Forest Pathology

For. Path. 43 (2013) 193–203

doi: 10.1111/efp.12020

Mortality and growth of dwarf mistletoe-infected red and white fir and the efficacy of thinning for reducing associated losses

By H. K. Mehl[1,3], S. R. Mori[2], S. J. Frankel[2] and D. M. Rizzo[1]

[1]Department of Plant Pathology, University of California, One Shields Avenue, Davis, CA 95616, USA; [2]USDA Forest Service, Pacific Southwest Research Station, Albany, CA, USA; [3]Email: hkmehl@ucdavis.edu (for correspondence)

Summary

In managed forests dominated by true fir (*Abies*) species, stands are often restocked using understory trees retained during timber harvest, making the effects of dwarf mistletoe (*Arceuthobium* spp.) infestation on small true fir a concern. This study examined the response of small red (*A. magnifica*) and white (*A. concolor*) fir and their dwarf mistletoes (*A. abietinum* f.sp. *magnificae* and *A. abietinum* f.sp. *concoloris,* respectively) to precommercial thinning treatments in fir-dominated stands in the Sierra Nevada Mountains of California. Tree diameters and dwarf mistletoe ratings were monitored from 1981 to 2001, and mortality was observed from 1981 to 2006. Red and white fir survival and radial growth decreased significantly with greater mistletoe ratings and increased with larger diameters and live crown ratios. Thinning significantly increased survival and growth of white, but not red fir. Over the course of the study, mistletoe ratings for both fir species did not change significantly in unthinned stands, but increased in thinned stands. However, while statistically significant, increases in mistletoe ratings in thinned stands were gradual and mistletoe ratings did not statistically differ between treatments 20 years post-thinning. Additionally, thinning did not significantly influence mistletoe spread to uninfected trees, indicating that precommercial thinning in lightly infested red and white fir stands will not likely result in substantial increases in dwarf mistletoe abundance over typical harvesting intervals. Overall, while severe dwarf mistletoe infection ratings reduced tree survival and growth, because ratings remained low, actual losses resulting from mistletoes during this study were minor and will not likely result in substantial economic losses over normal harvesting intervals. This finding indicates that precommercial thinning treatments designed specifically to compensate for mistletoe-associated losses may not be necessary when managing red and white fir for timber production.

1 Introduction

The dwarf mistletoes (*Arceuthobium* spp.) are native forest pathogens of many coniferous tree species throughout the northern hemisphere (Hawksworth and Wiens 1996; Mathiasen et al. 2008). Dwarf mistletoes are vascular plants that live as obligate parasites, deriving all of their water and mineral nutrients and much of their carbohydrates from their hosts (Hull and Leonard 1964; Glatzel and Geils 2009). By increasing water demands, depleting nutrients and reducing photosynthetic capacity of infected branches, dwarf mistletoe infection can result in reduced growth, increased susceptibility to drought stress, attack by other pathogens and insects and direct or indirect mortality (Hawksworth 1978; Knutson and Tinnin 1980; Meinzer et al. 2004). The effects of mistletoe infection are dependent on multiple interacting factors, including pathogen abundance, physiological status of the host, developmental stage of the host and environmental conditions such as stand density and water availability (Childs 1960; Parmeter 1978; Page 1981; Knutson 1983). Because of their wide distribution and broad host range, dwarf mistletoes cause more losses to timber production in western North America than any other group of pathogens (Hawksworth 1983; Hawksworth and Shaw 1984). For these reasons, foresters have long sought silvicultural methods for minimizing dwarf mistletoe infection and associated losses (Scharpf and Parmeter 1978; Hawksworth and Wiens 1996; Geils et al. 2002).

In the western United States, dwarf mistletoes are particularly damaging to red (*Abies magnifica* A. Murray) and white (*A. concolor* (Gord. & Glend.) Lindl. ex Hildebr.) fir. In the California Sierra Nevada, roughly 40% of trees in red fir stands and 30% of trees in white fir stands are infected (Parmeter and Scharpf 1963; Scharpf 1978). Red and white firs are economically and ecologically important trees in Sierra Nevada forests (Laacke 1990a,b; Fites-Kaufman et al. 2007). White fir is one of several dominant species in mixed-conifer forests, whereas red fir is the single dominant species in higher-elevation red fir forests. These species co-occur in the transitional zone between forest types (Laacke 1990a,b; Fites-Kaufman et al. 2007). Different form species of fir dwarf mistletoe infect red fir (*Arceuthobium abietinum* Engelmann ex Munz f.sp. *magnificae* Hawksworth and Wiens) and white fir (*A. abietinum* f.sp. *concoloris* Hawksworth and Wiens) and do not infect the reciprocal species (Parmeter and Scharpf 1963). However, disease development and symptoms in both of these host–pathogen systems are believed to be generally similar (Scharpf and Parmeter 1967). On both hosts, mistletoe infections occur on the bole and branches. Bole infections result in large swellings that provide an entry point for wound-decay fungi, thereby increasing susceptibility of the host to wind breakage (Parmeter and Scharpf 1982). Branch infections cause swellings that may be infected by the canker fungus *Cytospora abietis* Sacc., which often girdles and kills branches, thereby increasing mistletoe-associated damage (Scharpf 1969; Scharpf and Bynum 1975; Filip 1984).

The effects of dwarf mistletoe on small true fir are a particular concern in fir-dominated stands managed for timber because residual understory trees are often left after harvest to restock a stand. Understory fir are frequently infected with dwarf mistletoe, but the effects of infection on survival and growth of these small trees over time are not well quantified (Scharpf 1979). Scharpf (1979) hypothesized that water stress and competition in dense stands may increase dwarf

Received: 14.9.2011; accepted: 4.12.2012; editor: N. B. Klopfenstein

mistletoe-associated mortality and growth reductions. Red and white fir are known to respond well to thinning treatments that increase spacing between trees, with increased radial and height growth following release (Gordon 1973; Oliver 1988). Therefore, precommercial thinning, in which trees are removed from maturing stands prior to commercial harvest, has been proposed as a method for promoting overall tree vigour, thereby reducing dwarf mistletoe-associated losses in fir-dominated stands. Because red and white fir dwarf mistletoes have slow rates of vertical spread within tree crowns, thinning treatments were also expected to reduce over time the proportion of a tree's crown infected with dwarf mistletoe by stimulating host height growth sufficient to exceed the upward establishment of mistletoe infections (Scharpf and Parmeter 1976; Parmeter and Scharpf 1989).

The study presented here was initiated in the late 1970s by the USDA Forest Service, Pacific Southwest (PSW) Region, Forest Pest Management and the PSW Forest and Range Experiment Station. Data were collected for this study through 2006; however, results were neither analysed nor published by the original investigators. The analyses and interpretations presented here were conducted as a part of a broader project aimed at making available yet unpublished work from studies supported by the Pest Trend and Impact Plot System (PTIPS) program, which funded data collection for this study between 1990 and 2006. The objective of this study was to test the efficacy of increased tree spacing, created through precommercial thinning treatments, for reducing dwarf mistletoe-associated losses in overstocked, fir-dominated stands. To meet this objective, we first examine the effects of dwarf mistletoe infection on tree mortality and radial growth, to assess whether pathogen-associated losses justify expensive silvicultural measures. We then evaluate the efficacy of precommercial thinning by examining whether thinning treatments promote tree survival and radial growth. Finally, we examine how thinning influences dwarf mistletoe intensification and spread to uninfected trees.

2 Materials and methods

2.1 Study sites

Between 1979 and 1981, study sites were established in the Klamath, Lassen, Tahoe, Stanislaus and Sequoia National Forests (NF) and the LaTour Demonstration State Forest (DSF; Fig. 1). Study sites were established in stands composed of

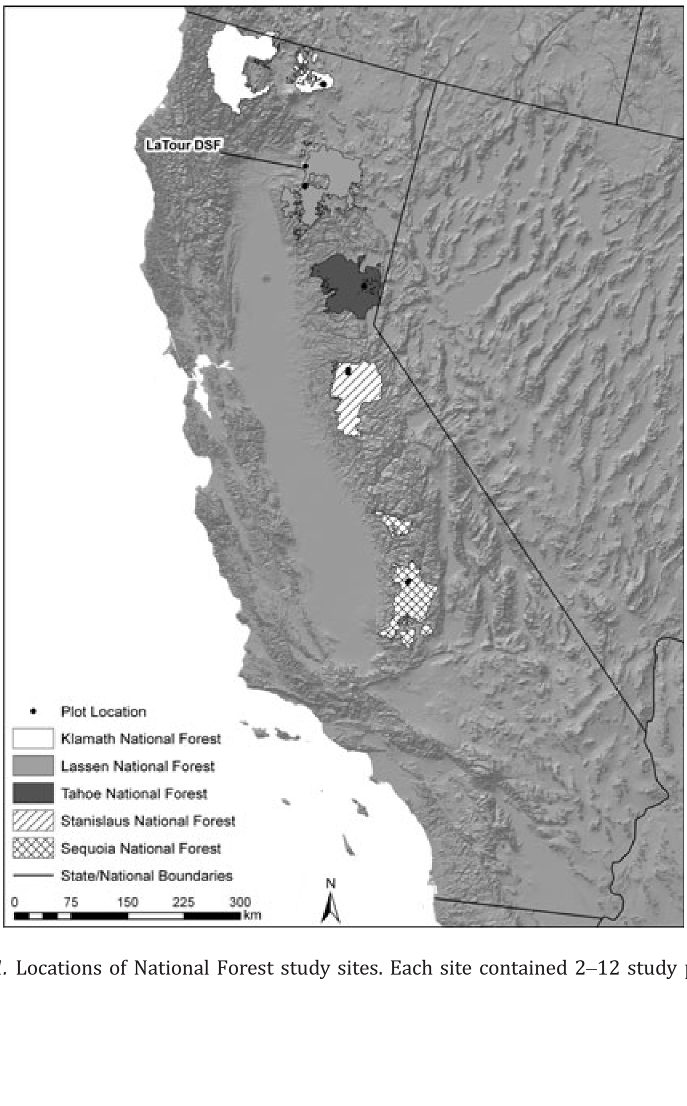

Fig. 1. Locations of National Forest study sites. Each site contained 2–12 study plots.

at least 50% red and/or white fir, and plots were installed only in areas overstocked with true fir less than 30.5 cm diameter at breast height (1.37 m; dbh). Study sites in Klamath NF were dominated by white fir, while sites in all other forests were composed predominantly of red fir (Table S1). All sites also contained other conifer species, including ponderosa pine (*Pinus ponderosa* C. Lawson), western white pine (*Pinus monticola* Douglas ex D. Don), lodgepole pine (*Pinus contorta* Douglas ex Louden), sugar pine (*Pinus lambertiana* Douglas) and Jeffrey pine (*Pinus jeffreyi* Balf.).

2.2 Thinning treatments

Thinning treatments to increase tree spacing were completed between 1979 and 1980 on 23 of 32 plots (Table 1). All forests contained both thinned and unthinned plots, except the Sequoia NF where all plots were thinned. The original study design specified that thinning was to be done to an average spacing of 3.7 m between all stems (including non-fir species), leaving approximately 740 trees per hectare. True firs were preferentially removed if they had dwarf mistletoe infections in the trunk, the upper half of the live crown or more than 50% of all branches in the lower half of the crown. However, firs meeting these infection criteria were sometimes retained if necessary to achieve desired spacing and stand stocking. Only trees less than 20.3 cm dbh were to be removed during thinning. Estimates of overall basal area and per cent dwarf mistletoe infection on true fir were determined for each plot before and after thinning (Table S1). However, individual tree data were only recorded for true fir located in sampling strips (described below) that were within the target diameter range (5.1–30.5 cm dbh) in 1981. Therefore, data on other tree species and true fir above or below this dbh range are not available. For this reason, precise stem densities and basal areas before and after thinning treatments cannot be calculated. Also, while the original study design specified that no overstory trees were to be present, we cannot be positive that there was a complete absence of overstory trees in all stands.

2.3 Stand surveys

Study sites were surveyed post-thinning in 1981, 1990, 1995, 2001, 2004 and 2006. Permanent sampling locations in each plot were established along 6.1-m-wide parallel strips spaced at 15.2-m intervals. In total, this method covered roughly 20% of a plot's area. During the first post-thinning survey, red and white fir in the 5.1–30.5 cm dbh range located within sampling strips were tagged for monitoring of individual trees over time; these trees constitute the study population followed throughout the study. Data recorded for these trees in the first post-thinning survey (1981) included location along the strip, dbh to the nearest tenth of an inch (approximately 0.3 cm increments), the uncompacted live crown ratio (lcr) using standard Forest Inventory and Analysis methodology (Anonymous 2005) and a dwarf mistletoe rating (dmr) based on the six-class system (Hawksworth 1977). Briefly, this rating is determined by visually dividing a tree's crown into thirds and assigning each third an infection rating based on the amount of dwarf mistletoe observed (0 for no apparent infection, 1 for <50% and 2 for >50% of the branches infected). These ratings are summed to obtain an ordinal measure of dwarf mistletoe intensity for the entire tree (dmr), ranging from 0 to 6. Data recorded in 1990, 1995 and 2001 included the same information collected during the first post-thinning survey, plus the occurrence of mortality. Additional mortality surveys were conducted in 2004 and 2006.

The final data set generated from this study included 20 years of data on dwarf mistletoe infection intensity (dmr), radial growth (from differences in dbh measures) and live crown ratio (lcr) and a 25-year record of tree mortality. Data

Table 1. Attributes of 5.1–30.5 cm dbh red and white fir at the beginning and end of the study. Forests are divided based on the dominant fir species present (see Table S1). Because red fir was dominant in multiple forests, an overall summary of red fir across all forests is also included. All values were calculated from data on the specified fir species only. Standard errors are reported in parentheses.

			1981					2001			2006
	Forest	Plots	N trees	% Infection	dmr[1]	lcr[1]	dbh[1]	dmr[1]	lcr[1]	dbh[1]	% Mortality
White fir	Klamath	9	1274	53 (10)	1.3 (0.3)	4.6 (0.3)	16.5 (1.0)	1.8 (0.3)	5.1 (0.2)	26.2 (1.3)	26 (2)
		3*	342	64 (17)	1.7 (0.5)	4.7 (0.8)	13.7 (0.3)	1.7 (0.5)	3.9 (0.1)	21.6 (0.5)	39 (12)
Red fir	Lassen	3	1078	50 (24)	1.8 (0.9)	5.6 (0)	15.2 (2.0)	**1.9 (1.1)**	**4.9 (0.5)**	**24.5 (2.2)**	14 (5)
		2*	339	47 (47)	2.1 (2.1)	5.4 (1.2)	15.7 (3.3)	**1.1 (1.3)**	**4.5 (0.7)**	**24.8 (2.7)**	13 (2)
	LaTour	4	319	46 (23)	1.8 (1)	4.7 (0.4)	16.5 (1.5)	1.7 (1.1)	4.7 (0.6)	26.7 (0.3)	25 (11)
		2*	205	95 (0)	4 (0.3)	4.2 (0.3)	13.2 (0.8)	**3.2**	**4.6**	**21.1**	31 (24)
	Sequoia	3	269	60	1.8 (0.6)	6.1 (0.1)	13.0 (0.8)	2.1 (0.1)	6.1 (0.2)	24.1 (1.8)	18 (9)
	Stanislaus	1	252	71	2.5	6.6	14.5	2.9	7	29.5	38
		1*	49	82	4	4.7	15.2	2.4	4.9	25.9	45
	Tahoe	3	386	50 (25)	1.4 (0.8)	4.3 (0.3)	16.5 (0.3)	2.2 (0.7)	5.2 (0.3)	25.4 (1.3)	26 (6)
		1*	152	38	0.7	4.9	17.5	1.1	4.6	23.1	21
	All forests	14	2304	55 (4)	1.9 (0.2)	5.5 (0.4)	15.1 (0.7)	2.2 (0.2)	5.6 (0.4)	26.0 (0.9)	24 (4)
		6*	745	66 (14)	2.7 (0.8)	4.8 (0.2)	15.4 (0.9)	2.2 (0.5)	4.6 (0.1)	23.7 (1.1)	28 (7)

*Unthinned plots, bold = data from 2001 were lost for these sites. For the LaTour DSF, data for one thinned plot were available, but for sites in Lassen NF all 2001 data were lost and so values presented here were predicted using mixed regression models. dmr, dwarf mistletoe rating; lcr, live crown ratio; dbh, diameter at breast height.
[1]Values are means across plots.

were complete for all forests and years except the 2001 growth, and mistletoe infection data were lost for all plots in Lassen NF and two of the four plots in the LaTour DSF.

2.4 Statistical analyses

Because red and white fir are infected by unique form species of dwarf mistletoes and these fir species generally occur in different forest types, data from red and white fir were separated for all analyses. Detailed descriptions of the models described here are included in the Supporting Information.

2.5 Survival

To first examine the sole effect of dwarf mistletoe infection on tree survival, exploratory analyses using Kaplan–Meier survival curves were used (Lee and Wang 2003). These analyses identified similar survival responses for trees with three categories of dwarf mistletoe infection intensity in 1981: no infection (dmr 0), low infection (dmr 1–3) and high infection (dmr 4–6). When trees were grouped based on these infection categories, survival response curves differed significantly between groups for both red and white fir (log-rank tests < 0.0001). These mistletoe rating categories were used in all further analyses of tree survival.

To examine the influence of multiple factors likely to influence tree survival, two types of survival models were used: (i) A mixed Poisson regression model from the family of the mixed generalized linear models (GLMs; McCullagh and Nelder 1989) estimated the number of years that a tree was alive during the study (survival time, up to 25 years) and (ii) the Cox proportional hazard model (Cox PH; semi-parametric regression model) for right-censored data (Lee and Wang 2003) estimated the probability of a tree surviving longer than a given time (survival probability). Both types of survival models included the fixed effects of thinning treatment, initial dmr, lcr and dbh (all measured in 1981) and the random effect of plot nested in forest. For the red fir models only, a random effect was also included to account for differences by forest. Contrasts were used to examine whether survival differed for: (i) trees with differing levels of initial dmr and (ii) trees growing in thinned *vs.* unthinned stands.

2.6 Radial growth

The effects of dwarf mistletoe infection intensity (dmr), live crown ratio (lcr) and thinning on average annual radial growth between surveys (1981–1990, 1990–1995 and 1995–2001) were examined using regression models from the family of mixed GLMs (McCulloch and Searle 2001). Because tree growth is related to diameter, growth–resource relationships can be obscured due to background variation in growth driven by a diversity of initial tree diameters in a study population (MacFarlane and Kobe 2006). To minimize this potential confounding effect, we also included initial dbh as a fixed effect in all growth models, allowing us to better isolate the effects of our factors of interest (dmr and thinning treatments) on radial growth over time (MacFarlane and Kobe 2006). Models also included the random effect of plot nested in forest and modelled the correlation matrix of the residuals to account for the repeated measurement of the same tree over time. The red fir model also included the random effect of forest. To examine the effect of thinning on radial growth over time, comparisons of predicted average annual radial growth in thinned *vs.* unthinned stands were conducted for each survey interval. Only trees that were still alive at the end of each observation period (1990, 1995 and 2001) were included in these analyses.

2.7 Intensification of dwarf mistletoe

The effects of thinning, diameter (dbh), live crown ratio (lcr) and initial infection intensity (dmr) on dwarf mistletoe intensity over time were examined using a regression model from the family of the mixed GLMs. The model response for intensification was the current dmr (0–6, for the year being examined) treated as a proportion (dmr/6). Only trees that were still alive at the end of each observation period (1990, 1995 and 2001) were included in these analyses. Model fixed effects included initial dbh, lcr, dmr, plot treatment (thinned or unthinned) and the year examined (1990, 1995 or 2001). Random effects included forest location and plot nested in forest. For the red fir model, the per cent fir composition in a stand was also included as a fixed effect; however, this effect was not included for the white fir model because it was not significant.

2.8 Spread of dwarf mistletoe to initially uninfected trees

A logit model from the family of the mixed GLMs was used to estimate the probability of an individual tree becoming infected (spread) under given initial tree conditions in 1981 (dbh, dmr and lcr), plot thinning treatment and per cent true fir present in 1981. This model also included random effects for forest, plot and tree (to account for repeated measurements of the same tree). By selecting trees with initial dmr equal to 0 (no initial infection), the fitted logit model was used to estimate the probability of spread by a given time, based on treatment level and initial tree conditions in 1981.

Exploratory analyses for the examination of mortality at differing infection ratings were made with the Kaplan–Meier estimator using the PROC LIFETEST in SAS 9.3 (SAS 9.3, Cary, NC, USA). For the survival analyses, model parameters were estimated using the PHREG and the GLIMMIX procedures in SAS 9.3. The SAS 9.3 GLIMMIX procedure was also used for models examining radial growth, intensification and spread.

3 Results

3.1 Survival

Over the 25-year course of the study, cumulative mortality for both fir species was 22.7%. However, mortality was quite variable between plots (range: 16–54% for white fir and 6–57% for red fir; Table S2a and b) and forests (13–45% for red fir; Table 1).

Results of the mixed Poisson survival models were generally similar for red and white fir. For both species, the number of years that a tree survived increased significantly with larger live crown ratios and greater initial diameters (Table 2). Contrasts of predicted survival times for trees with mean initial diameters and live crown ratios showed that for both fir species, trees with dmr 4–6 had significantly shorter survival times than trees with dmr < 4 ($p < 0.001$). For white fir, trees with dmr 1–3 also had significantly shorter survival times compared to trees without mistletoe ($p = 0.004$). The results of the Cox PH survival models generally agreed with and supported the findings of the Poisson models (Fig. 2, Table S3). Survival probabilities increased significantly for red and white fir with larger initial diameters and live crown ratios. Survival probabilities for both species were also significantly lower for trees with dmr 4–6 compared to trees with dmr < 4 ($p < 0.001$ for both species; Table S3). The results of the Cox PH models differed from the Poisson only in that dwarf mistletoe ratings of 1–3 were found to significantly decrease survival probabilities of red rather than white fir ($p < 0.001$; Table S3).

Overall, cumulative mortality was less in thinned compared to unthinned stands for both white (26 *vs.* 39%) and red (24 *vs.* 28%) fir (Table 1). However, contrasts of predicted survival times from the Poisson models and survival probabilities from the Cox PH models indicated that thinning treatments significantly increased the survival of white, but not red fir ($p < 0.001$ for the Poisson model, $p = 0.002$ for the Cox PH model; Fig. 2, Table S3).

3.2 Radial growth

For both red and white fir, radial growth was significantly greater for trees with larger initial diameters (dbh; Table S4) and live crown ratios (lcr) and significantly lower for trees with higher initial dwarf mistletoe ratings (dmr; Fig. 3). The effect of thinning on radial growth differed between fir species. For white fir, average annual radial growth was significantly greater in thinned *vs.* unthinned plots between 1981 and 1990 and 1990 and 1995 (Fig. 3, Tables S5 and S6). In contrast, for red fir, average annual radial growth did not differ between treatments during any survey period (Fig. 3, Table S6).

3.3 Dwarf mistletoe intensification

The dwarf mistletoe intensification models for both red and white fir indicated that, over the course of the study, dmr on individual trees decreased in trees with larger initial diameters and increased more rapidly in trees with greater initial dwarf mistletoe ratings (Table S7). A tree's initial live crown ratio did not influence changes in dmr for either fir species. For red fir, dmr increased more rapidly in trees growing in stands with a higher proportion of true fir (Table S7). Between 1981 and 2001, overall mean dmr (across all plots and forests) of trees growing in thinned stands increased by 38% for white fir (from 1.3 to 1.8) and 16% for red fir (from 1.9 to 2.2; Table 1). In contrast, mean dmr of trees growing in unthinned stands did not change for white fir and decreased by 19% (from 2.7 to 2.2) for red fir. Contrasts of dmr predicted by intensification models at the end of the study (20 years post-thinning) compared to earlier survey periods showed that for

Table 2. Estimated coefficients from the Poisson survival models. Positive or negative estimates for continuous covariate coefficients indicate that survival times increased or decreased with the increase or decrease (respectively) in the covariate. Estimates of class covariates indicate the values of survival times for each class, relative to the class covariate set at zero. Estimated values for the variance components due to random effects and residual errors are reported in the final rows of the table.

	White fir		Red fir	
Parameter	Estimate	p-value	Estimate	p-value
No dm (dmr 0) in 1981	0	–	0	–
Low dm (dmr 1–3) 1981	**−0.039**	**0.004**	0.001	0.917
High dm (dmr 4–6) 1981	**−0.240**	**<0.001**	**−0.149**	**<0.001**
lcr in 1981	**0.056**	**<0.001**	**0.044**	**<0.001**
dbh in 1981	**0.002**	**<0.001**	**<0.001**	**<0.001**
Thinned	**−0.520**	**<0.001**	**−0.523**	**<0.001**
Unthinned	**−0.680**	**<0.001**	**−0.626**	**<0.001**
Forest variance	*		0.027 (0.023)[1]	
Plot variance	0.003 (0.002)		0.020 (0.008)[1]	

Bold = Significantly different from 0 at $\alpha = 0.05$.
*All white fir were located in a single forest.
[1]Standard errors reported in parentheses.

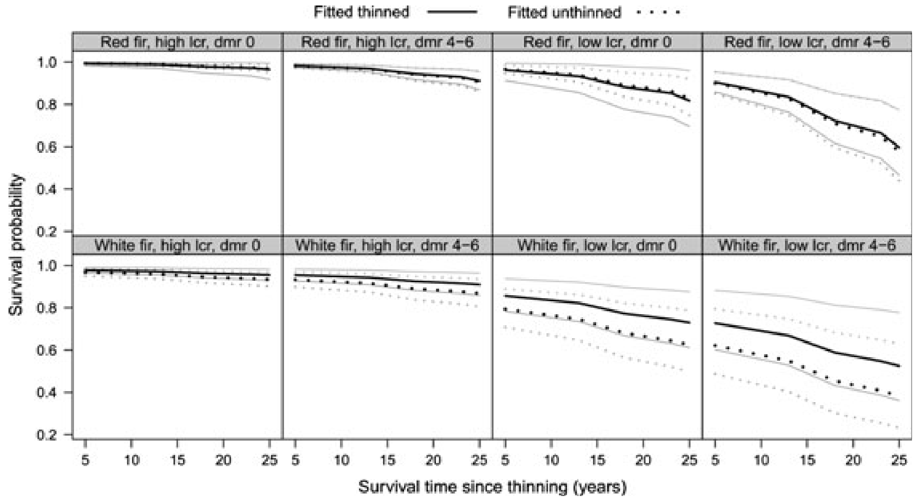

Fig. 2. Survival probability curves estimated from the Cox PH survival models. Changes in predicted survival probabilities post-thinning treatments (in 1981) are shown for trees with high (lcr = 9) and low (lcr = 2) live crown ratios and high (dmr 4–6) and no (dmr 0) dwarf mistletoe ratings at the start of the study. All survival probabilities were calculated for trees with initially large diameters (dbh = 30.5 cm) in 1981. Grey solid and dashed lines represent the upper and lower 95% confidence interval boundaries under thinned and unthinned conditions, respectively.

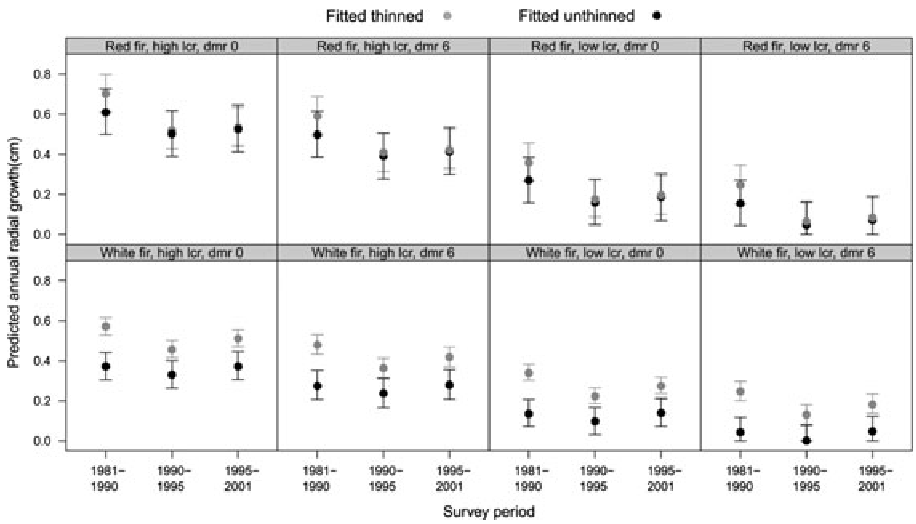

Fig. 3. Predictions of average annual radial growth between surveys (1981–1990, 1990–1995 and 1995–2001) from the mixed general linear models, for trees growing in thinned and unthinned stands. Differences in predicted average annual radial growth are shown across panels for trees with initially high (lcr = 9) and low (lcr = 2) live crown ratios and high (dmr 6) and no (dmr 0) dwarf mistletoe ratings in 1981. All growth rates were calculated for trees with initially large diameters (dbh = 30.5 cm), and so, these figures do not illustrate the influence of initial dbh on radial growth. However, if initial dbh is reduced by 50% compared to that shown here (15.2 cm), average annual diameter growth is reduced by roughly 70%. Grey and black dashes represent the upper and lower 95% confidence interval boundaries for thinned and unthinned treatments, respectively.

both red and white fir, predicted dmr increased significantly on trees growing in thinned stands, while there was no significant change in predicted dmr for trees growing in unthinned stands (Table 3). However, while statistically significant, the magnitude of dmr increases in trees in thinned stands has been small, and predicted dwarf mistletoe ratings at the end of the study did not differ significantly between trees growing under different treatments for either fir species (Table 3).

3.4 Spread of dwarf mistletoe to initially uninfected trees

For both red and white fir, the probability of becoming infected over the course of the study was greater for trees with smaller initial diameters (Fig. 4). For white fir, the probability of becoming infected also increased with greater initial live crown ratios, while for red fir, the probability of becoming infected also increased with higher proportions of true fir in a

Table 3. Comparisons of dwarf mistletoe ratings (dmr) predicted by the mistletoe intensity models for red and white fir, for trees growing under thinned *vs.* unthinned conditions at a given time and within the same treatment over time (20 *vs.* 9 years post-thinning). Estimated differences indicate the absolute difference in predicted dmr (0–6) between the conditions being compared, for a tree with mean initial dbh, dmr and lcr (in 1981). Positive estimated differences indicate that predicted dmr was greater under the condition listed first (thinned during a specified year or 20 years post-thinning).

	White fir		Red fir	
Comparison	Estimated difference	p-value	Estimated difference	p-value
Thinned *vs.* unthinned, 1990	**0.9**	**0.017**	0.03	0.93
Thinned *vs.* unthinned, 1995	0.4	0.303	0.3	0.391
Thinned *vs.* unthinned, 2001	0.4	0.277	0.3	0.428
2001 *vs.* 1990 (thinned)	**0.2**	**<0.001**	**0.1**	**0.001**
2001 *vs.* 1990 (unthinned)	−0.0	0.948	−0.1	0.136

Bold = differences statistically significant at $\alpha = 0.05$.

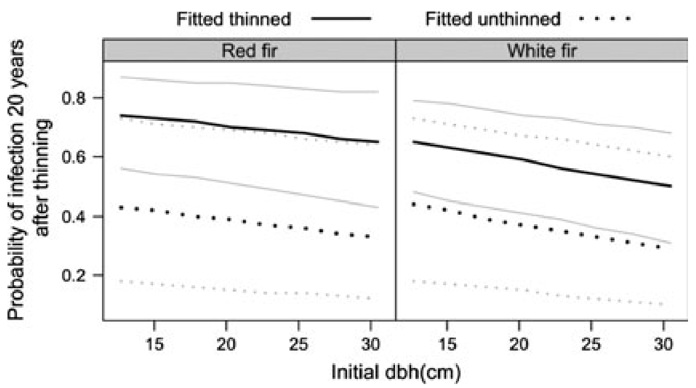

Fig. 4. Estimated probabilities that a tree uninfected at the start of the study (1981) will become infected by 2001 (20 years post-thinning), as a function of tree diameter (dbh) at the start of the study, under thinned and unthinned conditions. Values were calculated for trees with live crown ratios closest to the mean at the start of the study (lcr = 5). For the red fir model, probabilities were calculated for trees growing in stands with a mean value for overall per cent fir (87%) at the start of the study. Grey solid and dashed lines represent the upper and lower 95% confidence boundaries for thinned and unthinned treatments, respectively.

stand (Table S8). Over the course of the study, dwarf mistletoe incidence increased significantly in both thinned and unthinned stands, for both host species (Table S9). Thinning did not significantly influence dwarf mistletoe spread in either red or white fir (Table S9). However, while not statistically significant, there was a general trend for a higher probability of spread under thinned compared to unthinned conditions (Fig. 4).

4 Discussion

This study has demonstrated that dwarf mistletoe infections on small red and white fir can result in losses to stand productivity by increasing mortality and reducing radial growth. It is not surprising that the trees in this study were negatively affected by dwarf mistletoe infection, for red and white fir dwarf mistletoes are considered to be among the most damaging mistletoe species in the western United States (Hawksworth and Wiens 1996). In general, dwarf mistletoe-associated mortality is greatest in stands composed of small trees (Hawksworth and Geils 1990; Mathiasen et al. 1990; Hawksworth and Wiens 1996). However, few other studies have specifically monitored the survival of mistletoe-infected red or white fir over time. One study of small red fir observed over a 5-year period did not find any mortality attributable to dwarf mistletoe infection (Scharpf 1979). The apparent contradiction of our results is likely due to the fact that the previous study considered only mortality that appeared to be caused directly by mistletoe infection, whereas our analyses identify multiple contributing factors to mortality risk. It is interesting that we found evidence for trees with low ratings (dmr 1–3) to be significantly more likely to die than uninfected trees, because increased mortality at low ratings has been observed in few other studies (Mathiasen et al. 1990; Mallams 2008). However, these results were not consistent for both survival models and so may not bear strong biological significance. Our stronger, consistent finding that mortality increased at high ratings (dmr 4–6) for both red and white fir is consistent with many other studies in several dwarf mistletoe–host combinations (Knutson and Tinnin 1980; Mathiasen et al. 1990; Mallams 2008). However, while mistletoe infection did increase mortality at high ratings, it is also important to note that live crown ratio had an even stronger influence on tree survival. For example, for trees with large initial diameters (dbh = 30.5 cm) growing in unthinned stands, the increase in predicted mortality risk over 25 years with high infection ratings (dmr 4–6) compared to no infection was 7 and 6% for white and red fir, respectively, when the initial live crown ratio was high (lcr = 9). In contrast, the increase in predicted mortality risk over 25 years with a low (lcr = 2) compared to high (lcr = 9) live crown ratio was 33 and 14% for white and red fir, respectively, when a tree had no initial mistletoe infection (dmr 0).

Regarding radial growth, our findings that growth decreased significantly with higher dwarf mistletoe ratings for both red and white fir are consistent with previous studies on true fir that have shown growth reductions at infection intensities greater than a dmr of 3 (Scharpf 1979). Again, it is also important to note the importance of live crown ratio, which greatly influenced radial growth rates of small true fir. For example, a tree with a mean initial diameter (dbh = 15.2 cm) growing in an unthinned stand had a predicted decrease in radial growth with a maximum infection rating (dmr 6) compared to no infection of 25 and 21% for white and red fir, respectively, when the initial live crown ratio was high (lcr = 9). In contrast, the predicted decrease in radial growth with a low (lcr = 2) compared to high (lcr = 9) live crown ratio was 62 and 65% for white and red fir, respectively, when a tree had no initial mistletoe infection (dmr 0). Our finding that live crown ratio had a strong positive influence on radial growth and survival of red and white fir agrees with other studies where the living crown was highly influential on radial growth (Seidel 1980, 1985; Oliver 1985; Dolph 1992) and survival (Ferrell 1980, 1983; Oliver 1985) in small true fir.

The results of this study provide support for the use of precommercial thinning treatments that increase spacing between trees for promoting the survival and growth of small white, but not red fir. In terms of survival, a white fir with a large initial diameter (dbh = 30.5 cm), high initial mistletoe rating (dmr 4–6) and high initial live crown ratio (lcr = 9) was roughly 11% less likely to die over a 25-year period when growing in a thinned *vs.* an unthinned stand. It is not surprising that thinning improved the survival of small white fir. Tree death associated with dwarf mistletoe infection frequently results from complexes of factors, including site characteristics such as stand density, that are altered by thinning (Scharpf 1978; Filip and Schmitt 1990; Geils et al. 2002). Additionally, this result agrees with other studies that found dwarf mistletoe-associated mortality was reduced in thinned compared to unthinned stands (Conklin 2003). Thinning treatments also promoted diameter growth of infected white fir, with the predicted diameter growth of a tree with a maximum initial mistletoe rating (dmr 6), mean dbh (15.2 cm) and high initial live crown ratio (lcr = 9) being 43% greater when growing in a thinned *vs.* an unthinned stand, over the twenty-year length of study. The stimulatory effect of thinning on radial growth of white fir observed in this study agrees with other studies of true fir that found accelerated growth for up to 10 years following thinning (Seidel 1977, 1980, 1985; Oliver 1985). It is rather surprising that we did not find any significant benefits from thinning for the survival and growth of small red fir, as previous studies in dwarf mistletoe-infested red fir stands found increased growth following thinning (Scharpf 1979). The lack of significant thinning effects in this study could be partly due to insufficient replications for unthinned treatments (across all forests, 14 red fir plots were thinned and only six were left unthinned) and/or poor balance of thinned and unthinned treatments within the different forests. It is also possible that the lack of significant thinning effects resulted partly from variation by site in biotic and abiotic environmental conditions, which were not specifically quantified in this study, such as additional insects or pathogens, stand structure, water availability and/or site history. These differences also may have driven the high variation in mortality between forests.

We found evidence that thinning significantly promoted dwarf mistletoe intensification within white and red fir crowns, contrary to the hypothesis that thinning would result in reduced infection intensity over time by stimulating tree height growth (Scharpf and Parmeter 1976). Increased abundance of mistletoe shoots following thinning has been attributed to the emergence of latent infections (Knutson and Tinnin 1980; Roth and Barrett 1985; Conklin 2000, 2003; Jackson et al. 2006) and associated with increased resource acquisition by the host (Parmeter 1978; Bickford et al. 2005). Studies have also found increased abundance of mistletoe shoots in correlation with greater light availability (Shaw and Weiss 2000). However, it is important to note that while statistically significant, actual increases in red and white fir dwarf mistletoe ratings in thinned stands were minor over the course of the study, with overall mean dmr in thinned plots increasing by only 0.5 and 0.3 dmr units for white and red fir, respectively (Table 1). This differs from the findings of studies in many other dwarf mistletoe–host combinations that have shown more substantial increases in mistletoe infection ratings following thinning (for example, Knutson and Tinnin 1980, 1986; Roth and Barrett 1985; Shaw and Hennon 1991; Conklin 2000, 2003; Jackson et al. 2006). The slow amplification of dwarf mistletoe infections in small red and white fir crowns observed here agrees with previous studies (Parmeter and Scharpf 1989) and is not surprising, for these dwarf mistletoe species have: (i) some of the lowest within-tree vertical spread rates of any dwarf mistletoe–host combination, at <0.09 m yr^{-1} (Scharpf and Parmeter 1976; Parmeter 1978; Knutson and Tinnin 1980); (ii) long, multiyear generation times (minimum 5–6 years) and (iii) low rates of successful infection following seed dispersal (Scharpf and Parmeter 1967). Therefore, it takes several mistletoe generations and many years for infection intensity measured as dmr to increase substantially on an individual tree.

When evaluating the findings of this study regarding mistletoe spread, it is important to note that the available data did not allow for detailed examination of several important factors influencing dwarf mistletoe dispersal. The distance mistletoe seeds can travel and the likelihood they will be intercepted by a susceptible host are largely determined by stand density, structure and tree species composition (Robinson and Geils 2006). The lack of data for these stand characteristics and our inability to include them in the models for spread may partially explain why the effect of thinning was not statistically significant, despite the high increase in predicted infection probabilities in thinned compared to unthinned stands (33 and 42% for white and red fir with mean initial diameters, respectively). Dwarf mistletoe is known to increase more rapidly in low-density stands, and increased incidence following thinning has been observed for several other host–mistletoe combinations (Parmeter 1978; Knutson and Tinnin 1980; Jackson et al. 2006).

This study has provided long-term insights into the effects of dwarf mistletoe infection on small red and white fir in Sierra Nevada forests. Severe dwarf mistletoe infections did negatively impact the survival and growth of these trees, but mortality and growth reductions at low infection ratings (dmr < 4) have been negligible. Mistletoe intensification and spread have occurred slowly, and mean infection ratings in these stands have remained low. For these reasons, actual losses driven by these parasites have been minor over the course of this study. This suggests that in lightly infested red and white fir stands, dwarf mistletoes will not likely drive substantial economic losses over a typical 100- to 150-year timber-rotation cycle (Scharpf 1979). Therefore, precommercial thinning treatments designed specifically to compensate for mistletoe-associated losses may not be warranted when managing similar stands for timber production. While thinning may not be necessary for reducing dwarf mistletoe impacts, this study has also demonstrated that the use of precommercial thinning in lightly infested stands results in only slow increases in the build-up of dwarf mistletoe on individual trees over time. This suggests that, if thinning is implemented in lightly infested stands, it will not likely drive substantial and potentially detrimental increases in dwarf mistletoe abundance over normal periods of stand rotation. However, while the rates of mistletoe intensification and reductions in growth and survival associated with infection observed in this study are likely to have only minor impacts on the health and productivity of red and white fir stands managed for timber, today many fir-dominated forests in the Sierra Nevada are managed for various ecosystems services, including watershed protection and wildlife habitat (Fites-Kaufman et al. 2007). For this reason, fir growing in stands previously managed for timber may be retained for many decades past a typical rotation cycle. Dwarf mistletoe infection intensity increases markedly on mature trees that are past the active growing stage (Hawksworth 1978). Therefore, if mistletoe infection ratings continue to increase over a longer time horizon, greater levels of mistletoe-associated mortality may result in these and similar forests.

Acknowledgements

We would like to thank the original cooperators who established this project: Robert F. Scharpf, Richard S. Smith and Detlev R. Vogler. We would also like to thank Don Triplat, Gary Fiddler, John Kliejunas and Garey W. Slaughter for contributions to plot remeasurements and Beverly Bualon for data stewardship. Support for project establishment and data collection came from the USDA Forest Service, Pacific Southwest Research Station, Pacific Southwest Region, and support for data analysis came from USDA Forest Service, Forest Health Monitoring, Pest Trend Impact Plots: Analysis and Extension (WC-AR-09-03). We would also like to thank three anonymous reviewers for insightful comments, Richard Cobb and Margaret Metz for comments on earlier drafts of the manuscript and Clay DeLong and Matthew Hamilton for assistance with maps and figures.

References

Anonymous, 2005: Forest inventory and analysis national core field guide: field data collection procedures for phase 3 plots. Version 3.0. USDA Forest Service, Forest Inventory and Analysis. Arlington, VA.

Bickford, C.; Kolb, T.; Geils, B., 2005: Host physiological condition regulates parasitic plant performance: *Arceuthobium vaginatum* subsp. *cryptopodum* on *Pinus ponderosa*. Oecologia **146**, 179–189.

Childs, T. W., 1960: Drought effects on Conifers in the Pacific Northwest, 1958-59. PNW Old Series Res. Notes no. 182, pp. 1–5.

Conklin, D. A., 2000: Dwarf Mistletoe Management and Forest Health in the Southwest. USDA Forest Service Southwest Region Report, p. 30

Conklin, D. A., 2003: Comparison of Dwarf Mistletoe Behavior and Stand Development in Treated and Untreated Areas: 10-Year Monitoring on Jarita Mesa. USDA Forest Service Southwestern Region Forestry and Forest Health Report no. R3-03-02, p. 11.

Dolph, K. L., 1992: A diameter increment model for Red Fir in California and Southern Oregon. USDA Forest Service Pacific Southwest Research Station Res. Paper no. PSW-RP-210, p. 6.

Ferrell, G. T., 1980: Risk-rating systems for mature red fir and white fir in northern California. USDA Forest Service Gen. Tech. Rep. no. PSW-39, p. 29.

Ferrell, G. T., 1983: Growth classification systems for red fir and white fir in northern California. USDA Forest Service Gen. Tech. Rep. PSW-072, p. 18.

Filip, G. M., 1984: Dwarf mistletoe and *Cytospora* canker decrease grand fir growth in central oregon. Forest Sci. **30**, 1071–1079.

Filip, G. M.; Schmitt, C. L., 1990: Rx for *Abies*: Silvicultural options for diseased firs in Oregon and Washington. USDA Forest Service Gen. Tech. Rep. no. PNW-252, p. 34.

Fites-Kaufman, J. A.; Rundel, P.; Stephenson, N.; Weixelman, D., 2007: Montane and subalpine vegetation of the Sierra Nevada and Cascade ranges. In: Terrestrial Vegetation of California. Ed. by Barbour, M. G.; Keller-Wolf, T.; Schoenherr, A. A. Berkeley and Los Angeles: University of California Press, pp. 456–501.

Geils, B. W.; Cibrian, T. J.; Moody, B., 2002: Mistletoes of North American Conifers. USDA Forest Service Gen. Tech. Rep. no. RMRS-GTR-98, p. 123.

Glatzel, G.; Geils, B. W., 2009: Mistletoe ecophysiology: host–parasite interactions. Botany **87**, 10–15.

Gordon, D. T., 1973: Released advance reproduction of white and red fir - growth, damage, mortality. USDA Forest Service Res. Paper no. PSW-95, p. 12.

Hawksworth, F. G., 1977: The 6-class dwarf mistletoe rating system. USDA Forest Service Rocky Mountain Forest Range Experimental Station Gen. Tech. Rep. no. RM-48, p. 7.

Hawksworth, F. G., 1978: Biological factors of dwarf mistletoe in relation to control. In: Proceedings of the Symposium on Dwarf Mistletoe Control Through Forest Management Gen. Tech. Rep. no. PSW-31, Ed. by Scharpf, R. F.; Parmeter, J. R. (tech. coords.) Berkeley, CA: Pacific Southwest Forest and Range Experimental Station, USDA Forest Service, pp. 5–15.

Hawksworth, F. G., 1983: Mistletoes as forest parasites. In: The Biology of Mistletoes. Ed. by Calder, M.; Bernhardt, P. San Diego, CA: Academic Press, pp. 317–334.

Hawksworth, F. G.; Geils, B. W., 1990: How long do mistletoe-infected Ponderosa Pines live? West. J. Appl. For. **5**, 47–48.

Hawksworth, F. G.; Shaw, C. G., 1984: Damage and loss caused by dwarf mistletoes in coniferous forests of Western North America. In: Plant Diseases: Infection, Damage and Loss. Ed. by Wood, R. S.; Jellis, G. J. Oxford, UK: Blackwell Scientific Publications, pp. 285–297.

Hawksworth, F. G.; Wiens, D., 1996: Dwarf mistletoes: Biology, Pathology and Systematics. Agriculture Handbook 709, Washington, DC: USDA Forest Service, p. 410.
Hull, R. J.; Leonard, O. A., 1964: Physiological aspects of parasitism in mistletoes (*Arceuthobium* and *Phoradendron*): I. The carbohydrate nutrition of mistletoe. Plant Physiol. **39**, 996–1007.
Jackson, M. B.; Marsend, M. A.; Fergusion, B. A., 2006: Spread and intensification of Western Larch Dwarf Mistletoe (*Arceuthobium laricis*) following overstory removal of an infected overstory and (or) precommercial thinning: twelve-year remeasurements. USDA Forest Service Forest Health Protection Northern Region Report no. 06-06, p. 8.
Knutson, D. M., 1983: Physiology of mistletoe parasitism and disease responses in the host. In: The Biology of Mistletoes, Ed. by Calder, M.; Bernhardt, P. San Diego, CA: Academic Press, pp. 295–316.
Knutson, D. M.; Tinnin, R., 1980: Dwarf mistletoe and host tree interactions in managed forests of the Pacific Northwest. USDA Forest Service Pacific Northwest Research Station Gen. Tech. Rep. no. PNW-GTR-111, p. 21.
Knutson, D.; Tinnin, R., 1986: Effects of dwarf mistletoe on the response of young Douglas-fir to thinning. Can. J. For. Res. **16**, 30–35.
Laacke, R. J., 1990a: *Abies magnifica* A. Murr. California red fir. In: Silvics of North America, Volume 1: Conifers. Ed. by Burns, R. M.; Honkala, B. H. Washington, DC: USDA Forest Service Agricultural Handbook 654, p. 877.
Laacke, R. J., 1990b: *Abies concolor* (Gord. & Glend.) Lindl. ex Hildebr. White fir. In: Silvics of North America, Volume 1: Conifers. Ed. by Burns, R. M.; Honkala, B. H. Washington, DC: USDA Forest Service Agricultural Handbook 654, p. 877.
Lee, E. T.; Wang, J. W., 2003: Statistical Methods for Survival Data Analysis: 3rd edn New York: Wiley-Interscience, p. 534.
MacFarlane, D. W.; Kobe, R. K., 2006: Selecting models for capturing tree-size effects on growth-resource relationships. Can. J. For. Res. **36**, 1695–1704.
Mallams, K. E., 2008: Permanent plots for measuring spread and impact of Douglas-fir dwarf mistletoe in the Southern Oregon Cascades, Pacific Northwest Region: Results of plot remeasurement 2002-2007. USDA Forest Service Southwest Oregon Forest Insect and Disease Service Center Report no. SWOFIDSC-08-01, p. 8.
Mathiasen, R. L.; Hawksworth, F. G.; Edminster, C. B., 1990: Effects of dwarf mistletoe on growth and mortality of Douglas-fir in the Southwest. Great Basin Nat. **50**, 173–179.
Mathiasen, R. L.; Nickrent, D. L.; Shaw, D. C.; Watson, D. M., 2008: Mistletoes: pathology, systematics, ecology, and management. Plant Dis. **92**, 988–1006.
McCullagh, P.; Nelder, J. A., 1989: Generalized Linear Models: 2nd edn London: Chapman and Hall, p. 511.
McCulloch, C. E.; Searle, S. R., 2001: Generalized, Linear, and Mixed Models. New York: John Wiley and Sons, Inc., p. 325.
Meinzer, F. C.; Woodruff, D. R.; Shaw, D. C., 2004: Integrated responses of hydraulic architecture, water and carbon relations of western hemlock to dwarf mistletoe infection. Plant, Cell Environ. **27**, 937–946.
Oliver, W. W., 1985: Growth of California red fir advance regeneration after overstory removal and thinning. USDA Forest Service Pacific Southwest Forest and Range Experimental Station Res. Paper no. PSW-RP-180, p. 12.
Oliver, W. W., 1988: Ten-year growth response of a California red and white fir sawtimber stand to several thinning intensities. West. J. Appl. For. **3**, 41–43.
Page, J. M., 1981: Drought-accelerated parasitism of Conifers in the Mountain ranges of Northern California. Environ. Conserv. **8**, 217–226.
Parmeter, J. R., 1978: Forest stand dynamics and ecological factors in relation to dwarf mistletoe spread, impact, and control. In: Proceedings of the Symposium on Dwarf Mistletoe Control Through Forest Management. Gen. Tech. Rep. no. PSW-31, Ed. by Scharpf, R. F.; Parmeter, J. R. (tech. coords.) Berkeley, CA: Pacific Southwest Forest and Range Experimental Station, USDA Forest Service, pp. 16–30.
Parmeter, J. R.; Scharpf, R. F., 1963: Dwarf mistletoe on red fir and white fir in California. J. Forest. **61**, 371–374.
Parmeter, J. R.; Scharpf, R. F., 1982: Stem infection by dwarf mistletoe in California Firs. USDA Forest Service Pacific Southwest Forest and Range Experimental Station Res. Paper no. PSW-165, p. 12.
Parmeter, J. R.; Scharpf, R. F., 1989: Dwarf mistletoe in red and white firs in California - 23 to 28 years after inoculation. USDA Forest Service Pacific Southwest Forest and Range Experimental Station Res. Note no. PSW-RN-406, p. 5.
Robinson, D. C. E.; Geils, B. W., 2006: Modelling dwarf mistletoe at three scales: life history, ballistics and contagion. Ecol. Model. **199**, 23–38.
Roth, L. F.; Barrett, J. W., 1985: Response of dwarf mistletoe-infested ponderosa pine to thinning: 2. Dwarf mistletoe propagation. USDA Forest Service Pacific Northwest Forest and Range Experimental Station Res. Paper no. PNW-RP-331, p. 32.
Scharpf, R. F., 1969: *Cytospora abietis* associated with dwarf mistletoe on true firs in California. Phytopathology **59**, 1657–1658.
Scharpf, R. F., 1978: Control of Dwarf Mistletoe on True Firs in the West. In: Proceedings of the Symposium on Dwarf Mistletoe Control Through Forest Management. Gen. Tech. Rep. no. PSW-31, Ed. by Scharpf, R. F.; Parmeter, J. R. (tech. coords.) Berkeley, CA: Pacific Southwest Forest and Range Experimental Station, USDA Forest Service, pp. 117–123.
Scharpf, R. E., 1979: Dwarf Mistletoe-infected red fir: growth after release. USDA Forest Service Pacific Southwest Forest and Range Experimental Station Res. Paper no. PSW-RP-143, p. 9.
Scharpf, R. F.; Bynum, H. H., 1975: *Cytospora* canker of true firs. USDA Forest Service Forest pest leaflet no. 146, p. 5.
Scharpf, R. F.; Parmeter, J. R., 1967: The Biology and Pathology of Dwarf mistletoe (*Arceuthobium campylopodum* f.sp. *abietinum*) Parasitizing True Firs (*Abies* spp.) in California. USDA Forest Service Technical Bulletin no. 1362, p. 42.
Scharpf, R. F.; Parmeter, J. R., 1976: Population buildup and vertical spread of dwarf mistletoe on young red and white firs in California. USDA Forest Service Pacific Southwest Forest and Range Experimental Station Res. Paper no. PSW-122, p. 9.
Scharpf, R. F.; Parmeter, J. R., 1978: Proceedings of the symposium on dwarf mistletoe control through forest management, April 11-13. USDA Forest Service Pacific and Southwest Forest and Range Experimental Station Gen. Tech. Rep. no. PSW-31, p. 190.
Seidel, K. W., 1977: Suppressed grand fir and Shasta red fir respond well to release. USDA Forest Service Pacific North West Forest and Range Experimental Station Res. Note PNW-288, p. 7.
Seidel, K. W., 1980: Diameter and height growth of suppressed grand fir saplings after overstory removal. USDA Forest Service Pacific Northwest Forest and Range Experimental Station Res. Paper no. PNW-275, p. 9.
Seidel, K. W., 1985: Growth response of suppressed true fir and mountain hemlock after release. USDA Forest Service Pacific Northwest Forest and Range Experimental Station Res. Paper no. PNW-344, p. 28.
Shaw, C. G.; Hennon, P. E., 1991: Spread, intensification, and upward advance of dwarf mistletoe in thinned, young stands of Western Hemlock in Southeast Alaska. Plant Dis. **75**, 363–367.
Shaw, D. C.; Weiss, S. B., 2000: Canopy light and the distribution of hemlock dwarf mistletoe (*Arceuthobium tsugense* Rosendahl G.N. Jones subsp tsugense) aerial shoots in an old-growth Douglas-fir/western hemlock forest. North. Sci. **74**, 306–315.

Supporting Information

Additional Supporting Information may be found in the online version of this article:
Data S1. Statistical models.
Table S1. Individual plot attributes before and after thinning.
Table S2a. Attributes of 5.1–30.5 cm dbh fir trees in study strips at the start of the study (1981) and the end of the study (2001 or 1995) for white fir.
Table S2b. Attributes of 5.1–30.5 cm dbh fir trees in study strips at the start of the study (1981) and the end of the study (2001 or 1995) for red fir.
Table S3. Estimated hazard coefficients and their significance from the fitted Cox Proportional Hazard Survival models.
Table S4. Estimated coefficients (in cm units) from the Mixed General Linear models for diameter growth.
Table S5. Estimated average annual radial growth rates (in cm) from the fitted models for radial growth during each survey period, under thinned and unthinned conditions, for trees with mean initial dbh, dmr, and lcr.
Table S6. Comparison of average annual radial growth rates (in cm) in thinned *vs.* unthinned stands during each survey period.
Table S7. Estimated coefficients from the models for changes in the dwarf mistletoe rating ratio (dmr/6).
Table S8. Estimated coefficients from models examining the influence of initial diameter (dbh), live crown ratio (lcr), percent fir, and thinning on the probability of an initially uninfected tree becoming infected over the course of the study (spread).
Table S9. Contrasts for the presence of dwarf mistletoe predicted by the mistletoe spread models under thinned *vs.* unthinned conditions at a given time and within the same treatment over time (20 compared to 9 years post-thinning) for trees with mean initial dbh, dmr, and lcr (in 1981).