Modeling the incidence and severity of hemlock dwarf mistletoe in 110-year-old wind-disturbed forests in Southeast Alaska[1]

L.M. Trummer, P.E. Hennon, E.M. Hansen, and P.S. Muir

Abstract: A model was developed to predict the severity of dwarf mistletoe (*Arceuthobium tsugense* (Rosendahl) G.N. Jones) in western hemlock trees (*Tsuga heterophylla* (Raf.) Sarg.) that developed within forests of Southeast Alaska that experienced near-catastrophic windthrow in the late 1800s. The model suggests that the degree of dwarf mistletoe severity on western hemlock trees was significantly and positively correlated with levels of dwarf mistletoe infection and basal area (m^2/ha) in large and small residual trees that survived the wind disturbance. No significant relationships were found between severity level and any other factors, including site productivity, density of coexisting Sitka spruce (*Picea sitchensis* (Bong.) Carr.), or slope. The model demonstrates the overriding importance of infected residual trees to predict future severity of dwarf mistletoe; greater size and infection level of residual trees results in greater dwarf mistletoe levels on regenerating hemlock crop trees. The model, derived from 76 plots on Kuiu Island, was tested in 18 plots on Chichagof Island, providing a preliminary validation. Slower rates of dwarf mistletoe spread and intensification in forests of southeastern Alaska, as compared with similar coastal forests south of Alaska, provide an opportunity for managers to manipulate the parasite to desired levels in managed forests.

Résumé : Les auteurs ont élaboré un modèle pour prédire la sévérité du faux-gui (*Arceuthobium tsugense* (Rosendahl) G.N. Jones) chez la pruche de l'Ouest (*Tsuga heterophylla* (Raf.) Sarg.) qui croît dans les forêts du sud-est de l'Alaska où un chablis presque catastrophique est survenu à la fin des années 1800. Le modèle suggère que le degré de sévérité du faux-gui chez la pruche de l'Ouest est positivement et significativement corrélé avec le niveau d'infection du faux-gui et la surface terrière (m^2/ha) des petits et gros arbres résiduels qui ont survécu la perturbation causée par le vent. Il n'y avait pas de relation significative entre le degré de sévérité et tout autre facteur, incluant la productivité du site, la densité des épinettes de Sitka compagnes (*Picea sitchensis* (Bong.) Carr.) ou la pente. Le modèle démontre l'importance primordiale des arbres résiduels infectés pour prédire la sévérité future du faux-gui; la sévérité du faux-gui sur la régénération de pruche est directement reliée au niveau d'infection chez les arbres résiduels et à leur plus grande taille. Le modèle, qui a été construit avec les données de 76 parcelles établies sur l'île de Kuiu, a été testé dans 18 parcelles de l'île de Chichagof, permettant d'obtenir une validation préliminaire. Étant donné que les taux de propagation et de développement du faux-gui sont plus faibles dans les forêts du sud-est de l'Alaska, comparativement aux forêts similaires de la côte sud de l'Alaska, les gestionnaires ont la possibilité de garder le parasite aux niveaux désirés dans les forêts aménagées.

[Traduit par la rédaction]

Introduction

Hemlock dwarf mistletoe (*Arceuthobium tsugense* (Rosendahl) G.N. Jones) is an important pathogen of western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) in the coastal forests of Southeast Alaska (Laurent 1974; Drummond and Hawksworth 1979). The parasite is abundant in old-growth forests, but infection intensity varies among stands (Laurent 1974). Two factors, frequent small-scale disturbance (canopy gaps) and an old-growth forest composition dominated by western hemlock, favor horizontal and vertical parasite spread. Dwarf mistletoe is present at low levels in young-growth forests, primarily because of the presence of infected nonmerchantable hemlock trees left on site after clearcut harvesting (Shaw 1982). Damaging disease levels are not expected to develop within the planned 90- to 120-year rotation (Shaw 1982; Shaw and Hennon 1991).

Reduction of dwarf mistletoe in managed forests has traditionally been viewed as highly desirable because severe infestation increases growth loss and mortality of host trees (Wellwood 1956; Shea 1966; Smith 1969; Thompson et al. 1985). However, the parasite is also considered an important ecological component of forests influencing stand structure, species composition, and wildlife habitat (Parmeter 1978; Tinnin et al. 1982; Bennetts et al. 1996). Wildlife use of

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L.M. Trummer,[2] E.M. Hansen, and P.S. Muir. Department of Botany and Plant Pathology, Oregon State University, 2082 Cordley Hall, Corvallis, OR 97331-2902, U.S.A.
P.E. Hennon. USDA Forest Service, Forest Health Management and Pacific Northwest Research Station, Forestry Sciences Laboratory, Juneau, AK 99802, U.S.A.

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[2]Author to whom all correspondence should be addressed. Present address: USDA Forest Service, State and Private Forestry, 3301 C Street, Suite 522, Anchorage, AK 99503. e-mail: ltrummer/r10_chugach@fs.fed.us

Table 1. Stand characteristics on Kuiu and Chichagof Island.

Stand	Area (ha)	Estimated disturbance year[a]	Current age of hemlock trees (years)[b]		
			Large residual[c]	Small residual[d]	Post-disturbance[e]
Kuiu Island (57°N, 133°W)					
1	20.5	1881	305 (110)	192 (72)	98 (19)
2	4.0	1877	260 (59)	177 (62)	94 (10)
3	1.5	1884	320 (48)	157 (36)	98 (20)
4	7.3	1885	275 (86)	168 (49)	93 (17)
5	3.6	1880	246 (57)	164 (50)	99 (16)
6	3.6	1886	260 (39)	226 (63)	96 (19)
7	5.3	1882	392 (50)	181 (39)	102 (16)
8	4.5	1883	315 (71)	158 (28)	98 (9)
Chichagof Island (58°N, 135°W)[f]					
9	4.9	1876	—	—	—
10	5.0	1878	—	—	—

[a]Disturbance year was estimated as 3 years prior to the mode of release dates for at least five residual trees per stand.
[b]Values are mean, with SD given in parentheses.
[c]Large residual hemlock trees survived the wind disturbance, had a minimum diameter of 20 cm at that time, and contained past or present evidence of dwarf mistletoe infections.
[d]Small residual hemlock trees survived the wind disturbance, had a maximum diameter of 19.5 cm at that time, and contained past or present evidence of dwarf mistletoe infections.
[e]Post-disturbance hemlock trees established naturally after the wind disturbance or were less than 1 cm diameter at that time.
[f]Ages of hemlock trees were not determined on Chichagof Island.

brooms has not been quantified in Alaska but is expected to be at least similar to levels measured in other forest types (Burnett 1981; Smith 1982; Bennetts et al. 1996).

As forest management objectives have now come to include retaining biological and structural diversity, maintaining some level of the parasite may be desired. In Alaska, slower rates of spread and intensification, as compared with similar coastal forests south of Alaska, provide opportunities to manage the parasite at desirable levels and may justify a different management approach towards this disease than in other regions (Drummond and Hawksworth 1979; Shaw 1982; Shaw and Hennon 1991).

Dwarf mistletoe populations can be altered in predictable ways by silvicultural treatments. Clearcut harvest of infested stands substantially reduces parasite incidence (Shaw 1982; Shaw and Hennon 1991), while selective harvest increases incidence in future stands (Buckland and Marples 1952; Shea 1966; Stewart 1976). Partial harvest, or conversely, partial retention of a dwarf mistletoe infested overstory canopy, markedly enhances exposure of regenerating trees to the parasite since the residual trees are primary infection sources. Thus, some form of selective or partial harvest will be a silvicultural tool to maintain the parasite in managed forests. Reliable estimates of disease spread and intensification in multistoried forests in Alaska, however, are difficult because of the lack of critical information on disease distribution and development over time.

A spread and intensification model of dwarf mistletoe in young-growth western hemlock stands (Bloomberg et al. 1980) suggests that dwarf mistletoe infection levels on hemlock trees were proportional to the number of residual trees and inversely related to the density and growth rate of understory host trees as well as the percentage of nonhost trees (Bloomberg and Smith 1982). Application of the hemlock dwarf mistletoe model (Bloomberg et al. 1980) in multistoried forests in Southeast Alaska is limited because the size and distribution of residual trees used in the model did not represent our normal stand conditions. The model also utilizes variables that are poorly understood in Alaska (Shaw and Loopstra 1991). Development of a simplified model to determine parasite incidence and severity in multistoried forests in Southeast Alaska was initiated.

This paper describes and models the incidence and severity of dwarf mistletoe in hemlock trees following exposure to infested residual trees for approximately 110 years. We retrospectively studied wind-disturbed forests and developed a mathematical model that predicts infection levels using stand, site, and tree characteristics. Additionally, parasite location in the crown of hemlock trees is described.

Methods

Ninety-four field plots were established in 10 stands on Kuiu and Chichagof islands, in Southeast Alaska. Selected stands contain hemlock dwarf mistletoe, experienced near-catastrophic windthrow in the late 1880s, could be stratified into areas of complete and partial disturbance, and were minimally 1 ha in size (Table 1). Selectively harvested stands were not used in this study because older harvesting sites are typically under 1 ha, younger than 80 years, and adjacent to beaches where logging is no longer permitted.

Selected stands contained three types of hemlock trees: (*i*) large residual trees that survived the disturbance, were at least 20 cm diameter at that time, and contained past or present evidence of dwarf mistletoe infections; (*ii*) small residual trees that survived the disturbance, were less than 20 cm diameter at that time, and contained past or present evidence of dwarf mistletoe infections; and (*iii*) post-disturbance trees that established naturally since the disturbance or were less than 1 cm diameter at that time. The year of catastrophic disturbance for each stand was estimated from at least five residual trees per stand as the mode of release dates, determined from increment core analysis, minus 3 years. A 3-year lag time was estimated between wind disturbance and understory tree release response (Deal et al. 1991).

To assist in plot location, each stand was stratified in a preliminary walk-through survey into areas containing zero, low (1–32), and high (>32) density of large residual trees per hectare. Within most strata, three 20 m radius (0.125 ha) circular plots were randomly established. Areas with evidence of recent windthrow were avoided. Large residual trees, including live and recently dead trees, were confirmed by increment coring at 1-m height. Cores were examined for tree age and diameter at the time of the storm, 110 years ago. While a balanced sampling design was our intention, plot reconstruction revealed a different mix of large residual trees than anticipated. Only seven plots could be located that contained zero residual trees.

Within the 20 m radius plot, live and recently dead large and small residual trees were measured for diameter at 1.3 m (DBH; to the nearest centimetre); height (to the nearest metre); age, if cored; dwarf mistletoe rating (DMR) within the live crown (Hawksworth 1977); and presence of dwarf mistletoe infections on dead branches below the live crown. A 10 m radius nested plot (0.031 ha) that contained at least three post-disturbance hemlock trees was established in the center of each 20 m radius plot. Within the smaller plot, similar measurements were recorded for live post-disturbance and Sitka spruce (*Picea sitchensis* (Bong.) Carr.) trees that were greater than 10 cm DBH. At least one post-disturbance tree was cored per plot. The smaller 10 m radius plot size was chosen because the dwarf mistletoe seed source for the small plot was primarily from residual trees in the surrounding 20 m radius plot (Smith 1966).

Hemlock plot trees were classified as "large residual," "small residual," or "post-disturbance" primarily through increment core analysis. Over 800 tree cores were analyzed for total age, presence of a growth release pattern approximately 110 years ago, and tree diameter at the time of disturbance. The release pattern appeared as a series of narrow annual rings immediately followed by a series of rings at least twice as wide as those formed prior to release. Tree diameter at the time of disturbance, recorded as twice the distance from the pith to the onset of release, was used to calculate the basal area at that time for large and small residual hemlock trees and spruce trees. The location of the pith was estimated if it was not recovered in the core.

Live crown dwarf mistletoe rating (DMR) followed Hawksworth's (1977) six-class system, which assigns a 0, 1, or 2 to each third of the live crown based on visible infections: 0, no visible infections; 1, less than half of the branches contain infections; or 2, more than half of the branches contain infections. Dwarf mistletoe ratings were estimated without ocular aids by carefully inspecting standing trees from several aspects. A tree DMR was calculated by adding ratings for each crown third. A plot infection rating, or DMRpost, was calculated by averaging the ratings of all live post-disturbance trees per plot. An average DMR for all large and small residual trees was calculated for each plot. A relative appraisal of infection severity on post-disturbance trees was obtained by combining DMR classes: 0 (healthy), 1or 2 (light), 3 or 4 (moderate), and 5 or 6 (severe) (Shea 1964). Presence or absence of old dwarf mistletoe infections on dead branches below the current live crown was recorded.

Site measurements on each plot included elevation (m), aspect, slope (%), plant association classification series, and site index. Aspect was converted to heatload using a nine-point scale that relates aspect to soil moisture status (Muir and Lotan 1985). Classification of plant associations followed the series keys developed by the Stikine Area, Tongass National Forest (Pawuk and Kissinger 1989), which determines dominant overstory and understory plants. Site index was defined as the height of a 100-year-old Sitka spruce tree (Farr and Harris 1979). For plots without spruce trees, site index was estimated from the plant association series key (Pawuk and Kissinger 1989).

As a relative assessment of past mistletoe infection level in residual trees, 26 off-plot live dwarf mistletoe infections on branches were collected, measured, and aged on Kuiu Island. Branches were sawn in half and aged at the center of the swelling by counting annual rings on the cross-section. Our hypothesis was that dwarf mistletoe infections in residual trees, currently visible as large brooms, pre-dated the catastrophic wind events. The relationship between branch age and swelling diameter was tested by linear regression analysis. The age of the host tissue at time of infection was not determined but likely occurred when branches were less than 15 years old (Shaw 1982).

Multiple linear regression, using the ordinary least squares (OLS) method, was used to develop a model describing the relationship between dwarf mistletoe infection level on post-disturbance trees and stand, site, and tree variables (Statgraphics 1993). The model response variable was the average dwarf mistletoe rating of post-disturbance hemlock trees within a plot (DMRpost). Explanatory variables tested for inclusion in the model included elevation, aspect, slope, plant association series, site index, distance to nearest infected residual tree, density of co-existing spruce, density of residual trees, and dwarf mistletoe rating of residual trees.

Data for variables met the assumptions of normality and homogeneity sufficiently to allow use of multiple linear regression analysis. An α value of 0.05 was chosen as the significance level for all tested variables. One model was developed using pooled data from the eight stands, 76 plots, on Kuiu Island because differences between stands were not significant ($p \le 0.05$, extra sum of squares F tests). Forward and backward variable selection procedures yielded similar models; thus, results are reported for forward stepwise regression only. Data from 18 plots on Chichagof Island were then used to validate the dwarf mistletoe model.

Results

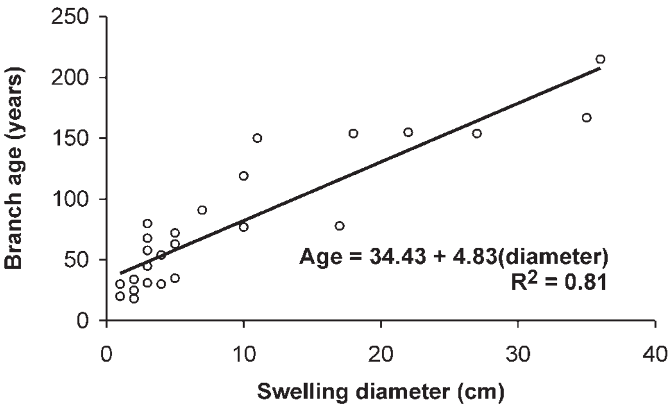
Sample population

The 10 sampled stands in this study represent a wide range of site conditions typical of western hemlock dominated forests in southeastern Alaska. All plots occurred within the western hemlock plant association series. Western hemlock/blueberry (*Vaccinium* spp.) was the dominant series described for 68% of the plots. Site index ranged from 75 to 131 at age 100 (98 ± 15; mean ± SD). Elevation ranged from 10 to 175 m (66 ± 41), slope ranged from 4 to 40% (17 ± 10%), and heatload (aspect) ranged from 1 (mesic) to 9 (xeric) (6 ± 2).

Pre-windthrow stand reconstruction

Prior to 1875, stands on Kuiu Island were likely old-growth multistoried forests, predominantly western hemlock, with a high incidence of dwarf mistletoe infection. Short growth release patterns were measured in increment cores of large and small residual hemlock trees (Trummer 1996), suggesting that small gaps periodically occurred in the overstory canopy prior to 1875, a pattern consistent with gap-phase processes in old-growth forests (Alaback 1982). Although it is probable that the Chichagof Island stands were old-growth and multistoried prior to disturbance, they may have been single- or multiple-cohort stands, as suggested by the lack of small residual trees in most plots. Increment

Fig. 1. Relationship between branch age and swelling diameter for 26 dwarf mistletoe infections.



cores from Chichagof Island were not retained for release pattern analysis, although cores were field analyzed to determine tree diameter at time of disturbance.

All hemlock trees older than 300 years (n = 44) at the study sites contained visible, often large, dwarf mistletoe brooms in the live crown; furthermore, 87% of them had old infections on dead branches below the live crown, suggesting that the parasite was not recently introduced to these trees. Analysis of dissected swellings indicates that infection age increased with swelling diameter (Fig. 1). Thus, large dwarf mistletoe swellings and brooms observed in the hemlock trees at sites on both islands were likely growing for centuries, pre-dating the catastrophic windthrow events.

Post-windthrow stand reconstruction

Study sites on both islands experienced windstorms that blew down most of the trees in the late 1800s. Within the Kuiu Island stands, some widely spaced individual large and small hemlock trees, with an average diameter of 43 and 10 cm, respectively, or clumps of trees remained alive after disturbance (Table 2). In Chichagof Island stands, the average diameter at disturbance for large and small residual trees was 45 and 13 cm, respectively (Table 2). Currently, the average DBH of large and small residual trees is 73 and 52 cm on Kuiu and 73 and 54 cm on Chichagof Island, respectively (Table 2).

Dwarf mistletoe infested multiple-cohort stands developed at all sites after windthrow. Large gaps within stands were filled in primarily with western hemlock as most plots contain less than 20% spruce. Less than 10% of the examined spruce trees on either island contained infections in the live crown. All infected spruce trees had only one swelling or broom per tree.

In all, 1030 and 380 post-disturbance western hemlock trees were examined on Kuiu and Chichagof islands, respectively. The average DBH and height of post-disturbance hemlock trees were 28 cm and 24 m on Kuiu Island and 30 cm and 26 m on Chichagof Island, respectively (Table 2). Dwarf mistletoe infection levels on post-disturbance hemlock trees ranged from none (DMR = 0) to severe (DMR = 6), with an average DMRpost = 2.1 on Kuiu Island and DMRpost = 1.4 on Chichagof Island (Table 2).

Dwarf mistletoe levels

The primary means of dwarf mistletoe spread on all plots has been from infected large and small residual trees to the post-disturbance western hemlock trees. Although infected residual trees within the overstory canopy contain a substantial level of dwarf mistletoe, the co-existing post-disturbance western hemlock trees have one third to one half the average current dwarf mistletoe rating of the residual trees (Table 2).

As the number of infected residual trees per hectare increased, infection severity and the incidence of infections in the upper crown third of post-disturbance trees also generally increased, even though dwarf mistletoe spread appears to be slow (Table 3). For example, on Kuiu Island 11% of post-disturbance trees are severely infected (DMR = 5 or 6) and 42% remain uninfected or lightly infected (DMR = 0, 1, or 2) after growing in the presence of 89–128 infected residual hemlock trees per hectare for nearly 110 years (Table 3). In addition, 59% of these post-disturbance trees appear uninfected or contain infections only in the lower two thirds of the crown (Table 3).

Dwarf mistletoe model

The dwarf mistletoe infection level of post-disturbance trees (DMRpost) showed a linear and significant correlation with both the DMR and basal area of large and small residual trees on Kuiu Island (Tables 4 and 5). The relationships were positive and highly significant, accounting for over 60% of the variation in DMRpost (Tables 4 and 5). No other factors, including percent slope, site index, plant association series, aspect, or spruce composition (all $p \geq 0.05$), were significantly correlated with the infection level of post-disturbance trees.

The equation, derived by multiple linear regression, is

$$[1] \qquad Y = -0.118 + 0.222X_1 + 0.322X_2 + 0.048X_3 + 0.761X_4$$

where Y is the estimated mean DMR of post-disturbance hemlock trees (DMRpost), X_1 is the mean DMR of large residual hemlock trees, X_2 is the mean DMR of small residual hemlock trees, X_3 is the basal area of large residual hemlock trees (m^2/ha), and X_4 is the basal area of small residual hemlock trees (m^2/ha).

The ranges of DMR and basal area used in the model were DMR = 0–6.0 and basal area = 0–32 m^2/ha (0–88 trees/ha) for large residual trees, and DMR = 0–6.0 and basal area = 0–1.5 m^2/ha (0–80 trees/ha) for small residual trees.

Model validation

A comparison of model predicted and measured dwarf mistletoe ratings for 18 plots on Chichagof Island indicated that predicted dwarf mistletoe ratings were within ±0.5 DMR of measured ratings in 10 of the plots and ±1.0 DMR in 14 of the plots (Table 6). In the remaining four plots, predicted ratings differed from measured values by less than ±2.0 DMR (Table 6). The majority (73%) of model-predicted ratings underestimated measured ratings.

Table 2. Characteristics of tree types in stands on Kuiu and Chichagof islands.

Tree type	Density (trees/ha)[a]	Diameter at disturbance (cm)[a,b]	Current DBH (cm)[a]	Current height (m)[a]	Current DMR (0–6)[a,c]
Large residual hemlock					
Kuiu Island	31 (25)	43 (22)	73 (19)	34 (8)	4.5 (1.5)
Chichagof Island	15 (18)	45 (18)	73 (15)	32 (8)	4.6 (1.3)
Small residual hemlock					
Kuiu Island	38 (27)	10 (5)	52 (9)	34 (5)	2.9 (1.7)
Chichagof Island	5 (10)	13 (4)	54 (10)	28 (9)	3.1 (0.7)
Post-disturbance hemlock					
Kuiu Island	435 (230)	—[d]	28 (11)	24 (7)	2.1 (1.7)
Chichagof Island	678 (192)	—[d]	30 (11)	26 (7)	1.4 (1.4)
Sitka spruce					
Kuiu Island	71 (88)	55 (35)	40 (17)	31 (7)	0.1 (0.3)
Chichagof Island	59 (55)	42[e]	40 (16)	31 (7)	0.1 (0.3)

[a]Values are mean with SD given in parentheses.
[b]Diameter at disturbance was calculated only for trees that were increment cored.
[c]Dwarf mistletoe ratings (DMR) follow the Hawksworth six-class system (Hawksworth 1977).
[d]Post-disturbance trees were not present or were less than 1 cm diameter at disturbance.
[e]Only one spruce was cored in the Chichagof Island stands.

Discussion

This study is the first to model hemlock dwarf mistletoe infection levels in mature (90–120 years) uneven-aged forests in Alaska. Measurement of dwarf mistletoe infection level on post-disturbance western hemlocks indicates that parasite spread and intensification is slow, even with an infected overstory. We developed a model to predict dwarf mistletoe severity on hemlock trees after partial disturbance of infected stands. Our model suggests that the basal area and dwarf mistletoe infection level of residual trees are directly proportional to the infection level of co-existing 110-year-old hemlock trees. No other factors, including those describing site or density of spruce, were significant in the model.

The proportion of Sitka spruce trees, a rare parasite host and barrier to dwarf mistletoe spread, did not influence dwarf mistletoe ratings of post-disturbance hemlock trees. Data from Bloomberg and Smith (1982) suggest that a decrease in hemlock infection levels could be predicted with as low as 20% immune or resistant tree component and that a substantial decrease could be expected with 30% or more. Our wind-disturbed stands typically contained less than 20% spruce, levels possibly too low to provide a barrier effect. On both islands, a low incidence of infection in spruce trees indicates that some dwarf mistletoe seeds are intercepted.

Accuracy of the model was tested in 18 plots on Chichagof Island (Table 6). We believe that predictions using the dwarf mistletoe model were sufficiently accurate in estimating measured DMR values to validate the model for use on Kuiu and Chichagof islands. Model testing is recommended in stands where dwarf mistletoe infested residual trees have been killed or removed during thinning operations.

Dwarf mistletoe ratings predicted by the model generally underestimated measured values in most plots on Chichagof Island. One explanation is that some proportion of infected residual trees survived the disturbance but have since died and are no longer visible on a plot. Since predicted values are based on the present stand condition, not accounting for some residual trees would result in underestimation of DMR on post-disturbance hemlock trees. Also, the model does not account for the spatial distribution of infected residual trees, which may provide valuable insight into parasite spread and intensification (Reich et al. 1991).

An important limitation of our study was the lack of measurement of dwarf mistletoe level on large and small residual trees immediately after catastrophic disturbance. Instead, we used current residual tree DMR in the model as a plausible approximation for DMR at the time of disturbance (Table 2). Large visible brooms within the live crown and on dead branches below the live crown were observed in the residual trees that currently have severe infection levels, suggesting that these trees were severely infected in the past. However, the relationship between current and past dwarf mistletoe levels in residual trees is poorly understood. Long-term monitoring of DMR on residual trees, ideally through a rotation period, will help to determine if our model is based on over- or under-estimation of this parameter.

This study was conducted in stands that experienced extensive past wind disturbance and was designed an analogue for understory stand structure and disease conditions expected after a partial harvest of a dwarf mistletoe infested overstory canopy. Differences between wind-disturbed and partially harvested stands may include the condition of residual trees following disturbance. Residual trees in wind-disturbed stands may sustain considerable live crown damage during storms, damaging or killing existing infections, while less damage to residual trees and dwarf mistletoe infections may occur in partially harvested stands, particularly if infested residual trees are retained in small clumps. However, if dwarf mistletoe infections survive the

Table 3. Dwarf mistletoe infection location and severity on post-disturbance hemlock trees on Kuiu and Chichagof islands.

No. of large and small residual trees/ha	DMR post[a,b]	No. of plots	No. of post-disturbance trees	Proportion of post-disturbance trees in DMR infection classes (% of trees)[a,c]				Infection location in crown thirds (% of post-disturbance trees)[a]			
				0	1 or 2	3 or 4	5 or 6	None	Lower only	Lower and middle[d]	Lower, middle, and upper[e]
Kuiu Island											
0	0.0 (0.1)	2	25	96 (5)	4 (5)	0 (0)	0 (0)	96 (5)	4 (5)	0 (0)	0 (0)
1–32	1.1 (1.1)	13	246	48 (32)	37 (25)	11 (16)	4 (12)	48 (32)	18 (14)	21 (18)	12 (17)
33–88	2.4 (1.2)	38	556	13 (19)	40 (22)	35 (25)	12 (17)	14 (19)	16 (16)	39 (22)	31 (23)
89–128	2.8 (1.2)	17	152	8 (11)	34 (29)	47 (36)	11 (17)	8 (12)	9 (14)	42 (26)	41 (30)
129–168	3.8 (0.8)	6	51	2 (6)	16 (15)	47 (12)	35 (23)	2 (6)	10 (13)	38 (15)	50 (13)
Chichagof Island											
0	0.3 (0.4)	5	106	72 (28)	28 (28)	0 (0)	0 (0)	72 (28)	28 (28)	0 (0)	0 (0)
1–32	1.7 (1.0)	11	237	25 (32)	47 (23)	24 (21)	4 (5)	25 (32)	24 (14)	32 (21)	19 (17)
33–88	2.2 (0.1)	2	37	12 (8)	45 (12)	38 (3)	5 (6)	13 (8)	14 (12)	60 (28)	13 (8)

[a]Values are mean with SD given in parentheses.
[b]The average dwarf mistletoe rating (DMR) of all live post-disturbance hemlock trees on a plot.
[c]Dwarf mistletoe infection severity classes are based on Shea (1964): 0, healthy; 1 or 2, light; 3 or 4, moderate; 5 or 6, severe.
[d]Includes trees with dwarf mistletoe in midcrown only.
[e]Includes trees with dwarf mistletoe in upper crow only, middle and upper crown only, and lower and upper crown only.

disturbance intact, behavior of the parasite, an aerial parasite of living branches, should be commensurate in both disturbances.

Rapid parasite spread from residual to young-growth trees has been both predicted and well documented in the Pacific Northwest coastal forests (Buckland and Marples 1952; Shea 1966; Smith 1966; Richardson and van der Kamp 1972; Stewart 1976; Smith 1977). In contrast, the results of our study indicated substantially slower rates of parasite spread despite the presence of dwarf mistletoe source trees in close proximity to host trees for nearly 110 years. Results are similar to those found in younger stands in Southeast Alaska (Shaw 1982, Shaw and Hennon 1991). Smith (1966) estimated that only 25 evenly scattered infected hemlock residual trees/ha could severely infect all regeneration on a hectare in coastal British Columbia. In contrast, our data indicate that 129–168 infected hemlock residual trees/ha are needed to severely infect at least one third of the hemlock regeneration after 110 years (Table 3).

Differences in parasite spread and intensification on western hemlock trees between the coastal forests of Alaska and similar forests further south on the western coast of North America are apparent and yet poorly understood (Drummond and Hawksworth 1979; Shaw 1982; Shaw and Hennon 1991; Shaw and Loopstra 1991). Isozyme analysis of dwarf mistletoe shoots from 21 populations, including Juneau, Alaska, indicates that the population is genetically distinct but shows great affinity to the more northern populations from Washington and Vancouver Island, British Columbia (Nickrent and Stell 1990). Parasite differences among regions may be attributed to climatic influences on pollen dispersal, fruit production, and seed spread (Shaw and Loopstra 1991). In Southeast Alaska, heavy rainfall during pollen dispersal may severely inhibit pollination. In addition, the timing of seed dispersal is affected by fruit maturity and weather factors (Smith 1973), and freezing temperatures can rupture mature dwarf mistletoe fruit capsules, reducing seed dispersal capacity by 95% (Baranyay and Smith 1974). Even in dwarf mistletoe inoculated trees in Southeast Alaska, loss of seeds or damage to dwarf mistletoe shoots is high (Shaw and Loopstra 1991).

Model application

To use the model, the manager inputs either the desired infection level of crop trees or the target stand conditions, expressed as the basal area and dwarf mistletoe rating of large and small residual trees, and solves the equation for the unknown parameter. For example, a low average hemlock tree dwarf mistletoe infection level (DMRpost = 1.0) is estimated by the model with the retention of 8.6 m^2/ha (24 trees/ha, average DBH of 68 cm) of large residual trees with an average DMR = 1.0 and 0.21 m^2/ha (12 trees/ha, average DBH of 15 cm) of small residual trees with an average DMR = 1.0:

$$[2]\quad 1.0 = -0.118 + 0.222(\mathrm{DMR} = 1) + 0.322(\mathrm{DMR} = 1) + 0.048(8.6\ \mathrm{m}^2/\mathrm{ha}) + 0.761(0.21\ \mathrm{m}^2/\mathrm{ha})$$

Similar examples can be developed to determine the stand conditions under which moderate or severe infection levels

Table 4. Analysis of variance of post-disturbance hemlock tree dwarf mistletoe infection level (DMRpost) for the Kuiu Island stands.

Source of variation	df	MS	*F*	*P*
Model	4	21.14	31.16	<0.001
Error	71	0.68		
R^2 value = 0.617 (adjusted for degrees of freedom)				

Table 5. Regression coefficients in the model of post-disturbance hemlock tree dwarf mistletoe infection level (DMRpost) for the Kuiu Island stands.

Parameter[a]	Estimate	SE	*t*	*P*
Intercept	–0.118	0.247	–0.478	0.634
DMR, large[a]	0.222	0.061	3.629	<0.001
DMR, small[b]	0.322	0.082	3.909	<0.001
BA, large[c]	0.048	0.014	3.324	0.001
BA, small[d]	0.761	0.315	2.419	0.018

[a]Mean current dwarf mistletoe rating (DMR) of large residual hemlock trees within a plot.
[b]Mean current dwarf mistletoe rating (DMR) of small residual hemlock trees within a plot.
[c]Basal area of large residual hemlock trees at the time of wind disturbance (m^2/ha).
[d]Basal area of small residual hemlock trees at the time of wind disturbance (m^2/ha).

Table 6. Model predicted and measured DMRpost values in 18 plots on Chichagof Island.

Plot	Predicted DMRpost[a] (0.0–6.0)	Measured DMRpost (0.0–6.0)	Difference (predicted – measured)
1	1.7	2.3	–0.6
2	1.1	0.9	0.2
3	1.0	1.0	0.0
4	1.1	0.0	1.1
5	0.0	0.0	0.0
6	2.9	2.2	0.7
7	0.4	0.5	–0.1
8	1.1	1.6	–0.5
9	0.0	0.2	–0.2
10	1.2	2.9	–1.7
11	0.0	1.0	–1.0
12	0.0	0.4	–0.4
13	1.9	2.4	–0.5
14	1.1	2.7	–1.6
15	2.4	1.7	0.7
16	2.1	2.1	0.0
17	1.1	2.7	–1.6
18	0.0	0.1	–0.1

[a]The average dwarf mistletoe rating of all live post-disturbance hemlock trees on a plot.

Table 7. Simulations using the hemlock dwarf mistletoe model developed in Alaska.

	Basal area (m^2/ha)[b,c]		DMR[d]	
Desired DMRpost[a]	Large residual	Small residual	Large residual	Small residual
3	13.8 (38)	1.3 (62)	3	3
3	32.0 (88)	0.0 (0)	6	0
3	0.0 (0)	1.5 (80)	0	6
4	21.7 (60)	1.3 (74)	4	4
5	29.0 (80)	1.3 (74)	5	5
6	32.0 (88)	1.5 (80)	6	6

[a] The average dwarf mistletoe rating of all live post-disturbance hemlock trees per hectare.
[b]All basal area calculations use a large and small residual tree diameter of 68 and 15 cm, respectively.
[c]The number of large or small residual trees used in basal area calculations is given in parentheses.
[d]Dwarf mistletoe ratings (DMR) follow the Hawksworth six-class system (Hawksworth 1977).

are predicted to occur (Table 7). Use of basal area and dwarf mistletoe data from local stand inventories will increase reliability of model estimates.

The model was developed as a simulation for disease levels expected after retention of infected residual trees in multistoried managed forests. Model outputs can be used by forest managers to manipulate the parasite to desired levels within the range of stand conditions included in this study. Growth loss estimates from studies in British Columbia, 40% growth loss from severely infested trees (DMR = 5 or 6) and 25% loss from moderately infested trees (DMR = 3 or 4) (Thompson et al. 1985), can be combined with model outputs to estimate future timber yields. The target level of the parasite, however, also may be influenced by noncommodity values. In stands where management goals include maintaining key elements of stand structure, biological diversity, and wildlife habitat, a higher level of the parasite may be desired.

In summary, slower rates of parasite spread and intensification in Alaska, as compared with similar coastal forests south of Alaska, may increase opportunities to manage the parasite at a desirable level. Some form of selective harvesting of dwarf mistletoe infested stands could be used to extract timber but maintain the disease at a level considered favorable for maintaining key elements of stand structure, biodiversity, and wildlife habitat. Wildlife use of dwarf mistletoe infections has not been quantified in Southeast Alaska; however, brooms caused by the parasite provide a unique structural component in the coastal forests. Research on the wildlife use of hemlock dwarf mistletoe brooms in Alaska would help managers evaluate the utility of maintaining different levels of the parasite in managed forests for wildlife habitat.

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