

Basal area growth impacts of dwarf mistletoe on western hemlock in an old-growth forest

David C. Shaw, Manuela Huso, and Howard Bruner

Abstract: We investigated the effect of western hemlock dwarf mistletoe (*Arceuthobium tsugense* (Rosend.) G.N. Jones ssp. *tsugense*) on the 13 year basal area growth of large (>45.7 cm diameter at breast height) western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) trees in an old-growth forest in southwestern Washington state. We controlled for spatial effects on tree growth by utilizing twenty-seven 0.4 ha plots that had uninfected, lightly, moderately, and severely infected classes of trees present on each plot. Basal area growth was analyzed using analysis of covariance of a randomized block design that was a balanced design with four treatments (infection classes) and 27 replicates (blocks or 0.4 ha plots), with initial diameter as the covariate. Basal area growth was found to be significantly different among the infection classes ($F_{[3,77]} = 10.09$ and $p < 0.0001$). Growth of the light and moderate infection classes was not detectably different from growth of uninfected trees. However, severely infected trees grew from 16% to 46% (mean = 36%) less than uninfected trees of the same initial diameter over the period of study (1991–2004). The large trees in this stand did not show growth impacts until they were severely infected.

Résumé : Nous avons étudié l'effet du faux-gui de la pruche (*Arceuthobium tsugense* (Rosend.) G.N. Jones ssp. *tsugense*) sur 13 années de croissance en surface terrière de grosses tiges (>45,7cm de diamètre au DHP) de pruches de l'Ouest (*Tsuga heterophylla* (Raf.) Sarg.) dans une forêt ancienne du sud-ouest de l'État de Washington, aux États-Unis d'Amérique. Nous avons contrôlé les effets spatiaux en utilisant 27 placettes-échantillons de 0,4 ha qui contenaient toutes des arbres non infectés ainsi que des arbres légèrement, modérément et sévèrement infectés. La croissance en surface terrière a été analysée au moyen d'une analyse de covariance avec un plan expérimental en blocs complètement aléatoires : un plan équilibré avec quatre traitements (classes d'infection) et 27 répétitions (blocs ou placettes-échantillons de 0,4 ha) et le diamètre initial comme covariable. La croissance en surface terrière était significativement différente entre les classes d'infection ($F_{[3,77]} = 10,09$ et $p < 0,0001$). Une différence de croissance n'a pas été détectée entre les classes d'infection légère ou modérée et les arbres non infectés. Cependant, les arbres sévèrement infectés ont eu une croissance 16 % à 46 % (moyenne de 36 %) inférieure à celle des arbres non infectés de même diamètre initial au cours de la période d'étude (1991–2004). La croissance des gros arbres dans ce peuplement n'a pas été affectée tant qu'ils n'étaient pas sévèrement infectés.

[Traduit par la Rédaction]

Introduction

Dwarf mistletoes (*Arceuthobium* spp., Viscaceae) are important agents of disease in the Pinaceae of western North America. Western hemlock dwarf mistletoe (*Arceuthobium tsugense* (Rosendahl) G.N. Jones ssp. *tsugense*) has been shown to cause growth loss, branch and stem deformation (brooming), reduced water use efficiency, and decreased photosynthetic capacity in its primary host, western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) (Hawskworth and Wiens 1996; Hennon et al. 2001; Meinzer et al. 2004). In severely infected trees every branch can have multiple dwarf mistletoe plants and complex brooms (Figs. 1a and 1b). The top branches of the tree may die first as the tree eventually declines and dies over the course of many years.

Historically, dwarf mistletoe in western hemlock and other species were considered destructive pests, however,

new research has determined that these native hemiparasites play a role in forest biodiversity and wildlife habitat through canopy brooming, vertical reorganization of foliage distribution, and canopy dieback (Watson 2001; Shaw et al. 2004a). Research on growth impacts of western hemlock dwarf mistletoe has focused on young and mature forests in managed stands, but there is interest in developing more data concerning old trees and old-growth forests because of a management emphasis on preservation of late-successional forests and forest conditions, and the retention of older trees in cut-over stands (Hawskworth and Wiens 1996; Kohm and Franklin 1997; Muir and Hennon 2007; Muir et al. 2007). Green tree retention in old-growth western hemlock forests of British Columbia has the potential to exacerbate dwarf-mistletoe-caused growth declines in managed forests (Muir et al. 2007), whereas preservation of some dwarf mistletoe in the canopy can be beneficial for wildlife (Shaw et al. 2004a).

In western North America, the six-class dwarf mistletoe rating system (DMR) is typically used to assess the intensity of infection in an individual tree (Hawskworth and Wiens 1996; Hawskworth 1977; Shaw et al. 2000). The system divides the live tree crown into thirds and rates each third 0 for no branches with dwarf mistletoe infections, 1 if <50% of the branches have at least one dwarf mistletoe infection, and 2 if >50% of the branches in that third have at least one dwarf mistletoe infection. The numbers assigned each third

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Fig. 1. (a) Severely infected western hemlock tree (dwarf mistletoe rating system (DMR) 6) in the T.T. Munger Research Natural Area (RNA). Note the broomy, compact branch patterns, the large number of dead branches, and the dead, flattened leader. Every branch of this tree is severely infected. The tree is approximately 50 m tall and 100 cm in diameter. (Shaw et al. 2004a). (b) Uninfected western hemlock tree (DMR 0). Note the unbroomed nature of the branches, the fewer number of dead branches, and the live leader. The tree is approximately 50 m tall and 100 cm in diameter. (From D.C. Shaw, D.M. Watson, and R.L. Mathiasen. 2004. Reproduced with permission of Aust. J. Bot., Vol. 52, p. 483, © 2004 CSIRO Publishing.)



are summed resulting in a total that ranges from 0, if there are no infections, to a maximum of 6, if each crown third has >50% of the branches infected.

Growth impacts are not detectable on host trees until the individual tree is moderately to severely infected (DMR 4, 5, or 6) (Hawksworth and Wiens 1996; Geils et al. 2002). Hawksworth and Wiens (1996) estimated that the general reduction in 10 year periodic diameter increment, compared with uninfected trees, is 10% for DMR 4, 30% for DMR 5, and $\geq 50\%$ for DMR 6. The impacts of western hemlock dwarf mistletoe on western hemlock tree growth have been recently summarized in Muir and Hennon (2007) and Muir et al. (2007). Studies using retrospective stem analysis have investigated the impact of western hemlock dwarf mistletoe on volume growth of western hemlock in second-growth western hemlock forests in British Columbia (Smith 1969; Thomson et al. 1984; Thomson et al. 1985). Estimated volume growth in moderately infected trees was 15%–25% less, and in severely infected trees 25%–41% less than uninfected trees.

Wellwood (1956) investigated some effects of hemlock

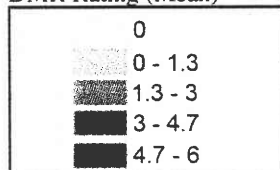
dwarf mistletoe on 10 western hemlock trees in an older forest of British Columbia and concluded that severely infected trees had lower tree vigor, lower wood specific gravity, and reduced wood moisture content. A study of the effect of dwarf mistletoe on hydraulic architecture, water, and carbon relations of old (>200 years) western hemlock showed reduced leaf nitrogen, water use efficiency, and photosynthetic capacity, resulting in an estimated reduction of carbon accumulation in a severely infected tree (DMR 6) of 60% (Meinzer et al. 2004). Meinzer et al. (2004) used five DMR 6 trees and three DMR 0 trees in their study, and also found that whole tree water use by severely infected trees averaged 55 kg-day⁻¹ versus uninfected trees, which averaged 90 kg-day⁻¹ during the peak of the summer drought.

In this study, we investigated an old-growth Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii*—western hemlock forest in the Cascades Range of southern Washington where hemlock dwarf mistletoe occurs in spatially discrete infection centers (Shaw et al. 2005; Swanson et al. 2006). The objective of our study was to investigate

Fig. 2. Map of the T.T. Munger Research Natural Area and plot system layout. Coded as mean DMR (dwarf mistletoe rating) for all hemlocks >47.5 cm within that 0.4 ha plot. The numbers below the plots indicate the 27 plots that were used for analysis in this paper and correspond to plots illustrated in Fig. 3. Figure adapted from (Swanson et al. 2006), courtesy of the Northwest Scientific Association.



DMR Rating (Mean)



whether western hemlock dwarf mistletoe infection was associated with reduced basal area growth of large western hemlock trees in an old-growth forest and to compare these results with those measured in young western hemlock stands by other authors.

Study site

The study site is located in the T.T. Munger Research Natural Area (TTM RNA) established in 1934 to exemplify old-growth forests in a natural condition (Franklin 1972). It

comprises a 478 ha, Douglas-fir–western hemlock forest approximately 500 years old. In 1947, nine transects comprising one hundred and five 0.4 ha (1 acre) adjacent plots were established at the TTM RNA (Fig. 2). The parallel transects are 401 m apart, centerline to centerline. Within each 0.4 ha plot, all trees ≥ 45.7 cm (18 in.) diameter at breast height (DBH) were surveyed for mortality every 5–7 years (Franklin and DeBell 1988) without permanently tagging the trees. In 1991, all trees ≥ 45.7 cm in diameter were tagged and measured for diameter. The trees were re-surveyed in 1997 and 2004 and basal area growth over this

interval was derived. In 1997, we also rated all 1661 western hemlock trees ≥ 45.7 cm in diameter using the six-class DMR system, and we calculated the mean DMR for each 0.4 ha plot (Fig. 2). We did not age our sample trees. Lyons et al. (2000) worked in the Wind River Canopy Crane Research Facility 12 ha plot, which is located between plots 1 and 9 in Fig. 2, and trees in their large tree class averaged 76.6 cm in diameter (range 50.6–93.5 cm) and 180 years of age (range 107–229 years).

The TTM RNA is located on the east and south slopes of Trout Creek Hill (elevation of summit 792 m), an approximately 340 000-year-old basaltic shield volcano. Soils are deep, well drained, generally stone free medial, mesic Entic Vitrandes derived from volcanic ejecta. Elevation of the TTM RNA varies from 335 to 610 m. The mean annual precipitation is 2223 mm·year⁻¹, with only about 5% of this falling during June–August (Shaw et al. 2004b). Much winter precipitation falls as snow, with the snowpack averaging over 100 mm during December and March, and approximately 300 mm during January and February near the lower elevation of the TTM RNA. The mean annual air temperature is 8.7 °C, with a January mean temperature of 0.1 °C and a July mean temperature of 17.7 °C (Shaw et al. 2004b).

Vegetation is transitional across the western hemlock and Pacific silver fir (*Abies amabilis* (Dougl. ex Loud.) Dougl. ex J. Forbes) Plant Associations, with the western hemlock Associations dominating lower elevations and the Pacific silver fir dominating the higher elevations (Franklin 1972). Understory vegetation in the TTM RNA is dominated by the woody shrubs salal (*Gaultheria shallon* Pursh), Oregon-grape (*Mahonia nervosa* (Pursh) Nutt.), vine maple (*Acer circinatum* Pursh), and herbaceous plants, such as vanillaleaf (*Achlys triphylla* (Sm.) DC.), common beargrass (*Xerophyllum tenax* (Pursh) Nutt.), and threeleaf foamflower (*Tiarella trifoliata* L.). Forest trees that dominate the site include western hemlock, Douglas-fir, Pacific silver fir, and western redcedar (*Thuja plicata* Donn ex D. Don). The forest originated after a fire or series of fires approximately 500 years ago. The initial forest was dominated by Douglas-fir, with some western white pine (*Pinus monticola* Dougl. ex D. Don) and western hemlock. Studies of the patterns of mortality by DeBell and Franklin (1987) and Franklin and DeBell (1988) indicate that western hemlock is slowly replacing Douglas-fir.

Two of the conifers associated with western hemlock at this site, Pacific silver fir and noble fir (*Abies procera* Rehd.), are considered occasional hosts. Only 5%–50% of trees of these species neighboring a severely infected western hemlock tree are typically infected, compared with >90% of the primary host (Mathiasen and Daugherty 2005). Grand fir (*Abies grandis* (Dougl. ex D. Don) Lindl.) is a rare host (<5% of neighboring trees are infected). Douglas-fir and western redcedar are not hosts (Hawsworth and Wiens 1996).

Methods

Study design

The original sampling design, which includes adjacent 0.4 ha plots in a series of transects, can lead to high spatial correlation. The qualities of the soil, available light, aspect,

and stand structure all have potential influence on how much a tree will grow. These qualities tend to be similar (have little variation) between places that are physically close to one another and have more variation as the places become physically more separated (Thomson et al. 1984). Since these qualities affect tree growth, the result is spatially autocorrelated growth responses. We took advantage of this spatial autocorrelation by blocking on the 0.4 ha plot. We assumed that the qualities of the soil, available light, aspect, and stand structure were fairly similar within a 0.4 ha sampling unit, but fairly dissimilar among 0.4 ha units. This blocking acknowledges correlation of growth among the trees within a block but assumes independence of growth of trees from two different blocks, whether contiguous or not. Within each block were trees with DMRs ranging from 0 to 6, with 0 indicating no western hemlock dwarf mistletoe observed in a tree and 6 indicating that a western hemlock was severely infected.

For this analysis DMRs were further grouped into four classes, uninfected (DMR 0), light infection (DMR 1 and 2), moderate infection (DMR 3 and 4), and severe infection (DMR 5 and 6). Only those plots for which there was at least one tree in each of the four DMR classes was used as a block. There were 27 plots that met this criterion (Fig. 2). There were sometimes as many as 20 trees in each DMR class, but most often two to four (Fig. 3). A total of 478 western hemlock trees ≥ 45.7 cm in diameter were included in the analysis; 192 uninfected, 67 lightly infected, 57 moderately infected, and 162 severely infected (Table 1). Each tree within a block was regarded as a sampling unit of the DMR treatment within each block. Although DMRs were determined in 1997, the diameter growth record from 1991 to 2004 (13 years) was used to determine basal area growth.

Statistical analysis

We analyzed basal area growth calculated over the period between 1991 and 2004. The response variable and the covariate were averaged across trees within each DMR class in each block, resulting in a balanced design with four treatments (DMR classes) and 27 replicates (blocks or 0.4 ha plots). Basal area growth has been found to be related to the diameter of trees at the beginning of their growth period (Hawsworth et al. 1992). In our study, initial diameter of the trees in 1991 was found not to be related to DMR class, and consequently, could potentially be included as a covariate. It was found to significantly reduce variance in this analysis. These data were analyzed using PROC MIXED in the SAS/STAT software, Version 9.1 of the SAS System for Windows (SAS Institute Inc. 2002). The data were modeled as randomized block design using analysis of covariance. Residual analysis indicated that assumptions of normality and homogeneous variance among treatments were better met for the response after log_e transformations of the response and covariate were made. Dunnett's adjustment for multiple comparisons was applied to account for multiple comparisons of DMR classes to a control (no infection).

Results

Basal area growth was found to be significantly different among the DMR classes ($F_{[3,77]} = 10.09$ and $p < 0.0001$)

Fig. 3. Distribution of trees by dwarf mistletoe rating (DMR) class in each 0.4 ha block. The block number corresponds to the map in Fig. 2. None, DMR 0; light, DMR 1 or 2; moderate, DMR 3 or 4; and severe, DMR 5 or 6.

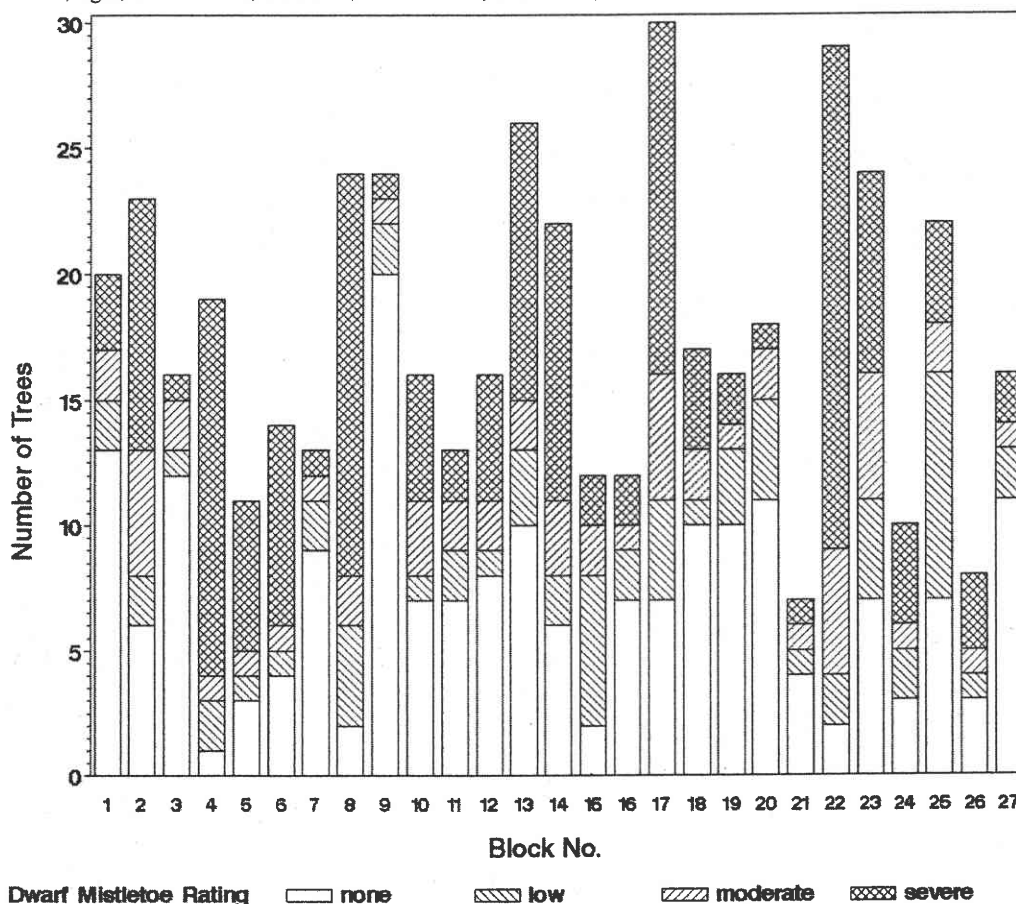


Table 1. Number of trees in each diameter class for each dwarf mistletoe rating class.

Diameter class (cm)	Uninfected (DMR 0)	Light (DMR 1 or 2)	Moderate (DMR 3 or 4)	Severe (DMR 5 or 6)
50–60	22	5	6	15
60–70	34	21	10	36
70–80	53	14	8	35
80–90	37	7	12	34
90–100	32	11	9	26
>100	14	9	12	16

Note: DMR, dwarf mistletoe rating system.

(Fig. 4 and Table 2). While basal area growth of trees with either light or moderate infection rates (DMR = 1 or 2 and DMR = 3 or 4) was not detectably different from growth of uninfected trees: basal area growth of severely infected trees (DMR = 5 or 6) was found to be quite different.

Although initial diameter was a significant covariate ($F_{1,77} = 4.64$ and $p = 0.034$), there was still a considerable amount of variation in basal area growth not attributable to initial diameter. In these data, basal area growth was estimated to increase between 2.5% and 86.6% when initial diameter was doubled (Fig. 5). Including initial basal area as a covariate reduced residual variation by only 3%. Severely infected trees were estimated to grow an average of 36% (95% confidence interval: 16%–46%) less than uninfected

trees of the same initial diameter over the period of study (Table 3).

Discussion

Our estimated basal area growth declines in severely infected western hemlock trees in this old-growth forest are consistent with our current understanding of the growth impacts of dwarf mistletoes on conifers (Hawksworth and Wiens 1996) except that we did not detect any basal area growth declines associated with moderate infection. We controlled for initial size of the tree and spatial correlation among trees, and estimated growth decline in severely infected trees to be 36% (95% confidence interval: 16%–48%), similar to that reported by Smith (1969) (41%) and Thomson et al. (1985) (39%), and Thomson et al. (1984) (25%). However, the growth declines reported by these authors refer to total tree volume, whereas we estimated basal area growth effects. Since dwarf mistletoes also influence height growth, volume growth impacts should be greater than basal area growth impacts (Hawksworth and Wiens 1996). Thomson and Smith (1983) found that height growth was reduced in young (22-year-old) western hemlocks by dwarf mistletoe, although radial growth was not.

The growth declines caused by severe dwarf mistletoe infection are likely a result of the multiple interacting factors

Fig. 4. Median annual basal area growth (m^2) and 95% confidence limits of trees with diameter = 69.2 cm (median of the diameter of all trees) from 1991–2004 in the four DMR classes. None, DMR 0 or 1; light, DMR 1 or 2; moderate, DMR 3 or 4; and severe, DMR 5 or 6.

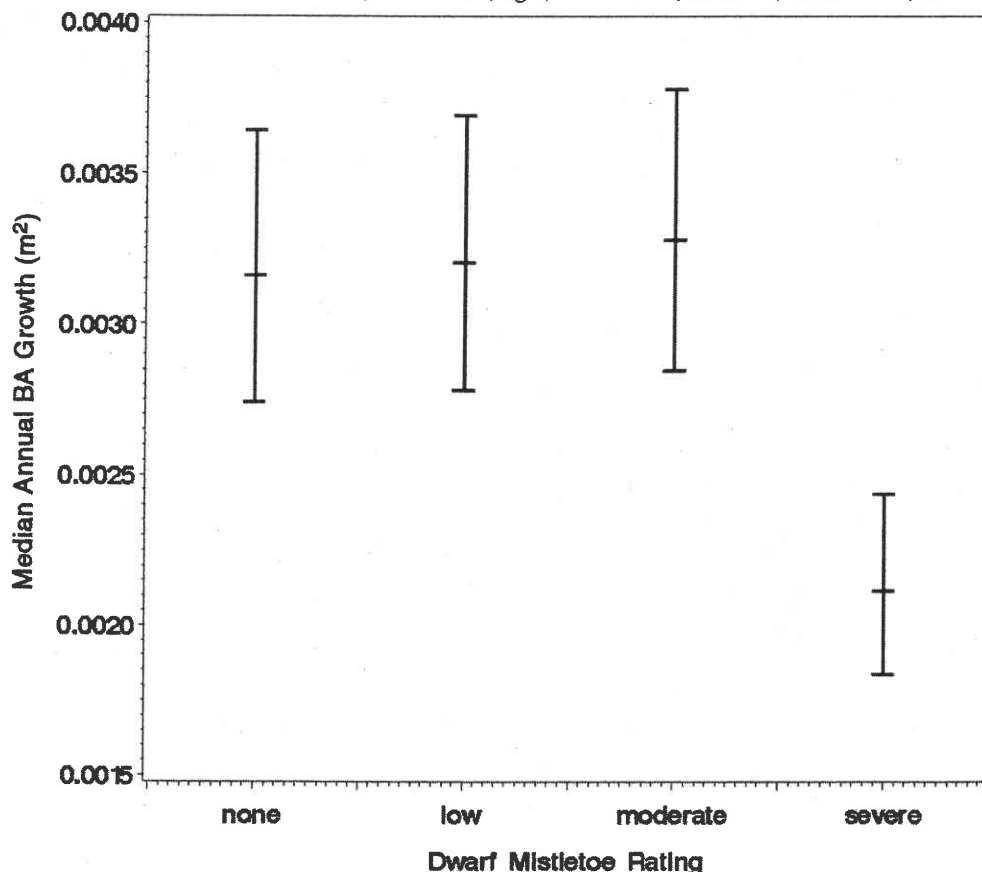


Table 2. Estimated basal area growth ($\text{cm}^2\cdot\text{year}^{-1}$ and 95% confidence intervals) for uninfected trees and infected trees in each dwarf mistletoe rating system (DMR) class.

DMR class	Basal area growth ($\text{cm}^2\cdot\text{year}^{-1}$)	95% Confidence interval
Uninfected (DMR 0)	31.6	28.1–36.4
Light (DMR 1 or 2)	32.1	27.8–36.9
Moderate (DMR 3 or 4)	32.8	28.5–37.8
Severe (DMR 5 or 6)	21.2	18.4–24.4

that influence hydraulic architecture, water, and carbon relations of trees infected with western hemlock dwarf mistletoe (Meinzer et al. 2004). One major effect reported by Meinzer et al. (2004), who did their study in the TTM RNA, was that maximum photosynthetic rates of severely infected trees (DMR 6) were approximately half of that of uninfected trees largely because of reduced leaf nitrogen, which was 35% lower in infected trees. In addition, they estimated the whole tree reduction in carbon accumulation was about 60% because of the combination of reduced photosynthesis and loss of leaf area from branch mortality. Infected trees also had fewer live branches than uninfected trees of equivalent size (Figs. 1a and 1b).

Our results show a 13 year mean basal area growth decline of only 36%, much less than 60%. However, results from Meinzer et al. (2004) may represent the potential for

future decline in growth associated with crown decline. As dwarf mistletoe infection intensifies in western hemlock trees, it is likely that the tree goes through a transformation in leaf area from an initial increase followed by a decline as branches die and the top dies back. Stanton (2006) recently reported a minor radial growth increase in low DMR trees in managed Ponderosa pine (*Pinus ponderosa* Dougl. ex P. & C. Laws.) that she hypothesized might be related to increased leaf area associated with broom formation.

A major problem in estimating the impacts of western hemlock dwarf mistletoe on growth is finding suitable controls that are healthy (Thomson et al. 1984). Thomson et al. (1984) determined that the uninfected trees they used for controls were not suitable because of differences in location and aspects of tree age and growth. Growth losses could only be estimated by making assumptions regarding the ratio of healthy to moderately infected tree growth and moderately infected to severely infected tree growth in their four study sites. Using growth curve projections, they estimated that moderate levels of infection (DMR 3 or 4) result in 15% volume losses and severe infection (DMR 5 or 6) result in 25% growth losses at a rotation age of 80 years or more.

Thomson et al. (1985) attempted to deal with the problem of control trees by using a sampling design that minimized the effects of site variability in five locations in British Columbia. However, they still considered the effects of suppression and release to be a major factor in comparing

Fig. 5. Relationship of median annual basal area growth (m^2) of trees from 1991–2004 to the median initial diameter in 1991, in each of the four DMR classes. None, DMR 0; light, DMR 1 or 2; moderate, DMR 3 or 4; severe, DMR 5 or 6.

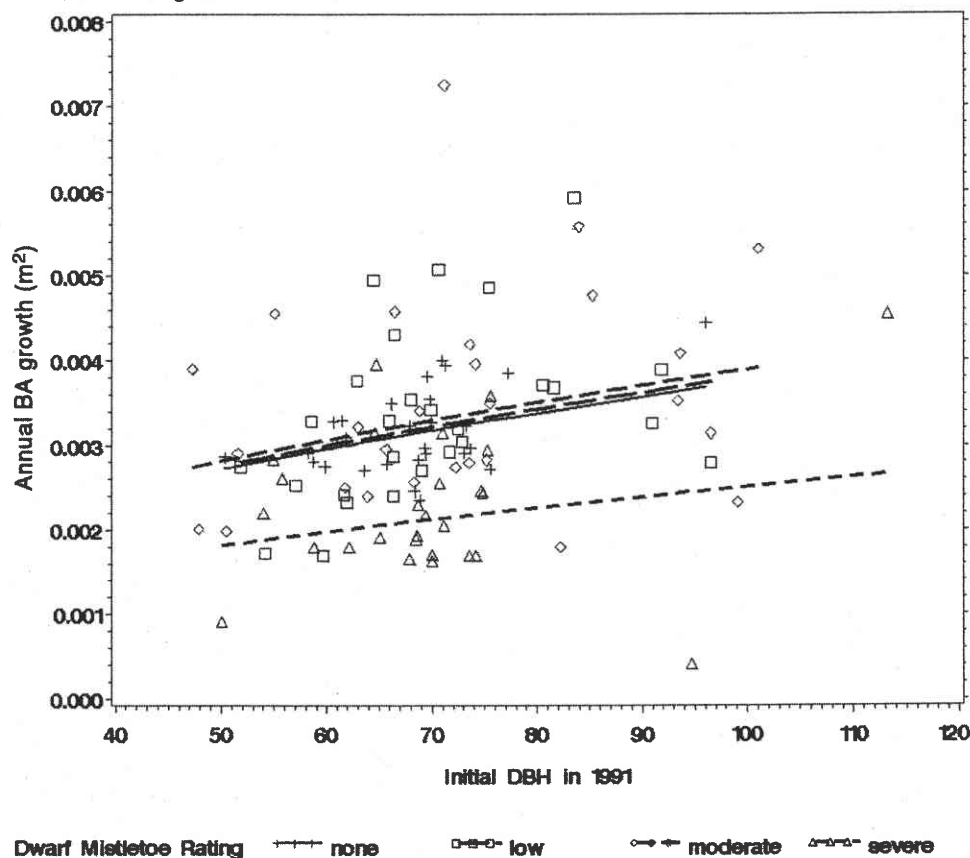


Table 3. Estimated percentage difference in basal area growth (with 95% confidence intervals) of infected trees in each DMR class relative to uninfected trees.

DMR class	Percentage difference in basal area growth (%)	95% Confidence interval (%)
Light (DMR 1 or 2)	+1.4	-19 to +27
Moderate (DMR 3 or 4)	+3.8	-17 to +30
Severe (DMR 5 or 6)	-36	-16 to -46

infection classes in some stands. They estimated that moderately infected trees averaged 23% less volume (range 17%–34%) and severely infected trees averaged 39% (range 30%–45%) less volume than healthy trees in pure western hemlock stands that ranged from 45 to 126 years old.

Our study dealt with the issue of suitable control trees by using only 0.4 ha plots that had all four infection classes, and included trees only >45.7 cm in diameter. The estimated age range of our sample trees was 107–229 years (Lyons et al. 2000). Basal area growth and initial diameter were averaged across trees within each DMR class in each block, resulting in a balanced design with four treatments (DMR classes) and 27 replicates (blocks or 0.4 ha plots) where residual analysis indicated that assumptions of normality and homogeneous variance were met.

This study helps fill the gap in our knowledge concerning the impacts of dwarf mistletoe in western hemlock forests by investigating growth impacts in large old trees. Old-

growth Douglas-fir–western hemlock forests have complex vertical structure, large old trees, large dead trees, and unique aspects of biodiversity (Franklin et al. 1981). Tree productivity, forest-stand productivity, and live-tree biomass accumulation all decline with age (Bond and Franklin 2002). Western hemlock dwarf mistletoe is an important tree pathogen in old-growth Douglas-fir–western hemlock forests that contributes to the reduction in tree and forest-stand productivity, increases the structural complexity of the stand, and increases biodiversity (Shaw et al. 2004a), which may make *Arceuthobium tsugense* a keystone species in western hemlock-dominated forests (Watson 2001). However, new forestry techniques that avoid clear-cutting old forests and that include such techniques as small patch clearcuts, selective harvest in old-growth, reserving large blocks of old-growth, and retaining individual older trees (green tree retention) will likely leave infected western hemlock trees in the overstory above regenerating host trees, and this may exacerbate the effects of dwarf mistletoe on tree growth and wood production (Muir et al. 2007). Silvicultural techniques for managing western hemlock dwarf mistletoe and maintaining it on site are well understood (Geils et al. 2002; Muir and Hennon 2007; Muir et al. 2007), so that the most important issue is not ignoring the problem.

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References

- Bond, B.J., and Franklin, J.F. 2002. Aging in Pacific Northwest forests: a selection of recent research. *Tree Physiol.* **22**: 73–76. PMID:11830404.
- DeBell, D.S., and Franklin, J.F. 1987. Old-growth Douglas-fir and western hemlock: a 36 year record of growth and mortality. *West. J. Appl. For.* **2**: 111–114.
- Franklin, J.F. 1972. Wind River Research Natural Area. In *Federal Research Natural Areas in Oregon and Washington: a guidebook for scientists and educators*. USDA Forest Service, Pacific Northwest Range and Experiment Station, Portland, Oregon. pp. WR1–WR8.
- Franklin, J.F., and DeBell, D.S. 1988. Thirty-six years of tree population change in an old-growth *Pseudotsuga-Tsuga* forest. *Can. J. For. Res.* **18**: 633–639. doi:10.1139/x88-093.
- Franklin, J.F., Cromack, K., Jr., Denison, W., McKee, A., Maser, C., Sedell, J., Swanson, F., and Juday, G. 1981. Ecological characteristics of old-growth Douglas-fir forests. USDA For. Serv. Gen. Tech. Rep. PNW-118.
- Geils, B.W., Tovar, J.C., and Moody, B. (Technical coordinators). 2002. Mistletoes of North American conifers. USDA For. Serv. Gen. Tech. Rep. RMRS-GTR-98.
- Hawsworth, F.G. 1977. The 6-class dwarf mistletoe rating system. USDA For. Serv. Gen. Tech. Rep. RM-48.
- Hawsworth, F.G., and Wiens, D. 1996. Dwarf mistletoes: biology, pathology, and systematics. USDA Agric. Handb. 709.
- Hawsworth, F.G., Moir, W.H., and Janssen, J.E. 1992. Effects of dwarf mistletoe in old-growth lodgepole pine stands at Fraser Experimental Forest, Colorado. In *Old-Growth Forests in the Southwest and Rocky Mountain Regions. Proceedings of a Workshop, 9–13 March 1992, Portal, Arizona*. M.R. Kaufmann, W.H. Moir, and R.L. Bassett (Technical coordinators). USDA For. Serv. Gen. Tech. Rep. RM-213. pp. 60–65.
- Hennon, P.E., Beatty, J.S., and Hildebrand, D.M. 2001. Hemlock dwarf mistletoe. US Department of Agriculture, Forest Service, Pacific Northwest Region, Portland, Oregon. Forest Insect and Disease Leaflet 135 (revised).
- Kohm, K.A., and Franklin, J.F. 1997. Creating a forestry for the 21st century. Island Press, Washington, D.C.
- Lyons, B., Nadkarni, N.M., and North, M.P. 2000. Spatial distribution and succession of epiphytes on *Tsuga heterophylla* (western hemlock) in an old-growth Douglas-fir forest. *Can. J. Bot.* **78**: 957–968. doi:10.1139/b00-064.
- Mathiasen, R.L., and Daugherty, C.M. 2005. Comparative susceptibility of conifers to western hemlock dwarf mistletoe in the Cascade Mountains of Washington and Oregon. *West. J. Appl. For.* **20**: 94–100.
- Meinzer, F.C., Woodruff, D.R., and 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. doi:10.1111/j.1365-3040.2004.01199.x.
- Muir, J.A., and Hennon, P.E. 2007. A synthesis of the literature on the biology, ecology and management of western hemlock dwarf mistletoe. USDA For. Serv. Gen. Tech. Rep. PNW-GTR-718.
- Muir, J.A., Hennon, P.E., and Negrave, R.W. 2007. Biology, ecology, and management of western hemlock dwarf mistletoe in Coastal British Columbia: a synthesis of the literature. Research Section, Coast Forest Region, BC Ministry of Forests and Range, Nanaimo, B.C. Tech. Rep. TR-037.
- SAS Institute Inc. 2002. SAS/STAT® software. Version 9.1, TS Level 1M0. SAS Institute Inc., Cary, N.C. Available from www.sas.com/technologies/analytics/statistics/index.html.
- Shaw, D.C., Freeman, E.A., and Mathiasen, R.L. 2000. Evaluating the accuracy of ground-based hemlock dwarf mistletoe rating: a case study using the Wind River Canopy Crane. *West. J. Appl. For.* **15**: 8–14.
- Shaw, D.C., Watson, D.M., and Mathiasen, R.L. 2004a. Comparison of dwarf mistletoes (*Arceuthobium* spp., Viscaceae) in the western United States with mistletoes (*Amyema* spp., Loranthaceae) in Australia—Ecological analogs and reciprocal models for ecosystem management. *Aust. J. Bot.* **52**: 481–498. doi:10.1071/BT03074.
- Shaw, D.C., Franklin, J.F., Bible, K., Klopatek, J., Freeman, E., Greene, S., and Parker, G.G. 2004b. Ecological setting of the Wind River old-growth forest. *Ecosystems* (N.Y., Print), **7**: 427–439. doi:10.1007/s10021-004-0135-6.
- Shaw, D.C., Chen, J., Freeman, E.A., and Braun, D.M. 2005. Spatial and population characteristics of dwarf mistletoe infected trees in an old-growth Douglas-fir–western hemlock forest. *Can. J. For. Res.* **35**: 990–1001. doi:10.1139/x05-022.
- Smith, R.B. 1969. Assessing dwarf mistletoe on western hemlock. *For. Sci.* **15**: 277–285.
- Stanton, S. 2006. The differential effects of dwarf mistletoe infection and broom abundance on the radial growth of managed ponderosa pine. *For. Ecol. Manage.* **223**: 318–326. doi:10.1016/j.foreco.2005.11.011.
- Swanson, M.E., Shaw, D.C., and Marosi, T.K. 2006. 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. *Northwest Sci.* **80**: 207–217.
- Thomson, A.J., and Smith, R.B. 1983. Growth patterns in a young western hemlock plantation infested with dwarf mistletoe. *Can. J. For. Res.* **13**: 972–978. doi:10.1139/x83-129.
- Thomson, A.J., Smith, R.B., and Alfaro, R.I. 1984. Growth patterns in immature and mature western hemlock stands infected with dwarf mistletoe. *Can. J. For. Res.* **14**: 518–522. doi:10.1139/x84-096.
- Thomson, A.J., Alfaro, R.I., Bloomberg, W.J., and Smith, R.B. 1985. Impact of dwarf mistletoe on the growth of western hemlock trees having different patterns of suppression and release. *Can. J. For. Res.* **15**: 665–668. doi:10.1139/x85-108.
- Watson, D.M. 2001. Mistletoe – a keystone resource in forests and woodlands worldwide. *Annu. Rev. Ecol. Syst.* **32**: 219–249. doi:10.1146/annurev.ecolsys.32.081501.114024.
- Wellwood, R.W. 1956. Some effects of dwarf mistletoe on western hemlock. *For. Chron.* **32**: 282–296.