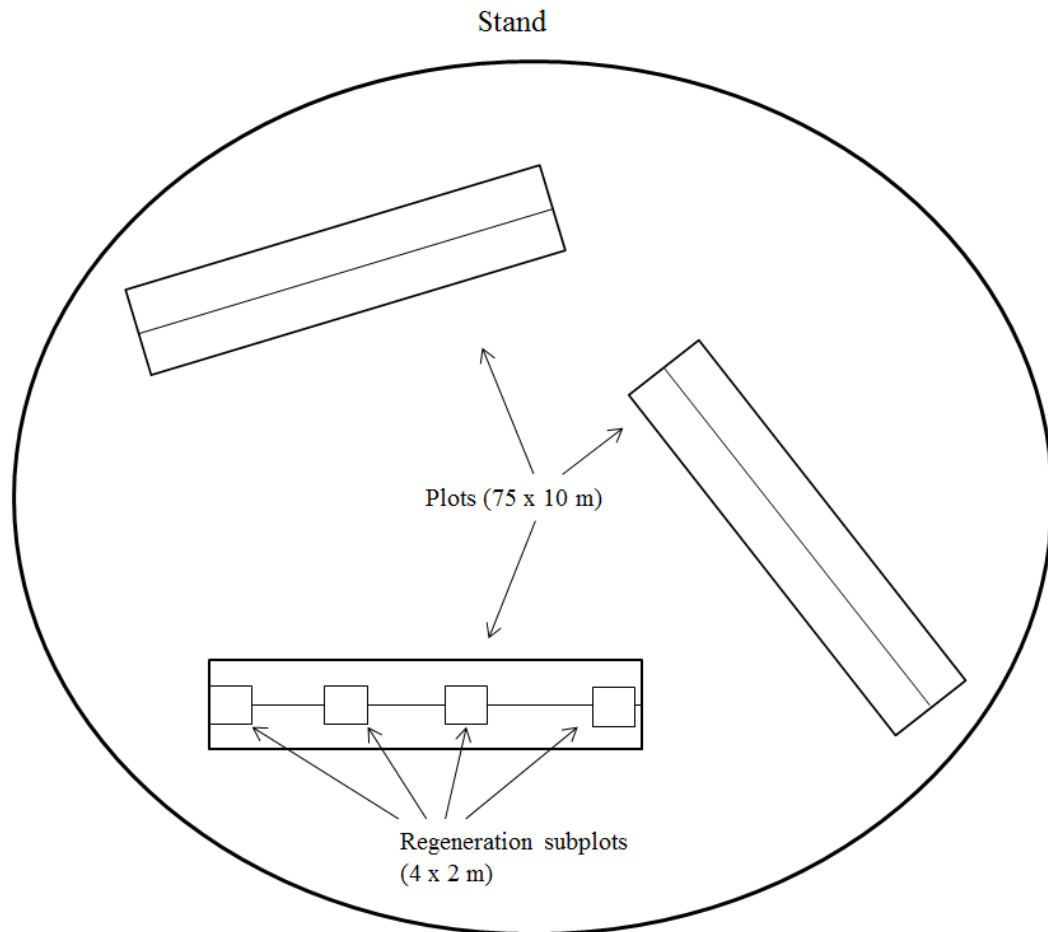


Figure 1.1. Plot layout.

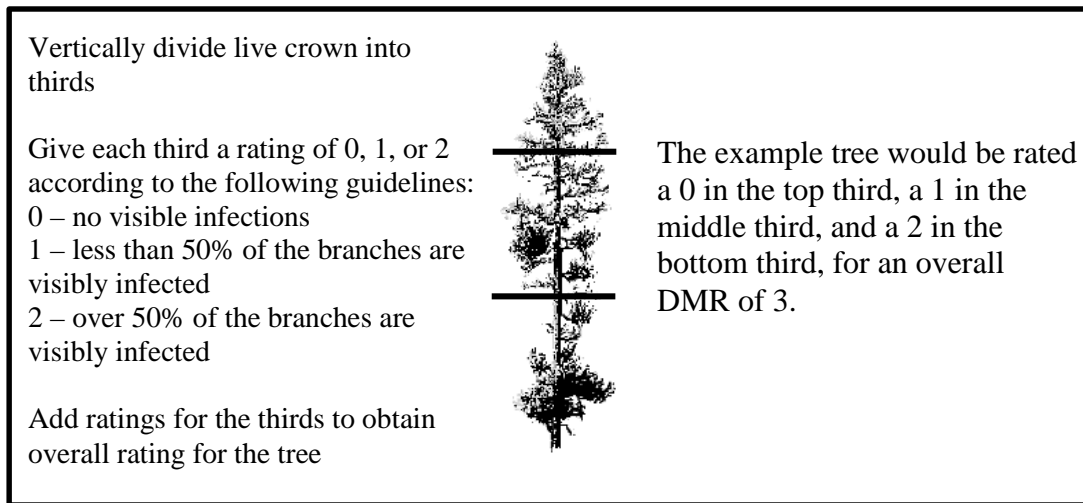


Figure 1.2. The Hawksworth 6-class dwarf mistletoe rating system.