Spatial and population characteristics of dwarf mistletoe infected trees in an old-growth Douglas-fir – western hemlock forest

David C. Shaw, Jiquan Chen, Elizabeth A. Freeman, and David M. Braun

Abstract: We investigated the distribution and severity of trees infected with western hemlock dwarf mistletoe (*Arceuthobium tsugense* (Rosendahl) G.N. Jones subsp. *tsugense*) in an old-growth Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) – western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) forest. With the use of Hawksworth six-class dwarf mistletoe rating system, infection status was assessed for 3516 hemlock and true firs ≥5 cm diameter on a 12-ha stem-mapped plot located in the Cascade Mountains of southwest Washington State. Within the plot, 33% of the area had some level of infection and 25% (719) of western hemlocks, 2.2% (12) of Pacific silver fir (*Abies amabilis* (Dougl.) Forbes), and 29% (2) of noble fir (*Abies procera* Rehd.) trees were infected. Infected trees are larger than uninfected trees, on average, and within the infected tree population, the severely infected trees averaged larger than lightly infected trees. Abundant dwarf mistletoe in larger trees definitely positions the dwarf mistletoe population for future spread. Ripley's *K* analysis indicates a negative association between infected and uninfected hemlock trees, confirming that the infected trees form distinct dwarf mistletoe infection centers. The infection centers are actively spreading at their margins, which was confirmed by nearest neighbor analysis. Heavily infected trees had a negative association with uninfected trees, while lightly infected trees had a positive association with uninfected trees.

Résumé : Les auteurs ont étudié la distribution des arbres infectés par le faux-gui de la pruche (*Arceuthobium tsugense* (Rosendahl) G.N. Jones subsp. *tsugense*) et la sévérité de la maladie dans une forêt ancienne de Douglas (*Pseudotsuga menziesii* (Mirb.) Franco) et de pruche de l'Ouest (*Tsuga heterophylla* (Raf.) Sarg.). Le degré d'infection, basé sur le système d'évaluation à six classes de Hawksworth, a été évalué pour 3516 pruches et espèces du genre *Abies* ≥5 cm de diamètre dans une placette cartographiée de 12 ha située dans la chaîne des Cascades, au sud-ouest de l'État de Washington. À l'intérieur de la parcelle, 33 % de la superficie était infectée et 25 % (719) des pruches de l'Ouest, 2,2 % (12) des sapins gracieux (*Abies amabilis* (Dougl.) Forbes) et 29 % (2) des sapins nobles (*Abies procera* Rehd.) étaient infectés. Les arbres infectés étaient en moyenne plus gros que les arbres non infectés et parmi les arbres infectés, les arbres sévèrement infectés étaient plus gros que les arbres légèrement infectés. L'abondance de faux-gui dans les plus gros arbres favorisera la dispersion future de la population de faux-gui. L'analyse du *K* de Ripley indique qu'il y a une relation négative entre les pruches infectées et non infectées confirmant que les arbres infectés constituent des centres d'infection distincts du faux-gui. Les centres d'infection s'étendent activement à la marge tel que confirmé par l'analyse du plus proche voisin. Les arbres sévèrement infectés avaient une relation négative avec les arbres non infectés alors que les arbres légèrement infectés avaient une relation positive avec les arbres non infectés.

[Traduit par la Rédaction]

Introduction

Western hemlock dwarf mistletoe (*Arceuthobium tsugense* (Rosendahl) G.N. Jones subsp. *tsugense*) is a canopy hemiparasite of western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), Pacific silver fir (*Abies amabilis* (Dougl.) Forbes), subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.), and noble fir (*Abies procera* Rehd.) (Hawksworth and Weins 1996). The plant causes deformation and brooming of woody structures within the crown of a tree, and in heavily infected trees dwarf mistletoe causes decreased wood production, increased cull, decreased water use, decreased photosynthetic capacity, and reduced water use efficiency (Smith 1969; Geils et al. 2002; Meinzer et al. 2004). Western hemlock dwarf mistletoe is one of many species in the genus *Arceuthobium* that impact trees in the Pinaceae family in North America (Kuijt 1960; Hawksworth and Weins 1996; Geils et al. 2002). Dwarf mistletoes are studied a lot, particularly from the perspective of forest disease impacts on timber production and pest management. Recently, however, research has demonstrated positive effects of dwarf mistletoes on stand-level biodiversity and wildlife habitat (Bennetts et al. 1996; Tinnin and Forbes 1999; Watson 2001), which has pointed

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to the need for a better understanding of dwarf mistletoes in the context of ecosystem and community ecology.

Dispersal of western hemlock dwarf mistletoe is accomplished by explosive discharge of the seed (Thomson 1979). The seed is covered with a sticky viscin and is forcibly expelled from the fruit up to 15 m, although slope and wind may influence this distance (Smith 1973). Birds, squirrels, and chipmunks may passively vector dwarf mistletoe seeds by carrying them on their bodies (Nicholls et al. 1984; Mathiasen 1996). The population dynamics of dwarf mistletoe involves spread into uninfected hosts, and intensification within these hosts (Geils and Mathiasen 1990; Shaw and Hennon 1991; Mathiasen 1996). Spread depends on a seed source. Intensification is the horizontal and vertical buildup of the mistletoe population within the host trees as numerous infections develop in tree crowns and the seed rain intensifies (Hawksworth 1969; Richardson and van der Kamp 1972; Geils and Mathiasen 1990). A tree may become so heavily infected that it will begin to decline and perhaps die. Intensification may result in the formation of distinct infection centers composed of heavily infected trees. In these centers, any susceptible hosts reproducing in the understory will become infected as they mature, possibly developing bole infections from mistletoe plants that established on the leader of the tree (Wellwood 1958; Shea and Stewart 1972).

Stand composition and structure control the vertical and horizontal spread and intensification of dwarf mistletoe at local scales because of limitations imposed by host specificity and seed dispersal (Hawksworth and Weins 1996; Mathiasen 1996; Geils et al. 2002). The spatial pattern of host versus nonhost, distance between trees, density of tree crowns, and density of foliage and branches have a major effect on distance that seed disperses (Hawksworth 1958; Parmeter 1978; Bloomberg et al. 1980).

Western hemlock dwarf mistletoe is thought to spread most rapidly in all-aged forests and old-growth (Shea and Stewart 1972), because small understory western hemlock trees can be continuously exposed to seed from the infected overstory of older western hemlock (Smith 1977), and the complex structured canopy has more vertically distributed light, which appears to be required for aerial shoot production (Smith 1969; Shaw and Weiss 2000). Spread may be much slower in younger, even-aged forests with dense foliage because of limitations in seed dispersal distance and reduction of light penetration of the canopy. However, if a young stand has an open canopy, the spread may be optimal.

In the Pacific Northwest of North America, western hemlock dwarf mistletoe is a major feature of old-growth forests (Shea and Stewart 1972; Hennon et al. 2001) and directly influences forest structure by creating crowns with many brooms, dead tops, and snags, while also influencing forest functions such as tree productivity, wildlife habitat, and carbon sequestration. A clear understanding of the ecology, population dynamics, and spatial patterns of dwarf mistletoe will be important to sustain the function of forests and provide necessary scientific basis for the management of these valuable resources (Hawksworth and Weins 1996). Quantitative information about the spatial distribution and influences on trees, in particular, are important to manage dwarf mistletoe spread and intensification.

Although western hemlock dwarf mistletoe is quite common in old-growth forests, there has been little research focused in this age-class (200+ years). Research efforts have investigated basic biology, epidemiology, and ecology in young managed stands in coastal forests of Alaska, British Columbia, Oregon, and Washington where western hemlock is an important plantation species and *A. tsugense* can have a significant effect on economics of timber management. In the Cascade Mountains of southern Washington State, typical forestry operations emphasize Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), which is not susceptible to western hemlock dwarf mistletoe. However, with the advent of ecological forestry and ecosystem management, selective harvests, commercial thinning, and green tree retention are now more widely utilized, especially on federal lands. Therefore, efforts to understand the dynamics of dwarf mistletoes in natural stands has become more critical, because managers are attempting to mimic natural ecosystem functions (Kolm and Franklin 1997).

We investigated the spatial distribution and infection characteristics of western hemlock trees infected with western hemlock dwarf mistletoe to aid in understanding the dynamics of western hemlock dwarf mistletoe in natural forests. We used a 12-ha research plot established in an old-growth (500 year) forest in the Cascade Mountains of southwest Washington State (Chen et al. 2004; Shaw et al. 2004*a*). Our specific study objectives were to (1) quantify the degree of dwarf mistletoe infections on all trees in an old-growth forest (i.e., free of human disturbances), (2) compare the structural features of infected hemlocks in the context of overall forest community, and (3) identify the spatial distribution of infections and explore the possible mechanisms for mistletoe dispersion across the stand.

Methods

Study site

The study site is on gentle topography (<10% slope) in the T.T. Munger Research Natural Area, a 478-ha research area established in 1934 to exemplify the old-growth Douglas-fir – western hemlock forest type (Franklin 1972), and includes the Wind River Canopy Crane Research Facility (WRCCRF) where a 75 m tall construction crane is in place for the study of the forest canopy (Shaw et al. 2004*a*). Located at 45°49′13.76″N and 121°58′06.88″W, the elevation of the 12-ha plot is 371 m, with average annual rainfall of 2467 mm (June through August precipitation is only 119 mm), average annual snowfall of 233 cm, and average annual temperature of 8.7 °C. The T.T. Munger Research Natural Area is located on the south and east flanks of a small shield volcano, Trout Creek Hill (890 m), with soil derived from volcanic flow breccias and pyroclastic airfall material, which overlays lahar and olivine basal bedrock. Soils are classified as Entic Vitrands, medial, mesic, and are coarse-textured, loamy sands, and sandy loams (Stabler series).

The research site is intermediate between the Pacific silver fir / salal (*Gaultheria shallon* Pursh) plant association and the western hemlock / salal and western hemlock / Oregon grape (*Berberis nervosa* Pursh) – salal plant association. Abundant understory plants include vine maple (*Acer circinatum*

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Table 1. Stand structural characteristics of the old-growth Douglas-fir forest based on measurements in a 12-ha research plot in the Wind River valley of southern Washington.

Species	Density (trees·ha^{-1})	Basal area (m^2·ha^{-1})	Foliage biomass (Mg·ha^{-1})	Biomass (Mg·ha^{-1})
Tsuga heterophylla	241.9 (55.3)	31.6 (44.0)	11.04 (58.5)	313.6 (47.2)
Taxus brevifolia	97.2 (22.2)	1.9 (2.7)	0.6 (3.1)	9.1 (1.4)
Abies amabilis	47.9 (11.0)	1.1 (1.6)	0.3 (1.6)	6.6 (1.0)
Pseudotsuga menziesii	31.1 (7.1)	29.2 (40.6)	5.4 (28.5)	289.1 (43.5)
Thuja plicata	14.1 (3.2)	6.8 (9.5)	1.3 (6.7)	35.6 (5.4)
Abies grandis	4.1 (0.9)	0.7 (0.9)	*	*
Other	1.2 (0.3)	0.5 (0.7)	0.3 (1.7)	10.0 (1.5)
Total	437.5	71.9	18.9	663.9

Note: Values in parenthesis are relative (%) to total. Data from Chen et al. (2004).
**Abies grandis* was included in "other" for these values.

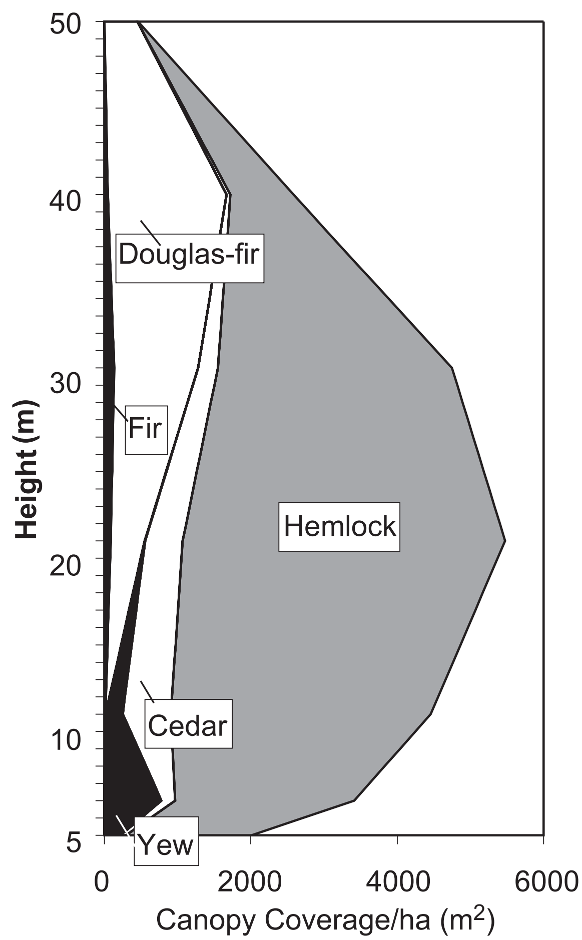
Pursh), salal, Oregon grape, red-huckleberry (*Vaccinium parvifolium* Smith), Alaska huckleberry (*Vaccinium alaskaense* How.), bear grass (*Xerophyllum tenax* (Pursh) Nutt.), and vanilla leaf (*Achlys triphylla* (Smith) DC.) (Shaw et al. 2004*a*). The salal and Oregon grape plant associations indicate drier soils and lower productivity than that of most other plant associations in the western hemlock series (Topik et al. 1986).

The forest, described by DeBell and Franklin (1987) and Franklin and DeBell (1988), originated following a fire or series of fires about 500 years ago. Douglas-fir and western white pine (*Pinus monticola* Dougl. ex D. Don) probably dominated the stand for the first 250 years, after which western hemlock and western redcedar (*Thuja plicata* Donn) became abundant. Western hemlock, western redcedar, Pacific silver fir, grand fir (*Abies grandis* (Dougl.) Lindl.), and Pacific yew (*Taxus brevifolia* Nutt.) are abundant species in the forest now. Douglas-fir is slowly dying out of the forest. Douglas-fir still dominates the forest in height and stature, although western hemlock predominates in amount of foliage, number of trees, basal area, and biomass (Chen et al. 2004).

A 12-ha stem map and research plot was established at the Wind River Canopy Crane Research Facility over several years to provide data on forest dynamics at this field station. Every tree ≥5 cm diameter at breast height (DBH, 1.3 m height) was measured, identified, and mapped beginning in 1994 with the 4-ha canopy crane research plot in the northeast corner (Shaw et al. 2004*a*) and two additional field seasons, 1996 (6 ha) and 1997 (2 ha), eventually totaling 12 ha (Chen et al. 2004). The entire 12-ha research plot was remeasured in 1999 and this data is reported here. Total stand density averages 437.5 trees·ha^{-1} with a basal area of 71.9 m^2·ha^{-1}. Western hemlock is the most abundant tree (241 trees·ha^{-1}) in all but the larger size classes with 44.0% of the basal area. Douglas-fir (31 trees·ha^{-1}) has 7.1% of the stems and 40% of the basal area. Western hemlock, Pacific silver fir (48 trees·ha^{-1}), and Pacific yew (97 trees·ha^{-1}), which are shade tolerant species, dominate the smaller size classes (Table 1). Western redcedar (14 trees·ha^{-1}) is patchy throughout the stand. Western hemlock dominates the stand in terms of foliage (58.5%) followed by Douglas-fir (28.5%).

Douglas-fir crowns dominate the canopy above 40 m, while western hemlock crowns dominate the canopy below 40 m (Fig. 1). Parker (1997), who investigated the light environment of this forest, divided the vertical profile into an upper canopy bright zone, above 40 m, where 90% of available light penetrates. The bright zone is dominated by individual Douglas fir crowns, where an occasional western hemlock crown reaches 55 m. The midcanopy transition zone extends from 40 to 12 m. Variation in the amount of light at any given point is very high, and the amount of light decreases steeply to a lower canopy dim zone, below 12 m. In the dim zone, less than 10% of available light typically penetrates.

Fig. 1. Vertical organization of crown cover (m^2·ha^{-1}) for the dominant tree species in the 12-ha research plot. Hemlock is western hemlock, Fir is all true firs, including grand fir, noble fir and Pacific silver fir, Yew is Pacific yew, Cedar is western redcedar. Data from Song (1998).



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Data collection and analysis

All western hemlock, grand fir, noble fir, and Pacific silver fir on the 12-ha research plot were surveyed in 1997 and 1998 utilizing the six-class dwarf mistletoe rating (DMR) system (Hawksworth 1977; Hawksworth and Weins 1996). One of two experienced people rated each tree, so that the variation in estimates was minimized (Shaw et al. 2000). Each tree was assigned a number from 0 (uninfected) to 6 (heavily infected). To rate a tree, the entire crown is divided into thirds and each third is rated 0, 1, or 2. Of the three ratings, 0 = no infected branches, 1 = <50% of the branches in that third are infected with at least one dwarf mistletoe plant, 2 = >50% of the branches are infected with dwarf mistletoe in that third. The score for each third is summed for the total DMR. This rating system estimates the infection level within a tree crown, but it is not an estimator of dwarf mistletoe populations. For example, a 45 m tall tree with 60 branches can get a rating of 6 by having 11 branches in each third infected (=33 branches with infections minimum), yet a 15 m tall tree with 30 branches can have the same rating if six branches in each third are infected (=18 branches minimum).

Infected and uninfected hemlock populations were compared for significant differences in infection rates using paired *t* tests (Neter et al. 1990). The number of trees in each DBH class (≤20, 20–40, 40–60, 60–80, 80–100, >100 cm) were compared by DMR class to determine whether any particular size class of tree was more heavily infected than other size classes. For example, the number of trees in the DBH class ≤20 cm that were DMR 1 was compared with the number of trees ≤20 cm that were DMR 2, and repeated for DMR 3, 4, 5, and 6. Percent difference from the mean for the DBH classes were also compared for uninfected, infected, infected rated 1–3, and infected rated 4–6 to further investigate size differences. Number of trees with infections in the low only, middle only, upper only, low and middle only, middle and upper only, low and upper only, and within all crown thirds were also compared in terms of mean DMR as a way of interpreting how the vertical distribution of dwarf mistletoe varies with tree size and infection intensity. The average DBH and height of trees were calculated and compared for each possible rating (0, 1, or 2) class of the lower, middle, and upper crowns to further understand vertical patterns. DBH was used to estimate height, crown length, and crown width using a nonlinear model (Chen et al. 2004), and mean dimensions were calculated for each DMR class and compared using paired *t* tests.

Spatial distribution of stems was investigated using Ripley's $\hat{K}$ to examine the spatial interactions between infected and uninfected western hemlock trees (i.e., is the distribution random or patterned). The purpose of bivariate Ripley's $\hat{K}$ is different from that of univariate tests. Univariate tests examine the spatial relationships within a single population, to check for clustering or regularity. For example, do hemlocks tend to grow near other hemlocks (clustering)? Or do they tend to avoid each other (regularity)? Bivariate tests examine the spatial relationships between two populations. For example, we can ask whether Pacific silver fir saplings tend to be intermixed with mature silver fir, or whether they tend to avoid the mature silver fir.

Bivariate Ripley's $\hat{K}$, with the $L(d)$ transformation suggested by Besag (in the discussion of Ripley (1977)), was used, where E is the expected value and

$$[1] \qquad K_{12}(d) = \frac{E(\text{no. of trees of type 1 within distance } d \text{ of an arbitrary tree of type 2})}{\text{density of trees of type 2}}$$

and

$$[2] \qquad L(d) = \left(\frac{K(d)}{\pi}\right)^{\frac{1}{2}} - d$$

The $L(d)$ transformation was used, because it linearizes $K(d)$, it stabilizes the variance, and because under complete spatial randomness, the expected value of $L(d)$ is approximately zero. In short, it is difficult to visually interpret $K(d)$, and using $L(d)$ makes graphs easier to read (Chen and Bradshaw 1999).

Ripley's $\hat{K}_{12}(d)$ was calculated for 50 distances, evenly spaced between $d = 0$ and $d = 150$ m. This maximum distance is half the shortest side of the 12-ha research plot. Interactions between infected and uninfected western hemlock were examined with 99 Monte Carlo simulations and the use of random labeling of infected trees. With random labeling, the locations of the western hemlock trees were considered fixed, as were the 724 infected and 2164 uninfected trees. Which particular trees were infected, however, was randomly shuffled 99 times. Therefore, for each of the 99 simulations, of the total 2888 western hemlock, 724 were randomly labeled as infected, and the rest as uninfected. Ripley's K was calculated for these 99 simulations, and the 95% confidence envelopes were constructed. The confidence envelope is not centered on zero, instead it curves slightly upwards. This slight curve occurs because with random labeling $\hat{K}_{12}(d)$ is conditioned on the distribution of western hemlock, and this species is clustered on this plot (Chen and Bradshaw 1999; Freeman and Ford 2002; Chen et al. 2004).

To infer whether the infection centers are actively spreading we compared the distribution of DMR-1 trees to the distribution of DMR-6 trees in relation to DMR-0 (uninfected) trees. We assumed that a DMR-1 tree was recently infected and a DMR-6 tree had been infected for a relatively much longer period. If DMR-1 trees tend to be closer to DMR-0 trees as a group, and DMR-6 trees tend to be statistically repulsed from DMR-0 trees as a group, then we contend that the infection center is actively spreading. No pattern would imply the infection centers are not spreading.

We used the nearest neighbor analysis to examine the spatial pattern. Ripley's $\hat{K}$ was used to understand the general spatial pattern, and it is an estimator for a second-order pa-

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Table 2. Frequency distribution by diameter at breast height (DBH) class of all western hemlock, all uninfected hemlock, all western hemlock dwarf mistletoe infected trees, infected with dwarf mistletoe rating (DMR) 1–3, and infected with DMR 4–6, within the 12-ha research plot in the Wind River valley of southern Washington.

DBH class (cm)	All stems	Uninfected	Infected	DMR 1–3	DMR 4–6
≤20	1402 (49.4)	1096 (51.7)	306 (42.4)	170 (46.6)	136 (38.1)
20–40	599 (21.1)	445 (21.0)	154 (21.3)	68 (18.6)	86 (24.1)
40–60	318 (11.2)	217 (10.2)	101 (14.0)	43 (11.8)	58 (16.2)
60–80	308 (10.8)	219 (10.3)	89 (12.3)	45 (12.3)	44 (12.3)
80–100	180 (6.3)	119 (5.6)	64 (8.4)	33 (9.0)	28 (7.8)
>100	33 (1.2)	22 (1.0)	11 (1.5)	6 (1.6)	5 (1.4)
Total	2836	2117	719	365	354

Note: Values in parenthesis are relative (%) to total (number at bottom of each column).

rameter. It analyses all the distances between all the trees, not just the distances between nearest neighbors. As a result, Ripley's $\hat{K}$ gives more information across the scale of patterns than do first-order parameters such as nearest neighbor distances. However, when an interaction occurs primarily between close neighbors, looking at all the distances with Ripley's $\hat{K}$ can swamp out the effects, and nearest neighbor tests would be more useful.

Dwarf mistletoe primarily spreads by the explosive projection of seeds from the plants in one tree to the neighboring host trees. Thus, when we examined the question "Are the infection centers spreading?" we used a bivariate form of nearest neighbor distances (Diggle 1983), where $G_{ij}(y) = P$ (distance from an arbitrary type i event to the nearest type j event is at most y) and

$$[3] \qquad \hat{G}_{ij}(y) = \frac{\text{no. of the nearest neighbor distances less than } y}{\text{no. of type } i \text{ events}}$$

where nearest neighbor distance is defined as the nearest type j neighbor to each type i event.

Monte Carlo testing was used to examine interactions between DMR-1 and uninfected western hemlock, and between DMR-6 and uninfected western hemlock. There were 137 western hemlock with DMR 1. $\hat{G}_{ij}(y)$ was calculated from the nearest uninfected neighbor of each of these 137 trees. Random selection among the infected western hemlocks was used to construct simulation envelopes. The null hypothesis was that all infected trees, independent of their locations within infection centers, were equally likely to have DMR 1. Of the 724 infected western hemlock, 137 were randomly selected, and $\hat{G}_{ij}(y)$ was calculated. This was repeated 99 times, and the 95% confidence values were used to construct the envelope. The sample mean, $\overline{G}_{ij}(y)$, of the simulations was used to linearize the plot. This same procedure was used to compare the DMR-6 trees with the uninfected trees.

To determine the influence of nonhosts we used a qualitative approach to visualize the distribution of nonhosts and the infection centers. We inferred that there was a relationship if the shape of the infection centers conformed to the pattern of nonhost distribution at the edge of the infection centers. We also looked at the patterns of DMR-6 hemlock and living and dead Douglas-fir, implying this may have had an influence in the past but currently may not be affecting the stand because of mortality of nonhosts from other factors, such as root disease and stem decay.

Results

Of the 2836 western hemlock, 554 Pacific silver fir, 48 grand fir, and 7 noble fir with ≥5 cm DBH present on the 12-ha research plot, infections were found in 719 western hemlock (25.4%), 12 Pacific silver fir (2.2%), 0 grand fir, and 2 noble fir (28.6%). The infected hemlock were evenly split; 365 were lightly infected (DMR 1–3) versus 354 that were heavily infected (DMR 4–6) (Table 2). However, 51.7% of the uninfected trees versus 42.4% of the infected trees were in the smallest size class (≤20 cm DBH), indicating that the infected trees tend to be larger. This is especially true for heavily infected trees (DMR 4–6), which had only 38.1% recorded in the smallest DBH class (Table 2).

The distribution of stem sizes is disproportional for the infected and uninfected hemlock populations. The average DBH (height) of uninfected, lightly infected, and heavily infected hemlocks were 30.1 cm (22.9 m), 34.8 cm (25.1 m), and 37.0 cm (27.0 m), respectively, indicating that on average, heavily infected trees are larger than lightly infected and uninfected trees. This was significant when we examined the differences from the overall mean for each DBH class (Fig. 2). For the uninfected population, the portion of stems ≤20.0 cm (51.7%) was 2.4% higher than the stand average (49.4%). In contrast, heavily infected populations ≤20.0 cm in DBH (38.1%) was 11.3% lower than the mean. Although the population size for infected populations of other host species was too small to generate a similar consensus that large (DBH and height) trees were more commonly infected, the average DBH of infected *Abies* stems was 23.5 cm, while the average DBH of all *Abies* stems was 15.7 cm. The DBH of two infected noble firs was 66.5 and 87.5 cm.

More than half (57.3%) of infected hemlocks were infected at all three crown thirds (Fig. 3). There were 84 (11.7%), 53 (7.4%), and 11 (1.5%) hemlocks that were infected only in their lower, middle, and upper portion of the crowns, respectively, while 19.6% of infected hemlocks had mistletoes at their lower and middle portions of the crowns. Only three individuals were infected in both the lower and upper part of the crown. Apart from those trees infected in all thirds, those with infections in the lower and midcrown, and those infected in the lower crown only were more abundant than trees in other categories (Fig. 3).

There are differences associated with size (DBH and height) among the infected western hemlock trees with different vertical infection ratings (Fig. 4). The DBH and height of trees

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Fig. 2. Deviation (measured as percent) of uninfected, infected, infected with dwarf mistletoe rating system (DMR) 1–3, and infected DMR 4–6 western hemlocks from the overall mean of all the western hemlock trees by DBH class on the 12-ha research plot.

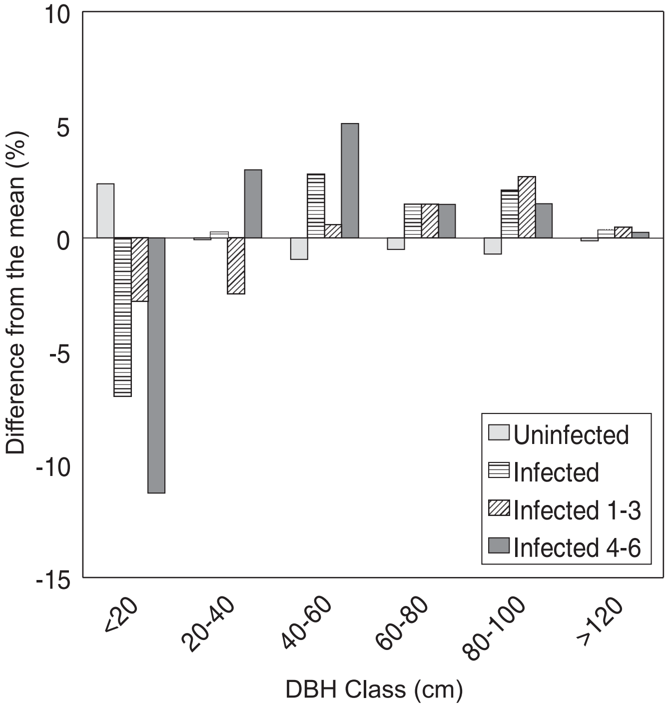
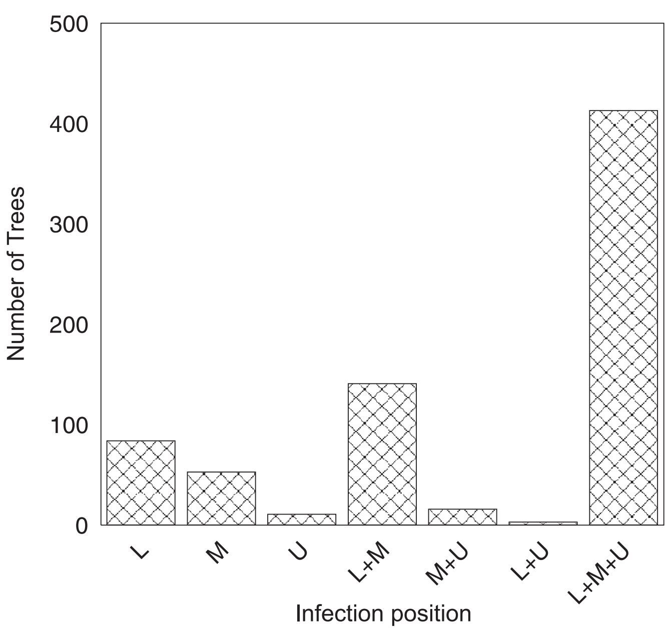
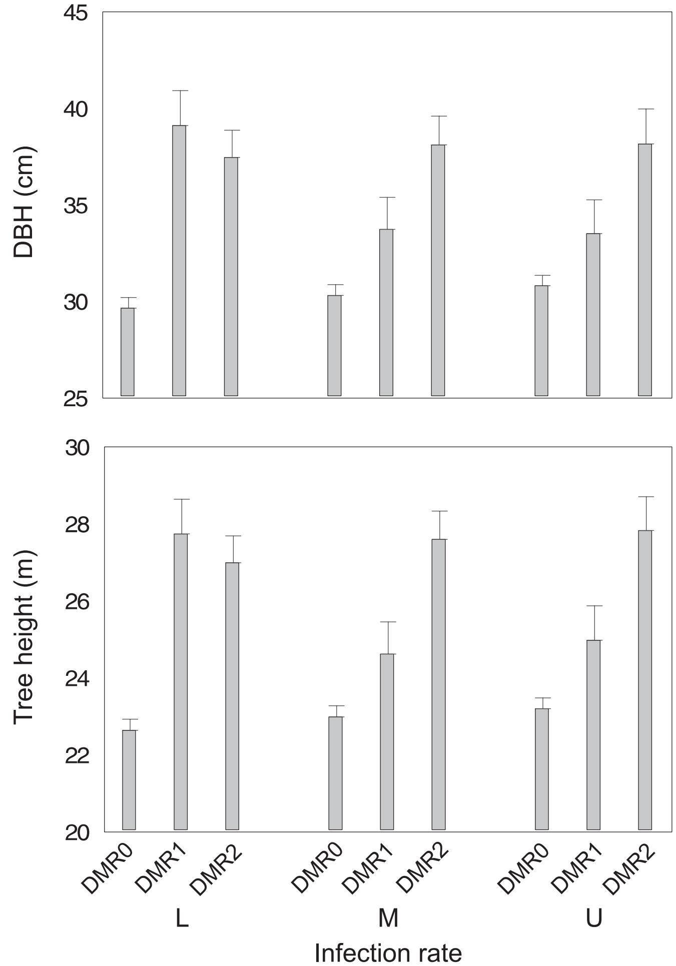


Fig. 3. Number of western hemlocks for each infected population within the 12-ha research plot. L, M, and U refer the lower, middle, and upper portion of a crown.



with lower crown free of infections were not significantly different from those with middle and upper crowns that are uninfected ($p > 0.47$). Hemlocks with middle and upper crown thirds lightly infected (DMR = 1 or <50% of the branches in that third are infected with at least one dwarf mistletoe plant) were significantly smaller ($p = 0.007$ and

Fig. 4. Comparisons of DBH and tree height among populations of uninfected (DMR0), lightly infected (DMR1), and heavily infected (DMR2) western hemlock trees at three different vertical portions of the crowns. L, M, and U refer the lower, middle, and upper portion of a crown.



0.002, respectively) than those with heavy infections (DMR = 2) (Fig. 4). No significant difference was found for DBH and height when trees were infected at the same level.

When tree characteristics of hemlocks were examined based on overall infection, a clear trend associated with increasing infection was evident; DMR 5 and 6 trees are larger (Fig. 5). All four measures (DBH, tree height, crown length, and maximum crown width) increased with total infection rate. However, the population with total infection rate of DMR 4 consisted of significantly smaller trees (Fig. 5).

Across the 12-ha research plot, 33% of the area had average DMR >0, while 28% has average DMR >0.5. The infected trees appeared to be grouped together, with heavily infected trees being especially clumped (Fig. 6). Bivariate Ripley's *K* analysis indicated a negative association between infected and uninfected western hemlocks on the 12-ha research plot (Fig. 7). The implication of a negative association is that infected trees are aggregated and repulsive from uninfected trees. A repulsive association between the infected and uninfected western hemlock trees occurs up to 140 m in scale, with the strongest repulsion occurring at 30 m. The simulation envelope curves slightly upward, indi-

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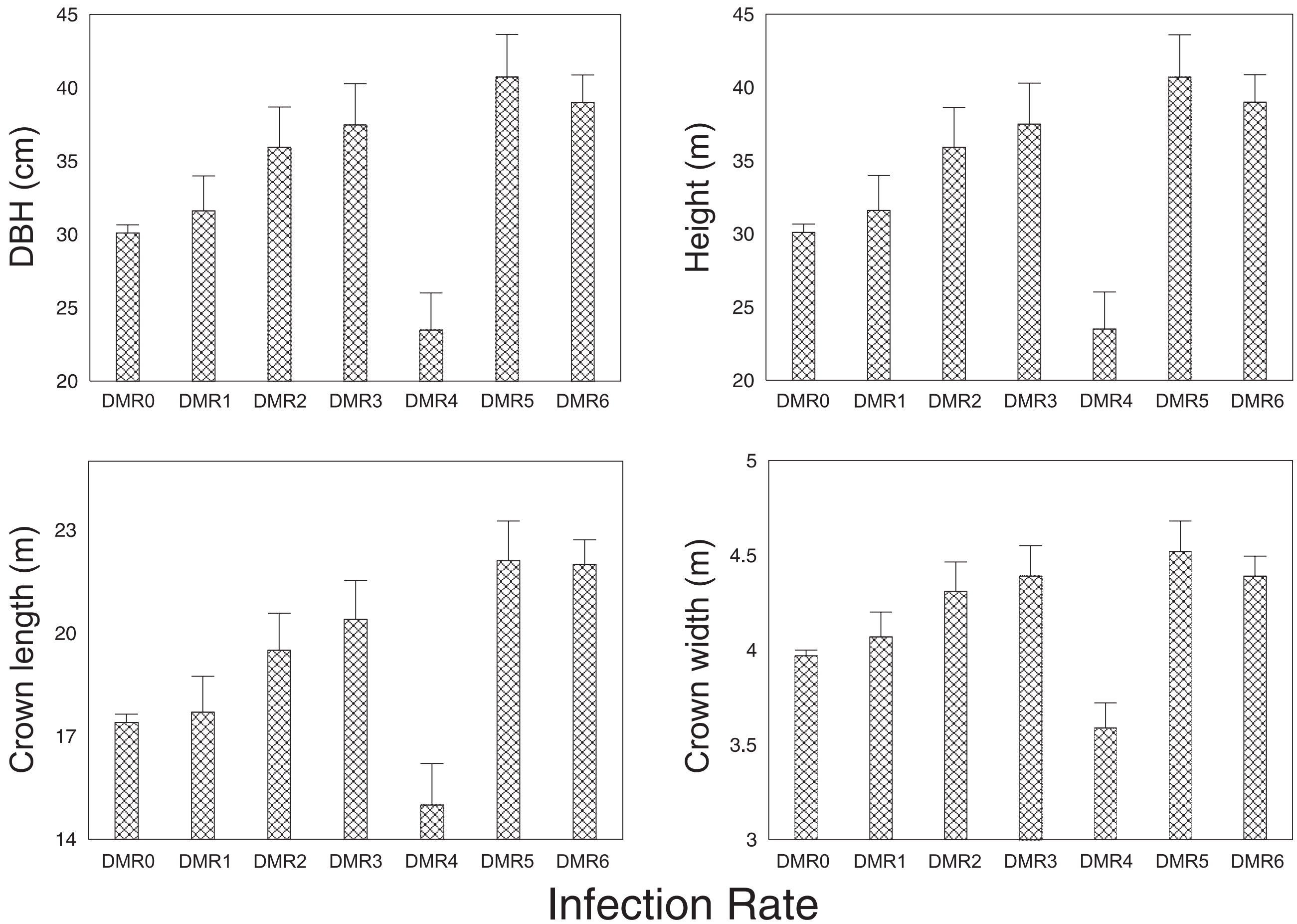
Fig. 5. Tree characteristics (DBH, height, crown length, and crown width) of western hemlock populations that had different infection rates in the 12-ha research plot.



cating western hemlock are clustered at the 20 to 80 m scale (Fig. 7). The spatial pattern forms discrete infection centers. There are also four lightly infected western hemlock trees in the southwest corner of the plot, three of these are clustered and one is about 20 m from these three (Fig. 6). This small cluster was more than 50 m from the nearest infection centers.

Trees with DMR 6 were clustered in the center of the infection centers and trees with DMR 1 were generally found in the periphery of the infection centers (Fig. 8). This pattern was confirmed by bivariate nearest neighbor analysis (Fig. 9). The DMR-1 (lightly infected) trees tended to be closer to uninfected western hemlock trees (Figs. 8A and 9A), while the DMR-6 (heavily infected) trees tended to be farther away from uninfected trees (Figs. 8B and 9B), suggesting that these infection centers are actively spreading. Qualitative visualization of host and nonhost distribution indicates that nonhosts may prevent spread of the infection centers in certain key areas, but that the entire shape of the infection center cannot be explained by the distribution of nonhosts (Fig. 10A). Comparison of the location of DMR-6 western hemlock trees and living and dead nonhosts draws a similar conclusion (Fig. 10B).

Discussion

The population of infected western hemlock trees on this plot is, on average, larger than the population of uninfected trees. Within the infected trees, those heavily infected are larger than those that are lightly infected (Figs. 2, 3, 4, and 5). There are several reasons that this pattern of infection has major implications for the future of dwarf mistletoe spread and intensification in this forest. Large trees make a better source for mistletoe spread because of the increased height of seed dispersal origin. In addition, Shaw and Weiss (2000) found that the distribution of aerial shoots is skewed to high light zones in the upper canopy at this site, usually above 40 m. This means infected taller trees that have more crown area in the upper canopy will most likely produce more vigorous dwarf mistletoe shoots and more seed. Mortality of western hemlock in the Wind River old-growth forest is much more likely in the smaller size classes (Bible 2001) and, therefore, plants that occur in larger trees have a higher likelihood of survival. Finally, larger trees can support more dwarf mistletoe plants than can small trees.

Parmeter (1978) noted that the distribution of dwarf mistletoes is usually skewed to larger trees within any stand. This may be because smaller trees make a smaller target area and, therefore, are less likely to be hit by seed. Younger trees may have been exposed to seed rain for less time than older trees, which also makes younger trees less likely to have heavy infection loads. Finally, host vigor promotes dwarf mistletoe vigor, and more robust aerial mistletoe shoots and larger amounts of seed are produced on vigorous host shoots,

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Fig. 6. Spatial patch patterns of infected western hemlock across the 12-ha research plot. Six distinct infection patches were identifiable.

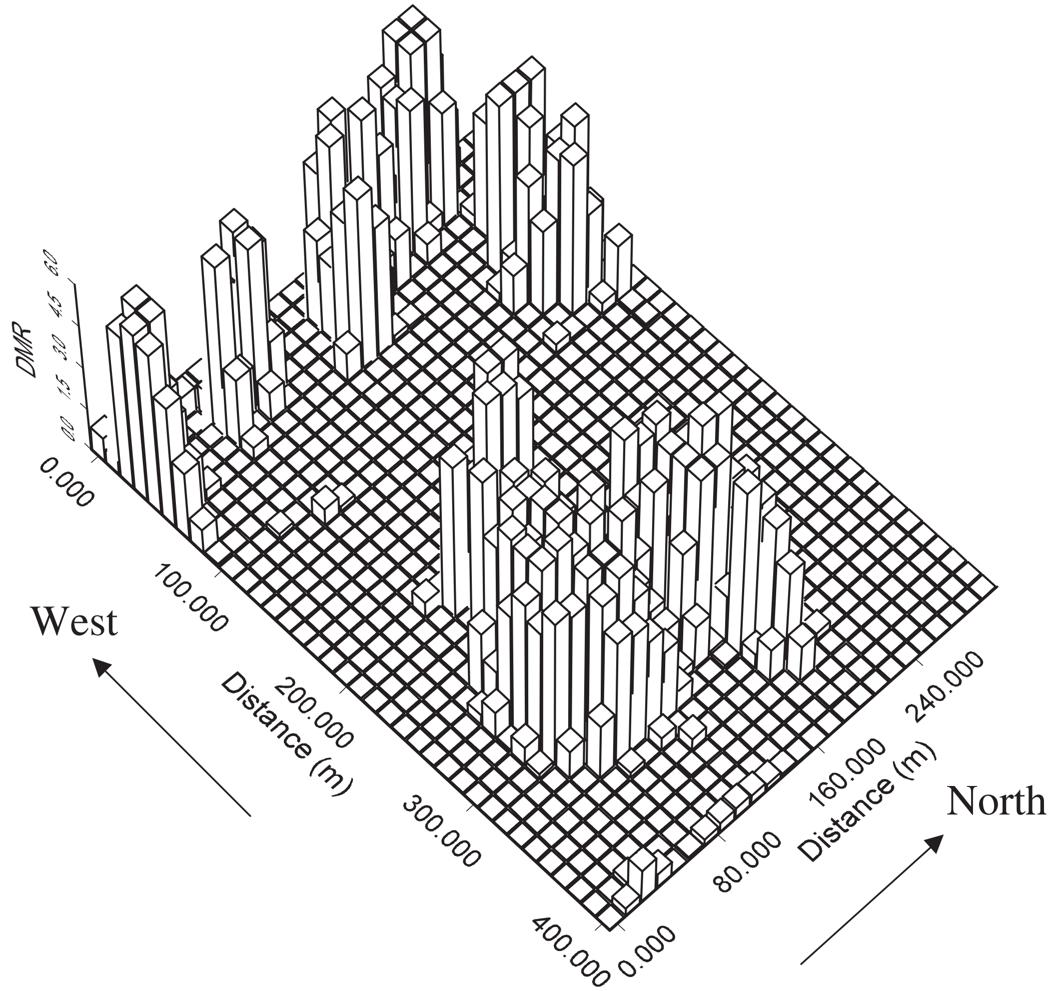
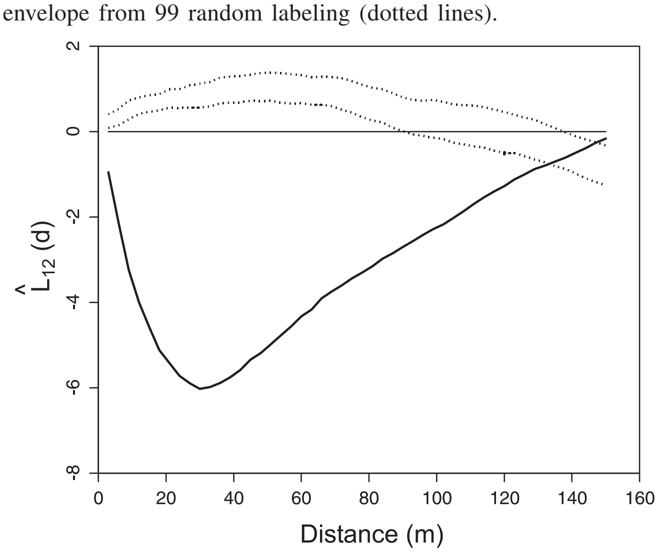


Fig. 7. Bivariate Ripley's $K(d)$ results for the interaction between infected and uninfected western hemlock. $\hat{L}_{12}(d)$ (solid line), and envelope from 99 random labeling (dotted lines).



which are higher in the canopy. Aukema (2003) reported that other Viscaceous mistletoes also tend to occur on the larger trees or shrubs within infested woody plant communities.

The majority of infected western hemlock trees in this stand have infections in all crown thirds (Figs. 3 and 4). Many stands infected with dwarf mistletoe, especially young stands, are predominantly infected in the lower and middle crowns (Sharpf and Parmeter 1976; Parmeter 1978; Shaw and Hennon 1991). Parmeter (1978) contended that as older trees reach their maximum height growth the upward advance of dwarf mistletoe eventually infects the entire crown.

Shea and Stewart (1972) and Hennon et al. (2001) describe the general distribution of hemlock dwarf mistletoe as occurring in patch-like patterns, with much variation in severity and distribution. Within this old-growth 12-ha research plot, 33% of the area had some level of infection, and this was in distinct infection centers, as shown by the Ripley's *K* analysis (Figs. 6 and 7).

The current spatial patterns of the infected trees in this old growth Douglas-fir – western hemlock forest (Figs. 6 and 8) indicate a classic pattern of isolated infection centers (Dixon and Hawksworth 1979) where intensification has likely occurred in the original areas of infection, and the infection centers are spreading, as indicated by the nearest neighbor analysis (Figs. 8 and 9). Spread in this forest will likely increase as the nonhosts decrease in abundance, because stands with multistoried canopies that are dominated by dwarf mistletoe hosts are considered the most susceptible to rapid spread (Parmeter 1978; Geils and Mathiasen 1990; Mathiasen

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Fig. 8. Stem map showing the locations of dwarf mistletoe rating system (DMR) 1 and all uninfected western hemlock (A) and locations of DMR 6 and all uninfected western hemlocks (B).

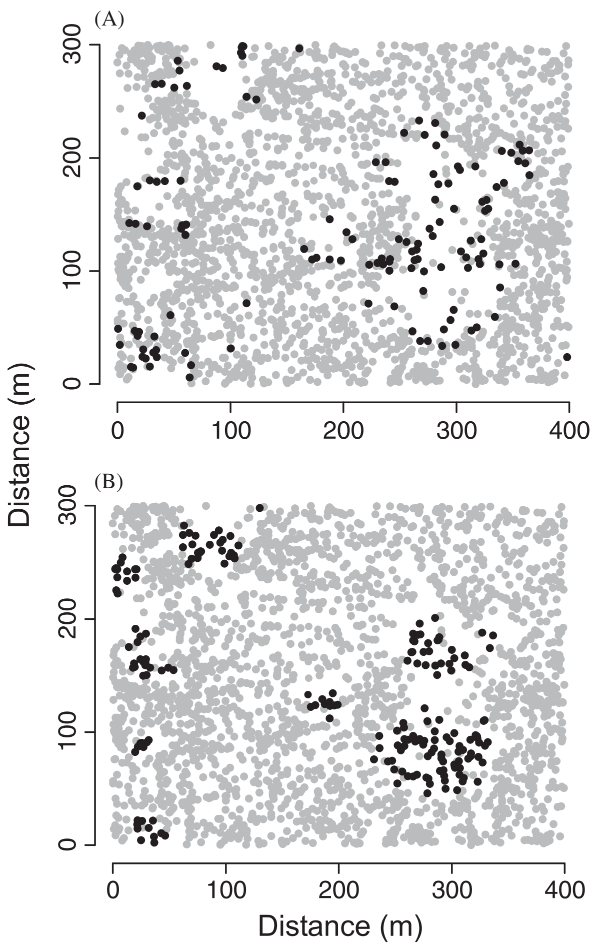
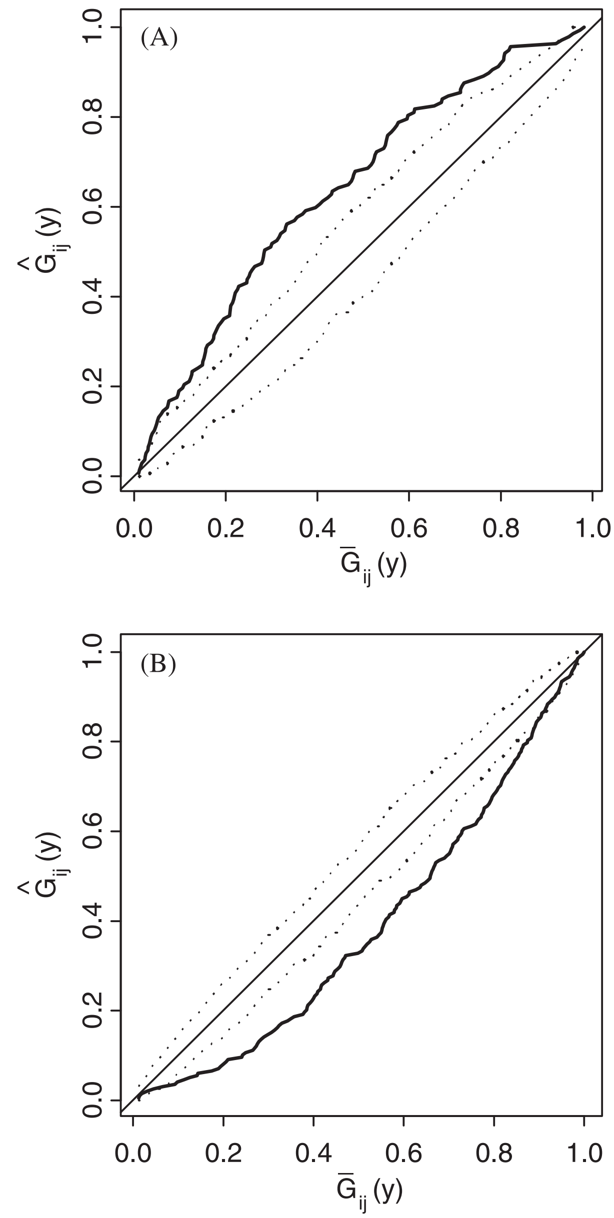


Fig. 9. Bivariate nearest neighbor analysis for the interaction (A) between dwarf mistletoe rating system (DMR) 1 and uninfected western hemlock trees, and (B) between DMR 6 and uninfected western hemlock trees $\hat{G}_{ij}(y)$ from the *n* trees of the specified DMR to their nearest uninfected neighbor (solid line), and envelope from 99 random selections of *n* infected western hemlock to their nearest uninfected neighbor (dotted lines).



1996). Hawksworth et al. (1992) investigated lodgepole pine dwarf mistletoe (*Arceuthobium americanum* Nuttall ex Engelmann) in a 300-year-old lodgepole pine forest in Colorado. The infected portion of the three 2.02-ha stands ranged from 34% to 60%, with no distinct infection centers. A nearby 70-year-old stand averaged 1.4 isolated infection centers per hectare. The implication is that succession leads to the coalescing of dispersed infection centers, and in old-growth forests dwarf mistletoe eventually becomes ubiquitous where the host trees are present.

Qualitative investigation of the host–nonhost distribution on this plot indicated that nonhosts certainly play a role in some elements of the current infection center pattern (Fig. 10). Nonhosts block mistletoe seed dispersal and may have played a much larger role in the past, especially several hundred years ago, when western hemlock was only beginning to become common throughout the forest (DeBell and Franklin 1987; Franklin and DeBell 1988). The current pattern of infection centers may reflect the distribution of hemlock and nonhosts early in stand development. Everett Hansen (personal communication, Oregon State University) suggested one possible scenario is that a root pathogen (*Phellinus weirii*) of Douglas-fir may have created gaps in the forest, which were colonized by western hemlock. Western hemlock is susceptible to *P. weirii*, but is more tolerant of the disease than is Douglas-fir and is rarely killed. Western hemlock is known to colonize and thrive in the gaps created by *P. weirii*, which caused Douglas-fir mortality (Holah et al. 1997; Hansen and Goheen 2000). At WRCCRF, western hemlock may have become more abundant in these gaps prior to other areas in the forest, and therefore dwarf mistletoe was more likely to arrive in the gaps.

Fire is a major factor that determines the distribution of dwarf mistletoe on a landscape basis (Alexander and Hawksworth 1975; Hawksworth and Weins 1996), particularly in the Douglas-fir forests of western Washington, which typically have stand replacement fires (Agee 1993). Mixed forests of

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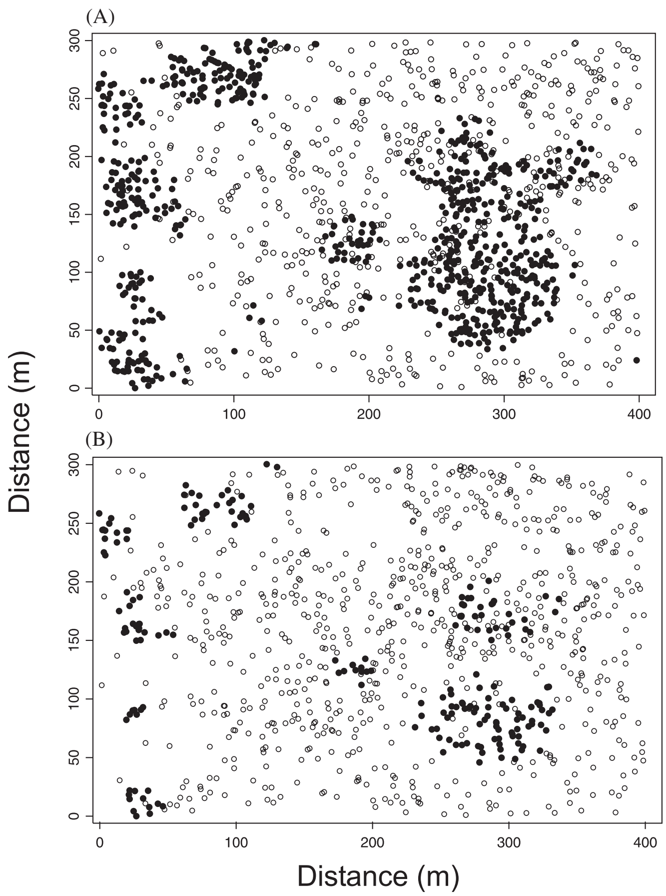
Fig. 10. (A) Stem map showing locations of living infected western hemlock trees and living nonhosts (Douglas-fir, grand fir, and western redcedar) on the 12-ha research plot. (B) Stem map showing location of living dwarf mistletoe rating system (DMR) 6 western hemlock trees and live and dead Douglas-fir trees on the 12-ha research plot.



western hemlock, western redcedar, and Douglas-fir are replaced primarily by Douglas-fir after fire, and western hemlock may not become abundant for several hundred years (Franklin and Dyrness 1973). The primary means of stand re-infection after fire disturbance by hemlock dwarf mistletoe is the survival of infected host trees (Wellwood 1956; Shea and Stewart 1972; Alexander and Hawksworth 1975). This is also the case for wind-disturbed forests of British Columbia and Southeast Alaska (Trummer et al. 1998). These infected trees act as a biological legacy and become the source for new infection centers. As western hemlock becomes more abundant in the vicinity of the infected trees, the dwarf mistletoe spreads into other western hemlock trees. The rate of spread is controlled by stand-level factors such as the distribution of hosts and nonhosts as well as the abundance and density of western hemlock. The result is a patchy distribution of the mistletoe within the forest (Shea and Stewart 1972).

Kipfmueller and Baker (1998) investigated dwarf mistletoe and fire in a Wyoming Rocky Mountain lodgepole pine ecosystem. Although dwarf mistletoe stand-level characteristics increased with increasing time (approximately 100 to 500 years) and tree size, there was much variation due to the distribution and abundance of trees that survived the original stand replacement fires. They concluded that dwarf mistletoe infection at the landscape scale is characterized by infection centers, which developed from infected trees that survived the fire.

Several hypotheses may explain the origin of the infection centers on the 12-ha research plot. The most obvious one is that infected western hemlock trees survived the fire of 500 years ago, and these trees became the source of today's infection centers. It is also possible that large trees, which survived the fire, occur just off the 12-ha plot. Although these trees provided the source for the infection centers, they would not be obvious in the 12-ha research plot analysis. Another alternative hypothesis is that long-distance dispersal via animal transport is coming from refugia that may have survived fire disturbance somewhere in the general vicinity of the 12-ha research plot. Finally, it is possible that the infection centers developed from all three methods of origin.

There are several characteristics expected to occur if these infection centers are 500 years old. These include large, dead western hemlock trees in the center of the infection areas, old heavily infected western hemlock trees, and bole infections on large trees, which form when dwarf mistletoe seed infects the leader of a tree. Bole infections commonly occur when overstory trees infect understory trees (Wellwood 1956). None of these characteristics occur on the 12-ha research plot. No large, dead western hemlock trees occur in the infection centers, but it is possible that infected hemlock trees that survived the fire died many (300–500) years ago and have decayed to a point where they would be unrecognizable. We have detected bole infections only in small size class trees in the understory of the infection centers, and none of the large infected trees have bole infections, implying these trees did not become infected under a seed rain from above. Lyons et al. (2000) did not age any western hemlock trees older than 250 years in the stand, but their sample included only 30 trees. Aging mistletoe brooms to determine infection timing could provide insight into the age of infection, but this requires destructive sampling that is not allowed at this site.

Evidence for seed dispersal by animals at the local scale can be found on the southwest portion of the 12-ha research plot where there is an isolated, small, infection center (Fig. 10A). This is >50 m away from the nearest infection center, 35 m farther than the maximum recorded distance of western hemlock seed dispersal (Smith 1973). The Douglas squirrel (*Tamiasciurus douglasii*) is common in the upper canopy during mistletoe seed dispersal times (Shaw and Flick 2002) and could potentially vector seed. Several birds (Shaw et al. 2002), which have been documented to vector seed in other regions, are also present in the T.T. Munger Research Natural Area old-growth forest during dwarf mistletoe seed dispersal periods, including Steller's jay (*Cyanocitta stelleri*), gray jay (*Perisoreus canadensis*), American robin (*Turdus migratorius*), dark-eyed junco (*Junco hyemalis*), red crossbill (*Loxia curvirostra*), brown creeper (*Certhia americana*), and red-breasted nuthatch (*Sitta canadensis*) (Nicholls et al. 1984; Mathiasen 1996; Hawksworth and Weins 1996).

The Steller's jay and gray jay were considered particularly important in carrying seed (Nicholls et al. 1984). They are both common in the upper canopy at the study site. In addition, red crossbills are common residents of this stand and specialize on western hemlock. The birds feed on hemlock

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cones during August, September, and October (D. Shaw, personal observation) and could be an important vector, because they move among individual western hemlock trees searching for cones in the zone where mistletoe aerial shoot occurrence is highest and during the time fruits are ripe and ready to explosively release seed. If birds are playing a role in dispersal of dwarf mistletoe seed, then the upper crowns may be infected first. This would lead to a top-down infection that results in the observed pattern of the majority of infected trees with dwarf mistletoe plants in all crown thirds.

Hemlock dwarf mistletoe is a native plant that is very common in western hemlock forests, especially old-growth Douglas-fir – western hemlock forests on the west slope of the Cascade Mountains. Bolsinger (1978) estimated that 21% of forest types classified as western and mountain hemlock in California, Oregon, and Washington were infected with dwarf mistletoe. In the western Oregon and Washington Douglas-fir forest type that includes our study site, Bolsinger concluded that western hemlock was the primary species infected with dwarf mistletoe, and only 10% of this type was infected. At the landscape level, dwarf mistletoe is important, because it creates forests of structural complexity and may play a positive role in forest biodiversity (Shaw et al. 2004*b*). The influence of dwarf mistletoes in natural areas and conservation set asides may be considered very positive. However, Hawksworth and Weins (1996) contend that gap sizes can be created within old infection centers that actually degrade old-growth forests for spotted owl habitat by lowering canopy cover and compromising interior forest conditions. Natural forest succession leads to this condition, and natural areas become the key study sites where the implications of such succession can be scientifically studied.

Management of dwarf mistletoes relies on scientific understanding of the ecology and epidemiology of these important pathogens in the context of on-the-ground forest conditions (Hawksworth and Weins 1996; Geils et al. 2002). In this study, the tendency of dwarf mistletoe to be on larger trees and occur vertically throughout the crowns in established infection centers implies hemlock dwarf mistletoe is well positioned to continue a long-term presence in this old-growth forest in the absence of fire. The potential ability of dwarf mistletoe to invade forest areas by long-distance transport of seed is significant, and should be a consideration in the ecology of hemlock dwarf mistletoe spread.

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