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Distribution of Western Hemlock Dwarf Mistletoe (*Arceuthobium tsugense* [Rosendahl] G.N. Jones Subsp. *tsugense*) in Mature and Old-growth Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) Forests

Abstract

We investigated the landscape distribution and spatial patterns of western hemlock dwarf mistletoe in old-growth and mature Douglas-fir forests of the Wind River Experimental Forest. The study was conducted in two settings: the old-growth forest (500 year) of the 478 ha T.T. Munger Research Natural Area (T.T. Munger RNA) and the higher-elevation, predominantly 157-year old stand of the 1,400 ha Panther Creek Division of the Wind River Experimental Forest. Existing transects and tagged trees were used in the T.T. Munger RNA to survey for dwarf mistletoe infection. We surveyed for dwarf mistletoe-infected trees in the Panther Creek Division by hiking roads, trails, and drainages. Eighty-three percent of the transect segments within the T.T. Munger RNA had some level of dwarf mistletoe infection. Dwarf mistletoe was found only in legacy old-growth patches in the Panther Creek Division, and these comprised only 2.4 percent of the division area. The three legacy old-growth patches containing dwarf mistletoe were restricted to drainage bottoms and well-watered benches. None of these patches burned completely in the 1800's, as evidenced by large, old trees > 300 yrs. Spatial analysis of transect segments (using Moran's I) in both T.T. Munger RNA and Panther Creek Divisions showed that within both old-growth and legacy patches in mature forest, western hemlock dwarf mistletoe infection is spatially aggregated. Dwarf mistletoe is maintained on this landscape by survival in refugia, most often in riparian areas, or, in the case of the T.T. Munger RNA, in low-density, low-productivity areas that do not burn completely during wildfire events. Dwarf mistletoe must persist in these refugia until host trees recover in burned areas, a process which may take many decades in intensely burned watersheds.

Introduction

Western hemlock dwarf mistletoe (*Arceuthobium tsugense* [Rosendahl] G.N. Jones subsp. *tsugense*) is a common hemi-parasitic plant on western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) and a few other shade-tolerant species in Alaska, British Columbia, Washington, Oregon and California (Hawksworth and Wiens 1996, Hennon et al. 2001, Geils et al. 2002). It is a subspecies of the more widely distributed hemlock dwarf mistletoe (*A. tsugense* [Rosendahl] G.N. Jones), which also occurs on mountain hemlock (*Tsuga mertensiana* (Bong.) Carr.) and shore pine (*Pinus contorta* Dougl. ex Loud. *var. contorta*) (Hawksworth and Wiens 1996). Western hemlock dwarf mistletoe causes deformation and brooming of infected branches, and in severely infected trees can cause growth loss, top-kill and tree death (Hennon et al.

2001, Geils et al. 2002). Dwarf mistletoes should not necessarily be considered detrimental to the forest ecosystem, as their contribution to forest structural diversity is important for wildlife and biodiversity (Hawksworth and Wiens 1996, Bennetts et al. 1996, Watson 2001).

Like other members of the genus *Arceuthobium*, western hemlock dwarf mistletoe spreads by explosively discharged seeds, shot up to 15 m or more (Smith 1973). The seeds are covered with a sticky substance called viscin, and they adhere to leaves and small twigs. Western hemlock dwarf mistletoe spreads slowly in dense, one-story stands of pure hemlock and in stands with many non-host trees. The greatest spread rate and best development of plants is in relatively open, multi-storied, pure western hemlock stands (Alfaro et al.1985). The distribution of western hemlock dwarf mistletoe on the landscape is patchy, and related to stand disturbance history, seed source, and spread rate interacting with forest composition and structure

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(Hawksworth and Wiens 1996, Hennon et al. 2001). Birds and mammals may passively transport dwarf mistletoe seed (Shaw et al. 2004b), complicating the model that assumes seeds are dispersing according to a locally contagious process.

Wildfire and other disturbances, such as wind storms, that kill trees and change forest composition and structure have a profound influence on dwarf mistletoes. In managed western hemlock stands, residual dwarf mistletoe infected trees not killed during logging were the source of subsequent infections in the regenerating stand (Bloomberg and Smith 1982, Shaw 1982, Alfaro et al. 1985, Shaw and Hennon 1991). Trummer et al. (1998) demonstrated that the distribution of infected trees that survived wind disturbance in natural forests of southeast Alaska could be used to predict the severity and distribution of dwarf mistletoe in the regenerating stand.

Western hemlock dwarf mistletoe occurs in coastal forests, where western hemlock is an early-successional species. Residual infected western hemlock can infect the regenerating stand that is dominated by western hemlock. However, western hemlock dwarf mistletoe also occurs in Douglas-fir forests of the Cascades Range where western hemlock is a late-successional species (Franklin et al. 2002). Periodic return intervals of wildfire are between 300 and 650 years in moist Douglas-fir forests of the southern Washington State Cascade Mountains and this often results in stand replacement (Gray and Franklin 1997). Stand-replacement fire shifts the composition of the forest from multi-species stands of old-growth Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco), western hemlock, Pacific yew (*Taxus brevifolia* Nutt.), true firs (*Abies* Mill.), and western redcedar (*Thuja plicata* Donn.) to early successional stands with a high proportion of Douglas-fir, and minor representation of associated species like western white pine (*Pinus monticola* Dougl. ex D. Don), western hemlock, and grand fir (*Abies grandis* (Dougl. ex D. Don) Lindl.). Residual hemlock trees or patches of old-growth forest, or legacy patches, that survive the fire may not be surrounded by host trees in the regenerating forest.

The purpose of this research is to describe spatial patterns of western hemlock dwarf mistletoe at landscape and patch scales (using transects) in forests of the Cascade Mountains where the principal host of the parasite may not become abundant for one to two centuries following disturbance. On the Wind River Experimental Forest in southwest Washington State, dwarf mistletoe is common in old-growth (500 yr) forests of the Thornton T. Munger Research Natural Area (T.T. Munger RNA). However, in the nearby Panther Creek Division of the Wind River Experimental Forest, where a forest of almost pure Douglas-fir has originated after a ~1845 fire, no mistletoe had been observed. However, legacy patches of hosts had been noted in some places in the Panther Creek Division. Information on how western hemlock dwarf mistletoe is spatially distributed as a function of time since stand-replacement disturbance in these forests is needed for long-term management of this important hemi-parasite, especially with regard to old-growth forests (Hawksworth and Wiens 1996).

Based on our understanding of western hemlock dwarf mistletoe life history, we predicted that in the old-growth stands of the T.T. Munger RNA, western hemlock dwarf mistletoe would be found somewhat evenly distributed across the landscape, whereas in the more recently disturbed Panther Creek Division, western hemlock dwarf mistletoe would be limited to legacy patches where western hemlock trees survived the 1845 disturbance. We also predicted that western hemlock dwarf mistletoe would be spatially aggregated in the T.T. Munger RNA and in legacy old-growth patches in the Panther Creek Division.

Study Site

The Wind River Experimental Forest (~ 4,000 ha) is separated into two divisions, Trout Creek (~ 2,600 ha) and Panther Creek (~ 1,400 ha) (Shaw and Greene 2003; Figure 1). The study was conducted within the T.T. Munger RNA, which is a 478 ha old-growth forest in the Trout Creek Division, and the entire Panther Creek Division, which is a 1115 ha watershed. The units are approximately 11 km apart. Mean annual temperature is 8.7°C, and mean annual precipitation is 2223 mm. There is a distinct summer dry season, when only about 5% of precipitation falls. Winter is characterized by snowpack in December through March in the lower elevations of the divisions, and December through April or May at the higher elevations of the divisions (Shaw et al. 2004a).

The T.T. Munger RNA (Franklin 1972) is located on the east and south sides of Trout

Figure 1. Map of the Wind River Experimental Forest showing the Trout Creek Division (location of the T.T. Munger Research Natural Area) and the Panther Creek Division. *Map courtesy of the U.S.D.A. Forest Service, Keith Routman.*

Creek Hill, a ~ 340,000 year old basaltic shield volcano. Soil parent material is air-deposited, mixed volcanic tephra, of relatively recent origin (between 3,500 and 12,000 years before present) from unknown stratovolcanic source. Soils are deep (2 m +), well drained, generally stone free, and medium textured. Elevation varies from 335 m to 610 m. Topography is gentle, and not deeply incised by drainages (Shaw et al. 2004a).

The Panther Creek Division includes the entire watershed of Mouse Creek, a tributary of Panther Creek. Elevation varies from about 275 m on the Panther Creek valley floor in the western edge of the division to approximately 1,200 m at the top of the ridge at the eastern border of the Mouse Creek watershed. The division is underlain by Eocene to Oligocene volcanic flows and breccias, with well-stratified volcaniclastics of a variety of origins (Woodfin et al. 1987). Broadly undulating terrain, dissected by streams results in a complicated mix of steep and gentle slopes in the division. Soils are characterized by three broad geomorphic types depending on slope position: alluvial soils

in the drainage bottoms, colluvial soils on lower slopes, and some alpine glacial till at higher elevations.

Vegetation in both units is characterized by *Tsuga heterophylla* plant associations below about 700 m elevation, and *Abies amabilis* plant associations above this, although the two vegetation zones are clearly intermixed with slope position, aspect, and exposure. Pacific silver fir (*Abies amabilis* Dougl. ex Forbes) types may occur as low as 300 m (Woodfin et al.1987). Common associations include salal (*Gaultheria shallon* Pursh.) and Oregon-grape (*Berberis nervosa* Pursh.) types and more mesic herb-dominated types, often with species such as foamflower (*Tiarella trifoliata* L.) and lady fern (*Athyrium filix-femina* (L.) Roth.) on toe slopes, wet benches, and near riparian areas. The old growth stand in the T.T. Munger RNA originated in a stand-replacement fire event about 500 years ago (part of the Medieval Optimum complex of fire events- Agee 1993). In the T.T. Munger RNA, the tree composition data from the mortality transects provided by Franklin and DeBell (1988) show that the forest is dominated by western hemlock, Douglas-fir, Pacific silver fir, and western redcedar . A stand-replacing fire event around 1845 (with possible reburn events) was the origin of the stand in the Panther Creek Division. Douglas-fir dominates the forest, with all other tree species less abundant at this successional stage (see Table 1 for stem densities by species for the two stands).

Methods

T.T. Munger Research Natural Area

Nine existing mortality transects (DeBell and Franklin 1987, Franklin and DeBell 1988) were used to survey the T.T. Munger RNA. These transects included 103 transect segments, five chains by two chains (100.6 m x 40.23 m, or approximately 0.4 ha) (Figure 2). This resulted in an area-wide sampling intensity of 41.2 ha out of 478 ha total (8.6%). All trees >45.7 cm diameter at breast height (dbh) were tagged and surveyed in 1998. Every tagged western hemlock, Pacific silver fir, noble fir (*Abies procera* Rehd.) and grand

fir was assigned a dwarf mistletoe rating (DMR) following the methods of Hawksworth (1977) and Hawksworth and Wiens (1996), in which the crown is divided into thirds and each third assigned an infection rating of 0 to 2. A DMR of zero indicates that no branches were infected, 1 indicates < 50% of the branches in that third were infected, and 2 indicates that > 50% of the branches in that third were infected. For a total per-tree DMR all thirds are summed. 0 = no infections and 6 = crown severely infected. A mean DMR was calculated in each transect segment within the mortality transect by dividing the sum of the per-tree DMR scores by the total number of potential host trees (western hemlocks, Pacific silver fir, noble fir, and grand fir). Using ArcView 3.2, transect segment-level infection levels were visualized on a coded map of the mortality transect (Figure 2). In order to assess the spatial dependence of average infection values on a transect segment-level basis, the transect segment-level data were exported to the R version 1.9.0 statistical analysis environment (R Development Core Team 2003), and analyzed using the permutation test for Moran's I statistic (Cliff and Ord 1981). This approach derives a random empirical distribution (or Monte Carlo) of the Moran's I spatial dependence statistic with a specified number of randomized simulations, and then compares the actual Moran's I statistic for the data to the random distribution.

Panther Creek Division

General Survey

Digital aerial photos (USFS 1:12,000) of the Panther Creek Division (Figure 3) were examined to gain clues as to probable legacy areas that may warrant closer examination. However, the resolution on the digital aerial photos was not sufficient for them to serve as a powerful investigative tool for occurrence of mistletoe in any stand. Walking surveys were made for western hemlock dwarf mistletoe following linear features in the landscape, such as trails, roads, ridgelines, and drainage bottoms (following methodology utilized by Keeton 2000). In areas where dwarf mistletoe was detected we surveyed the area of infection using mapping techniques.

Binoculars were used to aid in the identification of trees and presence of infections. Roads offered a transect that sampled across many environmental gradients and all roads in the division were walked. All observed occurrences of western hemlock dwarf mistletoe at a minimum of 25 m uphill from the road and 40 m downhill from the road were noted (distances verified with handheld laser distance measurement devices), and the locations were geo-referenced using handheld global positioning system (GPS) units. A section of the Pacific Crest Trail was used on the ridgeline transect. This section runs along the southeast and east border of the Panther Creek Division (Figure 1).

The main branch of Mouse Creek was surveyed, as were 3 smaller tributaries in the upper watershed. Walking transects were approximately 60 m wide, and 23.09 km of walking transect were conducted, resulting in a watershed-wide sampling intensity of 138.5 ha/1115 ha total (12.4%). However, since this sampling was weighted towards areas where biological legacies have a greater likelihood of surviving, a higher certainty existed of finding all western hemlock dwarf mistletoe infections present in the watershed.

Survey of Large Legacy Patch

Three legacy old-growth patches were intensively surveyed. The two smaller legacy old-growth patches were of insufficient size to conduct any form of spatial analysis. In the larger legacy old-growth patch, five belt transects were used to assess spatial distribution of western hemlock dwarf mistletoe and their host trees. The five transects, running north-south, were spaced at 100 meters throughout the patch. These transects were laid out in 25 m by 10 m segments. Transect lengths varied to conform to the extent of the stand. Within each segment of the transects, each western hemlock and Pacific silver fir was assigned a number, and dbh and a DMR (Hawksworth 1977) were recorded. No other potential host species were found.

Average DMR values for each transect segment were calculated in the same manner as for the T.T. Munger RNA data. Using the ArcView 3.2 geographic information systems software, the average DMR values for the transect segments were visualized on a digital aerial photo. Similar to the T.T. Munger RNA, a permutation test of the Moran's I statistic was performed on the average DMR values of the plot system in order to examine spatial dependence of the infections.
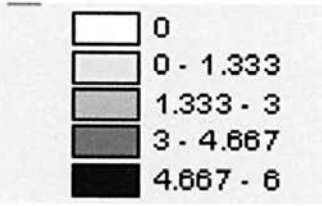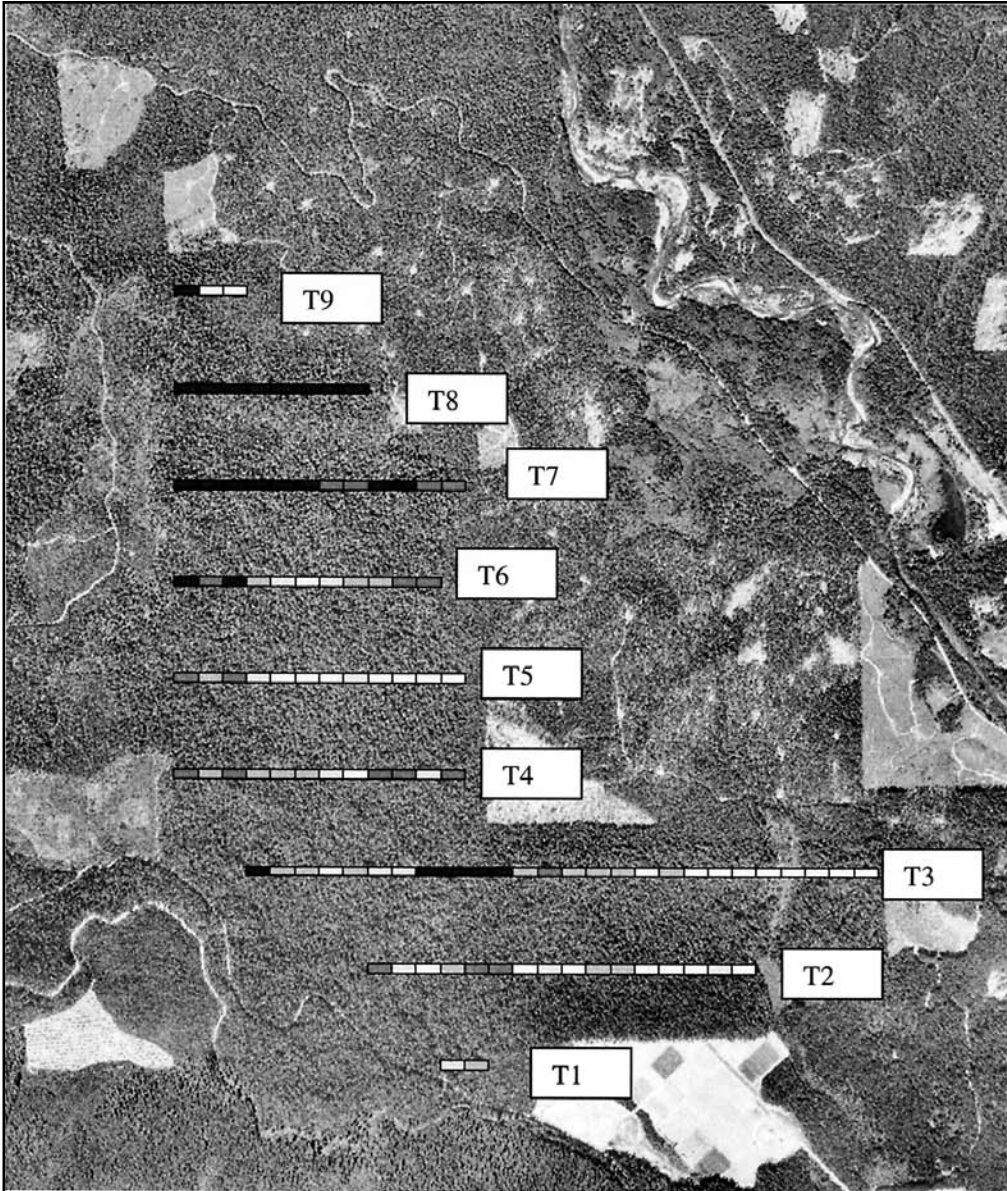
Figure 2. 1:12,000 aerial photo of the T.T. Munger RNA and adjacent forests to the west and north where a large dwarf mistletoe infection center occurs, and may be the source area for infections in the T.T. Munger RNA. Individual transect segment dwarf mistletoe ratings (DMR) averages are indicated by color coding for all host trees >5 cm diameter at breast height (dbh). "T1" represents transect 1, etc.

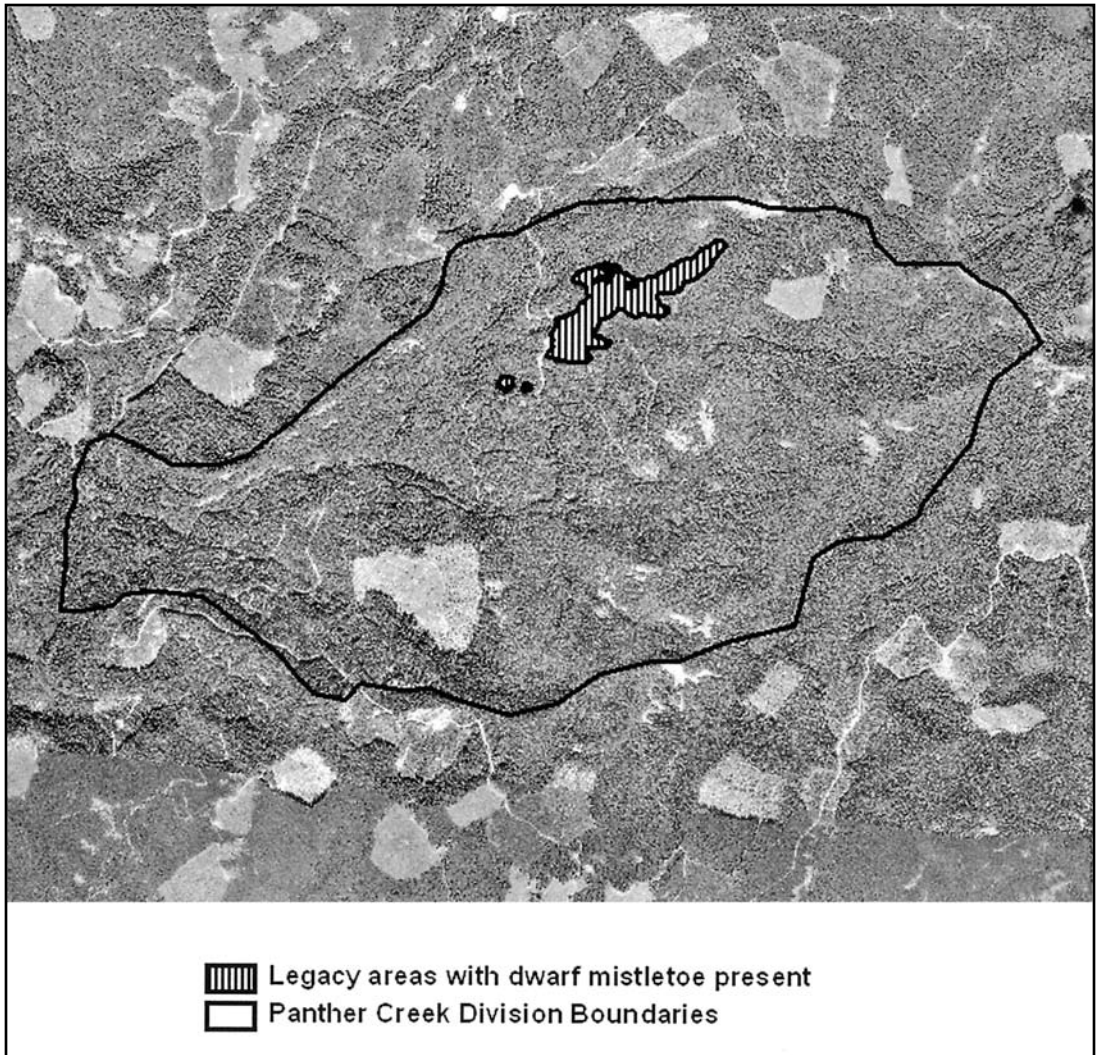Legend:
0
0 - 1.333
1.333 - 3
3 - 4.667
4.667 - 6

Figure 3. 1:12,000 aerial photo of the Panther Creek Division (including the Mouse Creek Drainage) watershed schematic with area of dwarf mistletoe occurrence outlined.

Results

T.T. Munger Research Natural Area

A total of 1,822 western hemlock, 170 Pacific silver fir, 26 grand fir, and 10 noble fir, $\geq$ to 45.7 cm were rated on 103, 0.4 ha transect segments in the mortality transects. Infected were 59% of the western hemlocks (1,075 infected trees), 26% of the Pacific silver firs (45 infected trees), 3% of the grand firs (1 infected tree), and 20% of the noble firs (2 infected trees). This represents the large tree component of susceptible host species in the T.T. Munger RNA. The non-hosts in these

transects include 1,555 Douglas-fir, 169 western redcedar, 17 Pacific yew, and 18 western white pine $\geq$ 45.7 cm. Of the 103 plots, 99 had western hemlock in them. Of these 99 plots, 82 had at least one infected western hemlock tree (82.8% of the plots containing the primary host), and 74 had an average rating $\geq$ to 0.5 (74.7% of the plots containing the primary host). The host trees in twenty-five of the plots averaged DMR 6, indicating a quarter of the plots in the T.T. Munger RNA were severely infected. A large infection center approaching 100 ha was present in the northern region of the RNA, as indicated by the

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pattern presented by the coded mortality transect map (Figure 2). A more complex mix of segment averages was present on transects T2, T3, and T4, indicating a series of infections centers, where a transect segment with an average of 5 or 6 is infrequently adjacent to a transect segment with an average of 0 (Figure 2).

The Monte-Carlo simulation of Moran's I on the T.T. Munger RNA transects demonstrated statistically significant ($P<0.001$) spatial dependence of the transect segments. The Moran's I statistic for the transect segment infection values was $I =$ 0.6421. The number of random permutations to establish the empirical distribution was 10^6, and the observed rank of the actual statistic was still the ultimate value. Through rejection of the null hypothesis that no spatial dependence exists, strong spatial dependence of transect segment infection values is demonstrated, *i.e.,* severely infected transect segments are more likely to be adjacent to each other.

Panther Creek Division

In the general survey, no mistletoe was observed along any of the roadsides or trails. There were very few western hemlock observed and these were free of infections. The area observed along the roadsides was similar in composition to the reference grid plots (Table 1). The stands observed along the ridgeline Pacific Crest Trail were dominated by noble fir. These stands had very few hemlock

TABLE 1. Tree densities (stems/ha > 5 cm diameter at breast height) of the T.T. Munger RNA mortality transects (Franklin and DeBell 1988) and Panther Creek reference grid (Swanson and Franklin, unpublished data). The reference grid does not include any large old-growth legacy patches.
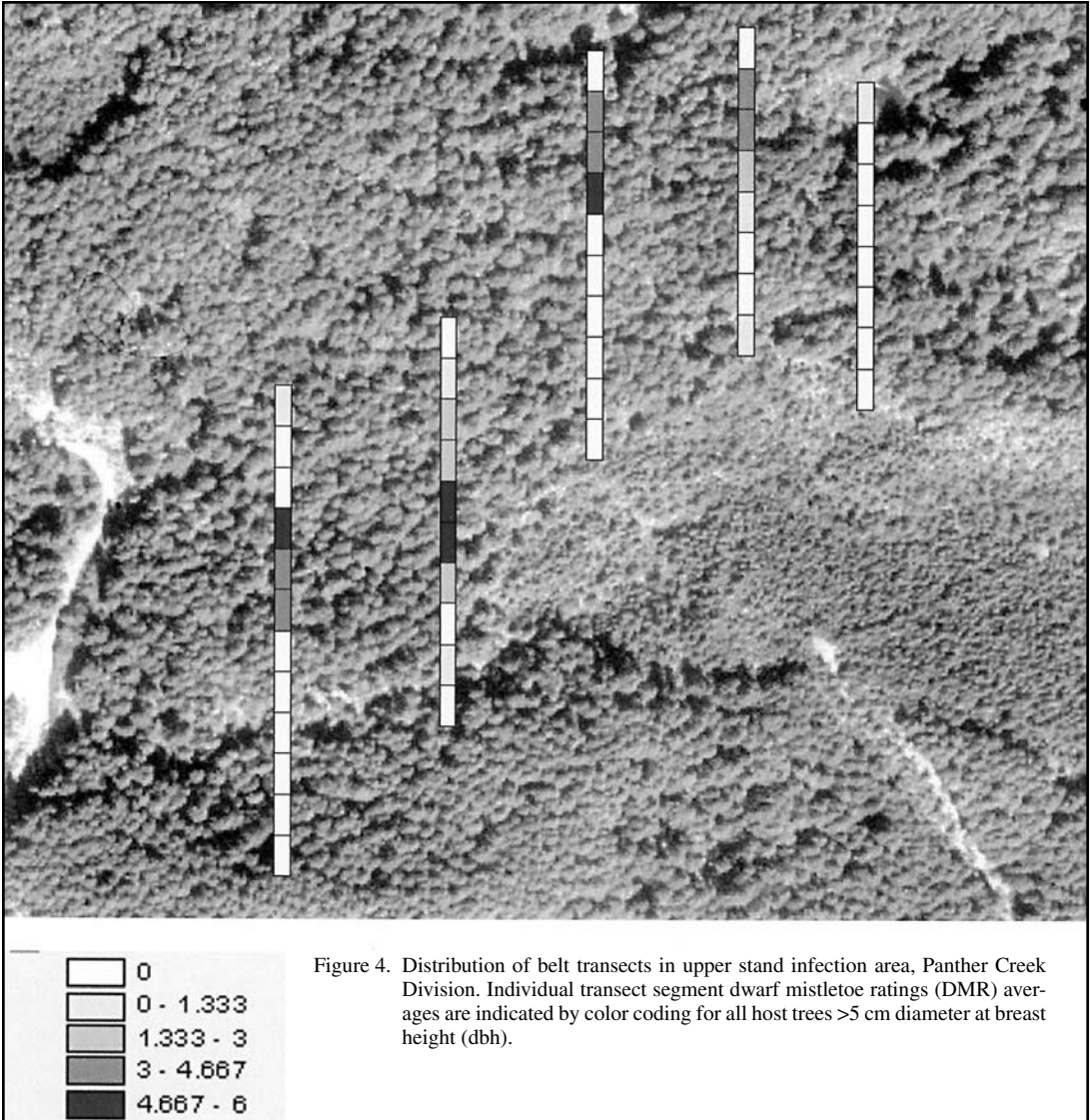
	T.T. Munger RNA	*Panther Creek* Plots
Total Density	444	244.71
Tsuga heterophylla	204	28
Pseudotsuga menziesii	55	211.8
Abies amabilis	96	0
Taxus brevifolia	59	0
Thuja plicata	17	40.0
Abies grandis	11	10
Pinus monticola	1	0
Abies procera	0.3	0
Cornus nuttallii	1	23.3

and no mistletoe was observed along the trail. The main branch of Mouse Creek did not have any infections, and of the three main tributaries that were further examined, three areas had dwarf mistletoe (Figure 3). These areas showed evidence that they were only minimally affected by the 1845 fires in terms of structure and composition (shade-tolerant trees at the margins of the legacy areas may have experienced fire mortality). Large legacy Douglas-fir and western hemlock (> 300 yrs) were present, including severely infected large legacy western hemlock. Topography played a role in the occurrence of legacy patches, since they primarily occurred on gentle topography near perennial watercourses.

We identified three distinct legacy old-growth patches where western hemlock dwarf mistletoe was present. These patches covered 27.9 ha, which is about 2.5% of the 1,115 ha Mouse Creek watershed. Western hemlock dwarf mistletoe was not evenly distributed through the larger of these three legacy old-growth patches (Figure 4). Of the 101 western hemlocks >5 cm dbh that were surveyed, and 46 of these were infected with western hemlock dwarf mistletoe (45.4%). Nine Pacific silver fir were also present in the transects, five of which (55.5%) were infected. Only four transect segments had an average DMR > 4.7 (for all host trees). The more severely infected transect segments, as well as the relatively mistletoe-free transect segments, were shown to be spatially aggregated with the application of the permutation test of the Moran's I statistic. The number of simulations run for the Monte Carlo distribution of the permutation test of the Moran's I statistic was 10^6, sufficient to give a reasonably precise P value. The Moran's I statistic for the actual transect segment infection data was $I = 0.5625$. This value has an observed rank of 99,992 in the Monte Carlo distribution of 10^6, yielding a P value <0.001. Therefore, the null hypothesis of no aggregation of transect segment infection values must be rejected.

Discussion

In the old-growth landscape of the T.T. Munger RNA,, western hemlock dwarf mistletoe was distributed over the vast majority of the area (~83% of the transect segments). In the maturing forest landscape of the Panther Creek Division, western hemlock dwarf mistletoe was restricted to three legacy old-growth patches covering 2.5% of the

Figure 4. Distribution of belt transects in upper stand infection area, Panther Creek Division. Individual transect segment dwarf mistletoe ratings (DMR) averages are indicated by color coding for all host trees >5 cm diameter at breast height (dbh).

Legend:
- 0
- 0 - 1.333
- 1.333 - 3
- 3 - 4.667
- 4.667 - 6

watershed area, and located in flat areas near major water courses and wetlands. These results support our prediction that topography and time since fire controlled the distribution of western hemlock dwarf mistletoe.

The origin of the T.T. Munger old-growth dwarf mistletoe centers appear to be the low productivity, low density forest area on the south and east side of Trout Creek Hill, including the northern portion of the RNA where all western hemlock in the plot transects had DMR ratings of 5 and 6. This region may have burned in a very patchy fashion during the 1500 AD fires due to the wide

spacing of trees and predominance of shrubs such as salal and rhododendron (*Rhododendron macrophyllum* G. Don). Tinnin et al. (1976) and Marshall and Filip (1999) have concluded that refugia for Douglas-fir mistletoe (*Arceuthobium douglasii* Engelmann) may be associated with low basal area, low density, old canopy layer, high elevation Douglas-fir forests where fire probably did not burn uniformly. Spread from these large refugia may be through both long distance (animal) and short distance spread.

The origin of the three Panther Creek Division infection centers is clearly the residual infected

western hemlock trees that survived the fire in the mid 1800's. Spread was very limited around these trees, making the distribution of dwarf mistletoe very patchy within the infection areas (Figure 4). The three distinct areas represent refugia associated with riparian, wetland sites, and low-gradient slopes (e.g., benches) that are generally characterized by patchy fire patterns. Keeton and Franklin (2004) have shown that topographical variation was highly significant in determining the post-disturbance spatial distribution of biological legacies, especially shade-tolerant trees (western hemlock) from the pre-disturbance ecosystem in the Wind River Basin. Drainage bottoms are the most likely refugia for shade-tolerant and other trees, while ridges and south- and west-facing slopes have few biological legacies due to more intense fire behavior and less available moisture. This is the pattern we found for western hemlock dwarf mistletoe and its host trees in the Panther Creek Division.

Two distinct types of refugia for western hemlock dwarf mistletoe were found in this survey, a pattern of drainage bottoms and riparian sites within the Panther Creek Division, and a low productivity and low density site within the T.T. Munger RNA. In both types of refugia, fire spread seems to have been patchy or absent, enabling the survival of legacy shade-tolerant trees. Upslope spread of western hemlock dwarf mistletoe from drainage bottoms may be slower than downhill spread (Bloomberg et al. 1980). Thus, the future distribution within the Panther Creek Division might be more limited than in the T.T. Munger RNA, where a large source area was available to facilitate downhill dispersal on the gentle slopes of the Trout Creek Hill shield volcano. Additionally, western hemlock and other host trees must first establish widely in the burned portion of the Panther Creek Division before spread of the western hemlock dwarf mistletoe from disturbance refugia. This case study demonstrates that expansion from isolated refugia in drainage bottoms may be slow in some situations due to limited post-disturbance distribution of primary and secondary hosts, which in this case are shade-tolerant, fire-sensitive species such as western hemlock and Pacific silver fir. Though not addressed by this analysis, the gravity-related limitation of uphill explosive dispersal may pose additional challenges in watersheds with steep slopes. The survey of the Panther Creek division

found uninfected western hemlock trees outside of the legacy patches, especially along the main branch of Mouse Creek. However, it will take some time for dwarf mistletoe to disperse into those areas, especially given the current lack of hosts in the intervening space.

In Wyoming, Kipfmueller and Baker (1998) surveyed American dwarf mistletoe (*A. americanum* Nutt. ex Engelm.) in 43 mature to old-growth lodgepole pine stands. At the landscape scale, dwarf mistletoe infection patterns were determined by the spatial distribution of surviving infected lodgepole pine after the fire, and subsequent stand development and impacts of fire suppression, although wildlife may vector seeds and establish new centers also. Trummer et al. (1998). found the distribution of western hemlock dwarf mistletoe in mature (110 yr old) western hemlock–Sitka spruce forests in southeast Alaska was strongly related to the distribution and size of infected western hemlock trees that survived major wind disturbance. The dwarf mistletoe infected trees that survived the disturbance rained dwarf mistletoe seed down on susceptible host individuals (Alfaro et al. 1985, Geils et al. 2002). However, these two examples are characterized by host species that are early-successional trees. In the Douglas-fir forests of the Cascade Mountains, western hemlock dwarf mistletoe must occasionally persist for long periods in fire refugia until host density increases in the surrounding burned landscape. In this case, the landscape distribution of the dwarf mistletoe refugia will strongly determine the future ability of dwarf mistletoe to spread. This case study demonstrates some of the variability in the spatial patterns of persistence of western hemlock dwarf mistletoe in landscapes of the southern Cascades.

Spatial aggregation of western hemlock dwarf mistletoe was similar in both the T.T. Munger RNA and the large legacy old-growth patch in the Panther Creek Division. The aggregated spatial patterns of western hemlock dwarf mistletoe that are typical of old-growth forest stands (Shaw et al. 2005) are apparently maintained in large legacy old-growth patches following stand-replacing disturbance. Spatial patterns of organisms are an important type of biological legacy (Franklin et al. 2000). In this case, the persistence of the spatial pattern associated with dwarf mistletoe in old growth is as notable a result as the persistence of the hemi-parasite itself, since any habitat values

or other functions associated with the spatial pattern of dwarf mistletoe infections in old growth are conserved.

The results of this research have potential application to forest management, especially since forest managers are increasingly cognizant of the importance of structural complexity in both managed forests and early-successional natural forests (Franklin et al. 2002, Lindenmayer and Franklin 2002). This research has shown that western hemlock dwarf mistletoe may not be able to expand out from fire refugia for long periods of time in some watersheds dominated by seral non-host species. This suggests that reintroduction of hemlock dwarf mistletoe in conjunction with underplanting of the shade-tolerant host tree (western hemlock) should be considered as an element of restoration plans for disturbed forest ecosystems in the Pacific Northwest, if the accelerated development of late-successional structural complexity is a management goal. The artificial seeding of dispersal-limited lichens into recovering forests has been proposed by Sillett et al. (2000). This type of restoration effort may well be applicable to the slow-dispersing dwarf mistletoes, which create canopy structures that are important to wildlife (Hawksworth and Wiens 1996). Since the spatial patterns in western hemlock dwarf mistletoe infection centers in both old growth (T.T. Munger RNA) and legacy patches in more recently burned areas (Panther Creek) were similar, (i.e., spatial aggregation of infected areas was a dominant feature in both of them), it is also possible that maintenance of these patterns of spatial aggregation should be an additional consideration in a late-successional restoration effort.

Future research should include extension of legacy mistletoe surveys to watersheds with varying levels of post-fire biological legacies in the western Cascades to better understand the spatial ecology of western hemlock dwarf mistletoe. Long-term monitoring in locations such as the Wind River Experimental Forest will eventually result in enhanced knowledge of the spatial and population dynamics of western hemlock dwarf mistletoe in landscapes with infrequent, high-severity fire regimes.

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