AN ABSTRACT OF THE THESIS OF

Katrina Marshall for the degree of Master of Science in Forest Science presented on June 8, 1995. Title: The Relationship of Douglas-fir Dwarf Mistletoe (*Arceuthobium douglasii*) to Environmental and Stand Conditions and Plant Communities in the Southern Oregon Cascades.

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Gregory M. Filip

This study examined the relationships between the frequency of occurrence and severity of Douglas-fir dwarf mistletoe (*Arceuthobium douglasii* Engelmann), environmental and stand conditions, and plant communities in the Southern Oregon Cascade Mountain Province.

Data for the study was collected from the same ecology plots that were previously used to define the plant associations in the province. A pilot study of the variability in the frequency of occurrence and severity of Douglas-fir dwarf mistletoe (DFDM) among plant associations was used to determine the sample size. The plant associations selected for the final sample were grouped into three climax series; Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), white fir (*Abies concolor* (Gord. and Glend) Lindl. ex Hildebr.) and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.). Environmental and stand conditions were sampled using the variables elevation, mean annual temperature, mean annual precipitation, dry season precipitation, site index, slope, total basal area, Douglas-fir basal area, percent basal area in Douglas-fir, number of tree canopy layers, age of each layer, diameter of

Douglas-fir at breast height, aspect, topographic position, topographic shape, and soil parent material.

DFDM was present in plots at significantly higher elevations, with lower mean annual temperatures and lower mean annual precipitation. The disease was never found in plots below 1066 meters elevation or at mean annual temperatures above 8°C. It occurred significantly more often in the white fir series than in the others. Within this series it was found more often in the coldest and driest plant associations. The relative frequency of DFDM among the series appeared to be related to the differences in their elevation, mean annual temperature and mean annual precipitation.

The geographic distribution of the plots where DFDM occurred suggested that past timber harvesting, fire history and fire behavior may have influenced the present distribution of the disease in the Southern Oregon Cascades.

The severity of DFDM was significantly associated with two stand variables. Severity increased as total basal area decreased and as the age of the oldest layer increased. Multiple regression analysis indicated that the disease was most severe in old, open stands on high, dry sites.

This study suggested that plant associations and climax series were useful indicators of the relative frequency of occurrence of DFDM in the Southern Oregon Cascades, but not of its severity. However, if the current distribution of DFDM was influenced by past harvesting and fire regimes, changes in these factors may change the diseases' distribution in the future. A return to widespread partial cutting would be of particular concern because partial cutting often creates the stand conditions that were associated with severe DFDM in this study.

The Relationship of Douglas-fir Dwarf Mistletoe (*Arceuthobium douglasii*)
to Environmental and Stand Conditions and Plant Communities
in the Southern Oregon Cascades

by

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Dean of Graduate School

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.

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Katrina Marshall, author

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INTRODUCTION

Douglas-fir dwarf mistletoe (*Arceuthobium douglasii* Engelm.) is a parasitic plant pathogen found almost exclusively on Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco). It is one of the most widespread diseases of Douglas-fir in the forests of southwestern Oregon (Hadfield, 1985).

All aspects of forest management including recovery plans for the northern spotted owl, ecosystem management, watershed restoration programs, and timber production require accurate methods of predicting stand development in order to prescribe activities that will achieve desired future conditions. Understanding the occurrence and severity of common diseases such as dwarf mistletoe is necessary to predict stand development.

Wildfire hazard is also affected by the presence of dwarf mistletoe in stands. The effects of dwarf mistletoe infection on fuel load and arrangement in stands may be of critical importance at the urban-forest interface (Bill Rose, Fire Management Officer, Siskiyou Zone, Rogue River N.F., pers. comm.). In the interior valleys of southwestern Oregon this interface occurs at relatively low elevations where Douglas-fir is the most common species and often grows in relatively pure stands.

At the same time, Douglas-fir dwarf mistletoe is an important component of stands managed for habitat for the northern spotted owl (*Strix occidentalis* var *caurina* Xantus de Vesey). In central and southwestern Oregon these owls use both Douglas-fir dwarf mistletoe brooms and cavities for nesting. Proposed treatments to improve habitat in areas managed for spotted owls include maintaining or even increasing Douglas-fir dwarf mistletoe to provide nesting platforms in stands otherwise lacking in suitable structures. Animals such as porcupines, squirrels, hawks and other owl species also use Douglas-fir dwarf mistletoe brooms. Silvicultural treatments that are used to eliminate and prevent dwarf mistletoe infection may create stand conditions that are incompatible with the habitat requirements of these animals. Therefore, some amount of dwarf mistletoe infection may be desirable even in stands managed for timber production.

The association of environmental and stand conditions with occurrence and severity of dwarf mistletoe would help resolve resource conflicts by providing information about conditions in which stands may have less likelihood of infection or in which infection is likely to remain at acceptable levels. It would help managers direct prevention and control efforts where they are needed. Association of Douglas-fir dwarf mistletoe with plant communities would provide the link to widely used systems of stand level vegetation classification.

There have been numerous studies that examined the relationships between the distribution of dwarf mistletoes, their severity, and environmental and stand conditions. Most of these studies have taken place in the Rocky Mountains. They focused primarily on ponderosa pine dwarf mistletoes (*A. vaginatum cryptopodum* Engelm. and *A. campylopodum* Engelm.), but some also investigated Douglas-fir dwarf mistletoe. Conflicting results were reported among studies in different geographic areas, on different hosts, and among dwarf

mistletoe species. This lack of consistency may be due in part to the differences in study design. However, it also suggests that the relationships vary depending on local conditions and cannot be extrapolated from one area, host or mistletoe species to another.

The objectives of this study were to determine if environmental or stand conditions or plant communities were associated with the occurrence and severity of Douglas-fir dwarf mistletoe in the Southern Oregon Cascades. Such relationships could be used to make growth and yield models used in southwestern Oregon, like Prognosis (Stage, 1973), more accurate and site-specific in their prediction of losses due to dwarf mistletoe. They could also be used to assess suitability of habitat for wildlife species that utilize mistletoe brooms and in models predicting fire hazard.

This study was observational in nature. It covered the west side of the Southern Oregon Cascades within the range of Douglas-fir dwarf mistletoe and included plant communities in which Douglas-fir is a major component.

A companion study by the U.S. Forest Service, Region Six, Forest Pest Management Group installed a system of permanent plots to quantify the spread and intensification of Douglas-fir dwarf mistletoe in southwestern Oregon. The information derived from these plots will be used to update the Prognosis model so it includes the effect of dwarf mistletoe on Douglas-fir growth and yield projections. The addition of information from this study about plant communities and stand or environmental conditions that are associated with Douglas-fir dwarf mistletoe to management planning using Prognosis or other models will allow more accurate assessment of the impact of this disease.

LITERATURE REVIEW

BIOLOGY OF DOUGLAS-FIR DWARF MISTLETOE

Dwarf mistletoes (*Arceuthobium* spp.) are obligate, parasitic angiosperms in the family Viscaceae. Species in this genus are found throughout the Northern Hemisphere on many hosts in the Pinaceae and Cupressaceae families. The greatest diversity of dwarf mistletoe species occurs in western North America (Hawksworth and Wiens, 1972).

Douglas-fir dwarf mistletoe occurs principally on Douglas-fir. Both the coastal and Rocky Mountain varieties of Douglas-fir have been demonstrated to be susceptible even though large areas of the range of coastal Douglas-fir are free of infection (Wicker, 1969). *Arceuthobium douglasii* sometimes infects true firs (*Abies* spp.) and spruces (*Picea* spp.) that are closely associated with infected Douglas-fir, but these are rare or occasional events (Scharpf, 1993; Mathiasen, 1984; Mathiasen and Loftis, 1987). Ed Wicker (1974) believes that the association between Douglas-fir and this parasite has existed at least since the end of the last glacial period.

The aerial shoots of dwarf mistletoes contain chlorophyll and photosynthesize but contribute little to the parasite's nutrition. They are believed to function mainly in reproduction. Male and female plants are found in separate infections on the same host (Gill and Bedwell, 1949; Pierce, 1960; Baranyay and Smith, 1972). Flowering and pollination of Douglas-fir dwarf mistletoe occurs in the spring (Kuijt, 1955). Although it was once believed that dwarf mistletoes were primarily pollinated by insects (Kuijt, 1955; Stevens and Hawksworth, 1970), research by Player (1979) showed that it is more likely that *A. douglasii* is wind-pollinated.

The seeds of dwarf mistletoes are disseminated in late summer or fall. They are ejected ten to fifteen meters from the fruit by the explosive force of water pressure. With favorable winds they have been observed to travel more than thirty meters from the tops of trees (Scharpf, 1993). Once an infection is initiated, the disease progresses through the stand as long as live host trees are available within the flight range of the seeds. The rate of lateral spread depends on the host-parasite combination and stand structure and density. Studies in the southwestern U.S. showed that *A. vaginatum* averaged 0.3 to 0.6 meters per year of lateral spread in ponderosa pine (*Pinus ponderosa* Doug. ex Laws) stands (Dixon and Hawksworth, 1979). Spread is greatest in multi-layered and open stands (Baranyay and Smith, 1972; Knutson and Tinnin, 1980). However, trees are rarely infected before they are one meter tall because the target area of the crown is a factor in the probability of successful infection (Wicker and Shaw, 1967). Birds and small mammals also spread dwarf mistletoe seeds, but little is known of the extent to which they are responsible for long distance spread and the initiation of new infection centers (Hawksworth and Johnson, 1989; Tinnin et al. 1982; Knutson and Tinnin, 1980). Nicholls et al. (1984) and Zilka and Tinnin (1976) suggested that the habitat specificity and general behavior of many birds may be factors in their success as long-distance dispersal agents of dwarf mistletoe seeds.

Dwarf mistletoe seeds are sticky and adhere easily to foliage and twigs. Precipitation washes them down to twig junctions or other crannies where they germinate in the spring, form a 'holdfast' and penetrate the branch by mechanical or enzymatic action (Kuijt, 1955; Gill and Hawksworth, 1961). From four to six years are needed from infection to production of flowers on aerial shoots (Baranyay and Smith, 1972).

Dwarf mistletoes parasitize their host via a system of longitudinal strands in the inner bark and sinkers that grow perpendicular to the cambium and become integrated with the host xylem rays (Alosi and Calvin, 1984). Gradients in solute and water concentrations between the host and parasite are believed to cause movement of photosynthates and water to the mistletoe plant (Alosi, 1978).

This endophytic system of dwarf mistletoes can develop into localized or systemic infections. All dwarf mistletoe species are believed capable of developing into localized infections. Only a few, including Douglas-fir dwarf mistletoe, develop systemic infections (Hawksworth and Wiens, 1972). In localized infections, the endophytic system is confined to the area near the site of the original infection. Masses of flattened, distorted adventitious branches known as 'witches-brooms' develop in many, but not all, host-parasite combinations (Tinnin et al. 1982; Alosi and Calvin, 1984).

When systemic infections occur, the endophytic system elongates synchronously with the terminal bud of infected twigs rather than remaining at the site of the original infection. Aerial shoots are produced along the twigs, especially at branch whorls. Large brooms of adventitious twigs are formed (Tinnin et al. 1982). In Douglas-fir these twigs become abnormally elongated, but not swollen. Production of abnormally large numbers of unusually long twigs results in more biomass in infected than non-infected branches (Tinnin and Knutson, 1980). Briede et al. (1991) found that flush growth of non-infected Douglas-fir branches on infected trees was reduced, especially in the upper crown. They suggested that carbohydrates fixed by foliage in the brooms were absorbed by the parasite. The non-infected branches maintained the trees but some of their photosynthates were probably translocated to

the brooms. Thus, the brooms became a resource sink for nutrients and water from the entire tree.

Douglas-fir dwarf mistletoe is associated with high levels of tree mortality compared to many other dwarf mistletoe-host combinations (Hawksworth and Wiens, 1972). The extent to which this dwarf mistletoe species colonizes its host may be a factor in its lethal nature.

EFFECTS OF DOUGLAS-FIR DWARF MISTLETOE PARASITISM

Nutrient and water depletion by *A. douglasii* are probably responsible for increased susceptibility of mistletoe-infected Douglas-fir to other pathogens and insects. Decay fungi invade infected branches through cracks caused by emerging mistletoe shoots or wounds caused by brooms breaking from trees (Weir, 1916; Tinnin et al. 1982). Knutson and Tinnin (1980) reported that death of infected trees was often caused by Armillaria root disease caused by *Armillaria* spp. fungi.

Douglas-fir dwarf mistletoe and insects often interact to cause tree mortality (Stevens and Hawksworth, 1984). The flat-headed borer (*Melanophila drummondii* Kirby) commonly attacks dwarf mistletoe-infected Douglas-fir (Furniss and Carolin, 1977; Ciesla, 1989). Early observers in the West believed that outbreaks of Douglas-fir beetle (*Dendroctonus pseudotsugae* Hopkins) often originated in heavily infected stands (Weir, 1916; Pierce, 1960). However, later studies by Furniss et al. (1980) in Idaho found no correlation between the two.

Dwarf mistletoe-infected Douglas-fir are attacked by the western spruce budworm (*Choristoneura occidentalis* Freeman) in eastern Oregon. Filip et al. (1993) found that mortality occurred most often in stands with heavy Douglas-fir dwarf mistletoe infection and heavy defoliation. But Briede et al. (1991) pointed out that it is not clear whether budworms

preferentially attack mistletoe-infected trees, because rapid budbreak and shoot elongation in infected trees may make their needles unpalatable to emerging insects. Filip and Parks (1987) found no preference by budworm for dwarf mistletoe-infected branches in northeastern Oregon.

The losses in timber yields due to reduced growth and higher mortality in Douglas-fir dwarf mistletoe-infected trees prompted much of the early interest in the disease (Weir, 1916; Pierce, 1960). Many studies have shown substantial reductions in yield from heavily infected Douglas-fir stands, including those by Baranyay and Smith (1972), Haglund and Dooling (1972), Filip et al. (1991) and Mathiasen et al. (1990a).

Reduced cone production or high percentages of sterile cones have also been reported from infected Douglas-fir by Weir (1916), Gill and Bedwell (1949), and Hawksworth and Wiens (1972).

Douglas-fir dwarf mistletoe infection is also of concern due to its contribution to extreme fire behavior and fire hazard. Brooms in trees or on the ground cause surface fires to be carried into tree crowns. They can become firebrands which cause spot fires (Alexander and Hawksworth, 1976). Brooms on the ground increase the residence time of surface fires, which increases the probability of tree cambium and soil damage (B. Rose, pers.comm.).

In recent years the role of dwarf mistletoes, especially Douglas-fir dwarf mistletoe in providing important elements of wildlife habitat has been recognized. The death of infected trees creates snags and gaps in the forest canopy. Douglas-fir dwarf mistletoe brooms provide animal nesting platforms, and thermal and hiding cover (Bull et al. 1989). Porcupines (*Erithizon dorsatum* Linnaeus) often roost in Douglas-fir dwarf mistletoe brooms during winter storms (Smith, 1982). Studies by Forsman et al. (1984) in western and central Oregon,

and Buchanan (1991) in central Washington, showed that northern spotted owls used Douglas-fir dwarf mistletoe brooms for twenty and sixty-six percent, respectively, of the nest platforms that were surveyed. Spotted owl nests have been found in Douglas-fir dwarf mistletoe brooms in the Southern Oregon Cascades (J. Goode and S. Armentrout, Wildlife biologists, Prospect and Butte Falls R.D., Rogue River N.F., pers. comm.). Seventy-five percent of the broom nests surveyed by Buchanan had also been used or constructed by northern goshawks (*Accipiter gentilis* Linnaeus). Reynolds (1982) found that cooper hawks (*A. cooperii* Vieillot) built nests in dwarf mistletoe-infected trees. Bull and Henjum (1990) observed great gray owls (*S. nebulosa* Forster) using the brooms for nest platforms. According to Larry Irwin (Wildlife biologist, National Council for Air and Stream Improvements, Corvallis, Oregon, pers.comm.) owls may prefer cavity nests where winters are wet (western Oregon) and platform nests where the climate is drier (eastern and southern Oregon). Since they do not construct their own nests, they are dependent on existing cavities or platforms. Nest site studies by Everett et al. (1992) have shown that spotted owls nested successfully in Douglas-fir dwarf mistletoe-infected stands with few large trees. They suggest that managing stands for Douglas-fir dwarf mistletoe might be one option to create components of spotted owl habitat in young stands in the future.

FACTORS AFFECTING THE OCCURRENCE AND SEVERITY OF DOUGLAS-FIR DWARF MISTLETOE

The primary environmental factors determining dwarf mistletoe occurrence and severity are the same as those affecting other plant species: light, moisture, temperature and nutrients (Tom Atzet, Ecologist, Siskiyou National Forest, pers.comm.). Of these factors, moisture and temperature have the greatest effect on plant distribution (Waring, 1969). These factors have direct effects on dwarf mistletoe, as well as indirect effects through the host trees (Merrill, 1983).

Sunny locations have been observed to favor dwarf mistletoes (Pierce, 1960). The reason is not well understood since dwarf mistletoes derive most, if not all their photosynthates from their hosts. Gill and Hawksworth (1961) cited studies showing the necessity of light for germination of some mistletoe seeds. However, Wicker (1974) reported that light was not necessary for germination of *Arceuthobium campylopodum* Engelm. or *A. laricis* Piper. Light may also affect dwarf mistletoe by its effect on host vigor. Parmeter (1978) cited several studies indicating that vigorous trees with full crowns had higher rates of infection, larger mistletoe shoots and more mistletoe seed production.

In shaded conditions dwarf mistletoe can remain alive without producing aerial shoots. If the level of light is increased, aerial shoots will be produced, allowing seed production and spread of the parasite (Baranyay and Smith, 1972). Thus, dwarf mistletoe might be expected to be more prevalent in open stands and in stands where the amount of sunlight is high due to aspect, slope, or topographic position.

Dwarf mistletoes need moisture for expulsion of the seed from the fruit and for germination (Kuijt, 1955). However, high levels of moisture can also promote the growth of

seed-destroying molds (Wicker, 1974). Precipitation can favor dwarf mistletoe establishment by washing seeds into suitable places for infection or inhibit it by washing the seeds onto the ground (Roth, 1959). Once established, moisture needed by the mistletoe plant is provided by the host. Kuijt (1960) pointed out "the value of the extreme morphological reduction of dwarf mistletoe to survival in xeric conditions". These studies suggest that the relationships between dwarf mistletoe infection and moisture are complex. Although very wet conditions might be unfavorable to Douglas-fir dwarf mistletoe infection and reproduction, it might thrive in droughty conditions.

Hawksworth (1969) hypothesized that cold temperatures limited the northern distribution of *A. vaginatum* and *A. douglasii* in the Rocky Mountains. Hawksworth and Johnson (1989) also suggested that the absence of *A. americanum* Nuttall ex. Engelm. from the highest elevation stands of Rocky Mountain lodgepole pine (*P. contorta* var. *latifolia* Engelm.) could be explained by the shortness of the growing season. The upper limit of *A. americanum* in the Rockies appeared to coincide with the -1°C mean annual isotherm. In general, dwarf mistletoes are believed to be more cold-sensitive than their hosts (Pierce, 1960). In laboratory studies *A. campylopodum* seeds required prolonged chilling periods but then germinated at a wide range of temperatures (Beckman and Roth, 1968). As far as is known, no such studies have been conducted with *A. douglasii*. However, this information suggests that Douglas-fir dwarf mistletoe might be less likely to occur at the lowest and highest elevations of the Douglas-fir range.

Nutrients required by dwarf mistletoes are absorbed from their host through the endophytic system of the parasite (Kuijt, 1955). Thus, Douglas-fir dwarf mistletoe, like other dwarf mistletoes, is dependent on the availability of nutrients that are translocated or

manufactured by the host. The soil type greatly affects the level of mineral nutrients available to the trees (Hobbs, 1992). Soil type can be identified directly or incorporated with climatic factors into measures of site productivity or 'site quality'.

The relationship between site quality and Douglas-fir dwarf mistletoe is complex because vigorous trees on good sites tend to have fuller crowns which intercept more mistletoe seeds, yet they are also more likely to have rapid height growth rates that confine the mistletoe to the lower crowns (Parmeter, 1978). This suggests that Douglas-fir dwarf mistletoe might be more likely to occur on good sites, but might be more severe on poor sites.

The variation in these four primary factors can be compared among sites by measurement of secondary environmental factors such as aspect, elevation, slope, stand density, etc. These factors act as surrogates for the primary factors. They are easier to measure, especially over large areas (T. Atzet, pers.comm.).

Hyper-parasitic fungi are another factor that may directly influence the occurrence and severity of Douglas-fir dwarf mistletoe. Several authors have suggested that their abundance and effect on dwarf mistletoes may be associated with favorable temperature and precipitation (Weir, 1915; Gill and Hawksworth, 1961; Wicker and Shaw, 1968; Knutson and Hutchins, 1979). However, the results of their studies varied widely. They were based on local observation and collections in various locations in the western United States, as well as on laboratory studies.

Because it is an obligate, host-specific parasite, disturbance and the patterns of forest succession that result also influence the occurrence and severity of dwarf mistletoes. According to Parmeter (1978), disturbance regimes that cause frequent changes in host species dominance tend to reduce dwarf mistletoe infestation, while perpetuation of the same

dominant host over time (whether a climax or seral species) favors the parasite. But, prolonged absence of disturbance where the host is seral may lead to its replacement by climax species and the elimination of the dwarf mistletoe that parasitizes it (Smith, 1972). Wicker and Leaphart (1976) observed that the greatest potential for development of dwarf mistletoes in the northern Rockies were in areas where their common hosts were the climax species. Yet Hawksworth (1969) stated that seral stages were generally more susceptible to dwarf mistletoes than climax forests, although he did not elaborate further.

Alexander and Hawksworth (1976) considered fire the most important natural disturbance agent affecting dwarf mistletoes in western North America. Mistletoe plants are killed by fire, but fire's most important effect on dwarf mistletoes is through its influence on forest succession (Wicker and Leaphart, 1976). Windthrow, insects and disease also affect dwarf mistletoes directly by killing host trees and influencing successional processes. Most recently, disturbance by humans in the forms of timber harvesting and fire suppression has affected dwarf mistletoe occurrence and severity.

DOUGLAS-FIR AND ITS ENVIRONMENT

Douglas-fir is one of the most widely distributed and commercially valuable conifers in western North America. Two varieties have been recognized, coastal Douglas-fir *(Pseudotsuga menziesii* var. *menziesii* (Mirb.) Franco) and Interior, or Rocky Mountain Douglas-fir (*P. menziesii* var. *glauca* (Beissn.) Franco). The Douglas-fir in the Southern Oregon Cascades is the coastal variety (Harlow et al. 1968).

Douglas-fir is intermediate in shade tolerance compared to its northwestern forest associates. Where moisture is limiting it may become less tolerant. Douglas-fir is considered

moderately drought tolerant. It is more tolerant of heat than any of its Southern Oregon Cascade associates other than ponderosa pine (*Pinus ponderosa*) or Oregon white oak (*Quercus garryana* Dougl. ex Hook.). It is moderately tolerant of nutrient deficiencies except nitrogen (Minore, 1979). These autecological characteristics suggest that conditions might be less than optimum for Douglas-fir on very dry sites in southwestern Oregon. When trees are weakened by unfavorable site and stand conditions, they may be less resistant to damage caused by insects and diseases (Oliver and Larson, 1990).

The fossil record indicates that Douglas-fir has been a major component of forests in the region since the mid-Pleistocene (one half million years b.p.), although its abundance has fluctuated greatly since then during climate changes associated with glacial and inter-glacial periods. During the warm, dry Xerothermic period (8,000 to 4,000 years b.p.) the abundance of Douglas-fir was greatly reduced in the Southern Oregon Cascades. It increased again after this period when a cooler, moister climate returned (Hermann, 1985; Hermann and Lavender, 1990).

Even though Douglas-fir is the most common conifer species in the southern Oregon Cascades today, its successional status is primarily that of a seral species in the predominant western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) and white fir (*Abies concolor* (Gord. and Glend) Lindl. ex Hildebr.) climax series. These series are found in comparatively warm, moist and cool, dry environments, respectively. Douglas-fir is intermediate in shade tolerance compared to either white fir or western hemlock. It is dependent on disturbance to maintain its presence in these series beyond the mid-successional stage (Agee, 1991). Today, many Southern Oregon Cascade stands in both the western hemlock and white fir series are at the mid-successional stage. Douglas-fir still dominates the overstory but is becoming less

abundant in the understory, especially in the western hemlock series (Atzet and McCrimmon, 1990).

Douglas-fir is a climax species in only about five percent of the area. These are typically the lowest elevation, warmest and driest forested sites in the Southern Oregon Cascade province (Atzet and McCrimmon, 1990).

VEGETATION CLASSIFICATION

The handbook Preliminary Plant Associations of the Southern Oregon Cascade Mountain Province (Atzet and McCrimmon, 1990) uses a classification system based on potential natural vegetation. This system was defined and implemented by R. and J.B. Daubenmire in the western United States in 1968 (Daubenmire, 1968). Associations are the most specific level in the hierarchy of this system. They are similar, stable combinations of species that occur across the landscape where environments are equivalent. Thus, associations are also indicators of the primary environmental factors on a site (Atzet et al. 1992). They are usually named after the climax species in the tree, shrub, and herb layers. Series are the associations grouped according to the climax tree species (Atzet and McCrimmon, 1990).

This classification system is useful to land managers because it provides, 1) a permanent system of land classification based on vegetation potential, 2) a system for classifying mature to near-climax plant communities, and 3) a framework for successional modeling. Also, the classification system can be used as a predictive system, since areas of the same type can be expected to show the same successional response to disturbance (Cooper, 1991). Layser

(1974) and Cooper (1991) suggest that predicting susceptibility to diseases would be a potentially appropriate use of plant community classifications.

Studies by McDonald et al. (1987) and Williams and Marsden (1982) have shown that plant communities can be used to predict the occurrence of Armillaria and laminated root rot diseases caused by the fungi *Armillaria ostoyae* (Romagnesi) Herink and *Phellinus weirii* (Murr.) Gilbertson, respectively, in the northern Rocky Mountains. Most studies that have reported relationships between dwarf mistletoes and plant communities were descriptive, rather than quantitative in nature (Mathiasen and Blake, 1984). However, Merrill's (1983) finding of a significant association between the occurrence and severity of *A. vaginatum* and the *Pinus ponderosa/Muhlenbergia montana* habitat type in Colorado suggests that habitat types may also be useful to predict occurrence and severity of other dwarf mistletoes such as *A. douglasii* if significant associations with plant communities exist.

OBJECTIVES

The specific objectives of this study were to determine:

Whether the frequency of occurrence of Douglas-fir dwarf mistletoe (DFDM) was significantly associated with environmental or stand conditions;

- whether it varied significantly among plant communities,

- and whether it would be significantly associated with the plant communities after accounting for the environmental and stand conditions.

Similarly, whether the severity of DFDM in infected plots was significantly associated with environmental and stand conditions;

- whether it varied significantly among plant communities,

- and whether it would be significantly associated with the plant communities after accounting for environmental and stand conditions.

HYPOTHESES

Hypothesis 1: Frequency of occurrence of DFDM is significantly associated with environmental or stand conditions.

Hypothesis 2: Frequency of occurrence of DFDM is significantly associated with plant communities.

Hypothesis 3: Frequency of occurrence of DFDM is significantly associated with plant communities after accounting for the environmental and stand conditions.

Hypothesis 4: Severity of DFDM is significantly associated with environmental or stand conditions.

Hypothesis 5: Severity of DFDM is significantly associated with plant communities.

Hypothesis 6: Severity of DFDM is significantly associated with plant communities after accounting for the environmental and stand conditions.

METHODS

This was an observational study. It was conducted on the Rogue River and Umpqua National Forests on the west side of the Southern Oregon Cascade Mountains in the Rogue and Umpqua River basins (Figure 1). The divide between the two river basins is also the boundary between the two National Forests. Plant communities in this area have been defined by climax series and plant associations in studies by Atzet and McCrimmon (1990).

The response variables, frequency of occurrence and severity of Douglas-fir dwarf mistletoe, were measured as the proportion of infected plots and the mean plot dwarf mistletoe severity rating, respectively. A plot was considered infected if DFDM was present on one or more trees.

Environmental and stand conditions at each plot were sampled by recording sixteen independent variables. These were selected through a review of the literature of previous studies of a variety of dwarf mistletoe species in the western U.S. The variables were: elevation (meters), mean annual temperature (°C), mean annual precipitation (centimeters), dry season precipitation (centimeters, May-September), site index (meters of height at 100 years of age), slope (percent), total basal area (square meters/hectare), Douglas-fir basal area (square meters/hectare), percent basal area in Douglas-fir (Douglas-fir basal area/ total basal area), number of tree canopy layers, age of each layer (years), diameter of the Douglas-fir at breast height (centimeters), aspect (north, east, south, west), topographic position (lower third, middle third, upper third of slope), topographic shape (concave, convex, flat) and soil

Middle Fork Willamette River

Cottage Grove RD
(not included in study area)

UMPQUA
NATIONAL FOREST

North Umpqua RD

North Umpqua River

Diamond Lake RD

Roseburg

Tiller RD

South Umpqua River

Crater Lake
National Park

I-5

Prospect RD

LEGEND

〰 River   *Rogue River*

—— District Boundary

▬▬ Forest Boundary

• Cities

Scale 1:1,000,000

Butte Falls RD

ROGUE RIVER
NATIONAL FOREST

• **Medford**

N

Ashland RD

Klamath Falls •

FIGURE 1. **Map of study area**

parent material (andesite, pyroclastic, basalt, granitic, sedimentary). These variables were not controlled in the study design.

The white fir (ABCO), western hemlock (TSHE), and Douglas-fir (PSME) climax series were chosen for this study from among the seven climax series in the Southern Oregon Cascades (Atzet and McCrimmon, 1990). Together they cover about 75 percent of the study area (Figure 2). They are the series where Douglas-fir is most commonly found. The plant associations that were sampled in these three series were chosen from those that had at least nine Ecology plots (to ensure the accuracy of association characteristics) and a high constancy of Douglas-fir.

In order to be assured of adequately sampling the plant associations and climax series, and to avoid making mistakes when identifying them, the plots used in this study were located at the centers of the permanent plots ("Ecology plots") that the ecologists used when they identified the plant associations. The ecologists selected the plot locations subjectively by driving throughout the entire study area and sampling what appeared to be mature, relatively undisturbed stands representing the range of vegetation types. Their location was random with respect to the occurrence and severity of dwarf mistletoe, because the presence or absence of the disease was not a factor in site selection and was unknown until the plots were visited (T.Atzet, pers. comm.).

I pre-selected a subset of the original Ecology plots from a master map to spread the plots in each association and series throughout the entire study area as much as possible. However, none of the plots on the Cottage Grove Ranger District of the Umpqua N.F. were

Legend:

Province Boundary
Forest Boundary

Climax Series

- ABAM
- ABCO
- ABCO/TSHE
- ABMAS
- TSHE
- TSME
- PICO
- PSME

Scale 1:920,000
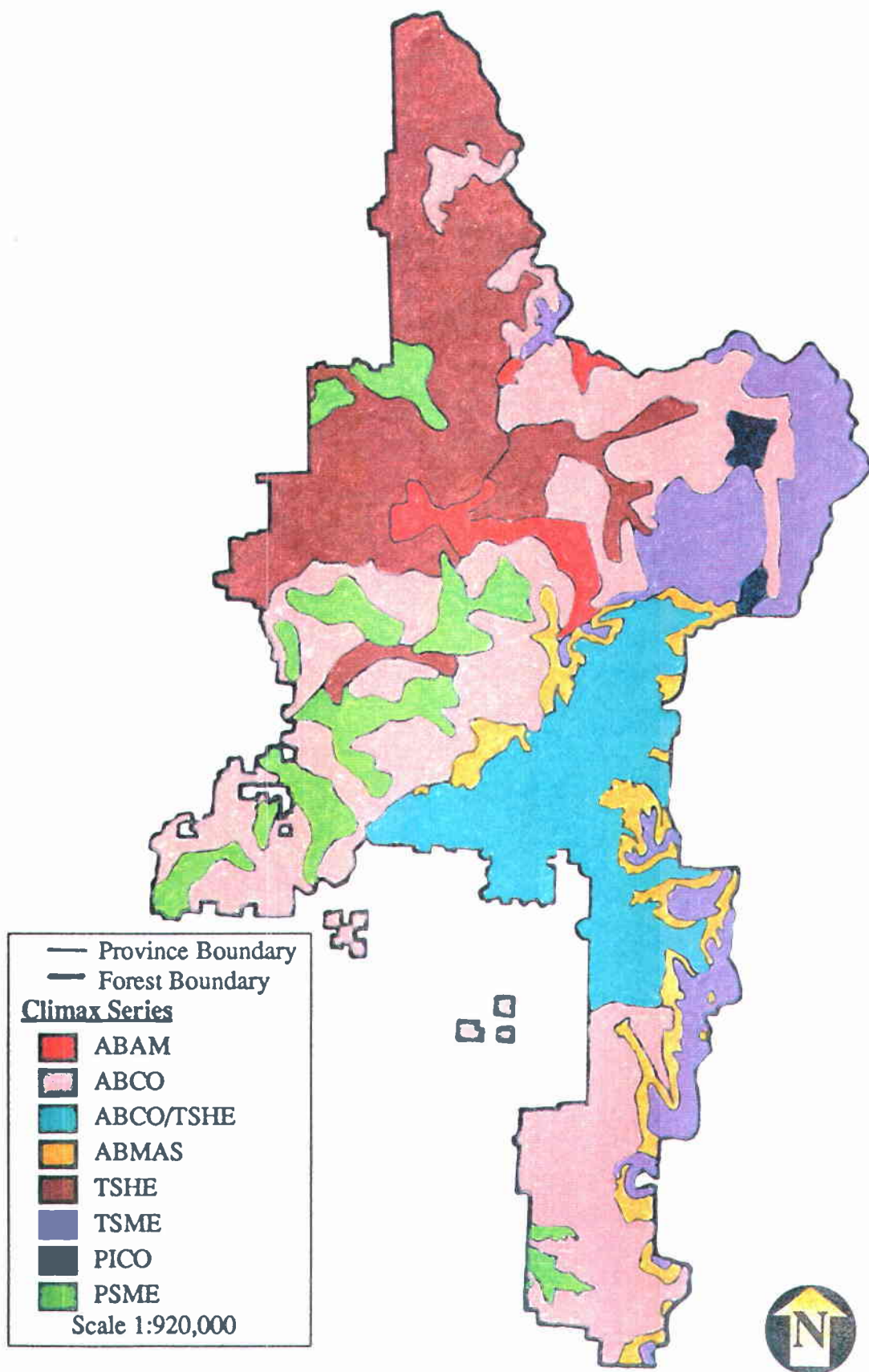
FIGURE 2. General location of climax series in the study area

included in this study because DFDM has never been observed on that district (Dave Ruppert, Silviculturist, Umpqua N.F., pers. comm.).

PILOT STUDY

In 1992 a preliminary survey of seventeen plant associations was conducted to estimate the variability in occurrence and severity of mistletoe among associations in order to calculate plot size and numbers. Two to five plots were sampled in each association, with a minimum of twenty Douglas-fir per plot (based on previous studies of DFDM and western spruce budworm in eastern Oregon by Filip and Parks (1987)).

The radius necessary to include twenty live Douglas-fir (greater than 12.7 cm dbh) in a full circle was estimated visually from the Ecology plot center. The distance from the plot center to each Douglas-fir was measured (to a maximum radius of seventy-five meters), and mistletoe severity estimated using the Hawksworth six-class rating system (Hawksworth, 1977). This system was developed by Frank Hawksworth in 1961 to rate dwarf mistletoe infections on ponderosa pine caused by *A. vaginatum cryptopodum*. The ratings were based on counting individual dwarf mistletoe plants. However, the system has also been used to rate *A. douglasii* on Douglas-fir in the southwestern U.S. (Hawksworth, 1977).

I used my own interpretation of Hawksworth's system to rate Douglas-fir dwarf mistletoe in this study. The area of each third of the live crown that was involved in a broom was estimated. If more than zero but less than half of the crown third was in a broom the rating was one. If more than half of the crown third was in brooms the rating was two. Thus one large broom could receive a higher rating than one small broom.

To determine plot size, the change in mean dwarf mistletoe rating (DMR) of infected plots was calculated as each Douglas-fir accumulated in the plot, adding outward from the plot center (Figure 3). The cumulative mean DMR with each additional tree was then averaged by plant association (Table 1). In five of the seven plant associations where DFDM was found, the mean DMR reached a plateau or declined by the fifteenth tree (Figure 4). This suggested that in most cases, fifteen Douglas-firs would include the most severe mistletoe present in a plot. Only one infected tree was required to determine the occurrence of DFDM in a plot. The data showed that an average of nine Douglas-firs per plot were accumulated before the first infected one was tallied. On this basis a minimum of fifteen Douglas-firs per plot were estimated to be adequate to measure both frequency of occurrence and severity.

The variability in frequency of occurrence of DFDM between plant associations was so large that most plant associations did not have enough Ecology plots available to provide an adequate sample. Thus, the associations were combined into their climax series. The proportions of infected plots in the three climax series were quite different (TSHE=10%, ABCO=41%, PSME=0%), so sample sizes were calculated for each series separately. Since no DFDM was found in the PSME series, the number of plots calculated for TSHE was used for PSME.

A formula for binomial distributions with a $Z_\alpha=0.05$ and $Z_\beta=0.2$ was used to calculate the sample sizes (T. Sabin, Statistician, OSU, pers.comm.). A practically significant difference (PSD) of 15% was selected as a compromise between 25% (which would have distinguished a change in mean DMR of two classes), and 10% (which would have required too many plots
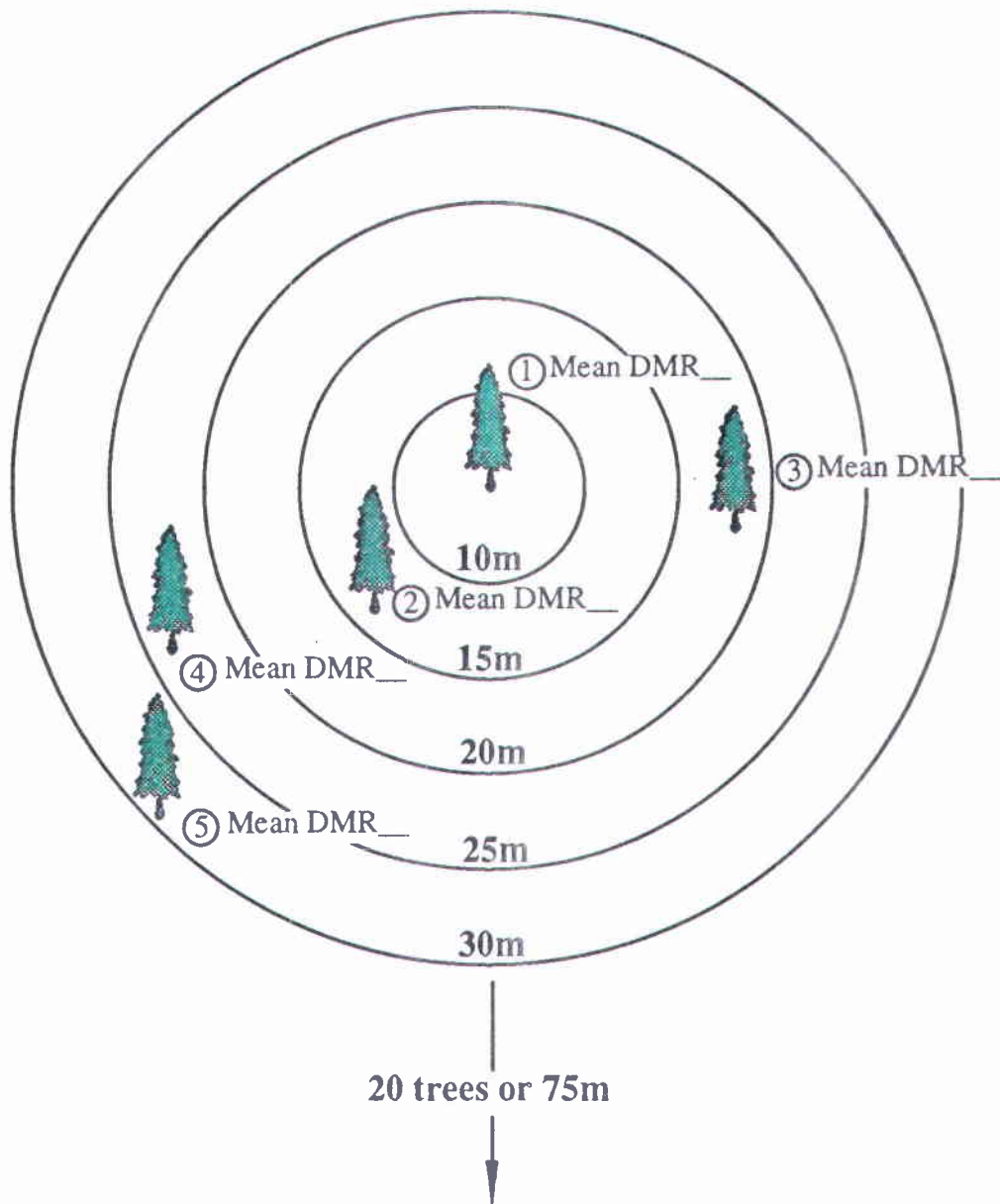
FIGURE 3. Pre-sample plot method

TABLE 1. Mean dwarf mistletoe rating as trees accumulate in plots [a]

TREE #	ABCO-ABMAS/CHUM	ABCO-CADE3/BENE	ABCO-PSME/BEPI	ABCO/ACGL/BENE	ABCO/AMAL/ANDE	ABCO/VAME/LIBOL	TSHE-ABAM/VAME
1	0.00[b]	1.00	0.00	1.00	1.50[c]	0.00	0.00
2	0.30	1.17[c]	0.00	0.50	1.13	0.00	0.00
3	0.27	0.89	0.00	0.33	0.92	0.00	0.00
4	0.35	0.92	0.00	0.25	0.81	0.00	0.00
5	0.32	1.00	0.00	0.35	0.90	0.00	0.00
6	0.40	0.94	0.00	0.29	0.75	0.17	0.00
7	0.43	0.90	0.14	0.32	0.68	0.14	0.00
8	0.53	0.92	0.31	0.35	0.69	0.13	0.00
9	0.58[c]	0.81	0.33	0.42	0.69	0.19	0.00
10	0.52	0.73	0.30	0.40	0.88	0.17	0.03
11	0.49	0.76	0.36	0.57	0.98	0.30	0.06
12	0.47	0.81	0.38	0.65	1.00	0.36	0.08
13	0.43	0.77	0.41[c]	0.71	1.00	0.38	0.08
14	0.44	0.71	0.38	0.75[c]	1.06	0.50	0.07
15	0.49	0.67	0.35	0.72	1.09	0.58	0.07
16	0.49	0.67	0.35	0.74	1.05	0.60	0.06
17	0.46	0.69	0.32	0.75	1.02	0.61	0.06
18	0.46	0.00	0.31	0.75	1.01	0.68	0.06
19	0.43	0.00	0.30	0.69	0.99	0.74	0.05
20	0.41	0.00	0.29	0.14	0.98	0.78[c]	0.05
21	0.43	0.00	0.28	0.13	0.95	0.76	0.05
22	0.41	0.00	0.26	0.13			0.05
23	0.41	0.00	0.25	0.12			0.10
24	0.39	0.00	0.24				0.14
25	0.38	0.00					0.15[c]
26	0.37	0.00					0.14
27	0.36	0.00					
28	0.34	0.00					
29	0.33	0.03					
30	0.33						
31	0.05						
32	0.05						
33	0.05						
34	0.00						
35	0.00						
36	0.00						
37	0.00						
38	0.00						
39	0.00						
40	0.00						
41	0.00						
42	0.00						
43	0.01						

a: average of plot ratings in each plant association

b: mean DMR = sum of plot DMRs / number of plots in association

c: highest cumulative mean DMR as trees accumulated outward from plot center
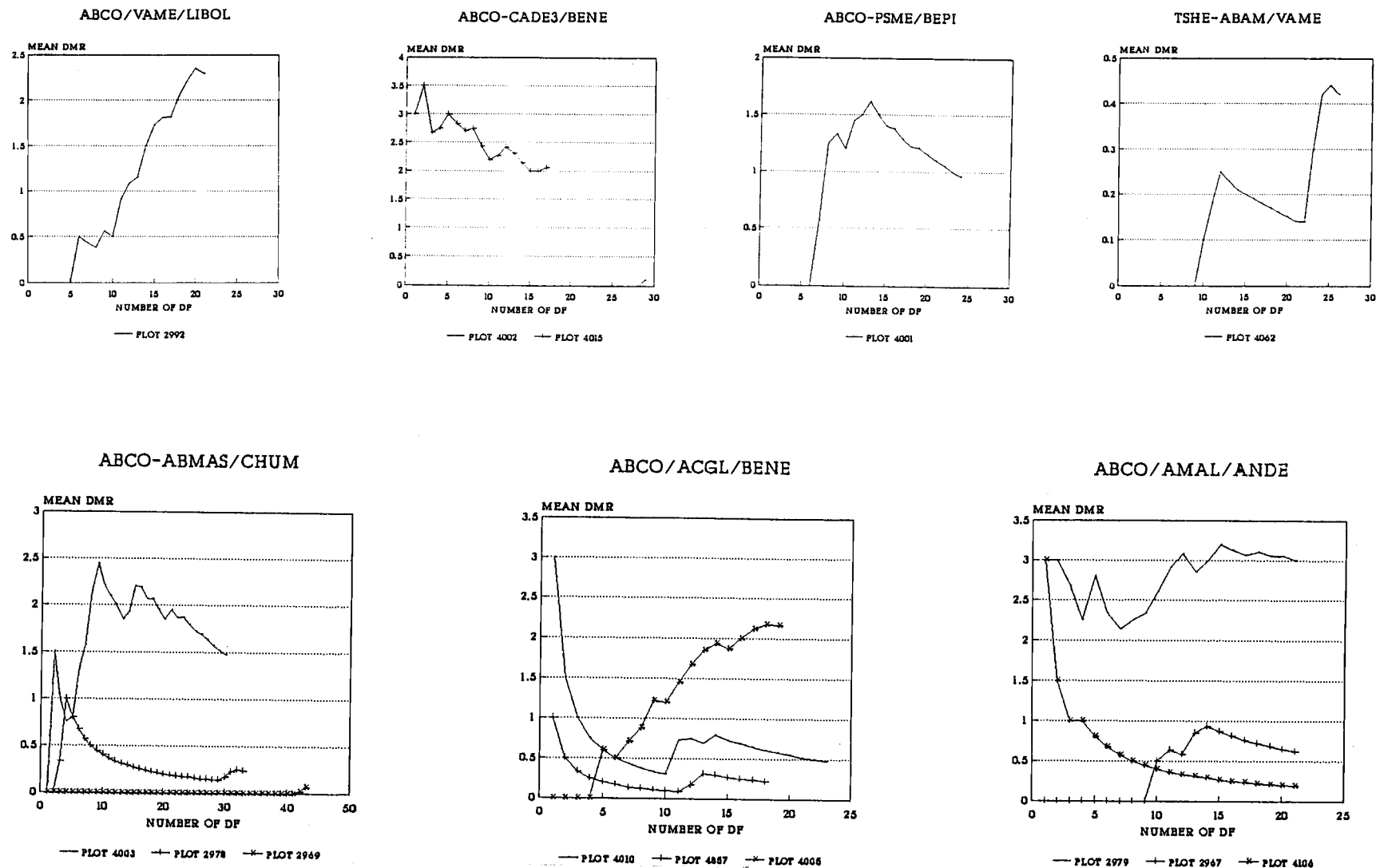
FIGURE 4. Mean dwarf mistletoe rating as trees accumulate in plots

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for the time available). The calculations resulted in a minimum sample of 167 plots; 41 plots each for the PSME and TSHE series and 85 plots for the ABCO series.

DATA COLLECTION

A total of 168 plots were sampled in 1993; 40 plots in the PSME series, 85 in the ABCO series and 43 in the TSHE series. One hundred and forty-two of these were Ecology plots, and 26 were new plots in mature stands identified previously by plant association by ranger district personnel. Data were collected for all the variables at each plot or from previously recorded Ecology plot data where appropriate. The plot centers were the original Ecology plot centers. In new plots the centers were selected by walking into the stand for fifty meters or the radius of the plot, whichever was greater, from a pre-selected point on the map.

The plot radius was determined at the Ecology plot center by visually estimating the distance necessary to include the nearest fifteen, live Douglas-fir, 12.7 cm DBH or larger in a full circle around the center. Once this radius was chosen, all trees meeting these criteria were included, even if there were more than fifteen of them. Each tree was rated for presence or absence, and severity of DFDM using the Hawksworth Six-class rating system (Hawksworth, 1977). Dwarf mistletoes on other host species were not recorded.

Studies of DFDM should exclude plots disturbed within the last ten years to give latent infections present before the disturbance time to develop enough to be visible. Although no studies have been conducted to determine the length of time needed for broom development, Tinnin and Knutson (1980) and Tinnin, et al (1982) suggested that a minimum of ten years would be necessary. For this reason, plots disturbed by logging or other human or natural causes within the last ten years were not sampled to avoid recording mistletoe as absent where

it may have actually been present, but removed by the disturbance. If plots were disturbed by partial cutting more than ten years old, the intensity of cutting was estimated as low, medium or high (low, no change in canopy closure or structure; medium, canopy opened but structure unchanged; high, canopy opened and structure changed). Disturbance greater than ten years old due to other factors was recorded only where mistletoe was present.

The mean values of the environmental and stand variables were calculated for each plant association and series over the whole study area (Tables 2-5) and for each series by Forest (Tables 6 and 7) to provide a comparison of conditions among the plant communities. The relative positions of the series according to mean annual temperature and precipitation were the same as that described by Atzet and McCrimmon (1990). Some of the plant associations had mean annual temperature or precipitation above or below those found by Atzet and McCrimmon. This indicates that the plots that were included in this study sampled above or below the average conditions province-wide for those associations (Figures 5 and 6). This was probably because not all of the original Ecology plots were used. In addition, eight new plots were sampled in the ABCO series and eighteen in the PSME series to compensate for Ecology plots that had been clearcut, recently burned, or could not be found.

TABLE 2. Mean values of continuous variables by plant association

Plant association	plots (number)	elevation (m)	matemp (°C)	maprecip (cm)	dsprecip (cm)	site index (m/100yr)	slope (%)	total ba (sq m/ha)	DF ba (sq m/ha)	% DF (%)	layers (number)	age (yrs)	meandbh (cm)
PSME/BENE/POMU[1]	7	925.7	8.4	146.6	19.0	38.7	49.0	81.7	80.4	98.3	2.1	150.7	46.1
PSME/GASH/POMU[1]	14	850.4	9.1	143.9	18.9	33.95	43.1	73.4	64.0	86.9	2.6	205.4	46.9
PSME/RHDI/PTAQ[1]	12	707.7	9.8	143.7	19.1	32.5	45.9	70.0	59.1	84.0	2.8	227.9	38.5
PSME/RHDI/CYGR	7	1010.7	8.0	86.6	15.0	33.5	35.4	71.0	53.1	74.7	2.3	167.1	35.1
ABCO-ABMAS/CHUM	11	1469.3	6.1	133.6	17.9	37.7	21.4	76.5	32.9	39.8	2.8	279.5	68.6
ABCO-CADE3/BENE	13	1182.0	7.4	135.5	18.1	37	30.8	73.1	47.8	65.3	2.7	236.5	64.3
ABCO-PSME/BEPI	12	1108.7	7.5	135.2	18.3	37.3	32.3	73.8	50.8	70.0	2.4	195.0	48.8
ABCO/ACCI/ACTR	9	1221.2	7.1	149.2	20.6	35.6	37.8	80.4	64.0	79.9	2.3	288.9	85.2
ABCO/ACGL/BENE	9	1230.1	6.9	116.8	15.8	36.2	23.0	72.7	32.0	41.2	2.6	152.8	40.2
ABCO/AMAL/ANDE	7	1357.7	6.6	126.9	17.4	37.9	26.4	79.7	45.4	49.0	2.7	243.6	70.7
ABCO/BENE-GASH[1]	11	955.2	8.4	146.3	19.5	36.0	33.3	68.5	50.2	70.2	2.7	270.0	59.5
ABCO/RUNI/ACTR	9	1212.7	7.1	154.8	20.6	37.2	20.9	77.9	56.2	75.3	2.6	203.3	72.1
ABCO/VAME/LIBOL	4	1379.3	6.3	120.5	17.0	37.3	11.3	64.5	26.3	41.8	3.0	322.5	78.3
TSHE-ABAM/VAME	5	1242.4	6.8	164.8	21.8	39.6	25.4	85.6	58.6	65.2	3.0	385.0	82.9
TSHE-PSME/GASH[1]	7	764.4	9.1	152.1	19.9	37.5	28.3	67.0	36.1	53.6	3.0	381.4	77.7
TSHE/ACCI/RUNI[1]	2	1180.5	7.0	171.0	20.0	33.5	47.5	71.5	34.5	48.5	3.0	375.0	68.4
TSHE/ACGL/LIBOL	5	1248.4	6.8	147.0	20.8	35.4	40.8	89.6	52.6	56.6	3.0	314.0	73.4
TSHE-ACMA/POMU[1]	5	528.6	10.4	149.6	19.4	40.8	56.2	74.6	41.4	57.0	3.0	276.0	80.5
TSHE/BENE/ACTR	5	1201.2	7.2	172.2	23.4	34.7	53.0	75.6	51.6	67.8	2.8	294.0	75.6
TSHE/BENE/LIBOL	8	1038.1	8.0	144.1	19.1	39.6	28.9	80.4	60.8	72.4	2.9	346.9	69.7
TSHE/RHMA/LIBOL	6	1081.7	7.7	166.8	21.3	32.5	28.2	73.0	52.0	71.3	2.8	337.5	82.0

1. plant associations where no DFDM was found

TABLE 3. Number of plots in each level of categorical variables by plant association

Plant association	soil parent material					plot aspect				topographic position			topographic shape			Forest	
	and	pyro	bas	gra	sed	north	east	south	west	lower	middle	upper	concave	convex	flat	Rogue	Umpqua
PSME/BENE/POMU[1]	1	2	3	1	0	0	1	3	3	1	2	4	0	6	1	2	5
PSME/GASH/POMU[1]	5	8	0	1	0	1	0	9	4	1	4	9	4	10	0	0	14
PSME/RHDI/PTAQ[1]	2	7	2	1	0	0	2	7	3	2	5	5	4	7	1	0	12
PSME/RHDI/CYGR	2	3	2	0	0	0	2	3	2	1	4	2	4	3	0	6	1
ABCO-ABMAS/CHUM	7	1	3	0	0	4	1	4	2	1	5	5	7	2	2	7	4
ABCO-CADE3/BENE	6	3	3	1	0	2	3	4	4	1	7	5	7	6	0	9	4
ABCO-PSME/BEPI	4	2	4	2	0	2	0	8	2	2	4	6	5	5	2	6	6
ABCO/ACCI/ACTR	2	1	6	0	0	2	3	1	3	0	3	6	5	4	0	1	8
ABCO/ACGL/BENE	6	0	3	0	0	2	1	4	2	4	2	3	7	1	1	9	0
ABCO/AMAL/ANDE	4	1	2	0	0	0	2	1	4	1	2	4	4	2	1	6	1
ABCO/BENE-GASH[1]	1	2	4	3	1	1	5	3	2	2	3	6	3	8	0	0	11
ABCO/RUNI/ACTR	3	0	4	2	0	2	2	2	3	4	3	2	7	2	0	4	5
ABCO/VAME/LIBOL	2	0	2	0	0	2	2	0	0	2	1	1	2	2	0	4	0
TSHE-ABAM/VAME	1	1	3	0	0	1	0	2	2	3	0	2	2	3	0	0	5
TSHE-PSME/GASH[1]	1	1	4	1	0	1	2	2	2	4	1	2	3	3	1	0	7
TSHE/ACCI/RUNI[1]	0	0	1	0	1	0	1	0	1	0	1	1	1	1	0	0	2
TSHE/ACGL/LIBOL	2	1	2	0	0	1	3	0	1	4	0	1	2	3	0	3	2
TSHE-ACMA/POMU[1]	3	0	2	0	0	3	1	0	1	4	0	1	2	3	0	0	5
TSHE/BENE/ACTR	1	3	0	1	0	0	0	3	2	0	2	3	3	2	0	1	4
TSHE/BENE/LIBOL	2	2	3	1	0	2	2	1	3	3	1	4	4	4	0	3	5
TSHE/RHMA/LIBOL	2	4	0	0	0	2	1	2	1	1	0	5	3	3	0	0	6

1. plant associations where no DFDM was found

TABLE 4. Mean, minimum and maximum values of continuous environmental and stand variables by series and Forest

Series		Elev (m)	Matemp (°C)	Maprecip (cm)	Dsprecip (cm)	SiteIndex (m/100yr)	Slope (%)	TotalBa (sq m/ha)	DFBa (sq m/ha)	%DF (%)	Layers (#)	Age (yrs)	Mean dbh (cm)
PSME	Minimum	451.0	7.0	76.0	15.0	21.3	0.0	27.0	23.0	39.0	2.0	75.0	26.1
	Mean	848.8	9.0	134.3	18.3	34.3	43.7	73.4	63.5	85.9	2.5	195.9	42.2
	Maximum	1295.0	11.0	177.0	22.0	48.8	77.0	116.0	106.0	100.0	4.0	400.0	77.6
ABCO	Minimum	774.0	6.0	101.0	15.0	18.3	0.0	41.0	0.0	0.0	1.0	70.0	24.3
	Mean	1215.7	7.1	136.7	18.4	36.9	27.7	74.4	46.3	60.9	2.6	238.4	63.7
	Maximum	1572.0	10.0	203.0	27.0	48.8	73.0	125.0	125.0	100.0	4.0	540.0	137.4
TSHE	Minimum	432.0	6.0	114.0	15.0	21.3	2.0	46.0	13.0	17.0	2.0	120.0	39.9
	Mean	1014.2	8.0	156.5	20.6	37.1	36.5	77.2	49.8	63.1	2.9	338.7	76.5
	Maximum	1426.0	11.0	190.0	25.0	54.9	77.0	111.0	92.0	100.0	4.0	800.0	110.8

TABLE 5. Number of plots in each level of categorical variables by series and Forest

Series	Soil parent material					Plot aspect				Topographic position			Topographic shape		
	And	Pyro	Bas	Gra	Sed	N	E	S	W	Lower	Middle	Upper	Concave	Convex	Flat
PSME	10	20	7	3	0	1	5	22	12	5	15	20	12	26	2
ABCO	35	10	31	8	1	17	19	27	22	17	30	38	47	32	6
TSHE	12	12	15	3	1	10	10	9	14	19	5	19	20	22	1

TABLE 6. Mean, minimum and maximum values of continuous environmental and stand variables by series and Forest

Series	National Forest		Elev (m)	Matemp (°C)	Maprecip (cm)	Dsprecip (cm)	SiteIndex (m/100yr)	Slope (%)	TotalBa (sq m/ha)	DFBa (sq m/ha)	%DF (%)	Layers (#)	Age (yrs)	Mean dbh (cm)
PSME	Rogue (n=8)	Minimum	963.0	7.0	76.0	15.0	27.4	0.0	41.0	27.0	39.0	2.0	80.0	29.1
		Mean	1050.0	7.9	93.3	15.5	35.4	25.3	68.0	55.3	81.6	2.3	153.8	36.1
		Maximum	1164.0	9.0	127.0	17.0	45.7	52.0	92.0	69.0	100.0	3.0	350.0	43.0
	Umpqua (n=32)	Minimum	451.0	7.0	101.0	15.0	21.3	9.0	27.0	23.0	39.0	2.0	75.0	26.0
		Mean	798.5	9.3	144.5	19.0	34.0	48.3	74.8	65.6	86.9	2.6	206.4	43.7
		Maximum	1295.0	11.0	177.0	22.0	48.8	77.0	116.0	106.0	100.0	4.0	400.0	77.6
ABCO	Rogue (n=46)	Minimum	914.0	6.0	101.0	15.0	24.4	0.0	41.0	0.0	0.0	2.0	70.0	28.9
		Mean	1297.0	6.8	121.5	17.0	37.7	21.6	73.6	37.7	49.4	2.7	220.0	59.2
		Maximum	1572.0	9.0	165.0	22.0	48.8	73.0	125.0	125.0	100.0	3.0	540.0	120.4
	Umpqua (n=39)	Minimum	774.0	6.0	101.0	15.0	18.3	4.0	46.0	9.0	11.0	1.0	80.0	24.3
		Mean	1119.9	7.6	154.7	20.2	35.9	34.9	75.4	56.5	74.5	2.6	260.0	69.0
		Maximum	1524.0	10.0	203.0	27.0	48.8	68.0	116.0	92.0	100.0	4.0	470.0	137.4
TSHE	Rogue (n=7)	Minimum	926.0	7.0	114.0	17.0	33.5	7.0	46.0	23.0	31.0	3.0	120.0	46.3
		Mean	1142.0	7.4	130.4	18.6	40.5	30.1	75.9	44.6	57.1	3.1	341.4	65.2
		Maximum	1286.0	8.0	165.0	25.0	51.8	62.0	97.0	78.0	84.0	4.0	800.0	108.2
	Umpqua (n=36)	Minimum	432.0	6.0	127.0	15.0	21.3	2.0	55.0	13.0	17.0	2.0	160.0	39.9
		Mean	989.3	8.1	161.6	21.0	36.4	37.8	77.5	50.8	64.2	2.9	338.2	78.7
		Maximum	1426.0	11.0	190.0	25.0	54.9	77.0	111.0	92.0	100.0	3.0	540.0	110.8
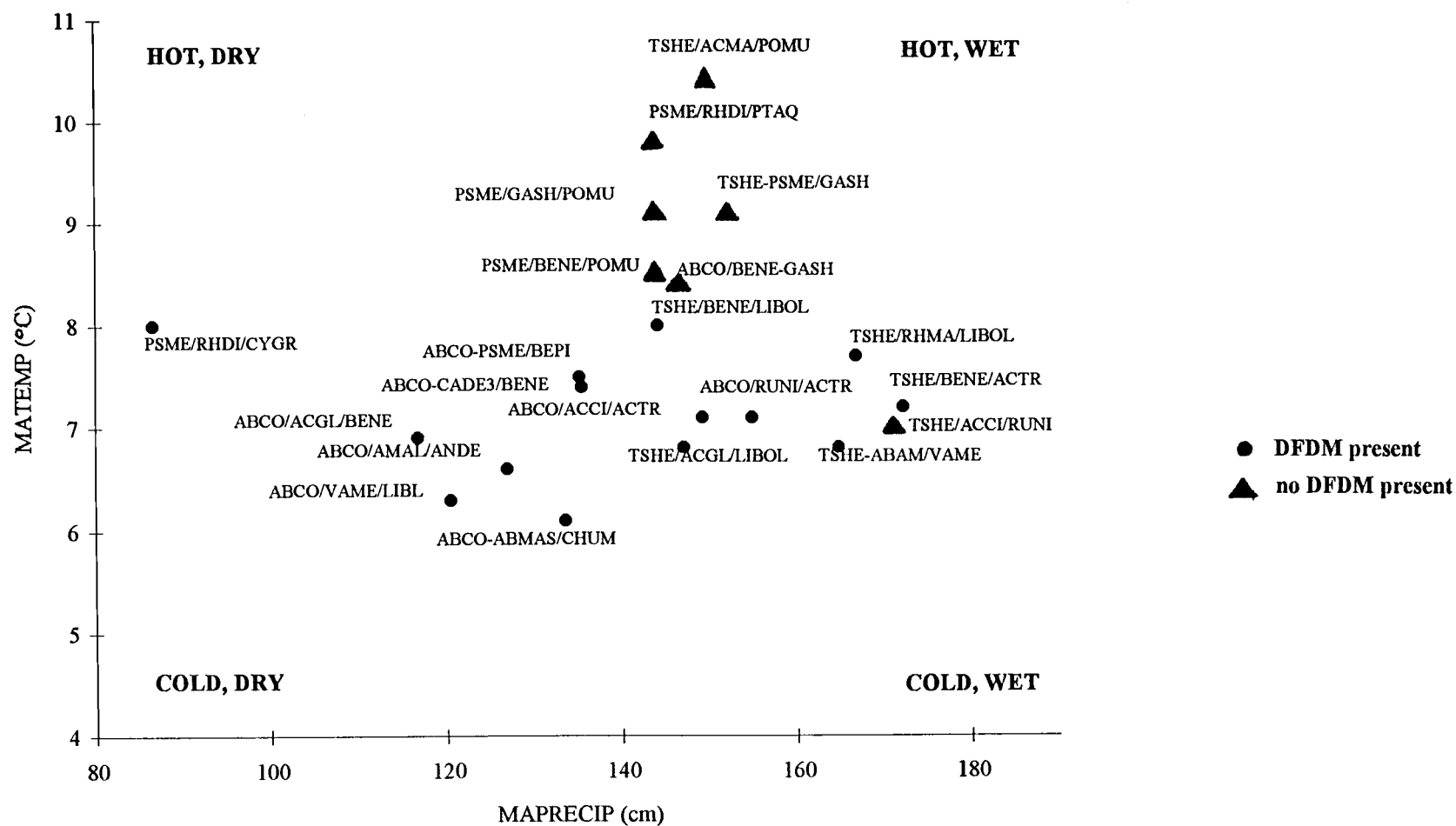
FIGURE 5. Ecograph of plant associations according to MATEMP and MAPRECIP of the sampled plots
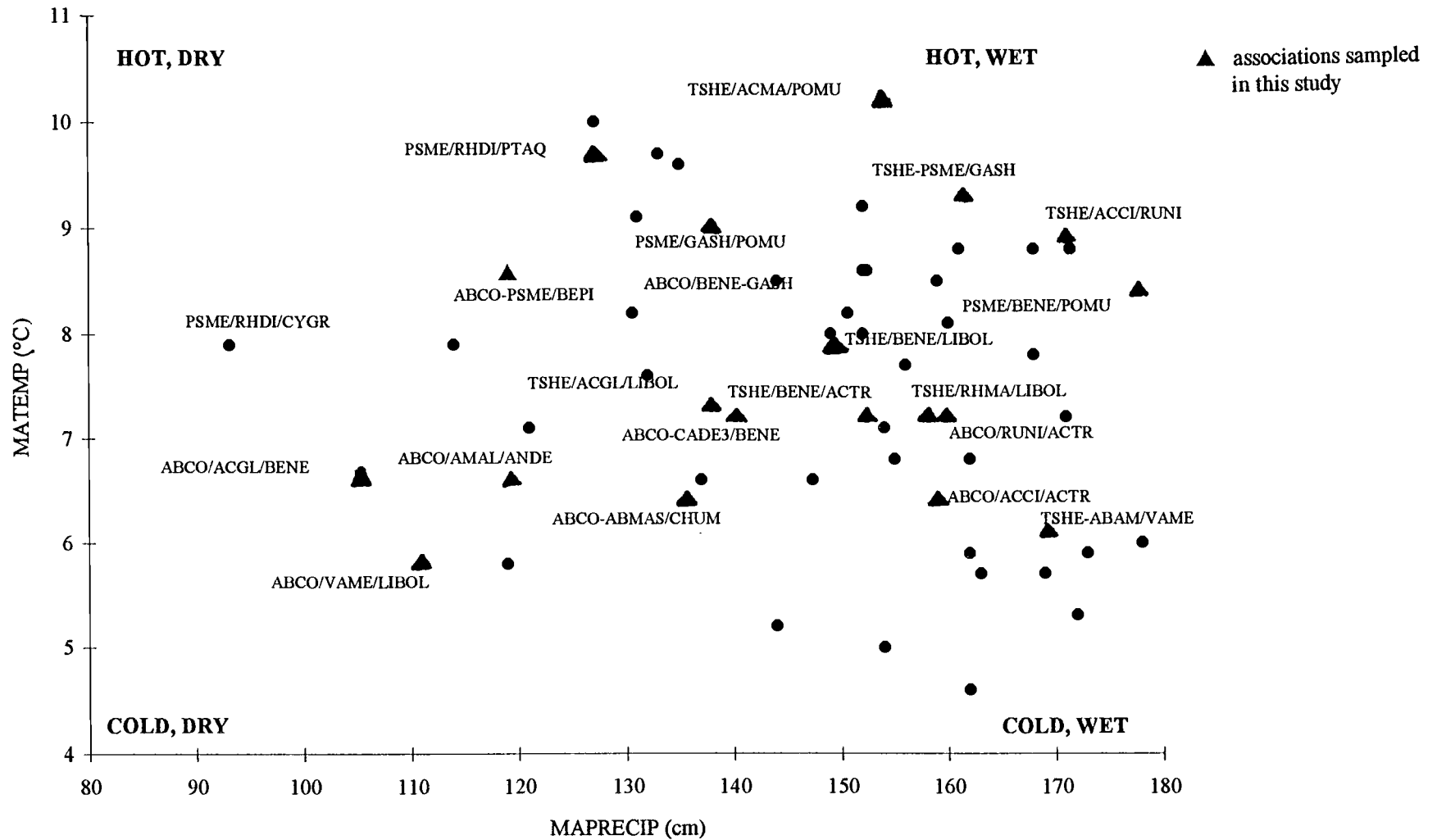
FIGURE 6. Ecograph of all plant associations with Douglas-fir in the Southern Oregon Cascade Mountain Province, using MATEMP and MAPRECIP from Atzet annd McCrimmon (1990)

TABLE 7. Number of plots in each level of categorical variables by series and Forest

Series	National Forest	Soil parent material					Plot aspect				Topographic position			Topographic shape		
		And	Pyro	Bas	Gra	Sed	N	E	S	W	Lower	Middle	Upper	Concave	Convex	Flat
PSME	Rogue	1	3	4	0	0	0	2	3	3	2	3	3	4	3	1
	Umpqua	9	17	3	3	0	1	3	19	9	3	12	17	8	23	1
ABCO	Rogue	25	2	16	3	0	11	6	15	14	12	18	16	31	11	4
	Umpqua	10	8	15	5	1	6	13	12	8	5	12	22	16	21	2
TSHE	Rogue	4	1	2	0	0	2	3	1	1	4	0	3	5	2	0
	Umpqua	8	11	13	3	1	8	7	8	13	15	5	16	15	20	1

STATISTICAL ANALYSIS

Frequency of Occurrence of DFDM

T-tests and the Wilcoxon rank sum test were used to test the significance (α=0.05) of the differences between the means of infected and non-infected plots among the continuous independent variables (Ramsey and Schafer, 1993). Chi-square analysis was used to test among the levels of the categorical independent variables (Ramsey and Schafer, 1993). Chi-square analysis was also used to test the homogeneity of the proportion of infected plots among the climax series and plant associations. Fischer's exact test was used instead of Chi-square when the expected cell counts were less than five (Ramsey and Schafer, 1993).

The stepwise logistic regression procedure identified which of the continuous environmental and stand variables contributed significantly to explaining the probability of occurrence of DFDM (keep and drop p-value = 0.05). Then, the slope and intercept of the regression lines for each series were compared to determine if they were significantly different among the series. Significant differences would indicate series-specific responses to the regression equation (Stafford and Sabin, 1994), which would suggest that there was something different about the occurrence of DFDM among the series that the individual variables did not explain.

To determine whether disturbance in the plots affected the frequency of DFDM, these procedures were repeated with several datasets. One dataset contained all the plots. A second dataset contained only plots where no cutting had taken place. Lastly, the T-tests and Chi-square analyses were repeated, excluding the infected plots that had other types of disturbance from the dataset of uncut plots.

Severity of DFDM

Since disturbance is known to affect the severity of DFDM (Parmeter, 1978), two datasets were also used in this analysis. One dataset contained only uncut, infected plots. The other had only totally undisturbed, infected plots. Mean DMR was calculated from the sum of individual Douglas-fir DMRs (0 to 6), divided by the number of Douglas-fir in the plot. The LOG transformation of the mean DMR was used in all the procedures because the ratio of the highest to lowest mean DMR was greater than 100. Simple linear regression was used to analyze the relationship between the LOG(mean DMR) and each of the continuous explanatory variables (Ramsey and Schafer, 1993). The stepwise multiple regression procedure (keep and drop p-value = 0.05) was then used to derive an equation that would best explain the variation in the LOG(mean DMR). One-way analysis of variance (ANOVA) and T-tests were used to test the equality of the LOG(mean DMR) among the three climax series and the plant associations, and among the levels of the other categorical explanatory variables (Ramsey and Schafer, 1993). The slope and intercept of the multiple regression lines for each series were compared to determine if they were significantly different using the same test that was used to compare the regression lines among the series in the analysis of DFDM frequency.

Disturbance by Partial Cutting

Chi-square was used to analyze the distribution of disturbance caused by partial cutting in the study area. The homogeneity in the proportions of cut and uncut plots was tested among series, plant associations, National Forests and Ranger Districts. To assess the effect of partial cutting on the distribution of DFDM, Chi-square analysis was used to test the homogeneity in the proportion of infected plots between cut and uncut plots overall, within series and among Forests and Ranger Districts.

RESULTS

ASSOCIATION OF FREQUENCY OF DFDM WITH ENVIRONMENTAL AND STAND VARIABLES

Among the continuous variables, there were significant differences in the mean elevation, mean annual temperature, mean annual precipitation, dry season precipitation, slope, Douglas-fir basal area and percent basal area in Douglas-fir between infected and non-infected plots when all the plots were compared (Table 8).

When only uncut plots were compared, the means of elevation, mean annual temperature, mean annual precipitation, and percent Douglas-fir were significantly different.

When infected plots with other disturbance were also excluded, the means of elevation, mean annual temperature, mean annual precipitation and dry season precipitation were significantly different. Percent basal area in Douglas-fir was suggestive, but not conclusively different. The mean site index, total basal area, number of layers, mean dbh and age of the oldest layer were not significantly different between plots with and without DFDM, whether all or only uncut plots were compared, or when the infected plots with other disturbance were also excluded.

For categorical variables, the proportions of infected plots were significantly different only among the types of soil parent material (Table 9). Plots on pyroclastic parent materials contributed most to the χ^2 value, having far fewer infected plots than expected. The proportions of infected plots were not significantly different among levels of aspect, topographic position or topographic shape. The results of these χ^2 tests were the same

TABLE 8. Differences in means of environmental and stand variables

Variable	Occur	All plots (no=127, yes=41)				Uncut plots (no=77, yes=20)				Without infected, disturbed plots (no=77, yes=14)[1]		
		Mean	SE	P_{TTest}	P_{Wilc}	Mean	SE	P_{TTest}	P_{Wilc}	Mean	SE	P_{TTest}
Elev	N	1000.11	23.83	0.00	0.0001	930.18	30.34	0.00	0.0001	930.18	30.34	0.00
	Y	1314.24	18.83			1297.90	25.40			1315.36	32.92	
Matemp	N	8.20	0.12	0.00	0.0001	8.52	0.15	0.00	0.0001	8.52	0.15	0.00
	Y	6.59	0.10			6.60	0.13			6.57	0.17	
Maprecip	N	145.36	2.22	0.0002	0.0003	146.48	2.67	0.006	0.01	146.48	2.67	0.0006
	Y	128.24	4.12			129.85	5.61			122.07	6.48	
DSprecip	N	19.29	0.25	0.009	0.005	19.31	0.30	0.13	0.09	19.31	0.30	0.01
	Y	17.95	0.46			18.25	0.73			17.21	0.81	
Site Index	N	36.30	0.63	0.91	0.91	35.80	0.79	0.85	0.73	35.80	0.79	0.65
	Y	36.40	1.14			36.10	1.67			34.80	2.16	
Slope	N	35.83	1.81	0.02	0.02	39.68	2.37	0.07	0.07	39.68	2.37	0.14
	Y	27.31	3.12			30.25	4.66			30.50	5.97	
TotalBA	N	75.48	1.43	0.42	0.34	76.58	1.96	0.51	0.63	76.58	1.96	0.32
	Y	73.06	2.83			79.50	4.34			81.71	5.17	
DFBA	N	54.45	1.96	0.003	0.001	56.18	2.44	0.17	0.08	56.18	2.44	0.52
	Y	41.56	4.21			48.25	6.35			51.93	7.98	
%BA in DF[2]	N	71.63	2.09	0.0001	0.0004	72.88	2.46	0.01	0.02	72.86	2.46	0.06
	Y	54.32	4.28			58.60	5.40			60.86	6.33	
# Layers	N	2.65	0.05	0.15	0.15	2.65	0.06	0.70	0.71	2.65	0.06	0.37
	Y	2.78	0.07			2.70	0.11			2.79	0.11	
Age	N	256.61	10.84	0.61	0.56	235.78	11.17	0.97	0.72	235.78	11.17	0.45
	Y	245.61	17.63			236.75	26.21			215.00	20.51	
Mean Dbh	N	60.37	2.20	0.17	0.15	56.66	2.79	0.16	0.19	56.66	2.79	0.68
	Y	66.50	3.77			65.59	6.08			59.68	6.93	

1. excludes plots with cutting or with blowdown, debris avalanches, road or spring edges or major skid trails
2. Analysis using the logit transformation caused no significant change in the results. The untransformed result is reported here.

TABLE 9. Chi-square and p values of categorical environmental variables

Variable	Level	All plots (n=168)					Uncut plots only (n=97)					Without infected, disturbed plots (n=91)				
		number plots	% total	% infected[1]	contribution to Chi-square[2]	P	number plots	% total	% infected[1]	contribution to Chi-square[2]	P	number plots	% total	% infected[1]	contribution to Chi-square[2]	P
aspect	north	27	16.1	40.7		0.14	15	15.5	20.0		0.99	13	14.3	7.7		0.68
	east	35	20.8	22.9			19	19.6	21.0			19	20.9	21.0		
	south	57	33.9	17.5			36	37.1	19.4			33	36.3	12.1		
	west	49	27.2	24.5			27	27.8	22.2			26	28.6	19.2		
topographic position	lower	41	24.4	14.6		0.16	24	24.7	16.7		0.74	23	25.3	13.0		0.81
	middle	50	29.8	32			27	27.8	18.5			25	27.5	12.0		
	upper	77	45.8	24.7			46	47.4	23.9			43	47.3	18.6		
topographic shape	concave	79	47	29.1		0.40	40	41.2	27.5		0.27	37	40.7	21.6		0.32
	convex	80	47.6	20.0			53	54.6	17.0			50	54.9	12.0		
	flat	9	5.4	22.2			4	4.1	0.0			4	4.4	0.0		
parent material	andesite	57	33.9	33.3	1.86	0.001	33	34.0	24.2	0.21	0.03	31	34.1	19.4	0.32	0.03
	pyroclastic	42	25.0	4.8	6.64		26	26.8	0.0	5.36		26	28.6	0.0	4.0	
	basalt	53	31.6	34.0	1.98		28	28.9	35.7	3.09		25	27.5	28.0	2.6	
	granitic	14	8.3	14.3	0.59		9	9.3	22.2	0.01		8	8.8	12.5	0.04	
	sedimentary	2	1.2	0.0	0.49		1	1.0	0.0	0.21		1	1.1	0.0	0.15	

1. Percentage of the total number of plots that were infected in each level of variable
2. includes contribution to Chi-square for variables with significant p-values

whether comparing all plots, only the uncut ones, or excluding infected plots with other disturbance.

Within the ABCO series, the means of elevation, mean annual temperature, mean annual precipitation, dry season precipitation, and percent of Douglas-fir between plots with and without DFDM were significantly different when all the plots were compared (Table 10). When the cut plots were dropped, the difference in means of percent Douglas-fir became insignificant.

The proportion of infected plots in this series was significantly different only among the types of parent material and then only when all the plots were considered (Table 11). Pyroclastic parent materials contributed most to the χ^2 value, having fewer plots than expected. When the cut plots were dropped the difference between the parent materials also became insignificant.

Within the TSHE series, only the means of elevation and mean annual temperature in infected and non-infected plots were significantly different when either all or only uncut plots were compared (Table 12). There were no significant differences among the levels of aspect, topographic position, topographic shape or parent material when either all or only uncut plots were tested (Table 13).

No comparisons were made of plots within the PSME series because only one infected plot was found.

TABLE 10. Differences in means of environmental and stand variables, ABCO series

Variable	Occur	All plots (No=53, Yes=32)				Uncut plots (No=28, Yes=16)			
		Mean	SE	P_{Ttest}	P_{Wilc}	Mean	SE	P_{Ttest}	P_{Wilc}
Elev	N	1138.62	31.09	0.000	0.0001	1087.21	40.65	0.0003	0.0006
	Y	1343.41	18.79			1318.13	27.39		
Matemp	N	7.53	0.15	0.000	0.0001	7.75	0.20	0.0002	0.0003
	Y	6.47	0.09			6.56	0.10		
Maprecip	N	144.17	3.43	0.0004	0.0008	151.68	4.06	0.002	0.005
	Y	124.31	3.86			127.44	6.41		
DSprecip	N	19.04	0.41	0.013	0.011	19.43	0.51	0.09	0.07
	Y	17.44	0.46			17.88	0.79		
Site Index	N	37.40	0.93	0.36	0.32	36.60	1.38	0.31	0.41
	Y	36.00	1.28			34.30	1.66		
Slope	N	27.91	2.36	0.89	0.73	31.36	3.30	0.90	0.92
	Y	27.34	3.71			32.13	5.50		
TotalBA	N	74.98	2.10	0.69	0.60	77.93	2.73	0.53	0.61
	Y	73.47	3.41			81.25	4.96		
DFBA	N	49.32	3.12	0.17	0.07	53.46	4.15	0.81	0.53
	Y	41.38	5.17			51.50	7.69		
%BA in DF[1]	N	65.53	3.62	0.05	0.06	67.71	4.44	0.39	0.42
	Y	53.25	5.16			61.00	6.54		
# Layers	N	2.58	0.08	0.39	0.39	2.57	0.12	0.77	0.79
	Y	2.69	0.08			2.63	0.13		
Age	N	245.00	14.48	0.46	0.39	228.39	18.65	0.51	0.55
	Y	227.30	18.58			208.75	22.21		
Mean Dbh	N	62.17	3.42	0.47	0.44	58.33	4.49	0.42	0.57
	Y	66.30	4.57			65.03	7.38		

1. Analysis using the logit transformation caused no significant change in the results. The untransformed result is reported here.

TABLE 11. **Chi-square and p values of categorical environmental variables, ABCO series**

Variable	Level	All plots (n=85)					Uncut plots only (n=44)				
		number plots	% total	% infected[1]	contribution to Chi-square[2]	P	number plots	% total	% infected[1]	contribution to Chi-square[2]	P
aspect	north	17	20.0	52.9		0.42	6	13.6	33.3		0.97
	east	19	22.4	31.6			10	22.7	30.0		
	south	27	31.8	29.6			15	34.1	40.0		
	west	22	25.9	40.9			13	29.6	38.5		
topographic position	lower	17	20.0	29.4		0.42	7	15.9	42.9		0.92
	middle	30	35.3	46.7			13	29.6	38.5		
	upper	38	44.7	34.2			24	54.6	33.3		
topographic shape	concave	47	55.3	38.3		0.97	23	52.3	43.5		0.50
	convex	32	37.7	37.5			19	43.2	31.6		
	flat	6	7.1	33.3			2	4.6	0.0		
parent material	andesite	35	41.2	42.9	0.25	0.03	15	34.1	46.7		0.11
	pyroclastic	10	11.8	0.0	3.76		8	18.2	0.0		
	basalt	31	36.5	48.4	0.95		15	34.1	46.7		
	granitic	8	9.4	25.0	0.34		5	11.4	40.0		
	sedimentary	1	1.2	0.0	0.38		1	2.3	0.0		

1. Percentage of the total number of plots thst were infected in each level of variable
2. includes contribution to Chi-square for variables with significant p-values

TABLE 12. Differences in means of environmental and stand variables, TSHE series

Variable	Occur	All plots (No=35, Yes=8)				Uncut plots (No=20, Yes=4)			
		Mean	SE	P_{Ttest}	P_{Wilc}	Mean	SE	P_{Ttest}	P_{Wilc}
Elev	N	965.17	47.66	0.01	0.008	860.80	69.87	0.04	0.04
	Y	1228.63	38.59			1217.00	51.97		
Matemp	N	8.26	0.23	0.01	0.01	8.80	0.33	0.02	0.02
	Y	6.88	0.30			6.75	0.48		
Maprecip	N	157.86	2.84	0.34	0.61	154.00	3.58	0.14	0.24
	Y	150.50	10.27			139.50	11.59		
DSprecip	N	20.69	0.41	0.76	0.68	20.60	0.58	0.58	0.46
	Y	20.38	1.19			19.75	1.89		
Site Index	N	36.70	1.40	0.59	0.61	36.60	1.48	0.07	0.13
	Y	38.50	2.88			43.40	3.38		
Slope	N	38.51	3.80	0.22	0.22	43.65	5.45	0.12	0.13
	Y	27.75	6.43			22.75	7.76		
TotalBA	N	78.40	2.60	0.29	0.37	81.35	3.73	0.35	0.46
	Y	72.00	5.36			72.50	9.14		
DFBA	N	52.29	3.62	0.10	0.12	53.45	4.96	0.13	0.13
	Y	38.88	5.65			35.25	4.87		
%BA in DF[1]	N	65.40	3.48	0.11	0.09	64.30	4.35	0.15	0.10
	Y	52.88	5.41			49.00	5.20		
# Layers	N	2.89	0.05	0.07	0.08	2.90	0.07	0.53	0.57
	Y	3.13	0.13			3.00	0.00		
Age	N	340.57	22.62	0.85	0.91	294.25	20.93	0.36	0.70
	Y	330.63	39.98			348.75	81.65		
Mean Dbh	N	77.90	3.46	0.34	0.33	77.80	4.79	0.39	0.37
	Y	70.43	5.74			67.82	8.94		

1. Analysis using the logit transformation caused no significant change in the results. The untransformed result is reported here.

TABLE 13. Chi-square and p values of categorical environmental variables, TSHE series

Variable	Level	All plots (n=43)					Uncut plots only (n=24)				
		number plots	% total	% infected[1]	contribution to Chi-square[2]	P	number plots	% total	% infected[1]	contribution to Chi-square[2]	P
aspect	north	10	23.3	20.0		0.88	8	33.3	12.5		1.00
	east	10	23.3	10.0			6	25.0	16.7		
	south	9	20.9	22.2			4	16.7	25.0		
	west	14	32.6	21.4			6	25.0	16.7		
topographic position	lower	19	44.2	5.3		0.11	13	54.2	7.7		0.22
	middle	5	11.6	20.0			3	12.5	0.0		
	upper	19	44.2	31.6			8	33.3	37.5		
topographic shape	concave	20	46.5	20.0		0.88	10	41.7	10.0		0.62
	convex	22	51.2	18.2			14	58.3	21.4		
	flat	1	2.3	0.0			0	0.0	0.0		
parent material	andesite	12	27.9	33.3		0.54	8	33.3	12.5		0.52
	pyroclastic	12	27.9	8.3			5	20.8	0.0		
	basalt	15	34.9	20.0			9	37.5	33.3		
	granitic	3	6.9	0.0			2	8.3	0.0		
	sedimentary	1	2.3	0.0			0	0.0	0.0		

1. Percentage of the total number of plots that were infected in each level of variable
2. includes contribution to Chi-square for variables with significant p-values

ASSOCIATION OF FREQUENCY OF DFDM AND PLANT COMMUNITIES

There were significant differences in the proportions of infected plots among the three climax series when all or only the uncut plots were compared, as well as when the infected plots with other disturbances were excluded (Table 14). Plots in the ABCO and PSME series contributed most to the χ^2 value. The level of infection was much higher in the ABCO series than either of the other two series. 37.6% of all plots in the ABCO series were infected, compared to only 2.5% of all PSME plots. 18.6% of all TSHE plots were infected. 34.6% of the uncut ABCO plots were infected, compared to 0% of uncut PSME plots and 16.7% of uncut TSHE plots.

There were no infected plots in the ABCO/BENE-GASH association (Table 15). The computer could not perform the χ^2 procedure when this association was included in the comparison of the proportion of infected plots among the associations. When the rest of the associations in the ABCO series were compared (which had DFDM in at least one plot), significant differences were found in the proportions of infected plots. In a comparison of all plots, the ABCO-ABMAS/CHUM, ABCO/ACGL/BENE, ABCO/AMAL/ANDE and ABCO/VAME/LIBOL associations had higher proportions of infected plots than expected (45%, 78%, 71%, and 75% respectively). ABCO/ACGL/BENE contributed most to the χ^2 value. The proportion of infected plots in the ABCO-CADE3/BENE, ABCO-PSME/BEPI, ABCO/ACCI/ACTR and ABCO/RUNI/ACTR associations was lower than expected (38%, 25%, 11% and 33% respectively). In this case, ABCO/ACCI/ACTR contributed most to the χ^2 value.

TABLE 14. Comparison of the proportion of infected plots among the climax series

Series	All plots (n=168)					Uncut plots only (n=97)					Without infected, disturbed plots (n=91)				
	number plots	% total	% infected[1]	contribution to Chi-square	P	number plots	% total	% infected[1]	contribution to Chi-square	P	number plots	% total	% infected[1]	contribution to Chi-square	P
PSME	40	23.8	2.5	7.9		29	29.9	0.0	6.0		29	31.9	0.0	4.46	
ABCO	85	50.6	37.7	6.1		44	45.4	36.4	5.3		40	44.0	30.0	5.55	
TSHE	43	25.6	18.6	0.59		24	24.7	16.7	0.18		22	24.2	9.1	0.57	
					0.00					0.001					0.008

1. Percentage of the total number of plots in each series that were infected

TABLE 15. Comparison of the proportion of infected plots among plant associations in the ABCO series

Plant association	All plots (n=85)					Uncut plots only (n=44)				
	number plots	% total	% infected[2]	contribution to Chi-square	P	number plots	% total	% infected[2]	contribution to Chi-square	P
ABCO-ABMAS/CHUM	11	14.9	45.5	0.01		2	5.6	0.0	0.89	
ABCO-CADE3/BENE	13	17.6	38.5	0.07		10	27.8	30.0	0.45	
ABCO-PSME/BEPI	12	16.2	25.0	0.92		8	22.2	37.5	0.09	
ABCO/ACCI/ACTR	9	12.2	11.1	2.15		4	11.1	0.0	1.78	
ABCO/ACGL/BENE	9	12.2	77.8	2.5		5	13.9	100.0	3.47	
ABCO/AMAL/ANDE	7	9.5	71.4	1.3		3	8.3	66.7	0.33	
ABCO/RUNI/ACTR	9	12.2	33.3	0.2		4	11.1	75.0	0.84	
ABCO/VAME/LIBOL	4	5.4	75.0	0.93		0.0	0.0	-	-	
ABCO/BENE-GASH[1]	11	-	0.0	-		8	-	0.0	-	
					0.05					0.03

1. this association was not included in statistical analysis
2. Percentage of the total number of plots that were infected in each plant association

When only uncut plots were compared, the ABCO/ACGL/BENE, ABCO/AMAL/ANDE and ABCO/RUNI/ACTR associations had higher proportions of infected plots than expected (100%, 67% and 75% of plots infected), while in the ABCO-ABMAS/CHUM, ABCO-CADE3/BENE, ABCO/ACCI/ACTR and ABCO-PSME/BEPI associations there was less infection than expected (0%, 30%, 0% and 38% of plots infected). Again, ABCO/ACGL/BENE and ABCO/ACCI/ACTR contributed most to the χ^2 value.

In the TSHE series, DFDM was found neither more or less frequently than would be expected from random occurrence of the disease. DFDM was not found at all in the TSHE-PSME/GASH, TSHE/ACMA/POMU or TSHE/ACCI/RUNI associations (Table 16). Among the TSHE associations where DFDM was found (in at least one plot) there were no significant differences in the proportions of infected plots. The frequency of infected plots in these associations ranged from 17% to 40% with all plots included, and 0% to 50% with only the uncut plots. Again, the computer could perform the χ^2 procedure only when the associations with no infected plots were excluded. These results were the same comparing all or only uncut plots.

The only infected plot in the PSME series was in the PSME/RHDI/CYGR plant association. It had been disturbed by cutting.

TABLE 16. Comparison of the proportion of infected plots among plant associations in the TSHE series

Plant association	All plots (n=43)					Uncut plots only (n=24)				
	number plots	% total	% infected[2]	contribution to Chi-square	P	number plots	% total	% infected[2]	contribution to Chi-square	P
TSHE-ABAM/VAME	5	17.2	40.0	0.28		4	28.6	50.0	0.64	
TSHE/ACGL/LIBOL	5	17.2	20.0	0.10		5	35.7	20.0	0.13	
TSHE/BENE/ACTR	5	17.2	40.0	0.28		2	14.3	0.0	0.57	
TSHE/BENE/LIBOL	8	27.6	25.0	0.02		2	14.3	50.0	0.32	
TSHE/RHMA/LIBOL	6	20.7	16.7	0.26		1	7.14	0.0	0.29	
					0.86					0.60
TSHE-PSME/GASH[1]	7	-	0.0	-		5	-	0.0	-	
TSHE-ACMA/POMU[1]	5	-	0.0	-		5	-	0.0	-	
TSHE/ACCI/RUNI[1]	2	-	0.0	-		0.0	-	0.0	-	

1. these associations were not included in statistical analysis
2. Percentage of the total number of plots that were infected in each plant association

ASSOCIATION OF FREQUENCY OF DFDM WITH PLANT COMMUNITIES, AFTER
ACCOUNTING FOR ENVIRONMENTAL AND STAND CONDITIONS

The logistic regression equation that best explained the probability of DFDM occurrence

in all the plots was:

$$LOG(\text{probability of DFDM occurrence}) = -33.72 + 11.23(MATEMP) - 0.03(MAPRECIP) - 0.91(MATEMP)^2 + 1.19(LAYERS)$$

There was a strong linear trend in the residual plot from this model. The fit was very poor

where the probability of mistletoe occurring was low. When the analysis was repeated using

only uncut plots, the 'best' model to explain the probability of DFDM occurrence was:

$$LOG(\text{probability of DFDM occurrence}) = 4.38 - 2.66(MATEMP) + 0.27(MAPRECIP) - 0.0012(MAPRECIP)^2$$

The residuals from this equation were closer to the estimated mean, but the linear trend

remained. It was not due to an interaction between MATEMP and MAPRECIP. The data

suggested this trend might be due to the lack of mistletoe in plots with mean annual

temperature greater than 8°C, or to some factor not included in the study (L. Ganio,

Statistician, OSU, pers. comm.). The analysis was repeated using plots with mean annual

temperatures less than 9°C but there was little change in the magnitude or trend of the

residuals. There was also little change in the residuals when the infected plots with other

types of disturbance were excluded. Therefore, although the terms in these two equations

suggested that mean annual temperature and mean annual precipitation were the most important factors associated with the probability of occurrence of DFDM, and the general nature of the relationship, the coefficients and T-statistics were of little value. According to David Hann (Biometrician, OSU, pers. comm.), even if the fit of these equations had been good, the results of logistic transformations are meaningful only for hypothesis testing. They have little value for predicting frequency.

Comparison of these regression lines among the climax series was not successful, probably because of the lack of fit of these models. Therefore, it was not possible to determine whether there were series-specific responses to the regression equations.

ASSOCIATION OF SEVERITY OF DFDM IN INFECTED PLOTS WITH ENVIRONMENTAL AND STAND CONDITIONS

There were significant linear relationships between LOG(mean DMR) and total basal area (p=0.04) and the age of the oldest layer (p=0.03) when the uncut plots were compared (Table 17). The relationship between the number of layers and LOG(mean DMR) was suggestive, but not conclusive (p=0.06). When the totally undisturbed plots were compared, LOG(mean DMR) showed a significant linear relationship only to total basal area (p=0.03, Table 19). The relationship to the age of the oldest layer became inconclusive (p=0.06). No other stand variables had significant linear relationships to the LOG(mean DMR) of infected plots. None of the environmental variables had significant linear relationships to the LOG(mean DMR) of infected plots (Tables 17-20). Since there were no significant differences in severity between the series (Table 21), the relationship of the LOG(mean DMR) to the environmental and stand conditions within series was not analyzed.

ASSOCIATION OF SEVERITY OF DFDM IN INFECTED PLOTS WITH PLANT COMMUNITIES

There was no significant difference in LOG(mean DMR) between the ABCO and TSHE series (Table 21). The average mistletoe rating in the ABCO series was 0.94. In the TSHE series it was 1.04. The PSME series was not included in the comparison because there were no uncut, infected plots.

The LOG(mean DMR) of uncut, infected plots was compared among plant associations in the ABCO and TSHE series where DFDM was found in at least one plot (Table 21). The average mistletoe rating ranged from 0.14 to 1.12 among associations in the ABCO series. Among associations in the TSHE series it ranged from 0.01 to 1.23. There was no significant difference in severity among associations in the ABCO series (p=0.42). The computer could not perform ANOVA with data from the TSHE series because there were not enough uncut, infected plots. Therefore, the analysis was repeated including plots with mean DMR of zero in plant associations where DFDM was found in at least one plot. This caused little change in the significance of differences among the mean DMRs of plant associations in the ABCO series (p=0.40). The difference among mean DMRs of plant associations in the TSHE series was also insignificant (p=0.21).

TABLE 17. **Results of regression analysis of LOG (mean DMR) on continuous independent variables, uncut plots**

Independent variable	Intercept	SE	Slope	SE	MSE	P	R^2
Elev	-0.48	3.16	-0.0001	0.002	1.46	0.96	>0.01
Matemp	3.05	2.93	-0.56	0.44	1.33	0.22	0.08
Maprecip	0.67	1.42	-0.01	0.01	1.38	0.36	0.05
DSprecip	0.08	1.55	-0.04	0.08	1.43	0.65	0.01
Site Index	-0.59	0.40	0.01	0.01	0.42	0.32	0.05
Slope	-1.10	0.46	0.02	0.01	1.33	0.24	0.08
TotalBA	1.57	1.03	-0.03	0.01	1.14	0.04	0.21
DFBA	-0.14	0.52	-0.01	0.009	1.36	0.3	0.06
% BA in DF[1]	-0.39	0.72	-0.004	0.01	1.44	0.72	>0.01
# Layers	-3.46	1.46	1.05	0.53	1.19	0.06	0.18
Age	-1.76	0.54	0.005	0.002	1.12	0.03	0.23
Mean Dbh	-0.86	0.72	0.003	0.01	1.44	0.74	>0.01

1. Analysis using the logit transformation caused no significant change in the results. The untransformed result is reported here.

TABLE 18. Results of analysis of variance (ANOVA) using LOG (mean DMR) of categorical independent variables, uncut plots

Independent variable	Level	Number plots	mean DMR	MSE	P	R^2
Aspect	north	3	1.10	1.26	0.95	0.02
	east	4	1.13			
	south	7	0.51			
	west	6	1.3			
Topographic position	upper	11	0.98	1.23	0.85	0.02
	middle	5	0.8			
	lower	4	1.1			
Topographic shape	concave	11	0.76	1.14	0.19	0.09
	convex	9	1.2			
	flat	0	-			
Parent material	andesite	8	0.65	1.12	0.17	0.19
	basalt	10	1.36			
	granitic	2	0.19			

TABLE 19. Results of regression analysis of LOG (mean DMR) on continuous independent variables, undisturbed, infected plots

Independent variable	Intercept	SE	Slope	SE	MSE	P	R^2
Elev	0.37	3.78	-0.0006	0.003	1.62	0.83	>0.01
Matemp	1.77	3.55	-0.34	0.54	1.57	0.54	0.03
Maprecip	1.00	1.76	-0.01	0.01	1.54	0.42	0.05
DSprecip	0.72	2.02	-0.07	0.12	1.58	0.57	0.03
Site Index	-0.56	0.46	0.01	0.01	0.46	0.36	0.07
Slope	-1.04	0.55	0.02	0.01	1.42	0.21	0.13
TotalBA	2.50	1.26	-0.04	0.02	1.10	0.03	0.32
DFBA	0.17	0.67	-0.01	0.01	1.49	0.32	0.08
% BA in DF[1]	-0.11	0.96	-0.005	0.01	1.61	0.72	0.01
# Layers	-1.62	2.31	0.42	0.82	1.59	0.62	0.02
Age	-2.19	0.90	0.008	0.004	1.20	0.06	0.26
Mean Dbh	-0.56	0.88	0.002	0.01	1.62	0.89	>0.01

1. Analysis using the logit transormation caused no change in the results. The untransformed result is reported here.

TABLE 20. Results of analysis of variance (ANOVA) using LOG (mean DMR) of categorical independent variables, undisturbed, infected plots

Independent variable	Level	Number plots	mean DMR	MSE	P	R^2
Aspect	north	1	2.18	1.75	0.77	0.10
	east	4	1.13			
	south	4	0.48			
	west	5	1.52			
Topographic position	upper	8	1.12	1.77	0.99	>0.01
	middle	3	1.00			
	lower	3	1.42			
Topographic shape	concave	8	0.9	1.41	0.21	0.13
	convex	6	1.5			
	flat	0	-			
Parent material	andesite	6	0.7	1.47	0.36	0.17
	basalt	7	1.68			
	granitic	1	0.26			

TABLE 21. Comparison of the LOG (mean DMR) of infected plots among series and associations with DFDM in at least one plot

		Number plots	Mean DMR	LOG Mean DMR	SE	P
Series	ABCO	16	0.94	-0.03	0.67	0.86
	TSHE	4	1.04	0.02		
	PSME	0	-	-		
ABCO plant associations[1]	ABCO-ABMAS/CHUM	2	0.00	0.00	0.41	0.40
	ABCO-CADE3/BENE	10	0.47	0.28		
	ABCO-PSME/BEPI	8	0.14	0.12		
	ABCO/ACCI/ACTR	4	0.00	0.00		
	ABCO/ACGL/BENE	5	0.89	0.49		
	ABCO/AMAL/ANDE	3	1.12	0.54		
	ABCO/RUNI/ACTR	4	0.33	0.25		
TSHE plant associations[2]	TSHE-ABAM/VAME	4	0.41	0.3	0.38	0.21
	TSHE/ACGL/LIBOL	5	0.01	0.01		
	TSHE/BENE/LIBOL	2	1.23	0.62		

1. includes 20 plots with mean DMR=0
2. includes 7 plots with mean DMR=0

ASSOCIATION OF SEVERITY OF DFDM WITH PLANT COMMUNITIES, AFTER ACCOUNTING FOR ENVIRONMENTAL AND STAND CONDITIONS

The multiple regression equation that best explained the variation in severity in uncut, infected plots was:

LOG(mean DMR) = - 2.086 + 0.006(ELEV) - 0.034(MAPRECIP) - 0.045(TOTALBA) + 0.0065(AGE)

$R^2 = 0.802$

TOTALBA and AGE were significant both when tested individually against LOG(mean DMR), and in this model (p_{totba}=0.0001, p_{age}=0.0002). ELEV and MAPRECIP were not significant when tested individually, but were significant terms in this model (p_{elev}=0.0009, p_{map}=0.0001). Regression of ELEV, MAPRECIP, TOTALBA and AGE terms on each other suggested linear relationships between ELEV and TOTALBA (p = 0.02) and MAPRECIP and AGE (p = 0.08). When the model was tested with these variables as interaction terms, none added significantly to the fit. However, added variable plots showed that ELEV and MAPRECIP did interact with TOTALBA and AGE in the model to explain the LOG(mean DMR) better than TOTALBA and AGE did alone. Together, TOTALBA and AGE explained only 34% of the variation in severity. When ELEV and MAPRECIP were added the four terms together explained 80% of the variation. Since this equation was based on a transformation of the response variable it is meaningful for testing hypotheses, but not as a predictor of severity (D. Hann, pers. comm.).

The best model to explain the variation in severity in totally undisturbed, infected plots was:

LOG(meanDMR) = 2.504 - 0.036(TOTALBA)

$R^2 = 0.325$

TOTALBA was the only variable with a significant linear relationship to LOG(mean DMR) in totally undisturbed plots. However, this model explained only 33% of the variation in severity. The spread of the residual plot away from the estimated mean was about twice that of the residual plot from the model using all the uncut plots. This suggested that there was not enough data in this model to determine significant relationships.

Since there were no significant differences in LOG(mean DMR) between series the regression lines were not compared. The lack of any significant differences between the series suggests that there would be no significant series-specific responses to the regression equations.

DISTURBANCE BY PARTIAL CUTTING

When comparisons of the proportion of partially cut and uncut plots or the proportion of infected plots in partially cut and uncut plots were made without regard to geographic location, there were no significant differences. 42.3% of the plots had been partially cut and 57.7% had no cutting. DFDM was present in 29.6% of the partially cut plots. 20.6% of the uncut plots were infected.

There were also no significant differences between the proportion of partially cut and uncut plots among the three climax series over the study area as a whole (p=0.09), (Table 22). There were significantly (p=0.005) fewer partially cut plots in the associations with no DFDM when they were compared to the associations with DFDM in at least one plot. There was also no significant difference in the proportion of infected plots between cut and uncut plots overall (p=0.18), or within the ABCO (p=0.8), or TSHE series (p=1.00), (Table 23).

Significant differences became apparent when the cutting was compared according to the geographic location of the plots. Partially cut plots were significantly more common south of the Rogue-Umpqua Divide (p=0.02), (Table 24). 54.1% of the plots on the Rogue River N.F. had been partially cut, compared to 35.5% on the Umpqua N.F. The frequency of partially cut plots ranged from 41% to 62% on ranger districts on the Rogue River N.F. On ranger districts of the Umpqua N.F. it ranged from 22% to 52%. The Butte Falls Ranger District on the Rogue River N.F. contributed most to the χ^2 value, having many more partially cut plots than expected. The Tiller Ranger District on the Umpqua N.F. had many fewer partially cut plots than expected.

When the proportions of <u>infected</u> plots were compared according to their location there were also significant differences found. DFDM was significantly more frequent south of the Divide, whether all plots, cut plots or uncut plots were compared (p<0.001), (Table 25). 54.1% of all the plots on the Rogue River N.F. were infected, compared to only 7.5% on the Umpqua N.F. 51.5% of the plots with partial cutting on the Rogue River N.F. were infected, compared to 10.5% on the Umpqua N.F. Among uncut plots 57.1% of those on the Rogue River N.F. were infectecd, compared to 5.8% on the Umpqua N.F. Again, the Butte Falls

Ranger District contributed most to the χ^2 value, with far more infected plots than expected. The Tiller Ranger District had fewer infected plots than expected.

Notice however, that there was little difference between the proportion of infected plots with and without cutting <u>within</u> the Forests. The changes in the frequencies of infected plots on the Rogue River N.F. from 51.5% to 57.1% and from 10.5% to 5.8% on the Umpqua N.F. were not significant ($p_{Rogue,}>0.5$, $p_{Umpqua}>0.25$), (Table 25).

TABLE 22. Comparison of partial cutting among series and associations with and without DFDM

		number plots	% total	% cut[1]	contribution to Chi-square[2]	P
Comparison of cutting among climax series	PSME	40	23.8	27.5		
	ABCO	85	50.6	48.2		
	TSHE	43	25.6	44.2		
						0.09
Comparison of cutting among plant associations where DFDM did and did not occur	associations with DFDM in at least one plot	110	65.5	50.0	1.56	
	associations with no DFDM at all	58	34.5	27.6	3.00	
						0.005

1. Percentage of the total number of plots with partial cutting in each level
2. includes contribution to Chi-square for variables with significant p-values

TABLE 23. Comparison of the proportion of infected plots by level of cutting, overall and within series

		number plots	% total	% infected[1]	contribution to Chi-square[2]	P
Comparison of the proportion of infected plots by level of cutting, overall study area	cut	71	42.3	29.6		
	uncut	97	57.7	20.6		
						0.18
Comparison of infected plots by level of cutting within the ABCO series	cut	41	48.2	39.0		
	uncut	44	51.8	36.4		
						0.80
Comparison of infected plots by level of cutting within the TSHE series	cut	19	44.2	21.1		
	uncut	24	55.8	16.7		
						1.00

1. percentage of the total number of plots that were infected in each level
2. includes contribution to Chi-square for variables with significant p-values

TABLE 24. **Comparison of partial cutting by geographic area**

Location	number plots	% total	% cut[1]	contribution to Chi-square	P
North of Divide (Umpqua)	107	63.7	35.5	1.15	
South of Divide (Rogue)	61	36.3	54.1	2.02	
					0.02
Districts north of Divide					
Diamond Lake	24	14.3	33.3	0.45	
Steamboat	26	15.5	42.3	0.00	
Glide	21	12.5	52.4	0.51	
Tiller	36	21.4	22.2	3.40	
Districts south of Divide					
Ashland	15	8.9	53.3	0.44	
Butte Falls	29	17.3	62.1	2.69	
Prospect	17	10.1	41.2	0.005	
					0.04

1. Percentage of the total number of plots with partial cutting at each location

TABLE 25. Comparison of the proportion of infected plots by geographic area and level of cutting

Location	All plots (n=168)					Uncut plots only (n=97)					Cut plots only (n=71)					P^3
	number plots	% total	% infected[1]	contribution to Chi-square	P^2	number plots	% total	% infected[1]	contribution to Chi-square	P^2	number plots	% total	% infected[1]	contribution to Chi-square	P^2	
North of Divide (Umpqua)	107	63.7	7.5	12.56		69	71.1	5.8	7.35		38	53.4	10.5	-		>0.25
South of Divide (Rogue)	61	36.3	54.1	22.04	<0.001	28	28.9	57.1	18.12	<0.001	33	46.5	51.5	-	<0.005	>0.50
Districts, Umpqua																
Diamond Lake	24	14.3	16.7	0.59		16	16.5	12.5	0.51							
Steamboat	26	15.5	7.7	2.98		15	15.5	6.7	1.42							
Glide	21	12.5	0.0	5.13		10	10.3	0.0	2.06							
Tiller	36	21.4	5.6	5.24		28	28.9	3.6	3.95							
Districts, Rogue																
Ashland	15	8.9	53.3	5.14		7	7.2	57.1	4.53							
Butte Falls	29	17.3	65.5	20.09		11	11.3	63.6	9.9							
Prospect	17	10.1	35.3	0.83	<0.001	10.0	10.3	50.0	4.19	<0.001						

1. Percentage of the total number of plots that were infected at each location

2. P-value of the comparison between plots on the Umpqua and Rogue NFs

3. P-value of the camparison between uncut and cut plots <u>within</u> each Forest

SUMMARY OF HYPOTHESES

In reference to Hypothesis 1, the null was rejected. The frequency of occurrence of DFDM was significantly associated with environmental conditions.

In reference to Hypothesis 2, the null was rejected. The frequency of occurrence of DFDM did vary significantly among the climax series. ABCO>TSHE>PSME.

In reference to Hypothesis 3, the null was not rejected. It was not possible to test whether the frequency of occurrence of DFDM was significantly associated with climax series after accounting for the relationships with the environmental variables.

In reference to Hypothesis 4, the null was rejected. The severity of DFDM was significantly associated with two stand variables, total basal area and the age of the oldest layer.

In reference to Hypothesis 5, the null was not rejected. The severity of DFDM did not vary significantly among the climax series.

In reference to Hypothesis 6, the null was not rejected. This hypothesis was not tested because the severity of DFDM did not vary significantly among the climax series.

DISCUSSION

FREQUENCY OF OCCURRENCE OF DFDM

The associations between the frequency of DFDM and three of the environmental conditions were consistent whether there was disturbance or not. DFDM was present at significantly higher elevations and on cooler, drier sites compared to where it was absent. It was never found in plots below 1066 meters elevation or at mean annual temperatures above 8°C.

The significance of the associations of DFDM and several other environmental and stand variables did change when disturbance was considered. DFDM was present in plots with significantly less dry season precipitation, lower basal area of Douglas-fir, a lower proportion of the basal area in Douglas-fir, on significantly gentler slopes and significantly less often on pyroclastic parent materials only when the partially cut plots were included in the analysis. When they were excluded, these differences became insignificant.

DFDM was much more common in the ABCO series than either of the other two series. One in three plots in this series were infected, compared to one in five TSHE plots and one in forty PSME plots.

Temperature, Precipitation and Elevation

The logistic regression equations suggested that mean annual temperature and precipitation were the most important factors explaining the probability of occurrence of DFDM. Both were negative, quadratic terms; suggesting that the probability of DFDM increased on cooler, drier sites, but not at a constant rate. Although the difference in elevation

between infected and non-infected plots was highly significant, it probably did not enter the regression equations because it is highly negatively correlated with mean annual temperature (Franklin and Dyrness, 1988).

An association between high frequencies of DFDM occurrence and high elevations was also found by Gottfried and Embry (1977) in Arizona. However, Hawksworth (1959) found no relationship between DFDM and elevation in New Mexico. Other species of dwarf mistletoes were more common at both high and low elevations in studies reported by Korstian and Long (1922), Hawksworth (1959), Gill and Hawksworth (1961), and Hawksworth (1969).

The results of this study were consistent with previous observations of the relationship between dwarf mistletoes and moisture although they associated occurrence with 'wet' or 'dry' sites or habitat types rather than precipitation. Weir (1916) found that most infected larch (*Larix occidentalis* Nutt.) were on dry slopes. Gill (1935) and Boyce (1938) associated heavy dwarf mistletoe infection with dry sites. Mathiasen and Blake (1984) cited studies by Daubenmire that associated *A. campylopodum* infection on ponderosa pine in Idaho with dry habitat types. Similarly, Merrill (1983) found that *A. vaginatum* was most prevalent on sites considered dry for ponderosa pine.

Douglas-fir Basal Area

The changes in significance of Douglas-fir basal area between analyses of datasets with various levels of disturbance made it difficult to interpret the role of this variable. But, the association of DFDM with plots that had lower percentages of the total basal area in Douglas-fir seemed consistent with the greater frequency of DFDM in the ABCO and TSHE series

than the PSME series. Both of these series had lower average proportions of basal area in Douglas-fir than the PSME series (Table 4). Acciaviatti and Weiss (1974) also found the incidence of *A. microcarpum* Engelm. on Engelmann spruce (*Picea engelmanii* Parry ex Engelm.) greatest in mixed conifer stands in the White Mountains of Arizona. However, Graham (1964) reported that DFDM in western Montana was most frequent in the Douglas-fir type, although he did not specify whether the Douglas-fir type was climax Douglas-fir or the early seral stage of stands with other climax species.

Soil Type

Although there is great variability in the soil types found in the study area, those derived from andesite and basalt parent materials are generally described as productive, deep and fertile. Soils derived from pyroclastic materials are described as generally young, shallow and infertile, except where they form a shallow layer over more developed soils (Atzet and McCrimmon, 1990). This suggests that the significant lack of DFDM on soils derived from pyroclastic parent materials was related to factors other than stress on the host caused by growing in shallow or nutrient-poor soil.

The association of DFDM with soil types in the literature is mainly anecdotal (Gill and Hawksworth, 1961). Korstian (1924) observed heavy *A. campylopodum* infection on basalt soils in central Idaho, but none on soils derived from granitic parent material. Very few studies have attempted to quantify a relationship between dwarf mistletoe and soil types. Larson et al. (1970) found significant differences in the frequency of *A. vaginatum* infection between two soil groups in Arizona. However, in a study in Colorado, Hawksworth (1968) found no association between the frequency of *A. vaginatum* and soil type.

Plant Communities

The differences in DFDM frequency among the plant communities appeared to reflect the plant communities' relationships to each other and to the variables associated with DFDM. Had I been able to compare the multiple regression equation containing the variables with significant associations to DFDM among the series, it might have been possible to test and quantify these apparent relationships. Thus, the significantly higher frequency of occurrence of DFDM in the ABCO series might have been associated with the fact that the ABCO series was found at comparatively higher elevations, and on cooler, drier sites with lower percentages of Douglas-fir basal area than either the TSHE or PSME series. The ABCO series occurred more often on andesite and basalt and less often on pyroclastic parent material than the TSHE or PSME series. DFDM was also associated with significantly higher, cooler and drier conditions and lower proportions of Douglas-fir basal area when the plots within the ABCO series were compared. These same characteristics also described ABCO plant associations where DFDM was most frequent.

Compared to the other two series, DFDM occurred in the TSHE series at about the level that would be expected from a random occurrence of the disease. This series was found over a greater range of elevations and mean annual temperatures than the other two series. It occurred about equally on andesite, basalt and pyroclastic parent materials. The variability in these conditions suggests that the series encompassed about equally environments both favorable and unfavorable to the occurrence of DFDM.

The low frequency of DFDM in the PSME series was consistent with the occurrence of this series on the lowest elevation, hottest sites, with the highest percentage of basal area in Douglas-fir. This series also had the highest proportion of plots on pyroclastic parent

materials. The significant association of DFDM with dry sites suggests that it should have occurred more often in the PSME series since this series occurs on the driest sites in the study area. However, most of the plots in the PSME series were on comparatively wet sites north of the Rogue-Umpqua Divide (Table 6). The only infected plot in the series was a partially cut plot south of the Divide in the highest, coldest and driest of the four plant associations.

The lack of DFDM in the PSME series was at odds with what Wicker and Leaphart (1976) reported from the Northern Rockies. There, they found the greatest development of DFDM on sites where Douglas-fir was the climax species. This difference may be due to differences in conditions between the Southern Oregon Cascades study area and the Northern Rockies. In the Northern Rockies, Douglas-fir apparently composes a majority of the stocking only where it is a climax species. Thus, where it is seral, the spacing between hosts may often be too great for tree-to-tree spread of DFDM. Fire frequency and fire behavior may also be different there, because the hottest, driest conifer forest sites are climax ponderosa pine rather than Douglas-fir as is the case in the Southern Oregon Cascades.

The lack of DFDM in the PSME series and higher frequencies in seral Douglas-fir in the ABCO and TSHE series is consistent with Hawksworth's (1969) suggestion that seral stages are more susceptible to dwarf mistletoes than climax forests.

When all the infected and non-infected plots were located on a map of the study area, striking regional patterns of DFDM occurrence were revealed (Fig. 7). The majority of infected plots were in the eastern half of the study area and south of the Rogue-Umpqua Divide. Based on information about the plant communities contained in the handbook Preliminary Plant Associations of the Southern Oregon Cascade Mountain Province (Atzet and McCrimmon, 1990), what is known about the history of timber harvesting in the study

area and review of the literature on the effects of fire on dwarf mistletoe; I would speculate that this regional distribution of DFDM could be associated with several factors that were not included as variables in this study, but may affect the relationships that were observed.

Timber Harvesting History

One of these factors is the distribution and history of cutting in the study area. This factor may explain some of the differences in the occurrence of DFDM among the plant communities. Cutting distribution and history may also explain some of the associations between environmental conditions and DFDM where these conditions were associated with plant communities that were concentrated in areas with different cutting histories.

Clearcutting appeared to be extensive at mid to low elevations on the North Umpqua Ranger District (pers. obs.). However, many Ecology plots were still available in mature stands at mid to low elevations on this district and elsewhere north of the Rogue-Umpqua Divide. These plots were sampled without finding any DFDM, suggesting that it might have been uncommon before clearcutting began in the area.

Clearcutting was also widespread on the Prospect Ranger District, especially east of Highway 62 and north of Red Blanket Mountain. In this area very few Ecology plots or mature stands were available for sampling. However, it is known that the district was aggressive about locating clearcuts where stands were infected with DFDM (D. Ruppert, Silviculturist, Umpqua N.F., pers. comm.). This policy was probably part of the Rogue River National Forest DFDM control program described by Kingsley (1978). Although it was impossible to confirm whether DFDM was present or absent prior to clearcutting the former

stands, this information suggests that DFDM may have been more common in this area in the past.

Many plots throughout the study area were disturbed by old selective, sanitation or salvage cutting. The extent of this cutting was not anticipated when the study was designed. According to Minore (1978), large-scale selective cutting began in the southern part of the study area (Ashland and south half of the Butte Falls Ranger Districts) in the early 1940s. In fact, most of the old cutting in plots throughout the study area appeared to be between twenty and fifty years old (pers. obs.). Minore (1978) attributed the demand for wood to World War II. This suggests that it is reasonable to believe that cutting in other parts of the study area might also have begun in the 1940s.

Although there were no significant differences in the occurrence of DFDM between cut and uncut plots overall or within the ABCO and TSHE series, differences in the results of analysis of some of the environmental and stand variables between data sets with and without the partially cut plots suggested that the partial cutting did have an effect on DFDM occurrence. The change in significance of these variables seemed consistent with the pattern of cutting in the study area. Early cutting on the Ashland and southern half of the Butte Falls Ranger Districts selectively removed large Douglas-fir (Minore, 1978). Where these trees were removed, the current basal area of Douglas-fir would be lower. Removing large trees could stimulate latent DFDM infections by increasing the amount of light reaching the remaining crowns. It might also favor mistletoe spread by reducing stand density (Baranyay and Smith, 1972; Parmeter, 1978). Partial cutting appeared to be concentrated on shallower slopes accessible with ground equipment (pers. obs.). Thus cutting may have been largely

responsible for the significant associations between Douglas-fir basal area, slope and the frequency of occurrence of DFDM that were observed (Table 8).

The mean dry season precipitation of infected plots increased and was no longer significantly different from non-infected plots when only uncut plots were compared (Table 8). This suggested that infected plots that were partially cut were in areas with less dry season precipitation. It seemed consistent with the fact that most of the partially cut plots were south of the Rogue-Umpqua Divide, where dry season precipitation was lower (Table 6). It did not explain why dry season precipitation became significant again when more infected, disturbed plots were excluded.

Similar studies of the relationship between environmental conditions and dwarf mistletoe frequency have also included selectively cut stands. Hawksworth (1968) used stands that had been cutover more than twenty years before they were sampled. Larson et al. (1970) used stands that had been cutover fifteen to twenty years prior to their study. Their results do not state any effect due to the cutting. According to Hawksworth (1959) the frequency of *A. vaginatum* would not be affected by partial cutting less than thirty years old. However, Graham (1959) found that districts on the Coeur d'Alene National Forest with a seventy year history of selective cutting and fire protection had a greater incidence of *A. laricis* than districts that had become accessible more recently. This information suggests that it might take twenty to seventy years for the frequency of dwarf mistletoes to increase by invasion of new sites after partial cutting. Since the age of most of the cutting in the study area appeared to be in this range, there may have been ample time for DFDM to spread into adjacent stands where no cutting was done.

Without baseline data on the frequency of DFDM prior to any timber harvest in the study area it is difficult to interpret the real significance of the relationships between the present level and distribution of cutting and DFDM. The level of infection may have been different in different areas to start with, and the criteria that were used to select trees for cutting may have favored or discriminated against DFDM.

Nonetheless, the match between districts with significantly more or fewer partially cut plots and the districts with significantly higher or lower frequencies of DFDM in uncut plots suggested that where cutting was extensive, DFDM may have spread into adjacent, uncut stands.

A similar pattern was observed among the plant associations. The ABCO/ACGL/BENE association had the highest frequency of DFDM in the ABCO series. It was sampled exclusively south of the Rogue-Umpqua Divide where the number of plots with cutting was significantly higher. The ABCO/ACCI/ACTR association, which had the lowest frequency of DFDM in the ABCO series, was sampled mainly north of the Divide where the number of plots with partial cutting was significantly lower. The effect of partial cutting might not have been significant when the series were compared using data from the whole study area, or even when comparisons were made within series, because plots in each series were dispersed throughout the study area enough to mask the effect on any particular group.

At the same time, there was no significant difference in the frequency of DFDM in partially cut and uncut plots within each Forest. Aho and Anderson (1959) reported that over 50% of the old growth Douglas-fir type on the Butte Falls and 12% on the Ashland Ranger Districts was already heavily infected with DFDM in 1958. This was only about fifteen years after cutting began in the area. According to the studies mentioned earlier, that would

probably not be enough time for a measurable increase in the occurrence of dwarf mistletoe. This suggests that DFDM might have been relatively more common on parts of the Rogue River N.F. even prior to the beginning of timber harvesting.

Even though the seven associations where DFDM was never found also had significantly fewer plots with partial cutting than the associations where there was DFDM infection, they did have cutting in 28% of the plots. Had DFDM been present prior to this cutting, it would be expected to have resulted in some DFDM still present due to development of brooms from latent infections. Yet this was not the case. This suggests that although cutting history seems to partially explain the presence and absence of DFDM, it does not explain all of it.

Fire History

Another factor that was not part of this study is the large-scale distribution of fire regimes in the study area and their relationship to the distribution of the plant communities. Fire regimes are an important factor in the distribution of dwarf mistletoes. Fire frequency and severity affect the distribution of host species through their effect on succession. Fire severity also affects the presence and distribution of infected trees. Low-severity surface fires can promote dwarf mistletoes by leaving infected overstory trees undamaged. Subsequent regeneration of the host species is then infected by seed from above. High-severity surface fires may reduce DFDM infection, because large brooms in heavily infected trees and brooms that fall and accumulate at their base create a fuel ladder that causes fires to burn into the crowns. High-severity crown fires eliminate or prevent dwarf mistletoe infection by removing the pathogen as well as its host from large areas. Subsequent re-establishment of host trees usually occurs much faster than mistletoe can invade from the edges or from isolated, infected

survivors (Alexander and Hawksworth, 1975; Parmeter, 1978; Zimmerman and Laven, 1984).

The TSHE series, which dominates the western two-thirds of the area north of the Rogue-Umpqua Divide, typically has a low frequency, high intensity fire regime (Atzet and McCrimmon, 1990). This type of fire regime typically occurs in areas of high precipitation where severe fires spread during dry, windy conditions (B. Kaufmann, Fire ecologist, OSU, pers.comm.). These types of fires may have prevented establishment of DFDM or eliminated it from much of the TSHE series. However, where the fire frequency is extremely low, or fire cannot spread or carry in tree crowns due to stand conditions, DFDM may be able to persist once established as long as Douglas-fir remains in the stand. This might explain why it was found only at elevations above 1200 meters or in stands with relatively open canopies (due to disturbance or site conditions) in the plots north of the Divide. Tinnin and Knutson (1973) and Tinnin et al. (1976) suggested a similar hypothesis to explain the rare, isolated occurrences of DFDM infection near the Calapooya Divide north of the study area on the Willamette National Forest. They suggest that these are relict patches of a previously more extensive distribution of the pathogen that have been protected from catastrophic disturbance for many years by protected locations and open or rocky conditions. Very infrequent but severe fire regimes may explain why there was DFDM in cold, wet associations such as TSHE-ABAM/VAME. Here, fires would probably occur only rarely; under the most extremely favorable weather conditions.

According to Atzet and McCrimmon (1990) the PSME series is affected by natural disturbance more than the other series, with fire being the primary agent. Descriptions of similar *Pseudotsuga*/hardwood and mixed conifer types by Agee (1993) suggest that surface

fires of varying intensity might be common, and severe crown fires might also occur. Severe surface and crown fires would tend to destroy infected trees or remove both host and pathogen from an area. Repeated fires might prevent establishment of DFDM. The three PSME associations where DFDM was absent were those found mostly on the hottest, but wettest PSME sites north of the Rogue-Umpqua Divide (Tables 2 and 3). The plots in the PSME series had the youngest average age of the oldest layer (Table 4). This suggests that these plots had the shortest time interval between severe, stand - replacing fires.

The fire regime of the ABCO series is extremely variable, due to the wide range of environments in which the series is found, according to Atzet and McCrimmon (1990). The one association where no DFDM was found, ABCO/BENE-GASH, was the warmest of the series and relatively wet. Atzet and McCrimmon (1990) suggest a fire regime of infrequent, high intensity fires with occasional surface fires, similar to much of the TSHE series. These infrequent, but stand replacing fires may have been enough to eliminate or prevent establishment of DFDM in this plant association.

Where DFDM was present in the ABCO series, fire regimes do not seem to offer much explanation of its occurrence. Both the ABCO/ACGL/BENE and ABCO/ACCI/ACTR associations were characterized by Atzet and McCrimmon (1990) as having a majority of fires that are infrequent and intense, with occasional underburns during dry years. Years of fire suppression could be a factor because periodic underburning has both positive and negative effects on dwarf mistletoe frequency (Alexander and Hawksworth, 1976). The great variability in the environment of this series coupled with the lack of specific fire history data discourages more speculation about the role of fire here. Other factors such as cutting history may have had a greater effect on DFDM in this series.

Other Disturbances

In addition to the disturbance caused by partial cutting that has been discussed already, other types of old disturbances had also occurred in eight infected plots (six were uncut and two were partially cut). These disturbances consisted of debris avalanches, blowdown and openings created by springs, rock outcrops and roadside clearing. When all these plots were excluded it left very few infected plots available for analysis. It became difficult to interpret the significance of the relationship between the occurrence of DFDM, dry season precipitation and Douglas-fir basal area because these disturbances also occurred in some non-infected plots, though they were not recorded during the data collection. Thus, those plots could not be excluded from analysis.

These confounding effects would not have occurred if all types of disturbance had been eliminated or controlled in the study design. Ideally, a study of dwarf mistletoe would be conducted only in undisturbed stands. Practically, this would be difficult due to the large sample required and the ubiquitous nature of partial cutting and other disturbances in the study area. One strategy to avoid partial cutting would have been to sample only in designated wilderness areas. For DFDM this would probably require enlarging the study area beyond the Cascades to include low elevation wilderness areas where Douglas-fir is common.

Where the other types of disturbances affected the entire plot, they would probably have caused a reduction in stand density similar to the effect of partial cutting (Parmeter, 1978). So, an increase in the occurrence of DFDM in disturbed plots should be reflected in infected plots having a lower mean basal area than non-infected plots. But, where disturbance created abrupt edges in otherwise dense stands, changes in DFDM occurrence would not be accounted for by the mean basal area.

The disturbances that were included in plots should have been quantified so they could have been used as covariates in the regression analyses (Stafford and Sabin, 1994). Total basal area or canopy closure might be sufficient, or the percent of basal area or canopy closure removed could be estimated. The length of time since the disturbance occurred should also have been estimated. Openings or abrupt stand edges that significantly changed the basal area or canopy closure should have been excluded from the plots.

Hyper-parasitic Fungi of DFDM

The effect of hyper-parasitic fungi on DFDM is another factor that was not considered in this study that may have affected the frequency of DFDM. Under environmental conditions that favor development of disease, fungi have been observed to destroy large proportions of the aerial shoots (Gill and Hawksworth, 1961). Three species that have been identified on DFDM in the western United States are *Wallrothiella arceuthobii* Peck, *Septogloeum gillii* Ellis and *Colletotrichum gloeosporioides* Penz (Wicker and Shaw, 1968). None have been identified in this study area, although fungal infection of DFDM shoots has been observed (pers. obs. and G. Filip, pers. comm). Information about the environmental conditions that are associated with these fungi is very sparse and variable so it would be difficult to speculate about their importance as limiting factors on DFDM in this area without further study.

SEVERITY OF DFDM

Where DFDM occurred, its severity in the absence of disturbance was most clearly associated with two stand variables, total basal area and age of the oldest layer. The severity of DFDM increased significantly as the total basal area decreased. In a similar study of *A. vaginatum* on ponderosa pine, mean DMR was also significantly higher in plots with low basal area (Merrill, 1983). Other studies suggest factors that might be responsible for this association. Higher light levels promote broom development (Kuijt, 1955). Brooms in open stands have higher levels of seed production than those in dense, shaded stands (Baranyay and Smith, 1972). According to Richardson and van der Kamp (1972) and Knutson and Tinnin (1980), an increase in severity is favored in open stands by the unobstructed seed flight within and between trees.

The severity of DFDM increased significantly as the age of the oldest layer increased. Hawksworth and Johnson (1989) and Mathiasen et al. (1990b) also reported an increase in mean DMR with increasing age, although their studies were conducted in stands that were younger than most of the stands in this study. Parmeter (1978) suggests that in old stands where height growth is minimal, severity will increase until the entire tree crowns are eventually affected.

The positive correlation between age and severity suggests that one would expect DFDM to become more severe when it occurred in areas with a history of infrequent, stand replacing fires because the long life of the host trees would allow infections to increase to high levels. However, once a fire did occur, high levels of infection would increase the potential for a surface fire to become a stand-replacing crown fire which would eliminate both host and mistletoe (Alexander and Hawksworth, 1976).

Stands with low basal area, especially those with minimal understory vegetation might escape being burned, even during catastrophic fires. If DFDM occurred on these sites it might be undisturbed for long periods of time (Tinnin et al. 1976). Stands with low basal area not caused by disturbance would be expected to occur on low quality sites. Typically these are found at high elevations where the growing season is short, where precipitation is low, or where the soil is rocky or shallow. Elevation and mean annual precipitation were significantly associated with severity in the multiple regression equation for uncut stands. This indicated that DFDM was most severe in older stands with low basal area on high, dry sites.

However, no significant relationship was found between severity and site index in this study (Tables 17 and 19). Previous studies have found dwarf mistletoes to be more severe on both high and low sites or to have no association with site (Gill and Hawksworth, 1961; Merrill, 1983; Hawksworth and Johnson, 1989). According to Parmeter (1978), the relationships between the two may be unclear due to the large number of factors that affect both tree growth (which is the basis of site indices) and the mistletoe parasite.

Previous studies also suggest that the severity of DFDM should have been significantly associated with the number of layers in the stands because the greatest spread of infection is from overstory to understory trees (Roth, 1953; Graham, 1959; Baranyay and Smith, 1972). But, in this study the relationship was only suggestive in uncut plots and insignificant when the plots with other disturbances were excluded. The lack of significance might actually have been due to a lack of sufficient data rather than a lack of association. In addition, the uncut plots were all in stands with either two or three layers, which may not have been enough variation to observe a difference in severity.

The association between high, dry sites and increasing severity suggests that DFDM would be more severe in the ABCO series, where it was also most frequent. Other studies of dwarf mistletoes have found that they were most severe where they occurred most frequently (Merrill, 1983; Mathiasen and Blake, 1984). Yet no significant difference in severity was found between the ABCO and TSHE series in this study. It is possible that the disease was about as severe in the TSHE series as it was in the ABCO series because the age of the trees in the oldest layer was greater in the TSHE series than in the ABCO series.

Had it been possible to include the PSME series in the comparison there might have been significant differences in severity among the series because the PSME series is not found on high, dry sites and had younger trees in the oldest layer than the other two series.

The significant increase in severity with decreasing basal area and increasing age raises concerns about the use of partial cutting in areas where DFDM occurs. Partial cutting often results in stands with low basal areas and is often prescribed because large, old trees are desired. Yet this would create the very stand conditions that were associated with severe DFDM in this study.

CONCLUSIONS

There were significant differences in the levels of environmental and stand variables between plots where DFDM did and did not occur. The plots where DFDM was present were at significantly higher elevations, had lower mean annual temperatures and lower mean annual precipitation compared to plots where DFDM did not occur. This was true whether the plots had been disturbed or not.

There were no significant associations between the occurrence of DFDM and aspect, topographic shape, topographic position, site index, total basal area, number of layers, age of the oldest layer or mean tree diameter.

The significance of the relationships between DFDM occurrence and dry season precipitation, slope, Douglas-fir basal area, the proportion of basal area in Douglas-fir and soil parent material changed depending on the level of disturbance in the plots being compared. In some cases the differences appeared to be due to differences in stand history among plots with various levels of disturbance. In other cases, the difference in significance may have been due to the fact that plots were dropped from the original dataset in order to make the comparisons among plots with different disturbance histories.

The occurrence of DFDM also varied significantly among the climax series. It was significantly higher than expected in the ABCO series, and lower than expected in the PSME series. The high frequency of DFDM encountered in the ABCO series was consistent with the occurrence of this series at relatively higher elevations and on cooler, drier sites compared to the PSME or TSHE series. Within the ABCO series, DFDM also occurred more frequently in plots and in plant associations found on higher, cooler, drier sites.

In the TSHE series, DFDM was found in about the proportion that would be expected if the disease had been distributed randomly across the landscape.

The occurrence of DFDM was significantly lower than expected in the PSME series. This came as a surprise, since the literature had suggested that DFDM would occur more frequently on warm sites, dry sites and on sites where a Douglas-fir climax would provide a high proportion of host trees in both over- and understory and easy tree-to-tree spread of infection.

The relative differences in the frequency of occurrence of DFDM among the series appeared to be related to the relative differences in their elevation, mean annual temperature and mean annual precipitation.

The geographic pattern of DFDM occurrence suggested that past timber harvesting practices, fire history and fire behavior might have had great influence on the present distribution of the disease in the Southern Oregon Cascades. Where clearcutting was aggressive, especially on the North Umpqua and Prospect Ranger Districts, little DFDM was found. The correlation with partial cutting was most evident when plots north and south of the Rogue-Umpqua Divide were compared. Districts north of the Divide had significantly fewer plots that had been disturbed by partial cutting and significantly lower frequency of DFDM. In contrast, districts south of the Divide had significantly more plots with evidence of partial cutting and significantly higher frequency of DFDM. This suggested that over a long period of time, partial cutting over large areas may have favored an increase in the occurrence of DFDM, even in adjacent, uncut stands.

However, other evidence suggests that DFDM may have been more common on parts of the Rogue River N.F. even before the advent of widespread timber harvesting. Baseline

data would be needed to thoroughly understand the effect cutting has had on the current distribution of DFDM in the study area.

In one third of the sampled plant associations, DFDM was never found, even though partial cutting had occurred in more than 25% of the plots in these associations. Six of the seven plant associations without DFDM were in the PSME and TSHE climax series. With one exception they were the warmest and wettest of all the plant associations that were sampled. The exception was an association in the TSHE series which was among the coldest and wettest sampled. The seventh plant association where no DFDM was found was in the ABCO series. It also was the warmest and wettest association in that series. This suggested that factors which are influenced by climate, like fire regimes, might also have influenced the frequency of occurrence of DFDM.

Fire regimes prior to organized fire suppression on wet sites, both warm and cold, probably included periodic, severe, stand-replacing fires which prevented the establishment of DFDM or eliminated most of the infection centers that were initiated. However, on the coldest, wettest sites and on rocky, open sites extremely infrequent fires may have allowed DFDM to persist where infection centers were initiated.

Thus, it could be that the significant associations between the occurrence of DFDM and the variables of elevation, mean annual temperature and mean annual precipitation were actually due to the relationship of these variables to the distribution of early timber harvesting practices and historic fire regimes in the study area, rather than to their direct effect on the mistletoe plants.

In contrast to the occurrence of DFDM, which was significantly associated with environmental variables, the level of severity was significantly related to two stand variables.

The severity of DFDM increased significantly as total basal area decreased and as the age of the oldest layer increased. The most severe DFDM was found in old, open stands on high, dry sites.

The lack of significant relationships between severity and the other environmental and stand variables may have been due to the small amount of data available for analysis from undisturbed plots. The lack of significance of the relationship between the number of layers and the severity of DFDM is especially questionable because it is at odds with what is known from previous research. It might be worthwhile to re-examine this relationship, particularly in light of plans to manage for multi-layered stand structure in areas designated as Late Successional Reserves (LSR) under the President's Forest Plan. Some areas designated as LSR in the Southern Oregon Cascades are infected with DFDM. If the severity of DFDM actually is associated with the number of layers in a stand, the effects of this disease may affect the ability to grow well-stocked stands of large, old Douglas-fir in these LSRs. At the same time, plant associations and climax series where DFDM was common may be appropriate areas to manage for habitat for the northern spotted owl because the DFDM brooms can provide the nesting platformas and thermal cover that these birds require.

The possible relationship of the occurrence and severity of DFDM to historic fire regimes and past timber harvesting practices also suggests implications for future forest management. Periodic stand-replacing fires and a history of clearcutting may be at least partially responsible for the lack of DFDM on low elevation, warm, wet sites in the Southern Oregon Cascades. Continuation of the current fire suppression policies and a reduction in clearcutting may allow conditions to develop that favor an increase in the frequency and severity of DFDM as long as stands on these sites are dominated by Douglas-fir.

The correlation between areas where partial cutting was extensive and areas with high frequency of DFDM, and the increase in DFDM severity in open stands and in older trees suggests that a return to partial cutting, which is often used in uneven-age management, may also favor an increase in the occurrence and severity of DFDM in the future. This is especially true where Douglas-fir is the climax species, because once established, DFDM will infect each new generation of its host. However, where Douglas-fir is seral, DFDM might actually decrease over the long run because partial cutting (or no cutting) and fire suppression may favor succession to non-host, climax species.

The amount of disturbance in the study plots and lack of differentiation among types and levels of disturbance when the data was collected was a major confounding factor that affected the analysis and results of this study. Disturbance is hard to avoid in large-scale field studies, so those planned in the future should include methods to account for disturbance in the study design. If the effects of disturbance are uniformly distributed within the plots and the amount of time since the disturbance is known or can be estimated, this information can be quantified and used as covariates in the analysis of the design variables. Otherwise, disturbed areas should be avoided. An option to avoid human caused disturbance would be to sample in designated wilderness areas.

Little data is available on the differences in spread and intensification of DFDM in mature trees after cutting to various densities. The extent of latent infections and the rate at which brooms develop in infected Douglas-fir are also unknown. Studies to determine the influence of site-specific fire history on the occurrence and severity of DFDM could provide important clues about the extent to which fire regulated this disease in the past. It may also help understand what the impact of re-introducing periodic underburning might be in DFDM-

infected stands. More thorough understanding of the use of Douglas-fir dwarf mistletoe-infected trees by spotted owls will also be needed before we can actively manage the level of infection in owl home ranges. The information gained from such studies would be useful to guide future management of the many stands containing Douglas-fir and Douglas-fir dwarf mistletoe in the Southern Oregon Cascades.

SUMMARY OF CONCLUSIONS

- A preliminary survey of 17 plant associations in 3 climax series in the Southern Oregon Cascades concluded that 15 Douglas-firs per plot would be adequate to measure both frequency of occurrence and severity of Douglas-fir dwarf mistletoe.

- Based on the same survey, a minimum of 167 plots (41 plots each for the PSME and TSHE series and 85 plots for the ABCO series) would be needed for a practically significant difference of 15%.

- The plots where DFDM was present were at significantly higher elevations, had lower mean annual temperatures and lower mean annual precipitation than plots where DFDM did not occur.

- DFDM occurred significantly more often in the ABCO series and less often than expected in the PSME series.

- The relative frequency of DFDM among the series appeared to be related to the differences in elevation, mean annual temperature and mean annual precipitation of the three series.

- DFDM was most common in the three coldest and driest plant associations in the ABCO series. These associations were: ABCO/ACGL/BENE, ABCO/AMAL/ANDE and ABCO/VAME/LIBOL.

- DFDM was not found at all in the six warmest, wettest plant associations: TSHE-ACMA/POMU, TSHE-PSME/GASH, ABCO/BENE-GASH, PSME/RHDI/PTAQ, PSME/GASH/POMU and PSME/BENE/POMU. It was also absent from one cold, wet association: TSHE/ACCI/RUNI.

- The geographic pattern of DFDM occurrence suggested that past timber harvesting, fire history and fire behavior may explain some of the differences in occurrence among the environmental and stand variables. These factors may have had a great influence on the present distribution of the disease in the Southern Oregon Cascades.

- The severity of DFDM was significantly associated with two stand variables. The average mistletoe rating increased as total basal area decreased and as the age of the oldest layer increased.

- This study suggested that if partial cutting becomes more widely used in the future, the occurrence and severity of DFDM may increase, particularly where Douglas-fir is the climax series.

REFERENCES

Acciavatti, Robert E. and Melvyn J. Weiss. 1974. Evaluation of dwarf mistletoe on Engelmann spruce, Fort Apache Indian Reservation, Arizona. Plant Disease Reporter. 58(5): 418-419.

Agee, James K. 1991. Fire history of Douglas-fir forests in the Pacific Northwest. Pp. 25-33. In Wildlife and vegetation of unmanaged Douglas-fir forests. Ruggiero, L.F., K.B. Aubry, A.B. Carey, and M.H. Huff, tech. coords. USDA-FS, PNW-GTR-285. 533 pp.

Agee, James K. 1993. Fire ecology of Pacific Northwest forests. Island Press, Washington, D.C. 493 pp.

Aho, Paul E. and Lyle N. Anderson. 1959. Office Report: Douglas-fir dwarf mistletoe aerial survey, Rogue River N.F., 1958. unpublished document on file, USDA-FS, Region 6, Forest Pest Management, Portland, Oregon. 12 pp.

Alexander, Martin E. and Frank G. Hawksworth. 1975. Wildland fires and dwarf mistletoes: A literature review of ecology and prescribed burning. USFS-FS, RM-GTR-14. 12 pp.

Alexander, Martin E. and Frank G. Hawksworth. 1976. Fire and dwarf mistletoes in North American coniferous forests. Journal of Forestry. 74: 446-449.

Alosi, M. Carol. 1978. The curious anatomy of *Arceuthobium* in regards to host/parasite water relations and translocation. Pp. 35-43. In Proceedings of the 26th annual Western International Forest Disease Work Conference. October 24-28, 1978. Tuscon, Arizona. Drummond, D.B., ed. 194 pp.

Alosi, M. Carol and Clyde L. Calvin. 1984. The anatomy and morphology of the endophytic system of *Arceuthobium* spp. Pp. 40-52. In Biology of dwarf mistletoes: Proceedings of the symposium on the biology of dwarf mistletoes, in conjunction with the A.I.B.S. meetings. August 8, 1984, Fort Collins, Colorado. Hawksworth, F.G. and R. Scharpf, tech coords. USDA-FS, GTR-RM-111. 131 pp.

Atzet, Thomas A. and Lisa A. McCrimmon. 1990. Preliminary plant associations of the Southern Cascade Mountain Province. USDA-FS, Pacific Northwest Region, Siskiyou National Forest. 330 pp.

Atzet, Thomas, David L. Wheeler, Brad Smith, Jerry Franklin, Gregg Riegel and Dale Thornburgh. 1992. Chapter 5: Vegetation. In Reforestation practices in southwestern Oregon and northern California. Hobbs, S.D., S.D. Tesch, P.W. Owston, R.E. Stewart, J.C. Tappeiner II, and G.E. Wells, eds. Forest Research Laboratory, Oregon State University, Corvallis. 465 pp.

Baranyay, J.A. and R.B. Smith. 1972. Dwarf mistletoes in British Columbia and recommendations for their control. Pacific Forest Research Center, Canadian Forestry Service, Victoria, British Columbia. BC-X-72. 18 pp.

Beckman, Kent M. and Lewis F. Roth. 1968. The influence of temperature on longevity and germination of seed of western dwarf mistletoe. Phytopathology. 58: 147-150.

Boyce, J.S. 1938. Forest Pathology. McGraw-Hill Book Company, New York. 600 pp.

Briede, J.W., J.G. Mexal, A.M. Lynch and F.G. Hawksworth 1991. Shoot growth and development of Douglas-fir and white fir in New Mexico. Pp. 155-159. In Interior Douglas-fir: the species and its management. Symposium proceedings. February 27-March 1, 1990, Spokane, Washington. Baumgartner, D.M., ed. Washington State University Cooperative Extension, Pullman. 301 pp.

Buchanan, Joseph Burton. 1991. Spotted owl nest site characteristics in mixed conifer forests of the eastern Cascade mountains, Washington. M.S. thesis, University of Washington, Seattle. 136 pp.

Bull, Evelyn L. and Mark G. Henjum. 1990. Ecology of the great gray owl. USDA-FS, PNW-GTR-265. 39 pp.

Bull, Evelyn L., Anthony L. Wright and Mark G. Henjum. 1989. Nesting and diet of long-eared owls in conifer forests, Oregon. The Condor 91: 908-912.

Ciesla, William M. 1989. Causes of tree mortality on Ashland District. unpublished report to Forest Supervisor, Rogue River N.F. USDA-FS, Region 6, Forest Pest Management, Portland Oregon. 3 pp.

Cooper, Stephen V., Kenneth E. Neiman and David W. Roberts. 1991. Forest land types of northern Idaho: a second approximation (revised). USDA-FS, GTR-INT-236. 143 pp.

Daubenmire, R. 1968. Plant communities. Harper and Row, New York. 300 pp.

Dixon, Gary E. and Frank G. Hawksworth. 1979. A spread and intensification model for southwestern dwarf mistletoe in ponderosa pine. Forest Science. 25(1): 43-52.

Everett, Richard, Sandra Martin, Monte Bickford, Richard Shellhaus and Eric Forsman. 1992. Variability and dynamics of spotted owl nesting habitat in eastern Washington. Pp. 35-39. In Getting to the future through silviculture. Proceedings, National Silviculture Workshop. May 6-9, 1991, Cedar City, Utah. Murphy, D., ed. USDA-FS, GTR-INT-291. 97 pp.

Filip, Gregory M., J.J. Colbert, Charles G. Shaw III, Paul F. Hessburg, Kevin P. Hosman and Catherina A. Parks. 1991. Some relations among dwarf mistletoe, western spruce budworm and Douglas-fir: Modeling and management implications. Pp. 161-163. In Interior Douglas-fir: the species and its management. Symposium proceedings. February 27-March 1, 1990,

Spokane, Washington. Baumgartner, D.M., ed. Washington State University Cooperative Extension, Pullman. 301 pp.

Filip, Gregory M., J.J. Colbert, C.G. Shaw III, Paul F. Hessburg and Kevin P. Hosman. 1993. Influence of dwarf mistletoe and western spruce budworm on growth and mortality of Douglas-fir in unmanaged stands. Forest Science. 39(3): 465-477.

Filip, Gregory M. and Catherine A. Parks. 1987. Simultaneous infestation by dwarf mistletoe and western spruce budworm decreases growth of Douglas-fir in the Blue Mountains. Forest Science 33 (3): 767-773.

Forsman, Eric D., E. Charles Meslow and Howard M. Wight. 1984. Distribution and biology of the spotted owl in Oregon. Wildlife Monograph #87. Wildlife Society, Washington, D.C. 64 pp.

Franklin, Jerry F. and C.H. Dyrness. 1988. Natural vegetation of Oregon and Washington, 2nd edition. Oregon State University Press, Corvallis. 452 pp.

Furniss, Malcolm M., R. Ladd Livingston and Mark D. McGregor. 1980. Development of a stand susceptibility classification for Douglas-fir beetle. Pp. 115-128. In Hazard rating systems in forest insect pest management, USDA-FS, WO-27. Proceedings of the symposium, Athens, Georgia, July 31-August 1, 1980. Hedden, Roy L., ed. 169 pp.

Furniss, R.L. and V.M. Carolin. 1977. Western forest insects. USDA-FS, Miscellaneous publication #1339. Washington, D.C. 654 pp.

Gill, Lake S. 1935. *Arceuthobium* in the United States. Transactions of the Connecticut Academy of Arts and Science. 32: 111-245.

Gill, Lake S. and Jess L. Bedwell. 1949. Dwarf mistletoes. Pp. 458-461. In Trees, The Yearbook of Agriculture, 1949. USDA, Washington, D.C. 944 pp.

Gill, Lake S. and Frank G. Hawksworth. 1961. The mistletoes: A literature review. USDA Technical Bulletin #1242. Washington, D.C.87 pp.

Gottfried, Gerald L. and Robert S. Embry. 1977. Distribution of Douglas-fir and ponderosa pine dwarf mistletoes in a virgin Arizona mixed conifer stand. USDA-FS, Research Paper RM-192. 16 pp.

Graham, Donald P. 1959. Dwarf mistletoe survey in the Coeur d'Alene N.F. USDA-FS, Research Note INT-68. 5 pp.

Graham, Donald P. 1964. Dwarf mistletoe survey in western Montana. USDA-FS, Research Note INT-14. 7 pp.

Hadfield, James S. 1985. Forest diseases of southwest Oregon, the quiet thieves. Pp. 7-12. In Forest pest management in southwest Oregon. Proceedings of a workshop. August 19-20, 1985. Grants Pass, Oregon. Helgerson, O.T. ed. Forest Research Lab, Oregon State University, Corvallis. 88 pp.

Haglund, Stephen A. and Oscar J. Dooling. 1972. Observations on the impact of dwarf mistletoe on Douglas-fir in western Montana. USDA-FS Northern Region, Insect and Disease Report, #D-72-1. 6 pp.

Harlow, William M., E.S. Harrar and F.M. White. 1968. Textbook of dendrology, 5th ed. McGraw-Hill Book Company, New York. 512 pp.

Hawksworth, Frank G. 1959. Distribution of dwarf mistletoes in relation to topography on the Mescalero Apache Reservation, New Mexico. Journal of Forestry. 57: 919-922.

Hawksworth, Frank G. 1968. Ponderosa pine dwarf mistletoe in relation to topography and soils on the Manitou Experimental Forest, Colorado. USDA-FS, Research Note RM-107. 4 pp.

Hawksworth, Frank G. 1969. Ecological aspects of dwarf mistletoe distribution. Pp. 74-82. In Proceedings, 16th Annual Western International Forest Disease Work Conference. October 28-November 1, 1968. Coeur d'Alene, Idaho. no editor cited. 164 pp.

Hawksworth, Frank G. 1977. The six-class dwarf mistletoe rating system. USDA-FS, RM-GTR-48. 7 pp.

Hawksworth, Frank G. and David W. Johnson. 1989. Biology and management of dwarf mistletoe in lodgepole pine in the Rocky Mountains. USDA-FS, RM-GTR-169. 35 pp.

Hawksworth, Frank G. and Delbert Wiens. 1972. Biology and classification of dwarf mistletoes (*Arceuthobium*). USDA-FS, Agriculture Handbook #401. Washington, D.C. 234 pp.

Hermann, Richard K. 1985. The genus *Pseudotsuga*: ancestral history and past distribution. Forest Research Laboratory, Oregon State University, Corvallis. Special pub. #26. 32 pp.

Hermann, Richard K. and D.P. Lavender. 1990. *Pseudotsuga menziesii* (Mirb.) Franco Douglas-fir. Pp. 527-540. In Silvics of North America. Volume 1. Conifers. Burns, Russell M. and B.H. Honkala, tech. coords. USDA Forest Service Agriculture Handbook #271, Washington, D.C. 675 pp.

Hobbs, Stephen D. 1992. Chapter 5: Seedling and site interactions. In Reforestation practices in southwestern Oregon and northern California. Hobbs, S.D., . Tesch, P.W. Owston, R.E. Stewart, J.C. Tappeiner II, and G.E. Wells, eds. Forest Research Laboratory, Oregon State University, Corvallis. 465 pp.

Kingsley, R. Duane. 1978. Dwarf mistletoe control on the Rogue River National Forest in Oregon. Pp. 82-85. In Proceedings of the symposium on dwarf mistletoe control through forest management. April 11-13, 1978. Berkeley, California. Scharpf, R.F. and J.R. Parmeter, Jr., tech. coords. USDA-FS, GTR-PSW-31. 190 pp.

Knutson, Donald M. and Anita S. Hutchins. 1979. *Wallrothiella arceuthobii* infecting *Arceuthobium douglasii*: culture and field inoculation. Mycologia. 71: 821-828.

Knutson, Donald M. and Robert Tinnin. 1980. Dwarf mistletoe and host tree interactions in managed forests of the Pacific Northwest. USDA-FS, GTR-PNW-111. 17 pp.

Korstian, C. 1924. Growth on cut-over and virgin western yellow pine lands in central Idaho. Journal of Agricultural Research. 28: 1138-1148.

Korstian, C. and W.H. Long. 1922. The western yellow pine mistletoe. USDA Bulletin #1112. Washington, D.C. 35 pp.

Kuijt, Job. 1955. Dwarf mistletoes. The Botanical Review. 21: 569-603.

Kuijt, Job. 1960. Morphological aspects of parasitism in the dwarf mistletoes. University of California Publications in Botany. 30(5): 337-436.

Larson, Fredric R., Peter F. Ffolliott and Warren P. Clary. 1970. Distribution of dwarf mistletoe in ponderosa pine stands on the Beaver Creek Watershed, Arizona. USDA-FS, Research Note RM-175. 4 pp.

Layser, Earle F. 1974. Vegetative classification: Its application to forestry in the northern Rocky Mountains. Journal of Forestry. 72(6): 254-357.

Mathiasen, Robert L. 1984. Comparative susceptibility of corkbark fir and Douglas-fir to Douglas-fir dwarf mistletoe. Forest Science. 30(3): 842-847.

Mathiasen, Robert L. and Elizabeth A. Blake. 1984. Relationships between dwarf mistletoes and habitat types in western coniferous forests. Pp. 111-116. In Biology of dwarf mistletoes: Proceedings of the symposium on the biology of dwarf mistletoes, in conjunction with the A.I.B.S. meetings. August 8, 1984, Fort Collins, Colorado. Hawksworth, F.G. and R. Scharpf, tech coords. USDA-FS, GTR-RM-111. 131 pp.

Mathiasen, Robert L., Carleton B. Edminster and Frank G. Hawksworth. 1990(b). Infection of young Douglas-firs by dwarf mistletoe in the Southwest. Great Basin Naturalist 50(1): 67-72.

Mathiasen, Robert L., Frank G. Hawksworth and Carleton B. Edminster. 1990(a). Effects of dwarf mistletoe on growth and mortality of Douglas-fir in the southwest. Great Basin Naturalist 50(2): 173-179.

Mathiasen, R.L. and L. Loftis. 1987. Douglas-fir dwarf mistletoe parasitizing Pacific silver fir in northern California. Great Basin Naturalist. 47(1): 161-162.

McDonald, Geral I., Neil E. Martin and Alan E. Harvey. 1987. Occurrence of *Armillaria* spp. in forests of the northern Rocky Mountains. USDA-FS, Research Paper INT-381. 7 pp.

Merrill, Laura M. 1983. Relationship of ponderosa pine dwarf mistletoe with habitat types and other ecological factors. M.S. thesis, Colorado State University, Ft. Collins. 85 pp.

Minore, Donald. 1978. The Dead Indian Plateau: A historical summary of forestry observations and research in a severe southwestern Oregon environment. USDA-FS, GTR-PNW-72. 23 pp.

Minore, Donald. 1979. Comparative autecological characteristics of northwestern tree species - A literature review. USDA-FS, PNW-GTR-87. 72 pp.

Nicholls, Thomas H., Frank G. Hawksworth and Laura M. Merrill. 1984. Animal vectors of dwarf mistletoe, with special reference to *A. americanum* on lodgepole pine. Pp. 102-110. In Biology of dwarf mistletoes: Proceedings of the symposium on the biology of dwarf mistletoes, in conjunction with the A.I.B.S. meetings. August 8, 1984, Fort Collins, Colorado. Hawksworth, F.G. and R. Scharpf, tech coords. USDA-FS, GTR-RM-111. 131 pp.

Oliver, Chadwick D. and B.C. Larson. 1990. Forest stand dynamics. Biological Resource Management Series. McGraw-Hill, Inc. New York. 467 pp.

Parmeter, John R., Jr. 1978. Forest stand dynamics and ecological factors in relation to dwarf mistletoes spread, impact and control. Pp. 16-30. In Proceedings of the symposium on dwarf mistletoe control through forest management. April 11-13, 1978. Berkeley, California. Scharpf, R.F. and J.R. Parmeter, Jr., tech. coords. USDA-FS, GTR-PSW-31. 190 pp.

Pierce, William R. 1960. Dwarf mistletoe and its effect upon the larch and Douglas-fir of western Montana. Bulletin #10. Montana State University, Missoula. 37 pp.

Player, Glade. 1979. Pollination and wind dispersal of pollen in *Arceuthobium*. Ecological Monographs. 19(1): 73-87.

Ramsey, Fred and D. Schafer. 1993. The statistical sleuth: an intermediate course in statistical methods. unpublished draft text. Oregon State University, Corvallis. Department of Statistics.

Reynolds, Richard T., E. Charles Meslow, Howard M. Wight. 1982. Nesting habitat of co-existing Accipiters in Oregon. Journal of Wildlife Management. 46(1): 124-138.

Richardson, K.S. and B.J. van der Kamp. 1972. The rate of upward advance and intensification of dwarf mistletoe on immature western hemlock. Canadian Journal of Forest Research. 2: 313-316.

Roth, Lewis F. 1953. Pine dwarf mistletoe on the Pringle Falls Experimental Forest. USDA-FS, Research Note PNW-91. 3 pp.

Roth, Lewis F. 1959. Natural emplacement of dwarf mistletoe seed on ponderosa pine. Forest Science 5 (4): 365-369.

Scharpf, Robert F. 1993. Diseases of Pacific coast conifers. USDA-FS, Agriculture Handbook #521. Washington, D.C., 199 pp.

Smith, Graham W. 1982. Habitat use by porcupines in a ponderosa pine/Douglas-fir forest in northeastern Oregon. Northwest Science. 56(3): 237-240.

Smith, Robert B. 1972. Relation of topography and vegetation to the occurrence of Douglas-fir dwarf mistletoe at its northern limits in British Columbia. Ecology 53(4): 729-734.

Stafford, Susan G. and T.E. Sabin. 1994. Statistical analysis for the natural resources and ecological sciences. unpublished draft text. Oregon State University, Corvallis. Department of Forest Science.

Stage, A.R. 1973. Prognosis model for stand development. USDA-FS, Research Paper. INT-137. 32 pp.

Stevens, Robert E. and Frank G. Hawksworth. 1970. Insects and mites associated with dwarf mistletoes. USDA-FS, Research Paper RM-59. 12 pp.

Stevens, Robert E. and Frank G. Hawksworth. 1984. Insect - dwarf mistletoe associations: an update. Pp. 94-101. In Biology of dwarf mistletoes: Proceedings of the symposium on the biology of dwarf mistletoes, in conjunction with the A.I.B.S. meetings. August 8, 1984, Fort Collins, Colorado. Hawksworth, F.G. and R. Scharpf, tech coords. USDA-FS, GTR-RM-111. 131 pp.

Tinnin, Robert O., Frank G. Hawksworth and Donald M. Knutson. 1982. Witches' broom formation in conifers infected by *Arceuthobium* spp.: an example of parasitic impact upon community dynamics. The American Midland Naturalist. 107(2): 351-359.

Tinnin, Robert O. and Donald M. Knutson. 1973. Douglas-fir dwarf mistletoe is west of the Cascade Divide. Plant Disease Reporter. 57(9): 716-718.

Tinnin, Robert O. and Donald M. Knutson. 1980. Growth characteristics of the brooms on Douglas-fir caused by *A. douglasii*. Forest Science. 26(1): 149-158.

Tinnin, Robert O., Peter J. Paquet and Donald M. Knutson. 1976. Factors limiting the western range of *Arceuthobium douglasii* in Oregon - a hypothesis. Northwest Science. 50(1): 1-6.

Waring, R.H. 1969. Forest plants of the eastern Siskiyous: their environmetal and vegetational distribution. Northwest Science. 43(1): 1-17.

Weir, James R. 1915. *Wallrothiella arceuthobii*. Journal of Agricultural Research. 4(4): 369-378.

Weir, James R. 1916. Mistletoe injuring conifers in the Northwest. USDA Bulletin #360. Washington, D.C. 39 pp.

Wicker, Ed F. 1969. Susceptibility of coastal form and central Montana Douglas-fir to Arceuthobium douglasii. Plant Disease Reporter. 53(4): 311-314.

Wicker, Edward F. 1974. *Arceuthobium douglasii*: Its absence from the flora of the Puget - Willamette lowlands. Northwest Science. 48(4): 239-245.

Wicker, Ed F. and Charles D. Leaphart. 1976. Fire and dwarf mistletoe (*Arceuthobium* spp.) relationships in the northern Rocky Mountains. Pp. 279-298. In Proceedings, 14th Tall Timbers Fire Ecology Conference and Intermountain Fire Research Council Fire and Land Management Symposium. October 8-10, 1974, Missoula, Montana. Komarek, E.V., general chair. 675 pp.

Wicker, Edward F. and C. Gardner Shaw. 1967. Target area as a klendusic factor in dwarf mistletoe infections. Phytopathology. 57: 1161-1163.

Wicker, Edward F. and C. Gardner Shaw. 1968. Fungal parasites of dwarf mistletoes. Mycologia. 60: 372-383.

Williams, Ralph E. and M.A. Marsden. 1982. Modelling probability of root disease center occurrence in northern Idaho forests. Canadian Journal of Forest Research. 12: 876-882.

Zilka, Paul J. and Robert O. Tinnin. 1976. Potential avian influence in the distribution of dwarf mistletoe. Northwest Science. 50(1): 8-16.

Zimmerman, G. Thomas and Richard D. Laven. 1984. Ecological inter-relationships of dwarf mistletoe and fire in lodgepole pine forests. Pp. 123-131. In Biology of dwarf mistletoes: Proceedings of the symposium on the biology of dwarf mistletoes, in conjunction with the A.I.B.S. meetings. August 8, 1984, Fort Collins, Colorado. Hawksworth, F.G. and R. Scharpf, tech coords. USDA-FS, GTR-RM-111. 131 pp.

APPENDICES

APPENDIX 1. Study data by plot

Obs	Plot	Series[1]	Plant association[1]	Elev[2] (m)	Matemp (°C)	Maprecip (cm)	Dsprecip (cm)	Site Index (m/100 yrs)	Slope (%)	Totalba (m²/ha)	DFba (m²/ha)	% ba in DF
1	2682	TSHE	TSHE/ACGL/LIBOL	1286	7	152	25	34	50	74	23	31
2	2711	ABCO	ABCO-ABMAS/CHUM	1298	7	152	17	37	4	74	32	43
3	2738	ABCO	ABCO-ABMAS/CHUM	1469	6	165	20	34	50	97	88	90
4	2745	ABCO	ABCO-ABMAS/CHUM	1524	6	165	22	46	59	83	37	44
5	2747	TSHE	TSHE-ABAM/VAME	1136	8	165	20	27	14	97	92	94
6	2751	TSHE	TSHE-ABAM/VAME	1426	6	177	22	55	36	78	41	52
7	2765	ABCO	ABCO/BENE-GASH	938	8	165	20	34	17	78	69	88
8	2774	TSHE	TSHE/BENE/LIBOL	1237	7	177	25	34	17	88	69	78
9	2794	TSHE	TSHE-ABAM/VAME	1359	6	152	25	46	44	78	27	34
10	2795	PSME	PSME/GASH/POMU	810	9	127	17	30	42	51	32	62
11	2797	PSME	PSME/RHDI/CYGR	655	9	101	15	37	68	78	55	70
12	2859	ABCO	ABCO/BENE-GASH	1194	7	165	20	40	49	69	65	94
13	2866	PSME	PSME/GASH/POMU	1258	7	165	20	40	65	78	78	100
14	2870	PSME	PSME/RHDI/PTAQ	688	10	127	15	49	40	83	74	89
15	2875	ABCO	ABCO-PSME/BEPI	816	9	114	15	40	40	51	51	100
16	2880	PSME	PSME/RHDI/PTAQ	804	9	152	17	30	51	69	27	39
17	2881	ABCO	ABCO/ACCI/ACTR	1402	6	165	25	49	53	83	69	83
18	2885	ABCO	ABCO/RUNI/ACTR	1408	6	177	25	18	14	74	60	81
19	2887	TSHE	TSHE/RHMA/LIBOL	1274	7	177	22	24	10	92	69	75
20	2892	ABCO	ABCO/ACCI/ACTR	1091	8	152	17	34	42	97	74	76
21	2894	TSHE	TSHE/ACMA/POMU	499	10	127	15	40	46	55	32	58
22	2901	PSME	PSME/GASH/POMU	640	10	127	17	37	13	60	55	91
23	2903	PSME	PSME/RHDI/PTAQ	780	9	152	20	30	9	65	55	84
24	2904	PSME	PSME/GASH/POMU	1091	8	152	20	37	27	27	23	85
25	2907	ABCO	ABCO/BENE-GASH	777	9	101	15	40	34	51	41	80
26	2908	PSME	PSME/BENE/POMU	902	8	114	15	37	60	83	78	93
27	2910	ABCO	ABCO/BENE-GASH	832	9	101	15	34	37	65	37	56
28	2912	PSME	PSME/GASH/POMU	911	9	114	15	27	30	65	51	78
29	2913	PSME	PSME/GASH/POMU	963	8	114	17	34	35	74	74	100
30	2914	TSHE	TSHE/BENE/LIBOL	1097	8	127	17	49	38	83	78	93
31	2922	TSHE	TSHE/RHMA/LIBOL	810	9	165	22	46	2	78	60	76
32	2931	ABCO	ABCO/BENE-GASH	1231	7	139	17	37	35	102	92	90
33	2933	PSME	PSME/RHDI/PTAQ	847	9	127	17	37	68	83	65	78
34	2936	ABCO	ABCO/BENE-GASH	908	9	139	20	37	37	65	32	49
35	2937	PSME	PSME/BENE/POMU	1295	7	177	22	27	60	83	83	100
36	2938	PSME	PSME/GASH/POMU	923	9	152	20	37	23	69	65	94
37	2949	ABCO	ABCO-CADE3/BENE	920	9	177	20	18	60	78	37	47
38	2950	PSME	PSME/RHDI/PTAQ	914	10	127	20	37	57	88	69	78
39	2951	PSME	PSME/RHDI/PTAQ	633	10	127	20	34	55	88	74	84
40	2955	ABCO	ABCO/BENE-GASH	917	8	165	25	30	20	51	27	52
41	2957	ABCO	ABCO/BENE-GASH	774	10	165	20	46	30	60	51	85
42	2959	TSHE	TSHE-PSME/GASH	499	10	152	20	34	69	92	55	59
43	2961	ABCO	ABCO-PSME/BEPI	877	9	152	20	40	20	88	69	78
44	2962	TSHE	TSHE-PSME/GASH	859	9	127	20	40	4	69	37	53

APPENDIX 1. (Continued)

Obs	Plot	Series[1]	Plant association[1]	Elev[2] (m)	Matemp (°C)	Maprecip (cm)	Dsprecip (cm)	Site Index (m/100 yrs)	Slope (%)	Totalba (m²/ha)	DFba (m²/ha)	% ba in DF
45	2965	TSHE	TSHE/ACMA/POMU	618	10	152	20	43	64	92	37	40
46	2967	ABCO	ABCO/AMAL/ANDE	1350	6	127	17	46	13	78	23	29
47	2969	ABCO	ABCO-ABMAS/CHUM	1408	6	127	17	30	14	60	4	6
48	2970	ABCO	ABCO-PSME/BEPI	813	8	152	20	34	38	65	60	92
49	2973	PSME	PSME/BENE/POMU	853	9	177	22	49	54	92	88	95
50	2974	PSME	PSME/GASH/POMU	841	9	177	22	43	56	83	83	100
51	2975	ABCO	ABCO/AMAL/ANDE	1322	7	114	17	43	50	74	37	50
52	2976	ABCO	ABCO/AMAL/ANDE	1359	7	127	17	27	6	51	0	0
53	2978	ABCO	ABCO-ABMAS/CHUM	1371	6	114	17	37	0	83	37	44
54	2979	ABCO	ABCO/AMAL/ANDE	1496	6	127	17	40	20	92	92	100
55	2981	ABCO	ABCO/RUNI/ACTR	1097	8	114	17	40	5	102	55	53
56	2989	ABCO	ABCO/AMAL/ANDE	1207	7	127	17	43	3	60	32	53
57	2990	ABCO	ABCO/RUNI/ACTR	1298	7	101	15	46	12	97	4	4
58	2992	ABCO	ABCO/VAME/LIBOL	1188	7	127	17	49	8	51	23	45
59	2996	ABCO	ABCO-PSME/BEPI	1176	7	127	17	37	9	74	23	31
60	2997	ABCO	ABCO/VAME/LIBOL	1444	6	114	17	34	7	55	18	32
61	2999	ABCO	ABCO-ABMAS/CHUM	1572	6	101	15	40	10	65	9	13
62	4001	ABCO	ABCO-PSME/BEPI	1432	6	127	20	40	40	78	51	65
63	4002	ABCO	ABCO-CADE3/BENE	1408	6	101	17	49	19	46	37	80
64	4003	ABCO	ABCO-ABMAS/CHUM	1560	6	101	15	49	18	83	13	15
65	4004	ABCO	ABCO-CADE3/BENE	1164	7	101	15	37	22	60	23	38
66	4005	ABCO	ABCO/ACGL/BENE	1246	6	101	15	43	47	41	13	31
67	4008	ABCO	ABCO-ABMAS/CHUM	1499	6	101	17	34	15	65	18	27
68	4011	ABCO	ABCO/VAME/LIBOL	1444	6	114	17	27	25	60	37	61
69	4012	ABCO	ABCO-ABMAS/CHUM	1475	6	127	17	34	15	74	13	17
70	4014	PSME	PSME/RHDI/CYGR	1100	7	101	15	34	31	41	32	78
71	4015	ABCO	ABCO-CADE3/BENE	1316	6	101	15	30	48	65	32	49
72	4035	ABCO	ABCO/RUNI/ACTR	1054	8	139	17	49	16	97	97	100
73	4036	TSHE	TSHE/BENE/ACTR	1152	8	165	20	40	62	69	51	73
74	4037	ABCO	ABCO-CADE3/BENE	1060	8	127	17	49	8	88	65	73
75	4038	ABCO	ABCO-CADE3/BENE	1091	8	165	20	30	49	55	46	83
76	4039	ABCO	ABCO/ACGL/BENE	975	8	165	20	30	18	65	18	27
77	4047	ABCO	ABCO/ACGL/BENE	1328	7	127	17	43	19	78	9	11
78	4048	ABCO	ABCO-CADE3/BENE	1085	8	127	17	46	28	69	46	66
79	4050	ABCO	ABCO/RUNI/ACTR	1264	7	177	22	46	35	46	46	100
80	4051	ABCO	ABCO/RUNI/ACTR	1170	7	203	27	24	29	78	69	88
81	4052	TSHE	TSHE/BENE/ACTR	1408	6	190	25	34	29	60	23	38
82	4053	ABCO	ABCO-CADE3/BENE	853	9	165	20	40	27	116	88	75
83	4054	ABCO	ABCO/RUNI/ACTR	1085	8	152	22	49	18	69	69	100
84	4055	ABCO	ABCO-CADE3/BENE	1505	6	165	20	43	35	92	60	65
85	4057	ABCO	ABCO/BENE-GASH	1054	8	165	22	37	40	60	23	38
86	4061	ABCO	ABCO/RUNI/ACTR	1335	6	165	20	34	49	78	60	76
87	4062	TSHE	TSHE-ABAM/VAME	1200	6	165	20	40	18	78	41	52
88	4067	ABCO	ABCO/VAME/LIBOL	1441	6	127	17	40	5	92	27	29

Obs	Plot	Series[1]	Plant association[1]	Elev[2] (m)	Matemp (°C)	Maprecip (cm)	Dsprecip (cm)	Site Index (m/100 yrs)	Slope (%)	Totalba (m²/ha)	DFba (m²/ha)	% ba in DF
89	4068	ABCO	ABCO-ABMAS/CHUM	1554	6	152	20	40	30	69	46	66
90	4101	ABCO	ABCO-PSME/BEPI	1374	6	101	15	37	6	55	37	67
91	4103	PSME	PSME/RHDI/CYGR	963	9	88	15	27	15	69	27	39
92	4105	PSME	PSME/RHDI/CYGR	1088	8	88	15	30	52	74	65	87
93	4106	ABCO	ABCO/AMAL/ANDE	1359	7	101	15	24	73	125	125	100
94	4108	ABCO	ABCO/ACGL/BENE	1225	6	101	15	27	72	69	27	39
95	4129	PSME	PSME/BENE/POMU	987	8	114	17	40	22	65	65	100
96	4131	ABCO	ABCO-PSME/BEPI	1530	6	139	20	40	20	92	23	25
97	4132	ABCO	ABCO-PSME/BEPI	1298	7	127	20	37	60	106	83	78
98	4134	ABCO	ABCO/RUNI/ACTR	1203	7	165	20	30	10	60	46	76
99	4140	ABCO	ABCO-CADE3/BENE	1331	7	152	22	34	40	83	60	72
100	4153	ABCO	ABCO-CADE3/BENE	1155	7	152	22	40	27	46	32	69
101	4155	TSHE	TSHE/BENE/LIBOL	926	8	127	17	43	12	92	78	84
102	4158	PSME	PSME/BENE/POMU	994	8	127	17	46	0	60	60	100
103	4662	TSHE	TSHE/ACGL/LIBOL	1191	7	165	20	21	47	111	83	74
104	4664	TSHE	TSHE/BENE/ACTR	1191	7	177	25	24	54	74	60	81
105	4665	TSHE	TSHE-PSME/GASH	963	8	165	22	55	16	69	37	53
106	4669	ABCO	ABCO/ACCI/ACTR	1295	7	165	22	40	42	83	69	83
107	4671	TSHE	TSHE/RHMA/LIBOL	1335	7	165	20	27	53	55	46	83
108	4672	TSHE	TSHE-PSME/GASH	1051	8	165	20	34	7	55	27	49
109	4675	TSHE	TSHE/RHMA/LIBOL	1066	8	177	22	40	19	74	69	93
110	4677	TSHE	TSHE/ACCI/RUNI	1249	6	177	20	34	60	69	46	66
111	4679	ABCO	ABCO/ACCI/ACTR	1149	7	177	25	24	47	92	83	90
112	4683	ABCO	ABCO/ACCI/ACTR	1219	7	152	20	34	19	83	55	66
113	4688	TSHE	TSHE-PSME/GASH	804	9	152	20	43	12	69	23	33
114	4691	TSHE	TSHE/ACGL/LIBOL	1371	6	177	25	43	72	78	51	65
115	4692	TSHE	TSHE/RHMA/LIBOL	966	8	165	20	21	32	65	55	84
116	4694	TSHE	TSHE/BENE/LIBOL	902	9	165	20	34	69	102	88	86
117	4699	ABCO	ABCO/ACCI/ACTR	1298	6	139	20	37	43	69	69	100
118	4762	ABCO	ABCO-ABMAS/CHUM	1432	6	165	20	37	20	88	65	73
119	4763	ABCO	ABCO/AMAL/ANDE	1411	6	165	22	43	20	78	9	11
120	4765	TSHE	TSHE/BENE/LIBOL	1030	8	177	20	43	5	65	41	63
121	4766	TSHE	TSHE/RHMA/LIBOL	1039	7	152	22	37	53	74	13	17
122	4768	TSHE	TSHE/ACCI/RUNI	1112	8	165	20	34	35	74	23	31
123	4774	TSHE	TSHE/BENE/LIBOL	877	9	152	20	27	38	102	78	76
124	4798	TSHE	TSHE-PSME/GASH	566	10	152	20	30	36	55	37	67
125	4802	ABCO	ABCO-PSME/BEPI	914	8	165	20	27	62	78	74	94
126	4808	TSHE	TSHE/BENE/ACTR	975	8	177	22	40	65	78	78	100
127	4809	ABCO	ABCO/ACCI/ACTR	1295	7	152	22	30	63	74	65	87
128	4811	ABCO	ABCO-BENE/GASH	999	8	152	20	40	15	92	88	95
129	4812	TSHE	TSHE-ABAM/VAME	1091	8	165	22	30	15	97	92	94
130	4816	TSHE	TSHE/ACMA/POMU	432	11	152	20	43	77	92	46	50
131	4818	TSHE	TSHE/ACMA/POMU	640	10	165	22	43	30	65	46	71
132	4824	TSHE	TSHE/ACMA/POMU	454	11	152	20	37	64	69	46	66

APPENDIX 1. (Continued)

Obs	Plot	Series[1]	Plant association[1]	Elev[2] (m)	Matemp (°C)	Maprecip (cm)	Dsprecip (cm)	Site Index (m/100 yrs)	Slope (%)	Totalba (m²/ha)	DFba (m²/ha)	% ba in DF
133	4826	TSHE	TSHE-PSME/GASH	609	10	152	17	27	54	60	37	61
134	4828	ABCO	ABCO-PSME/BEPI	780	9	152	17	34	12	60	41	68
135	4837	ABCO	ABCO/ACCI/ACTR	1328	7	127	17	40	13	65	65	100
136	4840	TSHE	TSHE/BENE/ACTR	1280	7	152	25	37	55	97	46	47
137	4841	ABCO	ABCO-PSME/BEPI	1075	8	152	20	46	68	65	60	92
138	4845	ABCO	ABCO/ACCI/ACTR	914	9	114	17	34	18	78	27	34
139	4846	TSHE	TSHE/ACGL/LIBOL	1200	7	127	17	37	7	88	46	52
140	4847	TSHE	TSHE/ACGL/LIBOL	1194	7	114	17	43	28	97	60	61
141	4848	TSHE	TSHE/BENE/LIBOL	1109	8	114	17	52	22	46	27	58
142	4849	TSHE	TSHE/BENE/LIBOL	1127	7	114	17	37	30	65	27	41
143	4857	ABCO	ABCO/ACGL/BENE	1328	7	101	15	40	23	97	60	61
144	5001	PSME	PSME/GASH/POMU	743	10	152	20	34	46	92	65	70
145	5002	PSME	PSME/GASH/POMU	950	9	152	20	27	64	116	88	75
146	5003	PSME	PSME/BENE/POMU	597	10	152	20	40	77	83	83	100
147	5004	PSME	PSME/BENE/POMU	853	9	165	20	34	70	106	106	100
148	5005	PSME	PSME/RHDI/PTAQ	536	11	152	20	40	55	78	78	100
149	5006	PSME	PSME/GASH/POMU	487	11	152	20	34	45	69	69	100
150	5007	PSME	PSME/RHDI/PTAQ	512	11	152	20	34	32	65	65	100
151	5008	PSME	PSME/RHDI/PTAQ	914	9	165	20	27	65	37	32	86
152	5009	PSME	PSME/GASH/POMU	499	11	152	20	30	48	78	65	83
153	5010	PSME	PSME/GASH/POMU	899	9	127	17	30	50	83	83	100
154	5012	PSME	PSME/RHDI/PTAQ	451	11	152	20	27	46	78	78	100
155	5013	PSME	PSME/GASH/POMU	890	9	152	20	37	60	83	65	78
156	5014	PSME	PSME/RHDI/PTAQ	609	10	152	20	21	27	41	32	78
157	5015	PSME	PSME/RHDI/PTAQ	804	9	139	20	24	46	65	60	92
158	5016	ABCO	ABCO/BENE-GASH	883	9	152	20	24	52	60	27	45
159	5017	ABCO	ABCO-CADE3/BENE	1143	8	114	15	34	14	83	27	32
160	5018	ABCO	ABCO/ACGL/BENE	1255	7	114	15	37	10	97	74	76
161	5019	ABCO	ABCO/ACGL/BENE	1231	7	114	15	34	9	69	37	53
162	5020	ABCO	ABCO/ACGL/BENE	1258	7	114	15	34	7	83	27	32
163	5021	ABCO	ABCO/ACGL/BENE	1225	7	114	15	40	2	55	23	41
164	5022	ABCO	ABCO-CADE3/BENE	1335	7	114	15	34	24	69	69	100
165	5023	ABCO	ABCO-PSME/BEPI	1219	7	114	15	40	12	74	37	50
166	5024	PSME	PSME/RHDI/CYGR	1164	7	76	15	40	40	92	69	75
167	5025	PSME	PSME/RHDI/CYGR	1066	8	76	15	34	23	69	69	100
168	5026	PSME	PSME/RHDI/CYGR	1039	8	76	15	34	19	74	55	74

1. see Appendix 2. for explanation of abbreviations of species
2. see Appendix 3. for explanation of abbreviations of variables and levels

APPENDIX 1. (Continued)

Obs	Layers	Age oldest (yrs)	Mean dbh (cm)	Aspect	Topopos	Toposhape	Parmat	Logging	Other disturb	Forest	Rngr Dist	Occur	Mean DMR
1	3	500	108.150	E	L	CV	AND	N	-	RR	PRO	N	0.00000
2	3	400	32.444	N	L	FL	PYR	N	-	UMP	DLK	N	0.00000
3	2	250	100.789	E	M	CV	AND	Y	R	UMP	DLK	Y	0.73684
4	3	250	77.821	S	M	CV	AND	Y	-	UMP	DLK	N	0.00000
5	3	250	78.105	W	L	CC	AND	N	-	UMP	DLK	N	0.00000
6	3	500	110.842	S	L	CV	BAS	Y	-	UMP	DLK	N	0.00000
7	3	250	54.550	E	L	CC	BAS	N	-	UMP	DLK	N	0.00000
8	3	425	91.950	S	L	CC	BAS	Y	-	UMP	GLD	N	0.00000
9	3	525	88.773	N	U	CV	BAS	N	R	UMP	STM	Y	1.00000
10	3	400	39.353	S	U	CV	AND	N	-	UMP	TIL	N	0.00000
11	2	200	33.813	W	M	CV	AND	N	-	UMP	TIL	N	0.00000
12	2	180	74.000	W	U	CV	AND	N	-	UMP	TIL	N	0.00000
13	2	160	55.882	S	U	CV	PYR	N	-	UMP	TIL	N	0.00000
14	3	250	57.435	E	U	CC	AND	N	-	UMP	TIL	N	0.00000
15	3	400	66.813	N	M	CC	GRA	Y	-	UMP	TIL	N	0.00000
16	3	300	30.647	S	M	CV	GRA	N	-	UMP	TIL	N	0.00000
17	2	150	84.000	N	U	CV	AND	N	-	UMP	TIL	N	0.00000
18	3	250	109.421	E	U	CC	GRA	N	-	UMP	TIL	Y	0.26316
19	3	350	85.607	W	U	CV	AND	Y	-	UMP	TIL	Y	0.03571
20	1	125	41.850	W	U	CC	BAS	N	-	UMP	TIL	N	0.00000
21	3	250	87.857	E	L	CC	AND	N	-	UMP	TIL	N	0.00000
22	3	260	39.353	S	U	CV	PYR	N	-	UMP	TIL	N	0.00000
23	3	300	27.875	S	M	FL	PYR	N	-	UMP	TIL	N	0.00000
24	3	300	36.941	S	U	CC	AND	N	-	UMP	TIL	N	0.00000
25	3	300	84.625	S	L	CV	GRA	N	-	UMP	TIL	N	0.00000
26	2	180	65.125	W	M	CV	GRA	N	-	UMP	TIL	N	0.00000
27	3	260	55.750	E	U	CV	GRA	Y	-	UMP	TIL	N	0.00000
28	3	180	57.150	W	U	CC	GRA	Y	-	UMP	TIL	N	0.00000
29	2	270	77.591	W	M	CC	PYR	Y	-	UMP	TIL	N	0.00000
30	2	160	61.000	W	L	CV	GRA	Y	-	UMP	TIL	N	0.00000
31	3	275	109.762	N	L	CC	PYR	N	-	UMP	TIL	N	0.00000
32	2	250	67.294	E	U	CC	GRA	N	-	UMP	TIL	N	0.00000
33	2	140	48.611	S	U	CC	PYR	N	-	UMP	TIL	N	0.00000
34	3	230	39.333	S	U	CV	BAS	Y	-	UMP	TIL	N	0.00000
35	3	350	44.263	S	U	CV	PYR	Y	-	UMP	STM	N	0.00000
36	2	140	49.882	S	U	CV	PYR	Y	-	UMP	STM	N	0.00000
37	4	350	100.800	S	U	CV	AND	N	-	UMP	STM	N	0.00000
38	4	350	29.579	S	M	CV	BAS	Y	-	UMP	STM	N	0.00000
39	3	260	72.000	S	M	CV	BAS	N	-	UMP	STM	N	0.00000
40	3	470	44.684	E	M	CV	BAS	Y	-	UMP	GLD	N	0.00000
41	3	250	96.294	S	M	CC	SED	N	-	UMP	STM	N	0.00000
42	3	260	41.385	E	L	CV	PYR	N	-	UMP	GLD	N	0.00000
43	2	170	48.176	W	U	CC	PYR	Y	-	UMP	STM	N	0.00000
44	3	350	98.944	W	U	CC	BAS	N	-	UMP	STM	N	0.00000

APPENDIX 1. (Continued)

Obs	Layers	Age oldest (yrs)	Mean dbh (cm)	Aspect	Topopos	Toposhape	Parmat	Logging	Other disturb	Forest	Rngr Dist	Occur	Mean DMR
45	3	160	39.947	N	U	CV	AND	N	-	UMP	GLD	N	0.00000
46	3	250	85.438	E	U	CV	AND	Y	-	RR	BUF	Y	1.43750
47	3	250	54.588	N	M	CC	AND	Y	B	RR	BUF	Y	0.05882
48	3	250	60.438	N	U	CV	PYR	N	-	UMP	STM	N	0.00000
49	2	75	35.278	S	U	CV	AND	N	-	UMP	GLD	N	0.00000
50	3	150	43.952	W	U	CV	AND	N	-	UMP	GLD	N	0.00000
51	3	300	77.944	S	U	CC	AND	Y	-	RR	BUF	Y	0.27778
52	3	350	63.750	W	M	CC	BAS	Y	-	RR	BUF	Y	3.81250
53	3	175	41.778	S	U	FL	BAS	Y	-	RR	BUF	Y	0.38889
54	3	250	75.500	W	U	CC	BAS	N	-	RR	BUF	Y	3.13636
55	3	270	55.294	N	L	CC	AND	Y	-	RR	BUF	N	0.00000
56	2	180	71.167	W	L	FL	AND	Y	-	RR	BUF	N	0.00000
57	3	160	57.000	W	M	CC	AND	Y	-	RR	BUF	N	0.00000
58	3	160	59.647	N	U	CV	AND	Y	-	RR	BUF	Y	2.82353
59	2	80	33.813	W	M	CC	AND	N	-	RR	BUF	N	0.00000
60	3	300	73.400	E	M	CC	BAS	Y	-	RR	ASH	Y	2.33333
61	3	250	70.222	W	U	CC	AND	Y	-	RR	ASH	N	0.00000
62	3	150	28.947	S	U	CV	BAS	N	-	RR	BUF	Y	0.52632
63	2	150	66.619	N	M	CV	BAS	Y	-	RR	BUF	Y	0.04762
64	3	250	71.455	W	M	CC	BAS	Y	-	RR	BUF	Y	1.45455
65	3	350	68.941	N	M	CC	BAS	N	-	RR	ASH	Y	2.17647
66	3	150	68.733	N	M	CC	BAS	Y	-	RR	ASH	Y	2.86667
67	3	280	79.545	N	M	CC	BAS	Y	-	RR	ASH	N	0.00000
68	3	400	89.150	N	L	CV	BAS	Y	-	RR	ASH	Y	0.05000
69	3	540	110.933	N	U	CC	AND	Y	-	RR	ASH	Y	0.73333
70	2	80	38.526	W	U	CV	BAS	N	-	RR	ASH	N	0.00000
71	2	200	33.500	E	U	CV	BAS	N	-	RR	ASH	Y	1.65000
72	2	150	62.889	E	M	CC	GRA	Y	-	RR	PRO	N	0.00000
73	4	250	54.400	S	U	CC	PYR	Y	-	RR	PRO	Y	0.70000
74	3	300	51.458	S	L	CC	GRA	N	-	RR	PRO	N	0.00000
75	3	200	58.600	W	U	CV	AND	Y	-	RR	PRO	N	0.00000
76	3	300	31.529	S	L	CC	AND	Y	-	RR	PRO	N	0.00000
77	2	80	42.000	W	U	CC	BAS	N	R	RR	PRO	Y	0.17391
78	2	80	46.813	S	M	CC	PYR	N	-	RR	PRO	N	0.00000
79	2	130	58.550	S	U	CC	BAS	Y	-	UMP	DLK	N	0.00000
80	3	210	60.208	W	M	CC	BAS	N	-	UMP	DLK	N	0.00000
81	3	350	88.500	W	M	CC	AND	Y	-	UMP	DLK	Y	1.62500
82	3	300	56.000	E	U	CV	AND	N	-	UMP	DLK	N	0.00000
83	2	140	61.941	S	L	CV	BAS	Y	-	UMP	DLK	N	0.00000
84	3	250	71.875	W	M	CV	AND	N	-	UMP	DLK	N	0.00000
85	3	400	65.133	E	M	CV	BAS	N	-	UMP	DLK	N	0.00000
86	3	350	94.435	W	L	CV	BAS	N	-	UMP	DLK	Y	0.91304
87	3	450	76.600	S	U	CV	BAS	N	R	UMP	DLK	Y	0.65000
88	3	430	91.053	E	L	CC	AND	Y	-	RR	ASH	N	0.00000

APPENDIX 1. (Continued)

Obs	Layers	Age oldest (yrs)	Mean dbh (cm)	Aspect	Topopos	Toposhape	Parmat	Logging	Other disturb	Forest	Rngr Dist	Occur	Mean DMR
89	3	350	73.789	S	U	CC	AND	Y	-	RR	PRO	N	0.00000
90	3	350	48.333	S	L	FL	BAS	Y	-	RR	ASH	N	0.00000
91	2	350	29.545	S	L	CC	BAS	N	-	RR	ASH	N	0.00000
92	3	200	29.091	S	U	CV	AND	N	-	RR	ASH	N	0.00000
93	2	200	77.722	W	M	CV	AND	N	-	RR	ASH	Y	0.22222
94	3	270	51.000	W	L	CV	BAS	N	-	RR	ASH	Y	3.26667
95	2	90	34.240	W	U	CV	BAS	Y	-	RR	PRO	N	0.00000
96	3	150	86.000	S	U	CC	AND	N	-	RR	PRO	Y	0.50000
97	2	150	59.182	S	M	CV	GRA	N	S	RR	PRO	Y	0.12121
98	2	170	89.333	N	L	CC	AND	N	D	RR	PRO	Y	0.13333
99	2	120	30.944	W	M	CC	PYR	N	-	RR	PRO	N	0.00000
100	3	350	120.400	S	M	CC	AND	N	T	RR	PRO	Y	0.86667
101	3	800	78.250	E	L	CC	BAS	Y	-	RR	PRO	N	0.00000
102	2	170	43.037	W	L	FL	BAS	N	-	RR	PRO	N	0.00000
103	3	400	73.955	E	L	CV	PYR	N	-	UMP	GLD	N	0.00000
104	3	320	90.412	W	U	CV	PYR	Y	-	UMP	GLD	N	0.00000
105	3	520	103.714	E	L	CC	BAS	Y	-	UMP	GLD	N	0.00000
106	2	450	137.412	E	M	CC	BAS	Y	-	UMP	GLD	N	0.00000
107	3	400	78.773	S	U	CC	PYR	Y	-	UMP	GLD	N	0.00000
108	3	540	43.800	S	L	FL	BAS	Y	-	UMP	GLD	N	0.00000
109	2	250	87.889	E	U	CV	AND	Y	-	UMP	GLD	N	0.00000
110	3	350	86.211	W	U	CV	BAS	Y	-	UMP	GLD	N	0.00000
111	2	300	97.316	E	M	CV	BAS	Y	-	UMP	GLD	N	0.00000
112	3	350	108.941	E	U	CC	BAS	N	-	UMP	GLD	N	0.00000
113	3	200	64.118	S	U	CV	AND	N	-	UMP	GLD	N	0.00000
114	3	350	85.133	E	U	CV	BAS	N	-	UMP	DLK	N	0.00000
115	3	250	78.000	W	U	CC	PYR	Y	-	UMP	DLK	N	0.00000
116	3	250	53.400	N	M	CV	BAS	N	-	UMP	DLK	N	0.00000
117	2	350	97.667	N	U	CC	PYR	Y	-	UMP	STM	N	0.00000
118	2	80	40.722	S	U	CC	AND	N	-	UMP	DLK	N	0.00000
119	3	175	43.667	E	U	CC	PYR	N	-	UMP	DLK	N	0.00000
120	3	300	64.333	W	U	CC	PYR	Y	-	UMP	DLK	N	0.00000
121	3	500	52.238	N	U	CV	PYR	Y	-	UMP	STM	N	0.00000
122	3	400	50.647	E	M	CC	SED	Y	-	UMP	STM	N	0.00000
123	3	320	92.267	W	U	CV	PYR	Y	-	UMP	STM	N	0.00000
124	3	350	90.938	N	M	CV	GRA	N	-	UMP	STM	N	0.00000
125	2	140	46.941	S	U	CV	BAS	N	-	UMP	STM	N	0.00000
126	2	300	73.053	S	U	CV	PYR	N	-	UMP	STM	N	0.00000
127	3	250	53.059	W	M	CV	BAS	Y	-	UMP	STM	Y	1.52941
128	2	130	45.360	N	U	CV	PYR	N	-	UMP	DLK	N	0.00000
129	3	200	60.267	W	L	CC	PYR	N	-	UMP	DLK	N	0.00000
130	3	350	96.824	N	L	CV	BAS	N	-	UMP	STM	N	0.00000
131	3	300	84.529	N	L	CC	BAS	N	-	UMP	STM	N	0.00000
132	3	320	93.474	W	L	CV	AND	N	-	UMP	TIL	N	0.00000

APPENDIX 1. (Continued)

Obs	Layers	Age oldest (yrs)	Mean dbh (cm)	Aspect	Topopos	Toposhape	Parmat	Logging	Other disturb	Forest	Rngr Dist	Occur	Mean DMR
133	3	450	98.300	W	L	CC	BAS	N	-	UMP	TIL	N	0.00000
134	2	300	24.250	S	U	FL	AND	N	-	UMP	TIL	N	0.00000
135	3	350	113.074	S	U	CC	AND	Y	-	UMP	TIL	N	0.00000
136	2	250	71.591	S	M	CC	GRA	N	-	UMP	TIL	N	0.00000
137	2	100	52.333	S	M	CV	BAS	N	-	UMP	TIL	N	0.00000
138	3	275	33.714	W	U	CV	BAS	N	-	RR	BUF	N	0.00000
139	3	200	53.345	W	L	CC	BAS	N	-	RR	BUF	Y	0.06897
140	3	120	46.318	N	L	CC	AND	N	-	RR	BUF	N	0.00000
141	3	220	52.550	E	U	CV	AND	N	-	RR	BUF	Y	2.45000
142	3	300	63.632	N	U	CC	AND	Y	-	RR	BUF	Y	3.10526
143	3	200	38.333	S	M	CC	AND	N	-	RR	BUF	Y	0.61111
144	3	200	28.294	W	M	CV	AND	N	-	UMP	GLD	N	0.00000
145	3	250	73.412	S	M	CV	PYR	N	-	UMP	GLD	N	0.00000
146	2	100	44.474	S	M	CV	PYR	N	-	UMP	GLD	N	0.00000
147	2	90	56.111	E	U	CV	BAS	Y	-	UMP	GLD	N	0.00000
148	2	90	52.625	W	U	CV	PYR	Y	-	UMP	STM	N	0.00000
149	2	90	31.800	S	U	CV	PYR	N	-	UMP	STM	N	0.00000
150	2	95	34.412	E	M	CC	PYR	N	-	UMP	STM	N	0.00000
151	3	250	26.067	W	U	CV	PYR	N	-	UMP	STM	N	0.00000
152	2	150	33.824	S	L	CC	PYR	Y	-	UMP	STM	N	0.00000
153	2	175	51.682	N	U	CV	AND	N	-	UMP	DLK	N	0.00000
154	3	250	26.300	S	L	CV	PYR	N	-	UMP	STM	N	0.00000
155	3	150	37.176	S	M	CV	PYR	N	-	UMP	TIL	N	0.00000
156	3	250	28.813	S	L	CV	AND	N	-	UMP	TIL	N	0.00000
157	3	200	27.813	W	U	CC	PYR	N	-	UMP	TIL	N	0.00000
158	3	250	27.895	W	U	CV	PYR	N	-	UMP	TIL	N	0.00000
159	3	350	96.882	E	U	CC	PYR	N	-	UMP	TIL	N	0.00000
160	3	150	30.476	E	U	CC	AND	N	-	RR	BUF	Y	0.14286
161	2	70	33.500	S	L	CC	AND	Y	-	RR	BUF	N	0.00000
162	2	70	35.333	S	U	CC	AND	N	-	RR	BUF	Y	0.26667
163	2	85	30.789	N	L	FL	AND	Y	-	RR	BUF	Y	0.05263
164	2	75	33.158	W	M	CC	AND	Y	-	RR	BUF	Y	0.68421
165	2	100	30.333	S	L	CC	AND	Y	-	RR	BUF	N	0.00000
166	2	90	37.040	E	M	CC	PYR	N	-	RR	BUF	N	0.00000
167	3	150	41.375	E	M	CC	PYR	Y	-	RR	BUF	Y	0.31250
168	2	100	36.048	S	M	CC	PYR	Y	-	RR	BUF	N	0.00000

APPENDIX 2. Plant species used to name the plant communities

Abbreviations	Scientific name	Common name
ABAM	*Abies amabilis*	Pacific silver fir
ABCO	*Abies concolor*	white fir
ABMAS	*Abies magnifica shastensis*	Shasta red fir
ACCI	*Acer circinatum*	vine maple
ACGL	*Acer glabrum*	Douglas maple
ACMA	*Acer macrophyllum*	big-leaf maple
ACTR	*Achlys triphylla*	vanillaleaf
AMAL	*Amelanchier alnifolia*	western serviceberry
ANDE	*Anemone deltoidea*	threeleaf anemone
BENE	*Berberis nervosa*	dwarf Oregongrape
BEPI	*Berberis piperiana*	Piper's Oregongrape
CADE3	*Calocedrus decurrens*	incense cedar
CHUM	*Chimaphila umbellata*	common prince's-pine
CYGR	*Cynoglossum grande*	Pacific hound's-tongue
GASH	*Gaultheria shallon*	salal
LIBOL	*Linnaea borealis longifolia*	western twinflower
POMU	*Polystichum munitum*	western swordfern
PSME	*Pseudotsuga menziesii*	Douglas-fir
PTAQ	*Pteridium aquilinum*	brackenfern
RHDI	*Rhus diversiloba*	poison oak
RHMA	*Rhododendron macrophyllum*	Pacific rhododendron
RUNI	*Rubus nivalis*	snow bramble
TSHE	*Tsuga heterophylla*	western hemlock
VAME	*Vaccinium membranaceum*	thin-leaved huckleberry

APPENDIX 3. Abbreviations used for the variables and levels

Continuous variables			Categorical variables			
Abbreviation	Variable	Units	Abbreviation	Variable	Abbreviation	Level
Elev	elevation	meters	Occur	occurrence	Y	yes
Matemp	mean annual temperature	°C			N	no
Maprecip	mean annual precipitation	centimeters	Aspect	aspect	N	north
Dsprecip	dry season precipitation	centimeters			E	east
Site Index	site index	meters			S	south
Slope	slope	percent			W	west
Totalba	total basal area	meters^2/ha				
DFba	Douglas-fir basal area	meters^2/ha	Topopos	topographic position	U	upper
% ba in DF	percent of total basal area in Douglas-fir	percent			M	middle
Layers	number of layers	number			L	lower
Age oldest	age of trees in the oldest layer	years				
Mean dbh	mean diameter at breast height	centimeters	Toposhpe	topographic shape	CC	concave
Mean DMR	mean dwarf mistletoe rating	1 through 6			CV	convex
					FL	flat
			Parmat	parent material	AND	andesite
					BAS	basalt
					GRA	granitic
					PYR	pyroclastic
					SED	sedimentary
			Forest	Forest	RR	Rogue River
					UMP	Umpqua
			Rngr Dist	Ranger District	ASH	Ashland
					BUF	Butte Falls
					DLK	Diamond Lake
					GLD	Glide
					PRO	Prospect
					STM	Steamboat
					TIL	Tiller
			Logging	previous logging	Y	yes
					N	no
			Other disturb	other disturbance	B	blowdown
					D	debris avalanche
					R	road edge
					S	spring edge
					T	skid trail