



Pruning high-value Douglas-fir can reduce dwarf mistletoe severity and increase longevity in Central Oregon



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ARTICLE INFO

Article history:

Received 4 May 2016

Received in revised form 7 July 2016

Accepted 11 July 2016

Available online 8 August 2016

Keywords:

Pseudotsuga menziesii var. *menziesii*

Arceuthobium douglasii

Pruning

Tree rings

Normalized Difference Vegetation Index

(NDVI)

Oregon

ABSTRACT

Mid- to very large-sized Douglas-fir (*Pseudotsuga menziesii* var. *menziesii*) that were lightly- to moderately-infected by dwarf mistletoe (*Arceuthobium douglasii*) were analyzed over a 14-year period to evaluate whether mechanical pruning could eradicate mistletoe (or at least delay the onset of severe infection) without significantly affecting tree vitality and by inference, longevity. Immediate and long-term pruning effects on mistletoe infection severity were assessed by comparing pruned trees ($n = 173$) to unpruned trees ($n = 55$) with respect to: (1) percentage of trees with no visible infections 14 years post-pruning, (2) Broom Volume Rating (BVR), and (3) rate of BVR increase 14 years post-pruning. Vitality/longevity (compared with unpruned trees) was assessed using six indicators: (1) tree survival, (2) the development of severe infections, (3) the development of dead tops, (4) tree-ring width indices, (5) Normalized Difference Vegetation Index (NDVI) from high-resolution multi-spectral imagery, and (6) live-crown ratio (LCR) and increment. Twenty-four percent of the pruned trees remained free of mistletoe 14 years post-pruning. Pruning is most likely to successfully eradicate mistletoe in lightly infected trees (BVR 1 or 2) without infected neighbors. Pruning significantly decreased mean BVR in the pruned versus the unpruned trees. However, the subsequent average rate of intensification (1.3–1.5 BVR per decade) was not affected, implying that a single pruning provides ~14 years respite in the progression of infection levels. Post-pruning infection intensification was slower on dominant and co-dominants than on intermediate or suppressed trees. The success of mistletoe eradication via pruning and need for follow-up pruning should be evaluated no sooner than 14 years after pruning to allow for the development of detectable brooms. Based on six indicators, foliage from witches brooms contribute little to long-term tree vitality since removal appears to have little effect on resources available for tree growth and maintenance. In the severely pruned trees, tree-ring width was reduced for several years post-pruning, but then compensated with larger ring width in later years. Both NDVI and LCR increment were significantly higher for the pruned trees than the control trees, while the development of severe infections and/or dead tops was significantly ($5\times$ and $3\times$) higher for the controls. If possible, multiple indicators of tree vitality should be evaluated. Pruning can be worthwhile even if all the mistletoe is not removed, because mistletoe intensification is delayed. The impact of removing the brooms seems to be minimal, and post-pruning crowns had greater NDVI values.

Published by Elsevier B.V.

1. Introduction

Large, old-growth Douglas-fir trees (*Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii*) are highly valued features in Pacific

Northwest campgrounds, parks, lakeshores, and other developed recreation areas. In these settings they provide wildlife habitat, shade, beauty, and confer a sense of wonder and tranquility. In many cases along the east slope of the Cascade Range, however, Douglas-fir is infected with dwarf mistletoe (*Arceuthobium douglasii* Engelm.). At high severity levels, *A. douglasii* can greatly decrease the vitality (ability to grow and survive under conditions

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present (Shigo, 1986)) and as a result, the longevity of these trees (Pierce, 1960; Mathiasen et al., 1990; Hawksworth and Wiens, 1996; Mallams, 2008b). Over time, when severely infected trees occur in recreation settings, the quality of the recreational experience may decrease as the large, severely infected trees die.

The principal and only common host of Douglas-fir dwarf mistletoe is Douglas-fir (Hawksworth and Wiens, 1996). Douglas-fir dwarf mistletoe has the greatest latitudinal range (3000 km) of any species in the genus (Hawksworth and Wiens, 1996). It occurs from southern British Columbia to central Mexico. It is common in eastern Washington, eastern Oregon, Idaho, western Montana, Utah, Colorado, Arizona, and New Mexico. Although there are abundant hosts west of the crest of the Cascade Mountains of Oregon, Washington, and British Columbia, *A. douglasii* is infrequent (Hawksworth and Wiens, 1996). It also occurs in southwestern Oregon and is common in northern California (Hawksworth and Wiens, 1996). *A. douglasii* is also characterized by its very small, aerial shoots, making it one of the smallest mistletoes in western North America (mean shoot length = 2 cm) (Hawksworth and Wiens, 1996).

Dwarf mistletoes (including *A. douglasii*) have an explosive seed dispersal mechanism and a sticky/slick seed coat that, together, increase the probability of proper seed placement for successful inoculation and infection. At maturity the seed (with a sticky seed coat) is forcibly ejected from the fruit. In order to successfully colonize a tree, however, the discharged seed must ultimately reach the base of a live needle. The seed coat assists this by being alternatively sticky and then slick. First, the sticky seed coat of the expelled seed increases its probability of adhering to needles that intercept its flight. Second, the seed coat becomes lubricated and slick when moistened by rain and often slides down to the needle base, germinates and sends a rootlet into the tree. Seeds can either re-infect the same tree or infect another tree (Hawksworth and Wiens, 1996).

Branch infection by dwarf mistletoe results in a malformation of the branch commonly called a “witches’ broom.” *A. douglasii* is characterized by the development of massive witches’ brooms (Tinnin and Knutson, 1980; Tinnin et al., 1982; Mallams et al., 2005). Compared to uninfected branches, dwarf mistletoe infections produce larger-diameter branches with twice as many twigs that are 50% longer. Consequently, broomed branches may weigh 2.5 times that of healthy branches (Tinnin and Knutson, 1980). Brooms accumulate dead foliage, lichens, water, snow, and ice, and may weigh >65 kg each, and thus are more prone to breakage (Hadfield, 1999; Filip et al., 2014).

The preferred method of rating dwarf mistletoe infection severity in Douglas-fir is broom volume rating (BVR), based on the volume of witches’ brooms (Tinnin, 1998). An alternative rating system is the Six-Class Dwarf Mistletoe Rating (DMR, Hawksworth, 1977), which is based on visible plants and the number of infected branches and their abundance in crown thirds. The small shoot size and characteristic dense brooming make DMR difficult for rating *A. douglasii* infection severity. Comparisons between the two ratings, however, show very little difference (Mallams, 2008a) and although a DMR of 0 means there is no mistletoe on the tree, a similar rating using the BVR system simply means there are no witches’ brooms.

Witches’ brooms caused by Douglas-fir dwarf mistletoe are often highly resistant to self-pruning that would naturally occur and therefore both affect the normal pattern of biomass/foliage allocation (Hawksworth and Wiens, 1996) and water balance (Fisher, 1983). Abnormal growth patterns (including dead tops and branches) and major changes in the biomass allocation are the result. Foliage on infected Douglas-fir has lower water use efficiencies (WUE) than non-infected branches or trees. This decrease in WUE is accompanied by increases in leaf area, water uptake, and

transpiration (sap flux) (Sala et al., 2001), provided there is enough available water to support this increase. Although amounts vary among studies, there is a consistent decline in tree growth and survival as infection severity increases from moderate (BVR rating of 3 or 4) to severe (BVR rating of 5 or 6) (Pierce, 1960; Filip and Parks, 1987; Wicker and Hawksworth, 1988; Mathiasen et al., 1990; Filip et al., 1993). Significant declines in radial bole increment (measured at 1.4 m from ground level on the uphill side of the tree) in larger trees usually begin at moderate infection severity levels. Severely infected trees exhibit dramatic growth reductions, sometimes less than half that of a healthy tree (Pierce, 1960; Wicker and Hawksworth, 1988; Filip et al., 1993). In addition to trees killed by dwarf mistletoe, breakage of large brooms and decayed dead tops can pose safety hazards to visitors in developed recreation sites (Hadfield, 1999). Management treatment(s) that arrested or delayed mistletoe intensification would be useful to managers and the public if the treatments improved longevity and structural integrity of these valuable trees.

The objective of this study is to refine current operational guidelines for mechanical pruning of dwarf mistletoe infected branches in larger Douglas-fir. These guidelines will address where and when it is likely that we can:

1. Remove all infected branches and brooms for the foreseeable future.
2. Significantly slow the increase in infection severity over time without seriously compromising the vitality and, by inference, the longevity of the tree.
3. Evaluate an approach that compares multiple indicators of vitality/longevity (e.g. survival, tree-ring width, BVR, and Normalized Difference Vegetation Index [NDVI]) between pruned and unpruned trees over the study period.

2. Methods

2.1. Study area

Suttle Lake and Scout Lake are located on the east slope of the Cascade Range in central Oregon in a moist mixed-conifer forest (1070 m elevation). The plant association for most of the area is White Fir (*Abies concolor* (Gord. & Glend.) Lindl. ex Hildebr.)-Grand Fir (*A. grandis* (Dougl. ex D. Don) Lindl.)/Twinflower (*Linnaea borealis* L.) (ABCO-ABGR/LIBO2) (Simpson, 2007). Average annual precipitation ranges from 33 to 150 cm (1960–2012). The shoreline of Suttle and Scout Lakes, where study trees are located, are managed by the USDA Forest Service (Sisters Ranger District, Deschutes National Forest), and there are several campgrounds, day-use recreation sites, a lodge and cabins, boat launching sites, and a hiking trail surrounding the lakes.

Douglas-fir dominates the overstory shoreline vegetation, although there are also ponderosa pine (*Pinus ponderosa* Douglas ex C. Lawson), white fir, Engelmann spruce (*Picea engelmannii* Parry ex Engelm), and western white pine (*Pinus monticola* Douglas ex D. Don). While there is a mixture of sizes and ages, old, large Douglas-fir are abundant. Dwarf mistletoe is distributed among all size classes of Douglas-fir. The Douglas-fir and white fir were severely defoliated by western spruce budworm (*Choristoneura freemani* Razowski) from 1985 to 1993. The Link Fire burned to the edge of the study area in 2003. The trees selected for study were not burned.

2.2. Study trees and pretreatment data

In 1998–99, stands surrounding Suttle Lake and Scout Lake were surveyed for larger diameter Douglas-fir infected with dwarf mistletoe that would be suitable for pruning; specifically trees

found with BVRs of 1–4, without dead tops. Two-hundred and twenty-eight Douglas-fir trees met the selection criteria and were tagged for study. Fifty-five of the 228 study trees were randomly chosen as unpruned controls. The rest were pruned ($n = 173$). Both pruned and unpruned trees were distributed throughout the study area, and the unit of replication was the tree.

All study trees were tagged and pre-treatment measurement data were collected, which included: BVR, diameter at breast height (1.4 m above groundline) (DBH), live crown ratio (LCR) (USDA Forest Service, 2014), and crown condition class (CCC). Mean DBH was 58 cm (range 17.8–139.8 cm) and LCR was 55% (range 25–95%). LCR was ocularly compacted where significant gaps in the crown occurred. Crown condition class, or position in the canopy with respect to other trees (Helms, 1998), was primarily dominant (21%) and co-dominant (68%), with some intermediate trees (11%).

2.3. Pruning

Trees were pruned by tree climbers in the fall of 1999 using chainsaws to remove dwarf mistletoe brooms and infected branches (Fig. 1). Additionally, all branches were removed two whorls above the highest visibly infected branches (e.g., those with dwarf mistletoe aerial shoots) to remove latent infections, unless this brought the LCR under 10%. At a minimum, the tree was pruned until all the major brooms were removed. Branches were pruned at the branch collar to reduce potential damage from decay fungi and insects. If trees had very large brooms (>3 m in diameter) with multiple branches close to the stem, the branch was pruned several inches away from the stem to the point where multiple branches began. This was done to avoid creating a large wound on the main stem.

We were more aggressive in crown reduction than is suggested in the current guidelines for dwarf mistletoe pruning (Hadfield, 2000; Lightle and Hawksworth, 1973; Scharpf et al., 1987), because we at times pruned more severely infected trees (up to BVR 4) and also often removed more live crown. Forty-one percent of the pruned trees had less than the recommended 30% LCR, with 7% having 10% or less LCR post-pruning. In addition, a majority of treated trees

was closer to other infected cohort trees than the recommended 15.2 m (Hadfield, 2000). Seventy-nine percent of the pruned trees had no infected cohort within 4.6 m, 53% none within 9.1 m, 42% none within 12.2 m, and 30% none within 15.2 m.

2.4. Post-treatment data and analysis

For each study tree, the following post-treatment data were also collected 5, 10, and 14 years post-treatment: BVR, DBH, LCR, tree condition (live or dead), and presence or absence of a dead top. Data collected 13 years after treatment included: a tally and distance to infected Douglas-firs of the same cohort, basal area (BA), DBH and species of neighboring trees within a 30-m radius of the study tree. In order to assess our ability to distinguish trees that were completely sanitized by pruning from those that still had residual mistletoe, (based on a BVR from the ground), study trees rated as free of mistletoe 10 years after treatment were climbed and the branches were examined for mistletoe shoots. If aerial shoots were observed, the tree was classified as “infected” for the comparison. A single increment core was taken to the center of 197 study trees (150 pruned trees; 47 unpruned trees) 13 years after treatment. The core was removed at DBH on the first defect-free area clockwise of the north side of the tree. The remaining study trees had heart rot or broken cores and were not included in the ring-width analysis. The cores were prepared and analyzed at the University of Arizona, Laboratory of Tree-Ring Research (Tucson, AZ, USA). Annual rings were cross-dated, measured, and de-trended for age and geometry with a cubic smoothing spline to produce ring width indices (Stokes and Smiley, 1968; Cook and Peters, 1981). Surprisingly, 26% of the cores were missing rings, with 11% missing multiple rings. The missing rings were a result of the multi-year western spruce budworm outbreak that ended in 1993.

Normalized Difference Vegetation Index (NDVI; Rouse et al., 1973) of the sunlit portion of the crown was derived from high-resolution (5.1 cm) multi-spectral, aerial imagery collected 12 years after pruning. This imagery was acquired using a digital sensor flown at 900 m for the study area on 9/29/2012. The visible wavelengths (red band included in analysis) and near infrared

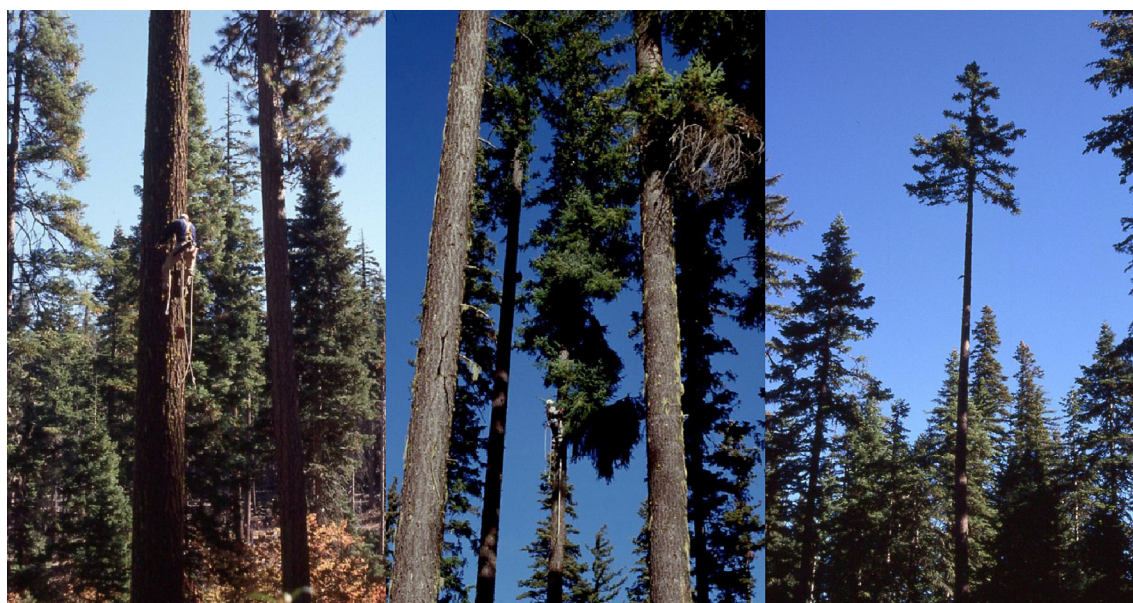


Fig. 1. Douglas-fir near Suttle Lake, Oregon that were pruned in 1999 to reduce dwarf mistletoe. (Left) Tree climber on a Douglas-fir. (Center) Tree climber pruning dwarf mistletoe “witches” brooms.” (Right) Douglas-fir with small live crown ratio (LCR) after pruning. All planned pruning in the study area was not completed when this photograph was taken.

(NIR) band had a spatial resolution of 5 cm. All geospatial processing, analysis, and image viewing was completed using ArcMap software version 10.0 (2010, Esri, Redlands, CA, USA). The sunlit portion of the study tree crowns was manually delineated based on visual interpretation of imagery. Larger, dead branches and tops were excluded from analysis after applying a supervised classification (dead branches had reflectance values $>130 \mu$ in the red band). Normalized Difference Vegetation Index was then calculated for each pixel within the sunlit portion of each crown and mean NDVI was calculated for each delineated sunlit crown.

We obtained monthly temperature and precipitation data (1960–2012) from Sisters, Oregon approximately 20 km away (Station identifier GHCND:USC00357857; <http://www.ncdc.noaa.gov/IPS/cd/cd.html>). Fifty year (1960–2009) annual precipitation (based on hydrologic year) and mean temperature were assessed for significant deviations ($\pm 20\%$ of 50-year averages) that might produce an anomalous growth response in either the pruned or unpruned groups.

2.5. Data analyses

We grouped our assessment of the effectiveness of mechanical pruning, and associated representative metrics, into three categories: (1) Mistletoe eradication by the end of the study; (2) Impact of pruning on dwarf mistletoe severity over time for those trees where pruning was unsuccessful at removing all the mistletoe; (3) Post-pruning monitoring of vitality/longevity using multiple indicators.

All statistical analyses were completed using JMP software, version 7 (2007, SAS Institute Inc., Cary, NC, USA). The two groups (unpruned and pruned) were compared for significant differences with respect to both the sample mean and variance of important tree and stand metrics including: DBH, BVR, 10-year average ring width index, LCR, and BVR. Residuals were evaluated, and Levene's test ($\alpha = 0.05$) was used to test for unequal variance to determine whether assumptions of analysis of variance (ANOVA) were met. ANOVAs were used to test for differences among means ($\alpha = 0.05$). If assumptions of ANOVA were not met, a Kruskal–Wallis test was used to test for differences among the two groups ($\alpha = 0.05$). In order to further test for pre-treatment differences between pruned and unpruned trees, we compared the 25-year de-trended ring widths of 30 non-infected trees (BVR = 0) scattered throughout the study area based on site factors, including: BA of surrounding trees measured with a prism, % slope, aspect, slope position, and distance to the lakeshore. All tests, and tests described hereafter, were evaluated for significance at the $p < 0.05$ level.

2.6. Mistletoe eradication

We used a BVR = 0, 14 years after pruning to represent successful long-term eradication of dwarf mistletoe. The small size of the aerial shoots and the height of our study trees (many > 30 -m tall) made the detection of shoots from the ground nearly impossible. As a result, the proxy of “no detectable brooms at year 14” was used instead. We assumed that latent infections would have produced aerial shoots by 10 years after treatment and that by year 14, brooms that were detectable from the ground would have developed. The trees were rated in 2014 independently without referring to BVR measurements in any previous year. This assumption was tested by comparing the trees rated as mistletoe free by the tree climbers with the trees rated as BVR 0 from the ground one year later. If the percentage of “false negatives” on the ground was $< 10\%$, we assumed that 14 years was an adequate time for broom expression to be a relatively reliable indicator of eradication.

We then developed a binary logistic equation predicting the probability that pruning would successfully eradicate dwarf mistletoe from an individual study tree given a set of site and tree characteristics. Potential explanatory variables representing conditions conducive to retaining mistletoe post-pruning and/or sources of re-infection were evaluated for inclusion in the equation. These included: (1) post-pruning BVR, (2) pre-pruning BVR, (3) post-pruning neighborhood BA, (4) CCC (dominant, co-dominant, intermediate and suppressed), and (5) number of dwarf mistletoe infected Douglas-fir cohort trees (represented by trees ≥ 53.3 cm) up to a maximum of 15 m away and the distance of these to each study tree. A tally of these trees was then placed in the following ordinal groups based on distance from the study tree: (a) 0–4.6 m; (b) 0–9.1 m; (c) 0–15.0 m. A Whole Model test and Lack of Fit test based on the chi-square statistic were evaluated for this and other regression analyses described hereafter. The Chi-square statistic was used to test the significance of potential explanatory variables. McFadden's R^2 statistic was used as a pseudo R^2 (i.e., to represent the proportion of the variance in the dependent variable that is explained by the variance in the independent variables (Long, 1997). Statistical tests employed for this logistic model were the same for other logistic regression analyses that follow.

2.7. The impact of pruning on dwarf mistletoe severity

Immediate and long-term pruning effects on dwarf mistletoe severity between the pruned and unpruned groups were compared with respect to: (a) mean post-pruning BVR (both immediately after pruning and 14 years subsequent), and (b) mean 14-year post-pruning BVR rate of change. Potential variates were also evaluated and included both pre- and post-treatment BVR, and the number of infected Douglas-fir within 0–15 m of each study tree. Comparison of pruned and unpruned groups included comparison of all pruned trees to the unpruned group followed by the same comparisons using the subgroup of pruned trees where mistletoe was not eradicated.

2.8. Post-pruning survival and vitality

Six metrics (12, 13 or 14 years post-treatment) were used to assess and compare the impact of pruning on inferred vitality of the pruned trees with the unpruned trees, including: (1) Post treatment survival, (2) tree-ring width indices, (3) change in LCR, (4) Mean NDVI, (5) percent top-kill, and (6) percentage of trees with severe infections (BVR of 5 or 6).

Tree-ring width indices were used as proxies of tree vitality in the pruned and the unpruned trees. We assumed trees with more vitality would be able to allocate more resources to ring growth (Gordon and Larson, 1968; Fogel and Hunt, 1979; Waring et al., 1980). Tree ring data were analyzed by first comparing mean ring-width index of the pruned tree group with that of the unpruned group over the study period. Mean ring-width index of the unpruned group and the pruned group was then compared on a year-by-year basis for each year after pruning. Potential covariate effects with treatment on ring width included: BVR before and after pruning; DBH; neighborhood BA; and mean DBH of nearest neighbors. LCR immediately post-pruning and percent reduction in LCR (from pruning) were used to represent the severity of pruning and assess its potential impact on ring width. Variables having a significant effect on ring width were then included, along with their interactions, in multiple linear regression models.

The capability of the pruned vs. the unpruned trees to re-grow live crown over the 14 year post-pruning period was an additional metric we used to assess post-pruning vitality. We believe this

comparison was most appropriately made over the lifespan of the study instead of shorter time intervals because we were not expecting, nor did we believe we could detect, shorter term response. In addition, there is built-in error in this metric since we had to “visually compress” the existing live crown, so a longer measurement time-frame was more desirable from that standpoint as well.

Mean Normalized Difference Vegetation Index (NDVI) of individual sunlit crowns, 12 years post-treatment, was also used as an indicator of relative vitality between the pruned and unpruned groups as NDVI is a measure of plant ‘greenness,’ and level of photosynthetic activity (Slayback et al., 2003). Thus, pruned study tree crowns might appear differently, overall, than unpruned tree crowns if the pruning treatment resulted in either loss or gain in vitality.

Percentage of trees that developed severe infections and/or top-kill over the study period in the pruned vs unpruned group was used as a comparative index of declining vitality. Trees with severe infection were assumed to have low vitality, and trees also with top-kill have even lower vitality. We assumed that once trees reached this level of infection, the decline in vitality was irreversible, and the expected longevity of the tree is dramatically reduced. We then used these data to develop a binary logistic equation to predict the probability that an individual study tree would increase to a BVR of 5 or 6 over the 14-years post-pruning. Potential explanatory variables tested that might logically influence this likelihood included: (1) pre-pruning BVR, (2) post-pruning BVR (if not pruned the BVR was assumed to remain the same), (3) post-pruning neighborhood BA, (4) crown competition class (CCC), (5) number of infected Douglas-fir cohort trees up to a maximum of 15 m away, and (6) DBH at the beginning of study. Variables were included in the equation if they had a significant effect.

2.9. Monitoring tools

As part of the above analysis, we evaluated the suitability of the metrics we used for their long- and short-term utility in monitoring the effects of pruning on study tree infection levels and vitality. These metrics (e.g. BVR, ring-width, NDVI) were compared with each other in terms of their ability to reasonably detect response from the mistletoe and/or host tree and when this response became apparent.

3. Results

3.1. Pre-treatment comparisons among pruned and unpruned groups

Based on ANOVA, pre-treatment populations of trees in the pruned vs. unpruned groups were not significantly different

($p > 0.29$) with respect to important tree and stand metrics (e.g. DBH, LCR, and BA) and ring width indices (Table 1). In addition, the relative distribution of replicates among mistletoe infection classes, CCC, site quality and LCR was very similar among the pruned and unpruned groups.

3.2. Post-treatment climate conditions

There were no unusual weather events (e.g. extreme drought, precipitation events or windstorms), or other significant disturbances during the study period that might have triggered an uncharacteristic response to pruning. Overall, post-pruning hydrologic year precipitation was almost always less than the 50-year average (81.8 cm); with four non-consecutive years falling below 20% of this average (Fig. 2). During the study timeframe, average annual temperatures were slightly above the 50-year average (7.6 °C) for most years, but never exceeded $\pm 20\%$.

3.3. Mistletoe eradication

Of 173 trees that were pruned, only 41 (24%) appeared to have successfully eradicated the mistletoe 14 years post-treatment. Visual ground inspection was not effective in detecting success of attempted dwarf mistletoe eradication until the end of the study. In the 5th year post-treatment, the majority (76%) of pruned trees appeared to be completely mistletoe free. By the 10th year post-treatment, 56% remained visually free of dwarf mistletoe from the ground. By the 14th year, only 24% of pruned trees were visually free of dwarf mistletoe based on ground inspection. By then, there was a high level of agreement between the ground and climbers' ratings, where there had not been 10 years after pruning. When climbed in the 13th year, mistletoe shoots were identified on 44% of those identified with a BVR = 0 in the 10th year. In contrast, mistletoe shoots were identified by climbers on only 6% of those rated with a BVR = 0 in the 14th year indicating that the brooms arising from these remaining infections had grown big enough to be detected from the ground by then.

Of the 41 trees that were successfully sanitized, the majority (82%) had a pre-treatment BVR of 1 or 2. Only 18% of trees that remained mistletoe free had pre-treatment BVR > 2. Pruning to eradicate dwarf mistletoe appeared to be equally successful among crown classes. Mistletoe was eradicated from 25% of the dominant and co-dominant crown classes and 23% of the trees with intermediate crown classes.

Based on regression analysis of pruned trees that remained mistletoe free 14 years after treatment, there were two significant variates that predicted the likelihood of failure to eradicate mistletoe in the long-term: (1) Number of other infected trees within 9.1 m of the pruned tree (# NN < 9.1 m), ($p = 0.006$) and (2) BVR before pruning (BVR_{T1}), ($p = 0.001$).

Table 1

Summary statistics (mean and standard error) for pruned and unpruned groups immediately before treatment.

Treatment	DBH (cm) ^a	BVR ^b	RWI in prior decade ^c	LCR ^d (%)	Age ^e	BA ^f	No. infected cohorts ^g	CCC ^h		
								1	2	3
Pruned	59.4 (1.8)	2.39 (0.07)	0.69 (0.02)	55 (1)	125 (4)	39 (1)	1.8 (0.14)	21	68	11
Control	56.1 (1.5)	2.46 (0.07)	0.70 (0.03)	55 (1)	117 (9)	42 (1)	1.6 (0.25)	22	69	9

^a Diameter at breast height (1.4 m).

^b Broom Volume Rating: severity ranges from 1 (low) to 6 (high).

^c Mean tree-ring width index in the decade prior to treatment.

^d Live-crown length divided by total tree height times 100.

^e Average tree age at breast height (1.4 m).

^f Basal area of all trees (m²/ha) surrounding the study tree measured using 40-BAF prism.

^g Average number of infected Douglas-fir in same canopy layer (or taller) within a 15.2 m radius from study tree.

^h Percentage of trees in each crown competition class; 1 = Dominant, 2 = Co-dominant, 3 = Intermediate.

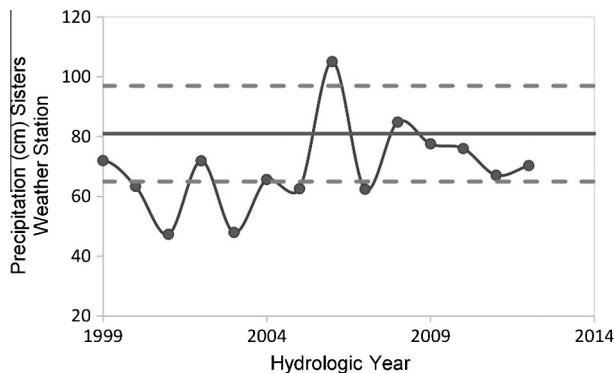


Fig. 2. Annual (based on hydrologic year) precipitation (cm) over 14-year study referenced to the 50-year average. Solid line is 50 year average; dashed lines represent 20% over and under average precipitation.

Probability of a tree remaining mistletoe free: $1/(1 + \text{Exp}(\text{Lin}[N]))$
 Where: $\text{Lin}[N] = -0.8591 + (0.9045 \times (\# \text{ NN} < 9.1 \text{ m})) + (0.6122 \times \text{BVR}_{T1})$
 McFadden's- $R^2 = 0.124$

The logistic regression model was statistically significant, $p < 0.001$, explained 12.44% of the variance in complete removal of dwarf mistletoe, and correctly classified 71.5% of cases (based on classification of probability > 0.50 for successful mistletoe eradication). Each additional infected tree within 9.1 m resulted in a pruned tree being 2.47 times more likely to not be mistletoe free. For each unit increase in BVR before pruning, a pruned tree was 1.84 times more likely to not be mistletoe free.

3.4. Impact of pruning on dwarf mistletoe infection severity

Pruning significantly ($p < 0.0001$) decreased BVR from pre-treatment levels in the pruned group, and BVR remained significantly lower (values of $p < 0.0001$) than BVR in the unpruned group 5, 10, and 14 years post-treatment (Fig. 3). Five years after pruning, mean BVR of the pruned group was 0.36 ± 0.07 SE, and 76% of the pruned trees were rated as broom free ($\text{BVR} = 0$). Of the remaining trees, 14% had a BVR of 1, 8% had a BVR of 2, and the remaining 2% rated 3 or 4. Over this 5-year period, mean infection severity of unpruned trees remained unchanged ($\text{BVR} = 2.6 \pm 0.13$ SE). Fifteen years after treatment, mean BVR for unpruned trees was 3.9 ± 0.2 SE and 1.8 ± 0.12 SE for pruned trees (Fig. 3). Proportionally, five times more unpruned trees (40%) than pruned trees (8%) were severely infected ($\text{BVR} \geq 5$). Unpruned trees had three times more

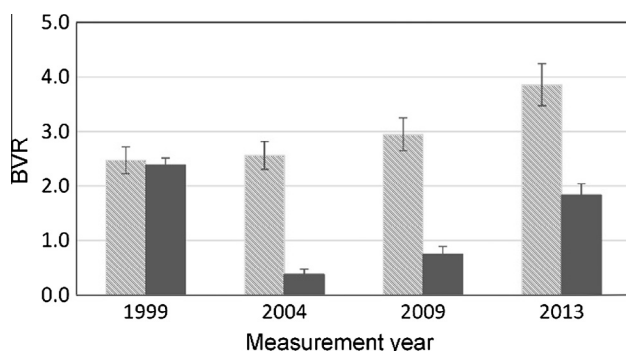


Fig. 3. Mean dwarf mistletoe broom volume rating (BVR) for pruned (solid) and unpruned groups (stripes) prior to mistletoe pruning treatment and up to 14 years post-pruning. Pruning occurred in the fall of 1999. Error bars are 95% CI of the mean.

dead tops (16%) than pruned trees (6%), and nine times more were also severely infected (9%) (Table 2).

In estimating the probability of a tree increasing to severe infection levels ($\text{BVR} \geq 5$), significant predictors included: (1) the BVR at 5-years post-pruning BVR_{T5} ; ($p < 0.0001$), (2) number of infected Douglas-fir neighbors within 9.1 m of the study tree ($\# \text{ NN} < 9.1 \text{ m}$), ($p = 0.002$), (3) BVR (BVR_{T1}) prior to pruning ($p = 0.04$), and (4) the intercept ($p < 0.0001$).

Long term probability to develop $\text{BVR}_{T14} > 5 = 1/(1 + e^{(\text{Lin } N)})$

Where: $(\text{Lin } N) = 5.79 + (-0.59 * \text{BVR}_{T1}) + (-1.27 * \text{BVR}_{T5}) + (-0.69 * \# \text{ NN} < 9.1 \text{ m})$;
 McFadden's- $R^2 = 0.40$.

The regression model was significant ($p < 0.0001$) based on the Whole Model test and correctly classified 91% of the cases (based on classification of probability > 0.50 for successful mistletoe eradication). Each additional infected tree within 9.1 m resulted in a study tree being twice as likely to become severely infected. For each unit increase in BVR before pruning, a study tree was 1.8 times more likely to become severely infected and for each unit increase 5 years after pruning, a tree was 3.6 times more likely to become severely infected.

The mean rate of increase in BVR (1.46 ± 0.11 SE) of the pruned group from years 5–14 after pruning was not significantly ($p = 0.72$) different than the mean of the unpruned group (1.29 ± 0.13 SE) (Fig. 3). Both groups increased by 1.3–1.5 mean BVR from years 5–14 after pruning. Five years after pruning, mean BVR for the unpruned and pruned trees was 2.6 and 0.4 respectively, which increased to 3.9 and 1.8, 14 years after pruning. For pruned trees where mistletoe was not successfully eradicated ($n = 132$), mistletoe-induced broom formation increased over the 14 years of observation to nearly pre-pruning infection severity levels, accelerating in the last 5 years (Fig. 4). Dominant and co-dominant trees in the pruned group that were not sanitized by pruning had a significantly lower mean rate of increase in dwarf mistletoe severity (1.6 BVR/decade, ± 0.10 SE) ($p = 0.005$) than did their intermediate tree counterparts (mean 2.4 BVR/decade ± 0.2 SE).

3.5. Post-pruning survival and vitality

Based on our indicators, pruning generally had a positive effect on vitality. Since pruning removed substantial amounts of living foliage in many cases, we expected a threshold where relief from mistletoe due to pruning was outweighed by the removal of so much crown that the tree would not recover, and might even die. This expected response, however, was not supported by any of our vitality indicators, even in the case of severely pruned trees.

Table 2

Summary statistics (mean and standard error) indicating vitality for pruned and unpruned groups 13–14 years post-pruning.

	% Survival	Ring-width index ^a	NDVI ^b	ΔLCR^c	% Dead top (DT) ^d	% Severely infected (HI) ^e	% DT and HI
Pruned	100	1.09 (0.01)	0.43 (0.01)	5.6 (0.4)	6	8	1
Control	100	1.11 (0.01)	0.40 (0.01)	2.6 (1.2)	16	40	9

^a Mean tree-ring width index for the 13-year post-pruning period.

^b Normalized Difference Vegetation Index (NDVI) of sunlit portion of crowns.

^c Change in live crown ration based on total bole height.

^d Percent of trees with a dead top 14 years post-pruning.

^e Percent of trees with mistletoe broom volume ratings of 5 or 6, 14 years post-pruning.

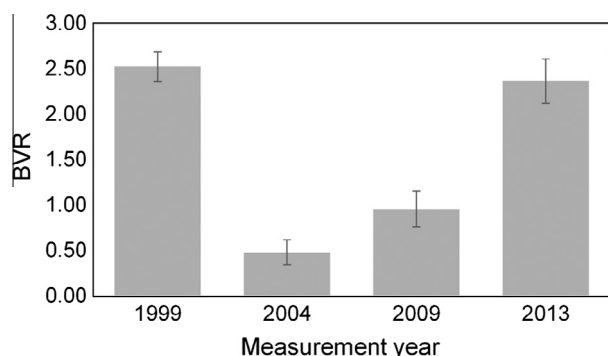


Fig. 4. Mean ($\pm 95\%$ CI) dwarf-mistletoe broom-volume rating (BVR) of pruned trees where mistletoe was not completely removed ($n = 132$ trees). Pruning occurred in the fall of 1999 after surveys.

No study trees died over the study period although two were felled because they were hazard trees (one pruned and one unpruned tree). There was a highly significant ($p < 0.0001$) positive relationship between pre-treatment BVR and the amount of live crown removed. Mean LCR of the pruned trees decreased from 55% (range of 25–95%) to 34% (range of 5–85%) as a result of pruning. Mean reduction from existing LCR for the pruned trees was 38% (range of 0–88%).

By the end of the study, there was strong evidence that observed NDVI was unaffected (or in some cases higher) by pruning, and the NDVI of the remaining crown was higher than that of the unpruned trees, implying that pruning resulted in improved photosynthetic activity. The 13-year average tree-ring width of pruned trees was similar to unpruned trees after pruning (Table 2). Other variates including BVR, DBH, BA, change in BVR and LCR pre and post-pruning did not affect these results.

Year-by-year comparisons of tree-ring growth revealed a more detailed picture. A temporary negative response in growth was compensated for by the end of the study period. In the 1st and 2nd years after pruning, the pruned trees had significantly lower mean ring width compared to unpruned trees ($p < 0.02$, Fig. 5a). By the 5th year post-pruning, ring growth of the pruned trees recovered to levels similar to, or exceeding that of unpruned trees (Fig. 5a).

The significant decrease in ring width immediately after pruning appeared to be temporary and was largely driven by the subset of trees that were severely pruned ($< 30\%$ remaining LCR) (Fig. 5b and c). Within this severely pruned subgroup, ring width in the 1st and 2nd years post-pruning was significantly negatively correlated with percent live crown removed (PLCR; Adjusted $R^2 = 0.26$, $p < 0.001$, $n = 76$). This relationship appeared somewhat stronger for intermediate trees than it was for the dominant and co-dominant trees; even so, it was transient. Percent live crown retained after pruning was also significantly correlated (Adjusted $R^2 = 0.14$, $p = 0.001$, $n = 76$) with tree-ring width. However, it was also highly correlated with PLCR, so this metric explained no additional variance.

Increased ring growth 10–13 years after pruning also appeared to be more common in the most severely pruned trees. In the 10th year after pruning, trees pruned to $\leq 30\%$ LCR had significantly higher mean ring width than unpruned trees ($p = 0.02$, Fig. 5c). There were no significant relationships ($p = 0.2$) between pre- or post-pruning BA (measured in 1999 and 2002) and the 13-year mean ring width post-pruning, nor with annual ring width post-pruning for the unpruned and pruned groups; even for the year immediately before and after pruning. From nearest neighbor measurements, mean DBH of conspecific neighbors had a significant, negative effect ($p = 0.02$) on mean ring width during the post-

treatment period for both pruned and unpruned groups. There was no significant co-linearity, however, between the ring width of pruned and unpruned trees with respect to nearest neighbor, indicating that there was no difference in the response to density induced by the pruning.

Mean NDVI in crowns (including all live and dead branches) of the pruned group was significantly greater than the unpruned group ($p = 0.005$), suggesting that pruned trees were more photosynthetically active. When the comparison was repeated with the dead vegetation excluded, the pruned group still had significantly higher mean crown NDVI ($p = 0.02$) than the unpruned group (Table 2).

Live crown increment was significantly higher for the pruned than the unpruned group ($p < 0.05$) (Table 2). This was the case even for severely pruned trees (i.e., those trees pruned to $\leq 30\%$ LCR). On average, there was a 6% recovery in LCR 14 years post-pruning among pruned trees, increasing mean LCR in 2013 to 40%. Over the same period, LCR increased by an average of 3% for the unpruned trees, which increased the mean LCR to 57%. For trees pruned to $\leq 30\%$ LCR, there was a significant but weak, ($p < 0.001$, adjusted $R^2 = 0.09$) positive relationship between regrowth of LCR from 2000 to 2014 and % LCR reduction from the pruning. Trees that had lower post-pruning LCR tended to regrow more crown than trees with more of their original crown remaining.

4. Discussion

This is the first long-term study of mistletoe pruning in Douglas-fir. Previous studies have examined the effects of mistletoe pruning on ponderosa pine (Lightle and Hawksworth, 1973) and Jeffrey pine (*P. jeffreyi* Grev & Balf); (Smith, 1978; Scharpf et al., 1987), and we assumed that Douglas-fir would respond similarly. Overall, this was true, with some specific differences. Our results support the use of mechanical pruning as a viable tool to delay, and in some cases eliminate, serious impacts of dwarf mistletoe in Douglas-fir. Our results also support Hadfield's guidelines (2000) recommending a 15.2 m buffer between pruned trees and other infected cohorts, since these trees may be a potential source of inoculum and lead to more rapid intensification. Like Scharpf et al. (1987), we found that pruning had minimal short- and long-term impacts on ring growth provided that at least 30% live non-broomed crown (based on total bole height) remained. This result was unexpected since we thought the removal of large systemic brooms characteristic of Douglas-fir would eliminate a key resource sink and result in a more dramatic increase in diameter growth than seen in ponderosa and Jeffrey pines. Some managers give dwarf mistletoe-infected Douglas-fir an automatic BVR rating of 2 if a tree has only one large broom on it because large brooms are thought to be important resource sinks. This study supports the argument that these brooms are probably not strong sinks. Therefore, trees normally rated as BVR 1 should remain so since the rationale for assigning extra rating points based on broom size appears to be unsupported.

Two important differences existed between the ponderosa and Jeffrey pine pruning studies and ours. First, the length of time required to evaluate the post-pruning effectiveness was much longer for our study. The aerial shoots of *A. douglasii* are small and inconspicuous and evaluation is dependent on the presence of witches' brooms, which can take years to develop after infection. In ponderosa and Jeffrey pine, aerial shoots are larger and more easily identified from the ground, making evaluation based on the presence of the dwarf mistletoe more accurate. This longer detection period might have resulted in lost opportunity with respect to identifying trees where early follow-up pruning could

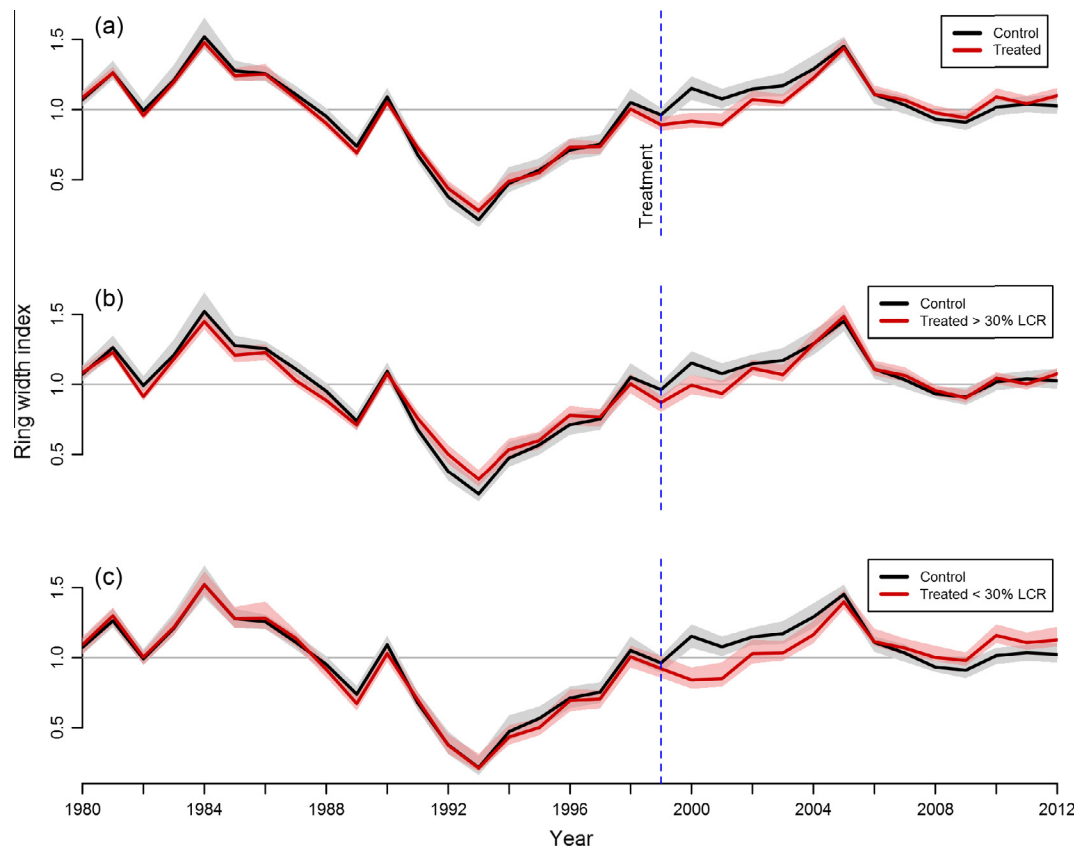


Fig. 5. Mean tree-ring width index chronologies for unpruned control trees compared to treated trees, before and after mistletoe pruning in the fall of 1999. (a) Control trees ($n = 47$) and all treated trees ($n = 150$). (b) Control trees and treated trees with $>30\%$ live crown ratio (LCR) after pruning ($n = 74$). (c) Control trees and treated trees with $\leq 30\%$ LCR after pruning ($n = 76$). Shaded 95% confidence intervals derived from 1000 bootstrap simulations.

have made a difference. Geils and Mathiasen (1990) described this difficulty where they found that the majority of young Douglas-fir could be accurately rated for DMR, but accuracy decreased for larger trees.

The second difference was the high degree of tolerance our study trees exhibited to severe pruning with respect to vitality indicators such as tree-ring width and survival. Although almost half of our study trees were severely pruned, all survived and while there was a short-term reduction in average ring growth for these trees, growth equaled (or exceeded) the unpruned trees in later years. This response appears similar to what has been reported by several researchers (and summarized by O'Hara, 1991) for younger *lightly-pruned*, non-infected Douglas-fir. In contrast, studies of *Pinus* spp. suggested that 30% or more of a live non-broomed residual crown was needed in order to avoid significant decline in vitality, even mortality. Hadfield (2000) appeared to draw his guidelines from pine mistletoe pruning and/or the general literature on Douglas-fir pruning to formulate his guidelines for Douglas-fir pruning since he recommended leaving, at a minimum, 30% live healthy crown for trees >25.4 cm DBH.

Using multiple monitoring indicators enabled us to evaluate tree vitality in different ways and time scales. The use of annual tree-ring width indices was a valuable technique for detecting and monitoring both the short- and long-term response to pruning. Annual ring-widths were needed to detect the subtle, ephemeral ring width decrease following pruning in Douglas-fir. This contrasts with ponderosa and Jeffrey pine where 5-year average radial growth was adequate (Scharpf et al., 1987). Moreover, tree rings could be collected at the end of the study and need not be collected at the beginning, an additional advantage. Other vitality indicators,

such as BVR, change in LCR, the occurrence of dead tops, and the development of severe mistletoe infection, were useful metrics over longer periods. Normalized Difference Vegetation Index derived from high-resolution, multi-spectral imagery shows promise as a sensitive indicator of crown response, which may differ from the response of woody tissue recorded by the tree rings. However, one acquisition of imagery (10 years after pruning) did not allow us to evaluate NDVI to the extent that we would recommend over the entire timeframe when differences in vitality may have been detected. Both Smith (1978) and Scharpf et al. (1987) reported that severe pruning markedly changed the appearance of Jeffrey pine resulting in a significant impairment of visual quality. We did not perform a formal survey with respect to the impact of the pruning on aesthetics. However, there was little reaction from campground users, both in the years immediately post-pruning as well as later years, implying that the pruning went largely unnoticed. Because of the height and large boles of the study trees as well as fact they were mixed in with trees of other sizes and species, the change in crown length of the pruned trees was perhaps not obvious to the casual recreationist.

5. Conclusions

We conclude that mechanical pruning can be an effective technique for delaying the deleterious effects of Douglas-fir dwarf mistletoe, and under certain circumstances eradicating it altogether. Lightly-infected dominant and codominant trees (without infected neighbors) should have the highest pruning priority, since pruning these trees affords the highest likelihood of complete removal of mistletoe or if not, lower intensification rates. However,

even under the most favorable circumstances, mistletoe will likely remain in at least half the trees. This failure of pruning to eradicate all dwarf mistletoe may not be detectable for at least 14 years, which delays the identification of trees for re-treatment. For other trees, mechanical removal of infected branches can result in a significant reduction in dwarf mistletoe infection intensity and possibly delay the onset of mortality-inducing infection levels for at least 15–20 years. Assigning a higher priority for treatment where it is most likely to successfully delay the onset of severe infection may seem appropriate. However, in recreation settings, at times, some trees with lower priority (e.g. intermediate trees) may be considered for pruning, depending on management objectives.

The foliage in infected brooms apparently contributes little to the vitality of the tree. Thus, removing witches' brooms has little immediate negative or positive effect on vitality; except in the case of severely pruned trees for a few years after pruning. Even if all the mistletoe is not eradicated from the crown, pruning can be a significant benefit to vitality and longevity by setting back the upward progression of mistletoe infection severity and stimulating the production of more efficient foliage. We believe that comparing vitality using multiple indices is a desirable way to monitor and cross-check the response to mechanical pruning of dwarf mistletoe in Douglas-fir or other tree species.

Acknowledgements

We gratefully acknowledge Paul Deignan, Sean Schroeder, Eze Ahanonu, and Stephanie Pickert for their long hours in the field and in data processing. Field assistance was also provided by Aaron Smith, Steve Fitzgerald, Christina Mead, and Kimberly Wesseler. We gratefully acknowledge Brian Tandy and Nita Rauch for their invaluable help in establishing the study. Additional support provided by the University of Arizona, Laboratory of Tree-Ring Research and Dr. Ann Lynch at the U.S. Forest Service – Rocky Mountain Research Station. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

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