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Source: Natural Areas Journal, 30(3) : 261-270

Published By: Natural Areas Association

URL: https://doi.org/10.3375/043.030.0302

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RESEARCH ARTICLE

Influence of Western Dwarf Mistletoe (*Arceuthobium campylopodum* Engelm.) on Surface Fuels and Snag Abundance in Mature Ponderosa Pine and Mixed Conifer Stands in Central Oregon

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Natural Areas Journal 30:261–270

ABSTRACT: We examined the influence of western dwarf mistletoe (*Arceuthobium campylopodum*) infestation on fuel loads in mature mixed-conifer forest in Crater Lake National Park and unmanaged ponderosa pine (*Pinus ponderosa*) stands in Lave Cast Forest, Oregon. We measured biomass of woody surface fuels (1-, 10-, 100-, and 1000-hr), litter and duff, and snag basal area in 29 stands infested with mistletoe and 21 non-infested stands. Univariate tests revealed no significant differences in total surface fuel loads or snag basal area between infested and non-infested plots in either stand type, but there were more fine fuels and litter in infested stands at Lava Cast Forest. Ordination analyses showed that stand level variables other than mistletoe abundance explained more variance in fuel loads. Ponderosa pine basal area and stand age were stronger predictors of fuel loads in pure ponderosa pine stands at Lava Cast Forest, while basal area of non-host fir was a key explanatory variable in the mixed-conifer stands at Crater Lake. Our results indicate that mistletoe has weak direct and indirect effects on fuel loads in mature forests, resulting primarily in greater accumulations of fine woody fuels.

Index terms: Arceuthobium campylopodum, fire ecology, fuel loads, mistletoe, old-growth, Oregon, *Pinus ponderosa*, ponderosa pine

INTRODUCTION

Human activities such as fire exclusion, grazing, and timber harvesting during the past 150 years have led to dramatic shifts in the stand structure and composition of ponderosa pine (*Pinus ponderosa* Dougl. ex P. & C. Laws) forests of the American West (Weaver 1959; Cooper 1960; Savage 1991; Covington and Moore 1994). Among these changes are increases in tree density, insect and disease problems, and fuel loads (Agee 1993). Fire exclusion has resulted in higher levels of insects and pathogens such as dwarf mistletoe (Dahms and Geils 1997; Fule et al. 2002), but the extent to which these agents influence fire behavior and wildfire hazard remains poorly understood.

Dwarf mistletoes (*Arceuthobium* M. Bieb. spp.) interact with a variety of biotic and physical factors (Geils and Hawksworth 2002), directly and indirectly influencing the quantity, quality, and spatial and temporal distribution of woody biomass in infested stands (Knight 1987; Wanner and Tinnin 1989). Dwarf mistletoes are strongly host-specific and have the potential to influence fuel loads through mortality of host trees, which can alter stand composition and the successional trajectory of an infested stand. Wanner and Tinnin (1989) noted high mistletoe-related mortality in lodgepole pine (*Pinus contorta* Dougl. ex Loud.) stands, and both Bennets et al. (1996) and Hoffman et al. (2007) report strong correlations between mistletoe infestation levels and snag abundance in ponderosa pine stands. Therefore, we expect severe mistletoe infestation to result in higher fuel loads in the form of dead standing or downed trees.

Live infected trees may also contribute to fuel loads through changes to crown structure and morphology. A typical host reaction to infection by dwarf mistletoe is the formation of "witches' brooms" characterized by branches swelling at the point of infection and the release of dormant buds following a loss of apical dominance. The result is an increased number of branches growing in abnormal patterns and orientation from a swollen main limb. These changes in crown and branch structure are ecologically important for a variety of reasons (Tinnin et al. 1982; Mathiasen 1996; Godfree et al. 2002), including their potential influence on fire behavior and fuel composition. The additional biomass in brooms is expected to increase fuel loads as needles or twigs senesce from brooms or as entire brooms fall to the ground.

Few studies have examined directly the influence of mistletoe on accumulation of surface fuels (Koonce 1981; Hoffman et al. 2007). Koonce (1981) quantified fuel loadings in young ponderosa pine stands and found that mistletoe increases both surface and aerial fuels, depending upon stand structure and the degree of infection. Koonce (1981) considered high fuel loadings in young infested stands a consequence of branch biomass both on the ground and persisting in the crown. Hoffman et al. (2007) found total fuel loads were significantly greater in se-

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verely infested stands of ponderosa pine in northern Arizona, primarily in the form of 100- and 1000-hr fuels. Koonce (1981) and Hoffman et al. (2007) examined the relationship between mistletoe and fuel loads in managed, relatively young forests, leaving a gap in our knowledge about the role of dwarf mistletoe in the fire ecology of relatively unmanaged, mature ponderosa pine and mixed conifer stands.

Our research investigated the effects of dwarf mistletoe infection on surface fuel loads and snag basal area in two mature, relatively natural forests dominated by ponderosa pine. Our specific objectives were to: (1) determine if fuel loads were greater in stands severely infested with dwarf mistletoe than in non-infested stands; (2) identify the specific fuel size classes most influenced by mistletoe infection; and (3) determine the relative influence of mistletoe on fuel accumulation relative to other stand variables such as age, density, and species composition.

METHODS

Study Areas

We conducted this research in two areas in central Oregon: the panhandle of Crater Lake National Park and Lava Cast Forest in Newberry National Volcanic Monument. Both areas support mature, mixed-conifer forests dominated by ponderosa pine with varying levels of dwarf mistletoe infection. The climate and management histories differ between the two study areas. The Crater Lake study area, which is more mesic and at lower elevation, was selectively logged until the 1920s and has experienced fire suppression and prescribed fire management. In contrast, the climate at Lava Cast Forest is more arid and there is minimal evidence of active management, including logging or fire suppression. A comparison between the two study sites revealed the stand structure for Crater Lake and Lava Cast Forest study areas were too dissimilar for data to be pooled. All stand structure variables we measured, except fir basal area, differed significantly between Crater Lake and Lava Cast Forest (Table 1).

Crater Lake

The Crater Lake study site was an 81.5-ha unit situated within the southern boundary of Crater Lake National Park (42º36'N, 122º05W). Located along the east flank of the Cascade Mountain range, the Crater Lake site included gentle slopes (3%) with a south-facing aspect, ranging in elevation from 1340 to 1400 meters above sea level (asl). Crater Lake was designated a national park in 1902, but the panhandle region was not included until 1932. U.S. Forest Service records indicate that selective logging occurred between 1909 and 1927.

The climate at Crater Lake is strongly seasonal. Average annual precipitation at Chiloquin (1274 m asl), ca. 30 km southeast of Crater Lake, was 51.3 cm (1971 to 2000), with the majority of precipitation occurring as snow between November and March (OCS 2006). Average monthly temperatures ranged from a low of -2 ºC in January to a high of 17 ºC in July (OCS 2006).

Vegetation in the panhandle region of Crater Lake National Park is dominated by ponderosa pine-white fir (*Abies concolor* Gordon and Glend. Lindl.) forest. Sugar pine (*Pinus lambertiana* Dougl.) and lodgepole pine occur in small numbers, with occasional incense cedar (*Calocedrus decurrens* Torr.) and Douglas-fir (*Pseudotsuga menziesii* Mirb. Franco). Common understory species include wax currant (*Ribes cereum* Douglas), snowbrush (*Ceanothus velutinus* Douglas ex Hook.), dogbane (*Apocynum androsaemifolium* L.), pinemat manzanita (*Arctostaphylos nevadensis* A. Gray), grasses, and sedges. Western dwarf mistletoe (*Arceuthobium campylopodum* Engelm.) has a patchy distribution at the Crater Lake study site with infestation levels ranging from low to severe. Mean fire-return intervals for the area that includes our study site were nine to 42 years from 1748 to 1902 (McNeil and Zobel 1980), and the panhandle region was scheduled for low-intensity prescribed burns following our sampling.

Lava Cast Forest

Lava Cast Forest is located in the Newberry National Volcanic Monument east of the Cascade crest (43.69ºN, 121.25ºW). Our study site is characterized by 11 kipukas (forested islands) isolated among shallow, mid-Holocene lava flows (Peterson and Groh 1969). Kipuka areas range from 0.4 to 113 ha with maximum elevations from 1590 to 1820 m asl. A rain shadow effect from the Cascade Mountains to the west strongly influences the regional climate of the study area. The moisture regime is semi-arid, with the majority of precipitation occurring from October to March, typically as snow during the winter. Average annual precipitation between 1971 to 2002 was 30 cm and average temperatures ranged from a low of 0 ºC in January to a high of 18 ºC in July (OCS 2006).

Kipukas are dominated by three tree species with distributions appearing to be topographically and edaphically controlled. Ponderosa pine (the primary host for western dwarf mistletoe) is most common on south-facing slopes, whereas north-facing slopes and interior stands are dominated by grand fir (*Abies grandis* Douglas ex D. Don Lindl.). Flat areas are typically covered with dense stands of lodgepole pine. Common understory species include snowbrush, green manzanita (*Arctostaphylus patula* Greene), and bitterbrush (*Purshia tridentata* Pursh DC.). The infestation intensity of dwarf mistletoe across the Lava Cast Forest study site is highly variable, with some kipukas lacking mistletoe while others support mistletoe in the majority of pine stands. The mistletoe infections are moderate to severe, with the majority of trees in infested stands supporting mistletoe in over half of their crowns. The mean fire-return interval on the kipukas included in our study site is six years (Arabas et al. 2006).

Sampling Strategy

We sampled 14 plots at Crater Lake (seven plots moderately- to severely-infested with mistletoe and seven plots non-infested) and 36 plots at Lava Cast Forest (22 moder-

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Table 1. Stand structure and fuel composition comparisons between infested and non-infested plots. Means (standard deviations) for stand structure variables and fuel loads, and t-test results comparing non-infested and mistletoe-infested plots within each study site - Crater Lake (CLP) and Lava Cast Forest (LCF).

Stand Structure Variables	CLP all plots (N=14)	CLP non-infested (N=7)	CLP infested (N=7)	LCF all plots (N=36)	LCF non-infested (N=14)	LCF infested (N=22)
Total basal area (m2/ha)	43.9 (21.5)	50.6 (27.3)	37.1 (12.2)	48.4 (18.8)	55.8 (18.4)	43.6 (17.9)
Ponderosa pine basal area (m2/ha)	19.3 (12.9)	21.4 (7.4)	16.8 (14.8)	37.8 (20.0)	43.6 (18.9)	34.0 (20.1)
White fir basal area (m2/ha)	4.4 (6.0)	5.7 (10.8)	3.5 (4.8)	7.7 (9.9)	8.9 (6.1)	7.0 (11.9)
Tree density (trees/ha)	782 (381)	875 (414)	688 (350)	379 (192)	487 (112)*	310 (202)
Tree age (yrs)	97 (15)	91 (12)	102 (17)	194 (42)	185 (35)	200 (46)
Maximum tree age (yrs)	295 (124)	312 (128)	278 (128)	413 (108)	412 (126)	414 (97)
Ponderosa pine age (yrs)	183 (90)	99 (31)	105 (35)	250 (59)	266 (45)	240 (65)
Sapling/seedling density (#/ha)	1663 (2103)	1617 (3116)	1709 (3150)	261 (275)	302 (266)	235 (284)
Ponderosa sap/seed density	498 (690)	519 (762)	476 (680)	91 (102)	60 (43)	123 (133)*
White fir sap/seed density	4816 (4561)	4539 (4553)	(4932)*	257 (305)	358 (330)*	146 (242)
Lodgepole sap/seed density	772 (938)	606 (994)	(2022)*	101 (126)	107 (144)	89 (92)
Understory % cover	5.03 (7.62)	2.23 (1.55)	5.84 (10.2)	0.14 (0.07)	0.14 (0.06)	0.14 (0.08)
Understory species richness	4 (3)	4.6 (3.2)	3.4 (2.8)	5 (2)	5.2 (2.3)	4.7 (1.9)
Years since last fire	27 (0)	27 (0)	27 (0)	112 (69)	136 (68)*	96 (67)
Fuel Variables						
1-hr (Mg/ha)	0.06 (0.04)	0.06 (0.04)	0.06 (0.04)	0.13 (0.12)	0.05 (0.03)	0.17 (0.14)*
10-hr (Mg/ha)	0.65 (0.28)	0.53 (0.24)	0.76 (0.27)	0.68 (0.34)	0.53 (0.22)	0.78 (0.38)*
100-hr (Mg/ha)	0.54 (0.34)	0.41 (0.40)	0.66 (0.25)	0.92 (0.70)	0.60 (0.39)	1.13 (0.78)*
1000-hr (Mg/ha)	2.49 (1.94)	1.69 (1.83)	3.29 (1.83)	11.7 (12.9)	12.0 (16.2)	11.5 (10.6)
Litter (Mg/ha)	0.03 (0.01)	0.03 (0.01)	0.03 (0.01)	0.03 (0.05)	0.02 (0.01)	0.05 (0.06)*
Duff (Mg/ha)	3.32 (3.32)	3.4 (3.0)	3.3 (3.8)	4.54 (3.35)	5.0 (3.6)	4.2 (3.2)
Total (Mg/ha)	7.08 (3.58)	6.1 (3.3)	8.1 (3.8)	18.02 (14.64)	18.2 (18.2)	17.9 (12.3)
Snags (m^2/ha)	5.98 (5.65)	4.3 (4.8)	7.6 (6.3)	4.83 (4.55)	4.8 (5.3)	4.8 (4.2)

* Significantly greater in this group at this study site ($P < 0.05$).

ately- to severely-infested plots, 14 non-infested plots). We visually estimated infection intensity using the dwarf mistletoe rating system (DMR), which ranges from 0 (non-infected) to 6 (severely-infected) (Hawksworth 1977). Individual tree DMRs were averaged across each plot and only plots with mean DMR ≥ 3 were included. Plots with DMR < 3 were excluded because they were too rare for meaningful statistical comparisons among different infestation levels. Plot sizes at both sites varied (15 m^2 to 50 m^2), based on the minimum area needed to include at least 20 live trees for stand structure analysis.

Stand Structure Variables

We measured stand structure variables within each plot (see plot establishment protocol above) to determine their relative influence on fuel composition in relation to dwarf mistletoe abundance. Stand structure variables included diameter measurements for all live and dead trees > 4 cm dbh (diameter at breast height, 1.4 m above ground) and tallies of all saplings and seedlings growing within each plot. We used four 1 m^2 quadrats per plot to estimate percent cover and richness of understory plants. We estimated stand age by collecting a single increment core as close to the root collar as possible (30 to 50 cm above ground) from all live trees (> 4 cm dbh) in our plots using standard dendrochronological procedures (Stokes and Smiley 1996).

Arabas et al. (2006) provided fire history information for Lava Cast Forest that includes years since the most recent fire-scar recorded or stand-replacing fire and the mean fire return interval for each stand. We excluded low-intensity surface fires (i.e., those that did not scar trees) from the analyses because of the incomplete historical record (Arabas et al. 2006). Fire history is not included in Crater Lake analyses because park records indicate the entire study area has not experienced fire

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since prescribed burning in 1976.

Fuel Load Comparisons

Fuel loads were measured in each plot using the planar intercept method (Brown 1974; Brown et al. 1982). Transects were placed randomly within each plot with the number of transects per plot ranging from one to five, varying according to plot size. Total transect length was 15 m; fuels in the 1-h size class (0 to 0.64 cm diameter at the intersection with the transect) were sampled from 0 to 2 m along each transect; 10-h fuels (0.65 to 2.54 cm) from 0 to 3 m; 100-h fuels (2.55 to 7.62 cm) from 0 to 5 m; and 1000-h fuels (> 7.62 cm) were sampled from 1 to 15 m. We used dbh to calculate the basal area of all snags in each plot and extrapolated to m^2/ha.

We measured litter and duff depth to the nearest centimeter with a ruler at 0, 3, and 6 m along each transect. Litter samples were collected from each transect and oven-dried to obtain bulk density measurements for use in biomass calculations. Fuel biomass calculations followed the procedures of Brown et al. (1982).

Data Analysis

Distributions of each variable were tested for normality using Kolmogorov-Smirnov tests ($P \leq 0{,}05$), histograms, and standard deviations. All fuel variables were square-root transformed to correct for skewed distributions and to avoid domination by the larger fuel types. Fuel and stand structure data were standardized using *z*-scores to account for different measurement units (fuel loads versus basal area for snags).

Stand structure and fuel load comparisons

We used descriptive statistics and t-tests to compare stand structure variables between the two study sites to determine if Crater Lake and Lava Cast Forest data could be pooled for subsequent analyses. We used independent samples t-tests ($P \leq 0.05$) to compare fuel loads and stand structure between infested and non-infested plots. We tested for differences in both total fuel loads and individual fuel size classes.

Influence of mistletoe and stand structure on fuel loads

We used a combination of indirect and direct gradient analysis to quantify the importance of mistletoe on fuel composition. Gradient analyses allowed us to test all fuel size classes separately but simultaneously, which is more relevant ecologically compared to univariate tests that investigate each fuel class independently. Principal components analysis (PCA), an unconstrained, indirect gradient analysis, was used to identify patterns in fuel distribution among the samples and to visually assess patterns in fuel composition among plots (Jongman et al. 1995). PCA revealed the covariance structure within the fuel data and identified the amount of variability in the fuels that can be interpreted with direct gradient analysis (RDA).

We used redundancy analysis (RDA), a constrained or direct gradient analysis, to identify the linear combinations of the stand structure variables that best explain variations in fuel loads among our samples. RDA also approximates the distributions of fuel data along the range of sampled values for each stand variable, indicating correlations between fuel data and the environment (ter Braak 1986). We chose a forward-selected RDA to determine which stand structure components accounted for the greatest amount of variance in the distribution of fuels and to reduce multicollinearity among independent variables (CANOCO v. 4.0, ter Braak 1998). This iterative process selects variables that uniquely and significantly ($P \leq 0.05$) explain variation in the distribution of fuels. The significance of each added variable and the final canonical axes were verified using Monte Carlo permutation tests with 999 unrestricted permutations ($P \leq 0.05$). We used Spearman rank-order correlations to identify any significant relationships between mistletoe infection level (mean DMR) and fuel loads for each plot. We also used one-way analysis of variance (ANOVA) with Bonferroni post-hoc tests to locate significant differences ($P \leq 0.05$) among infection levels (noninfected, moderate, and severely infected) for fuel size classes identified as significant in the ordination analyses.

Based on initial PCA and RDA results for Lava Cast Forest, we removed snag basal area and 1000-hr fuels as a dependent variable in the final RDA model. PCA indicated that snags contributed little to the covariance structure of fuels at Lava Cast Forest, and the initial forward-selected RDA model showed that snag basal area and 1000-hr fuels were not correlated with mistletoe infection. We removed slope angle and aspect from our subsequent analyses because of their low variability and minor influence on our dependent variables.

RESULTS

Crater Lake

Statistical tests revealed few differences between infested and non-infested plots at Crater Lake. The density of white fir and lodgepole seedlings and saplings was significantly greater in infested than non-infested plots (Table 1). Total fuel loads and individual fuel size classes showed no significant differences between infested and non-infested plots (Table 1). The first four PCA axes explained 85% of the variance in fuel composition among Crater Lake plots. The first axis explained 36% of the variance in fuels, representing 10- and 100-hr classes (Table 2; Figure 1). The second axis explained an additional 22% of the variance in fuels corresponding to a gradient of duff accumulation. Infested plots formed two distinct groups, representing low versus high accumulations of duff (Figure 1). PCA results indicated that infested plots generally had higher than average accumulations of 1-, 10-, and 100-hr fuels and high variations in litter, duff, 1000-h fuels, and snags. Non-infested plots showed greater variation overall in fuel accumulation (Figure 1).

RDA results identified five significant stand structure variables explaining fuel composition at Crater Lake: fir basal area, mistletoe infection, ponderosa basal area, density of seedlings and saplings, and maximum tree age (Table 3). The first four RDA axes explained 51% of the variance in

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Table 2. Principal components analysis (PCA) results for fuel composition at the Crater Lake (CLP) and Lava Cast Forest (LCF) study sites. Eigenvalues represent variance explained by each axis. Species scores indicate coordinates along each ordination axis.

	CLP		LCF	
	Axis I	Axis II	Axis I	Axis II
Eigenvalues	0.36	0.22	0.34	0.20
Species Scores				
1-h (Mg/ha)	0.68	-0.53	0.70	0.33
10-h (Mg/ha)	0.85	-0.17	0.80	0.24
100-h (Mg/ha)	0.77	-0.25	0.74	0.04
1000-h (Mg/ha)	0.64	0.53	0.52	-0.60
Litter (Mg/ha)	-0.22	0.34	0.24	0.76
Duff (Mg/ha)	-0.28	-0.80	0.48	-0.28
Snag Basal Area (m^2/ha)	-0.17	-0.42	0.39	-0.44

fuel composition among Crater Lake plots. The first constrained axis explained 28% of the variance, representing a gradient in fir basal area and mistletoe infection (Table 3; Figure 2). The second axis explained 15% of fuel load variation corresponding to basal area of ponderosa pine and density of seedlings and saplings (Table 3; Figure 2). RDA revealed positive correlations between dwarf mistletoe and 10-, 100-, and 1000-hr fuels and negative correlations with litter and duff accumulation (Figure 2). Plots with high ponderosa pine basal area generally exhibited larger accumulations of litter and duff, and fir basal area was positively correlated with 1-h fuel loads (Figure 2). Seedling and sapling density at Crater Lake was positively correlated with 1000-h fuel loads (Figure 2).

Spearman correlation confirmed the RDA results showing DMR was significantly and positively correlated with 1000-hr fuel loads ($r = 0.58$, $P = 0.03$). ANOVA results showed no differences in total, total fine (1 to 100-hr), or 1000-hr fuel loads among non-infested, moderately, and severely infested plots.

Lava Cast Forest

Infested plots at Lava Cast Forest experienced more recent fires, had significantly lower densities of live trees and white fir seedlings, and significantly higher densities of ponderosa pine seedlings compared to non-infested plots (Table 1). Infested and non-infested plots had similar total fuel loads, but infested plots contained more 1-, 10-, and 100-h fuels and litter (Table 1).

The first four PCA axes explained 79% of the variance in fuels at Lava Cast Forest. The first axis, representing a gradient in 10- and 100-h fuels, explained 34% of the variance in fuels (Table 2; Figure 3). The second axis explained 20% of the variance among plots, representing 1000-h fuels and litter (Figure 3). PCA did not show a distinct separation between infested or non-infested plots. Infested plots showed more variation in fuel composition and generally had higher than average 1-, 10-, and 100-h fuel loads (Figure 3). Non-infested plots had the least litter accumulations and 1-, 10-, and 100-h fuels.

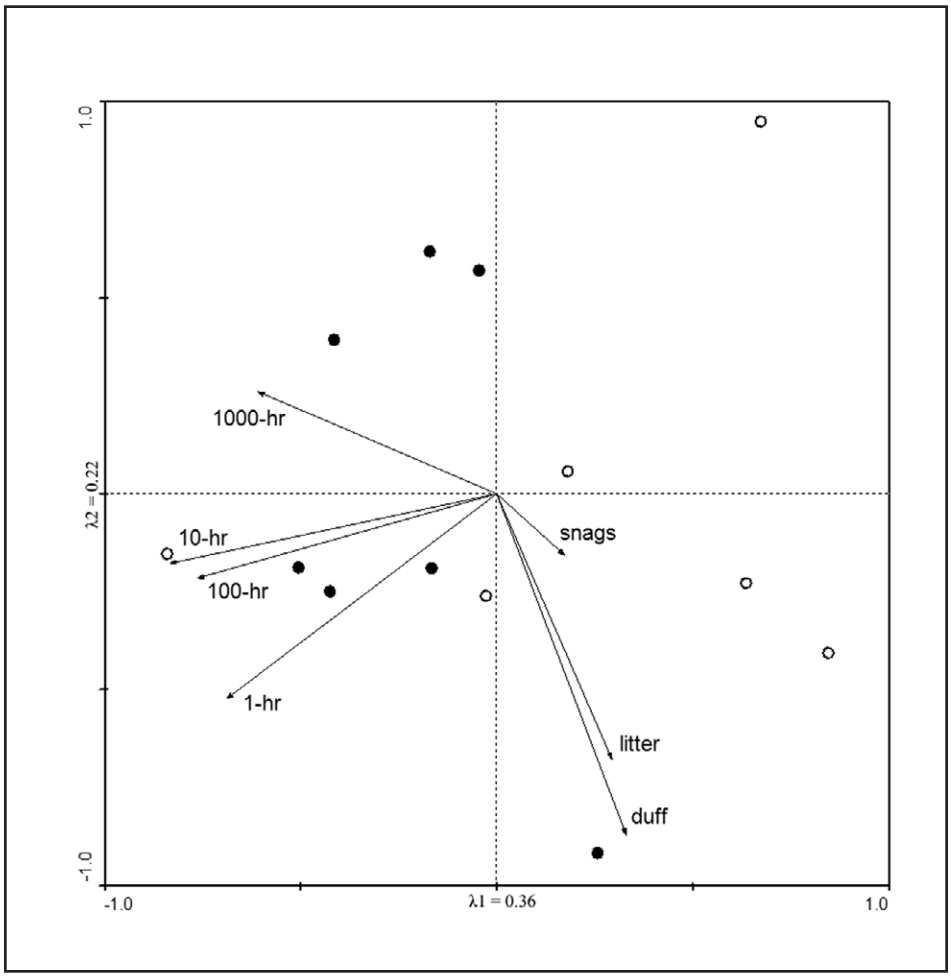

Figure 1. PCA diagram for fuel composition in Crater Lake plots. Dark circles represent plots infested with mistletoe; open circles represent non-infested plots. The first axis represents a gradient of 1-, 10-, and 100-hr fuels; the second axis 1000-hr fuels and duff.

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Table 3. Results from forward-selected redundancy analysis (RDA) for Crater Lake (CLP) and Lava Cast Forest (LCF) plots. Eigenvalues represent variance explained by each axis. Species-environment correlations indicate how well the included environmental variables explain the fuel composition among the samples. Inter-set correlations indicate the strength of the relationship between environmental variables and fuel composition along each axis.

	CLP		LCF	
	Axis I	Axis II	Axis I	Axis II
Eigenvalue:	0.28	0.15	0.16	0.09
Species-environment correlation:	0.86	0.72	0.63	0.68
	Inter-set Correlations			
Environmental Variables				
Mistletoe infection	0.42	-0.43	0.36	0.33
Fir basal area	0.46	0.12	n/a	n/a
Sapling / seedling density	-0.26	-0.46	n/a	n/a
Maximum tree age	0.26	0.15	0.25	-0.22
Ponderosa pine basal area	-0.22	0.64	-0.17	-0.10
Ponderosa pine average age	n/a	n/a	0.20	-0.44
Time since last fire	n/a	n/a	0.05	-0.56

The final RDA model for Lava Cast Forest identified five significant stand structure variables: maximum tree age, mistletoe infection, ponderosa basal area, time since the last fire, and average age of ponderosa pine trees (Table 3). The first four RDA axes explained 34% of the variation in fuel composition among Lava Cast Forest plots. The first axis explained 16% of the variance in fuels corresponding to differences in mistletoe infection and maximum tree age (Table 3; Figure 4). Axis two explained 9% of the variance corresponding to years since the most recent fire and mean ponderosa pine tree ages (Table 3; Figure 4). Ponderosa pine basal area was negatively correlated or uncorrelated with all fuel size classes (Figure 4). Maximum and mean tree ages of ponderosa pine were positively correlated with duff, 10- and 100-h fuels, while tree age and time since last fire were negatively correlated with litter accumulation (Figure 4). Plots not experiencing recent fires had the oldest trees, the highest accumulations of duff, and the lowest litter accumulations.

Redundancy analysis showed that dwarf mistletoe infection was positively correlated with 1-hr fuels and litter biomass at Lava Cast Forest and negatively correlated with duff accumulations (Figure 4). Mistletoe infection showed a weak positive correlation with 10- and 100-h fuels (Figure 4). Spearman correlation revealed significant, positive relationships between DMR and litter ($r = 0.35$, $P = 0.04$), 10-hr ($r = 0.45$, $P = 0.01$), and 100-hr ($r = 0.41$, $P = 0.02$) fuels. The RDA results were supported by ANOVA with severely infested plots having significantly greater fine fuel accumulation (1-hr df = 35, $F = 7.4$, $P = 0.002$; 10-hr df = 35, $F = 2.6$, $P = 0.04$; 100-hr df = 35, $F = 5.3$, $P = 0.01$) than lightly infested or non-infested plots (Figure 5) but no difference in total fuel loads.

DISCUSSION

Fuel loads were highly variable within and between the Crater Lake and Lava Cast Forest study sites and dwarf mistletoe was only one of several factors that influenced fuels. Our results suggest that stand composition, especially abundance of non-host tree species, exerts a strong influence on fuel accumulation that overshadows the direct effects of mistletoe infection. Our observations of mature ponderosa pine trees (300 to 600 years old) in central Oregon indicate that many trees survive infection (Stanton 2007), suggesting a complex relationship among infection, mistletoe-induced mortality, and fuel accumulation. In the absence of a natural disturbance regime, many ponderosa pine stands in central Oregon are developing dense understories of shade-tolerant and fire-intolerant fir species. Mistletoe may be contributing to this conversion to fir by increasing mortality rates among understory ponderosa pine and providing a competitive advantage to non-host tree species, thereby indirectly altering fuel composition.

Mistletoe infestation resulted in greater fuel loads for a subset of fuel size classes and under certain site conditions. Both study sites exhibited significant, positive correlations between mistletoe infestation and fine woody fuel loads, but the relative effect of mistletoe on fuel composition differed between study sites. Dwarf mistletoe exhibited a weak influence on fuel composition relative to stand density and basal area of dominant tree species in mixed-conifer stands at Crater Lake. In the pure ponderosa pine stands at Lava Cast Forest, mistletoe was a significant, but weaker, predictor of fuel load composition when compared with Crater Lake. This difference may be partly explained by the greater range of stand ages and environmental conditions (such as slope aspect and elevation) at Lava Cast Forest. More variables emerged as explanatory because the landscape was more diverse and there was more fuel load variation to be accounted for at Lava Cast Forest.

Fine Woody Fuels

The relationship between mistletoe infestation and fuel loads was most pronounced among the fine fuel classes. Infested plots at both study sites tended to have higher accumulations of 1-, 10-, and 100-h fuels. These results were similar to those reported by Koonce and Roth (1985) for 100-hr fuels in infested, thinned stands where brooms were left behind as slash, as well as those of Hoffman et al. (2007) who found infested stands in northern Arizona had greater fine fuel loads (< 7.6 cm diameter). Witches' brooms are the likely source for the additional fine woody fuels accumulating in infested areas as abundant twigs senesce or are dislodged from brooms by wildlife activity (Mathiasen 1996; Shaw et al. 2004).

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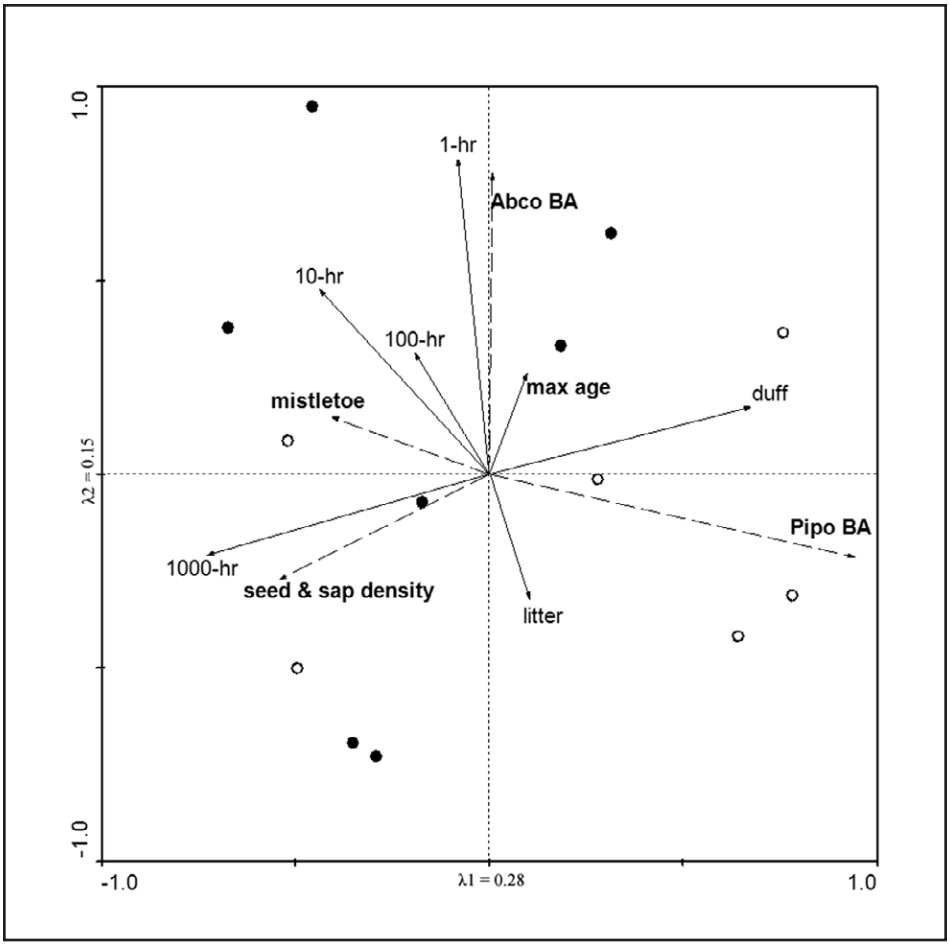

Figure 2. RDA diagram for Crater Lake plots. Dark circles represent plots infested with mistletoe; open circles represent non-infested plots. Environmental variables are indicated by bold text and dashed vectors. Fuel variables are indicated by solid vectors.
Pipo = ponderosa pine; Abco = white fir; BA = basal area.

Litter Accumulation

The relationship between mistletoe abundance and litter biomass differed between the two study sites, being positive at Lava Cast Forest and negative at Crater Lake. High litter accumulation at Lava Cast Forest may be a consequence of changes in needle growth and morphology, as well as stand structure and composition. Studies report greater needle surface areas on broomed branches (Tinnin and Knutson 1980; Wanner and Tinnin 1986), while others report decreases in the number, length, and mass of needles in lodgepole pine brooms (Broshot et al. 1986) and longer needle retention under stressful conditions (Nebel and Matile 1992; Richardson and Rundel 1998). We are unaware of published research that has examined the effects of mistletoe on needle morphology in ponderosa pine, leaving the relationship between infection and litter accumulation unresolved. Infested plots at Lava Cast Forest also experienced more recent moderate to severe fire than non-infested plots, adding to the uncertainty of the role of mistletoe infection leading to understory host mortality and lower stand densities. Although recent fire and lower tree densities would appear to decrease fine fuel loadings, our Lava Cast Forest results indicate that needle and fine fuel accumulation may increase following recent, low-intensity fires that scorch lower branches.

The negative correlation between mistletoe infestation and litter at Crater Lake may be: (1) a direct result of mistletoe causing changes in host needle retention; (2) an indirect result of mistletoe causing changes to stand structure; or (3) the result of changes in stand structure unrelated to mistletoe infection. In addition to altering host tree growth, mistletoe infection can alter stand structure through host mortality. The more severely infested plots at Crater Lake were young, mixed cohorts of several species.

Mistletoe-related mortality of ponderosa pine trees could explain the shift in stand age and structure to young and non-host species, resulting in an indirect link between infection and litter accumulation. Non-host species such as grand fir and Douglas-fir possess small needles in greater densities compared to long-needled species such as ponderosa pine (Grier and Running 1977).

Coarse Fuels

The relationship between mistletoe infestation and coarse fuels (1000-hr and snags) was inconsistent between the two study sites. Infested plots at Crater Lake had more coarse fuels in the form of downed logs when compared with uninfested plots, but mistletoe had little influence on the accumulation of coarse fuels at Lava Cast Forest. Infested plots at Crater Lake had more shade-tolerant fir seedlings and saplings with relatively little ponderosa pine regeneration. The 1000-h fuels in these infested plots appeared to be the result of self-thinning among the dense fir cohorts occupying the understory of the infested mature pines, rather than mistletoe-related mortality among host trees as reported in previous studies (Wanner and Tinnin 1989; Bennets et al. 1996; Hoffman et al. 2007). Previous research at Lava Cast Forest indicated that infection does not decrease growth or increase mortality rates among mature host trees (Stanton 2007). Stand age at Lava Cast Forest was most strongly correlated with coarse fuel loads. Older stands have more logs and snags regardless of the presence of mistletoe, and we found no correlation between stand age and mistletoe infection level at this site.

Our Lava Cast Forest results differ from those reported by Hoffman et al. (2007) who found infested stands in northern Arizona have greater fuel loads of coarse (> 7.6 cm) fuels. Hoffman et al. (2007)

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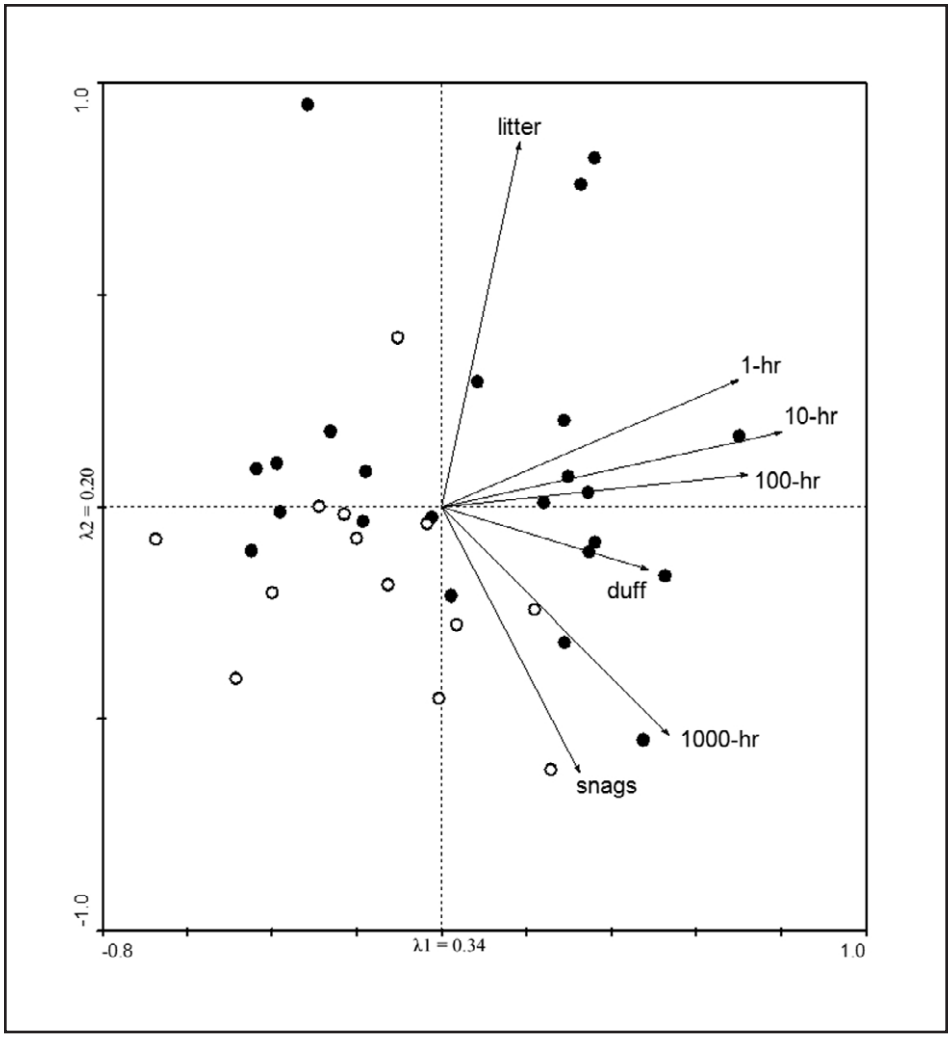

Figure 3. PCA diagram for fuel composition at Lava Cast Forest. Dark circles represent plots infested with mistletoe; open circles represent non-infested plots. The first axis represents a gradient of 1-, 10-, and 100-hr fuels; the second axis 1000-hr and litter.

reported average fuel loads ranging from 8.8 Mg/ha for uninfested stands to 51.9 Mg/ha for infested stands compared to Lava Cast Forest (18.2 Mg/ha for uninfested and 17.9 Mg/ha for infested stands). Our lower total fuel loads were also consistent with the lower tree density and greater basal area at Lava Cast Forest compared to northern Arizona (Hoffman et al. 2007) and may be a function of differences in climate and site productivity, as well as management or fire histories not addressed by Hoffman et al. (2007).

CONCLUSIONS

Our results indicate that severe mistletoe infestation in central Oregon ponderosa pine forests leads to greater accumulations of fine woody fuels, but the influence of mistletoe is complex, often indirect, and appears to change with stand development. Additional studies are needed to investigate the effects of mistletoe infection on fuel loads in other forest types and stand conditions, as well as the influence of infection on fire behavior. Prescribed fire is often used as a restoration tool in ponderosa pine stands, yet it is unclear if mistletoe alters fire behavior and, therefore, the outcome of prescribed burns. Fire behavior models would benefit from direct canopy and surface fuel data derived from severely infested trees during the various stages of stand development and a better understanding of how mistletoe interacts with other disturbance agents.

Environmental variables, including mistletoe infection level, explained little of the variance in fuel loads, indicating the absence of some key explanatory variables in our study or an inability to accurately model fuel accumulation processes. Stand history appears to play a critical role in fuel accumulations, but the history or successional trajectory of a stand is difficult to quantify and summarize. Other important stand-related variables need to be assessed, including measures of mistletoe-induced needle density, determination of how mistletoe influences tree stress and insect and pathogen infestation, and more detailed, stand-level fire histories that include low-intensity surface fires.

Our results suggest that mistletoe may increase the risk of wildfire in mature forests through the addition of easily ignited fine woody fuels, but the severity of fire may not be altered because infestation does not increase coarse fuel loads or snags. Frequent, low severity prescribed fires could be used to offset the additional fuels related to mistletoe infestation in ponderosa pine stands. Prescribed fires also would reduce densities of non-host species that appear to directly contribute more to fuel loading than mistletoe infestation.

ACKNOWLEDGMENTS

We thank Karen Arabas for her assistance throughout this research and Willamette University students for their help and good humor in the field. The manuscript was substantially improved by the comments of an anonymous reviewer. This research was partially funded by a Forbes-Lea Research Grant from Portland State University.

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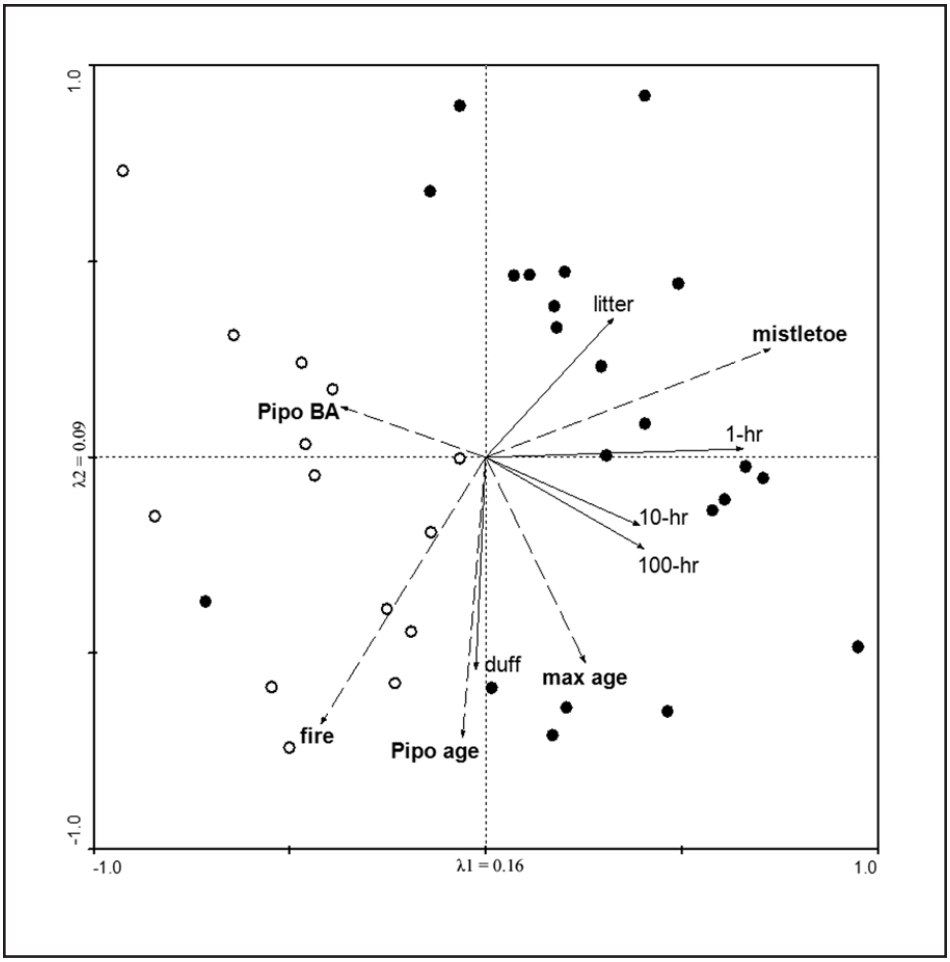

Figure 4. RDA results for Lava Cast Forest plots. Dark circles represent plots infested with mistletoe; open circles represent non-infested plots. Stand structure variables are indicated by bold text and dashed vectors. Fuel variables are indicated by solid vectors.
Pipo = ponderosa pine; BA = basal area; fire = years since last fire.

include vegetation dynamics, island biogeography, landscape ecology, dendrochronology, and climate change.

LITERATURE CITED

Agee, J.K. 1993. Fire Ecology of Pacific Northwest Forests. Island Press, Washington, D.C.

Arabas, K.B., K.S. Hadley, and E.R. Larson. 2006. Fire history of a naturally fragmented landscape in central Oregon. Canadian Journal of Forest Research 36:1108-1120.

Bennets, R.E., C.G. White, F.G. Hawksworth, and S.E. Severs. 1996. The influence of dwarf mistletoe on bird communities in Colorado ponderosa pine forests. Ecological Applications 6:899-909.

Broshot, N.E., L. Larsen, and R.O. Tinnin. 1986. Effects of *Arceuthobium americanum* on twig growth of *Pinus contorta*. Research Note PNW-453, U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, Ore.

Brown, J.K. 1974. Handbook for inventorying downed woody material. General Technical Report INT-16, U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station, Ogden, Utah.

Brown, J.K., R.D. Oberheu, and C.M. Johnston. 1982. Handbook for inventorying surface fuels and biomass in the interior west. General Technical Report INT-129, U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station, Ogden, Utah.

Cooper, C.F. 1960. Changes in vegetation, structure, and growth of southwestern pine forests since white settlement. Ecological Monographs 30:129-164

Covington, W., and M.M. Moore. 1994. Southwestern ponderosa forest structure: changes since Euro-American settlement. Journal of Forestry 92:39-47.

Dahms, C., and B.W. Geils. 1997. An assessment of forest ecosystem health in the Southwest. General Technical Report RM-295, U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colo.

Fulé, P.Z., W.W. Covington, H.B. Smith, J.D. Springer, T.A. Heinlein, K.D. Huisinga, and M.M. Moore. 2002. Comparing ecological restoration alternatives: Grand Canyon, Arizona. Forest Ecology and Management 170:19-41.

Geils, B.W., and F.G. Hawksworth. 2002. Damage, effects, and importance of dwarf mistletoes. Pp. 57-65 *in* B.W. Geils, J.C. Tovar, and B. Moody, eds., Mistletoes of North American Conifers, General Technical Report RMRS-98, U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colo.

Godfree, R.C., R.O. Tinnin, and R.B. Forbes. 2002. The effects of dwarf mistletoe, witches' brooms, stand structure, and site characteristics on the crown architecture of lodgepole pine in Oregon. Canadian Journal of Forest Research 32:1360-1371.

Grier, C.G., and S.W. Running. 1977. Leaf area of mature northwestern coniferous forests: relation to site water balance. Ecology 58:893-899.

Hawksworth, F.G. 1977. The 6-class dwarf mistletoe rating system. General Technical Report RM-48, U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colo.

Hoffman, C., R. Mathiasen, and C.H. Sieg. 2007. Dwarf mistletoe effects on fuel loadings in ponderosa pine forests in northern Arizona. Canadian Journal of Forest Research 37:662-670.

Jongman, R.H.G., C.J.F. ter Braak, and O.F.R. van Tongeren. 1995. Data Analysis in Community and Landscape Ecology. Cambridge University Press, Cambridge, U.K.

Knight, R. 1987. Parasites, lightning, and the vegetation mosaic in wilderness landscapes. Pp. 59-83 *in* M.G. Turner and D.J. Boqucki, eds., Landscape Heterogeneity and Disturbance. Springer-Verlag, New York.

Koonce, A.L. 1981. Interactions between fire and dwarf mistletoe in ponderosa pine. Ph.D. diss., Oregon State University, Corvallis.

Koonce, A.L., and L.F. Roth. 1985. The effects of dwarf mistletoe on fuel in precommercial ponderosa pine stands. Pp. 66-72 *in* L.R. Donoghue, and R.E. Martin, eds., Proceed-

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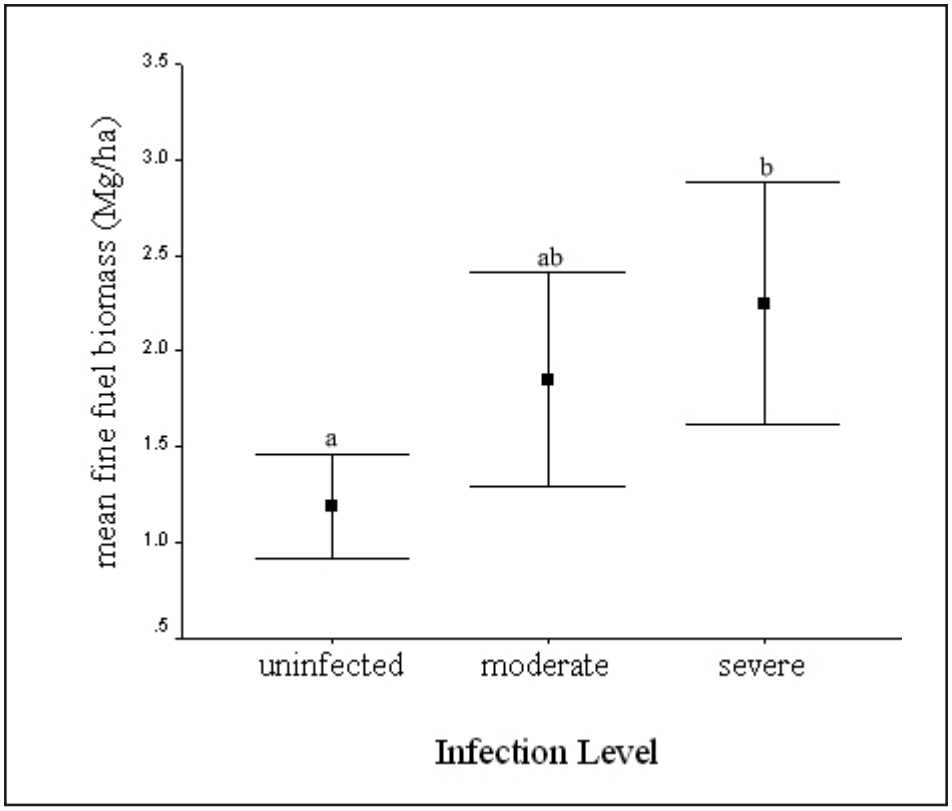

Figure 5. Sum of fine woody fuel loads (1-, 10- and 100-hr fuels; mean ± 1 SE) by dwarf mistletoe infection level (moderate = mean plot DMR 3 or 4; severe = mean plot DMR 5 or 6) for Lava Cast Forest, Oregon. Different letters (a or b) denote statistically different means determined by one-way ANOVA ($P \leq 0.05$).

ings 8th Conference of Fire and Forest Meteorology, Detroit, Mich.

Mathiasen, R.L. 1996. Dwarf mistletoes in forest canopies. Northwest Science 70:61-71.

McNeil, R.C., and D.B. Zobel. 1980. Vegetation and fire history of a ponderosa pine – white fir forest in Crater Lake National Park. Northwest Science 54:30-46.

Nebel, B., and P. Matile. 1992. Longevity and senescence of needles in Pinus cembra. Trees – Structure and Function 6:156-161.

[OCS] Oregon Climate Service. 2006. Oregon climate zone data. Available online http://ocs.oce.orst.edu.

Peterson, N.V., and E.A. Groh. 1969. The ages of some Holocene volcanic eruptions in the Newberry Volcano area, Oregon. Oregon Geology 31:73-87.

Richardson, D.M., and P. Rundel. 1998. Ecology and biogeography of *Pinus*: an introduction. Pp. 3-40 *in* D.M. Richardson, ed., Ecology and Biogeography of *Pinus*. Cambridge University Press, Cambridge, N.Y.

Savage, M. 1991. Structural dynamics of a southwestern pine forest under chronic human disturbance. Annals of the Association of American Geographers 81:271-289.

Shaw, D.C., D.M. Watson, and R.L. Mathisen. 2004. Comparison of dwarf mistletoes (*Arceuthobium* spp., Viscaceae) in the western United States with mistletoes (*Amyema* spp., Loranthaceae) in Australia – ecological analogs and reciprocal models for ecosystem management. Australian Journal of Botany 52:481-498.

Stanton, S. 2007. Effects of dwarf mistletoe on climate response of mature ponderosa pine trees. Tree-Ring Research 63:69-80.

Stokes, M.A., and T.L. Smiley. 1996. An Introduction to Tree-Ring Dating. University of Arizona Press, Tucson.

ter Braak, C.J.F. 1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. Ecology 67:1167-1179.

ter Braak, C.J.F. 1998. CANOCO v 4.0 program for canonical community ordination. Agricultural Mathematics Group, Wageningen, The Netherlands.

Tinnin, R.O., F.G. Hawksworth, and D.M. Knutson. 1982. Witches' broom formation in conifers infected by *Arceuthobium* spp.: an example of parasitic impact upon community dynamics. American Midland Naturalist 107:351-359.

Tinnin, R.O., and D.M. Knutson. 1980. Growth characteristics of the brooms on Douglas-fir caused by *Arceuthobium douglasii*. Forest Science 26:149-158.

Wanner, J.L., and R.O. Tinnin. 1986. Respiration in lodgepole pine parasitized by American dwarf mistletoe. Canadian Journal of Forest Research 16:1375-1378.

Wanner, J.L., and R.O. Tinnin. 1989. Some effects of infection by *Arceuthobium americanum* on the population dynamics of *Pinus contorta* in Oregon. Canadian Journal of Forest Research 19:736-742.

Weaver, H. 1959. Ecological changes in the ponderosa pine forest of Warm Springs Indian Reservation in Oregon. Journal of Forestry 57:15-20.

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