AN ABSTRACT OF THE THESIS OF

Loreen M. Trummer for the degree of Master of Science in Botany and Plant Pathology presented on March 15, 1996. Title: Modeling Hemlock Dwarf Mistletoe (*Arceuthobium tsugense* subsp. *tsugense*) Spread and Intensification in Mature Uneven-aged Forests in Southeast Alaska.

Abstract Approved: Redacted for privacy
Everett M. Hansen

Hemlock dwarf mistletoe (*Arceuthobium tsugense* (Rosendahl) G.N. Jones subsp. *tsugense* (western hemlock race)) is the most important and widespread disease of old-growth western hemlock forests in the Pacific Northwest. Although heavy infection of dwarf mistletoe can significantly increase growth loss and mortality of host trees, the parasite is also considered an important ecological component of forests influencing stand structure, species composition, and wildlife habitat.

This retrospective study was conducted in stands that sustained extensive windthrow in the past and was designed as a simulation for stand structure and disease conditions expected after use of silvicultural systems that retain overstory canopy trees in a managed forest. The specific objectives were to: 1. characterize the forest structure and dwarf mistletoe component of stands that developed after catastrophic wind storms in the late 1800's; and 2. develop and validate a model, using site, plot, and tree variables, that predicts the dwarf mistletoe rating of hemlock trees that have been exposed to the pathogen for approximately a century.

Results indicated that retention of overstory infected hemlock trees in southeast Alaska forests will result in pathogen spread to and intensification on hemlock trees that have developed since the late 1800's (post-disturbance trees), but not to the devastating levels predicted by previous research in the coastal forests of British Columbia, Washington, or Oregon. On Kuiu Island, the retention of an average of 3 heavily infected overstory residual trees/plot (83 residual trees/ha) resulted in nearly 100 percent infection

of post-disturbance hemlock trees within a plot. Of those trees infected, less than one-fifth had heavy infection (a dwarf mistletoe rating of 5 or 6), and approximately one-half had moderate infection (a dwarf mistletoe rating of 3 or 4). On Chichagof Island, the retention of an average of 2 heavily infected residual trees/plot (69 residual trees/ha) resulted in nearly 100 percent infection of post-disturbance hemlock trees within a plot. Of those trees infected, less than ten percent had heavy infection and approximately one-third had moderate infection.

A mathematical model that predicted dwarf mistletoe rating on post-disturbance hemlock trees was developed from eight stands on Kuiu Island and the generality of the variables was tested in two stands on Chichagof Island. The Kuiu Island model predicted that the mean dwarf mistletoe rating of post-disturbance hemlock trees within a plot increased with increasing numbers and dwarf mistletoe ratings of residual and advanced regeneration trees within a plot. No other factors that described site or tree conditions within a plot appeared important in the model. Sitka spruce trees, though rare hosts of dwarf mistletoe, did not appear to increase the mean dwarf mistletoe rating of post-disturbance hemlock trees within a plot. When present in sufficient numbers, spruce trees may act as barriers to pathogen spread, although further analysis is needed to confirm a barrier effect.

The Chichagof Island models, developed separately for the two stands, also predicted that the mean dwarf mistletoe rating of post-disturbance hemlock trees within a plot increased with increasing numbers and dwarf mistletoe rating of residual trees within a plot. The importance of advanced regeneration trees could not be verified in either stand on Chichagof Island since most plots lacked this tree type.

Modeling Hemlock Dwarf Mistletoe (*Arceuthobium tsugense* subsp. *tsugense*) Spread and Intensification in Mature Uneven-aged Forests in Southeast Alaska.

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Loreen M. Trummer

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APPROVED:

Redacted for privacy

Major Professor, representing Botany and Plant Pathology

Redacted for privacy

Chair of Department of Botany and Plant Pathology

Redacted for privacy

Dean of the Graduate School

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To my grandmother,

Christine Elizabeth Revord,

the beloved matriarch of my family.

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Chapter 1. Introduction and Literature Review

INTRODUCTION

Hemlock dwarf mistletoe (*Arceuthobium tsugense* (Rosendahl) G.N. Jones subsp. *tsugense* (western hemlock race)) is the most important and widespread disease of old-growth western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) forests in the Pacific Northwest, causing an estimated annual timber loss of 159 million cubic feet due to growth reduction and mortality (Drummond 1982). Infection has adverse effects on host growth and vigor, survival, reproductive potential, and wood quality and predisposes trees to insect attack and decay fungi (Weir 1915, Wellwood 1956, Hawksworth 1978).

National Forest managers have historically viewed dwarf mistletoes as forest pests that impede timber production goals. Although heavy infestation of dwarf mistletoe can significantly increase growth loss and mortality of host trees (Smith 1969, Thompson et al. 1984), the parasite is also considered an important ecological component of forests influencing stand structure, species composition, and wildlife habitat (Parameter 1978, Tinnin et al. 1982, Tinnin 1984, Bennetts 1991). Management of the National Forests at the ecosystem level provides an opportunity to maintain critical structural and biodiversity characteristics of the original forest. Under this management philosophy, hemlock dwarf mistletoe can be viewed as a forest component providing unique structure and biodiversity to forests primarily through formation of palmate brooms. Thus, the hemlock dwarf mistletoe may be desired at a particular level within the forest rather than viewed as a pest to be eradicated. This research was designed to provide managers with a simulation model for predicting the long-term spread and intensification of dwarf mistletoe in mature uneven-aged forests.

In southeast Alaska hemlock dwarf mistletoe is prevalent in old-growth forests, 250-300 years old (Laurent 1974, Drummond and Hawksworth 1979). The stand structure and composition of old-growth forests, multiple-storied and almost entirely western hemlock, perpetuates pathogen spread and intensification from large overstory trees to smaller developing trees. The pathogen is present at low levels, an average of less than 20 percent infection, in young managed forests up to 44 years old which developed after clear-cut harvest operations (Shaw 1982a). The low number of dwarf mistletoe infections coupled with the lack of additional dwarf mistletoe seed from overstory trees indicated the pathogen would die out of developing stands within the planned harvest rotation of 90-120 years (Shaw and Hennon 1991). It is possible that the pathogen may be completely eliminated for several centuries from even-aged managed forests which develop after clear-cut harvesting (Paul Hennon, pers. comm. 1995)

Since clear-cut harvesting may eradicate hemlock dwarf mistletoe in managed forests, other silvicultural systems that retain infected trees from the previous stand will need to be used to maintain a desirable level of the pathogen. We currently have a poor understanding of the extent of parasite intensification after partial harvest of an infected old-growth canopy and future uneven-aged stand development. Resource managers are understandably reluctant to use harvesting practices other than clear-cut because of the concern that dwarf mistletoe will intensify and cause unacceptable growth loss in the developing stand.

Studies that quantify long-term hemlock dwarf mistletoe spread and intensification following partial harvest of the overstory canopy are lacking from southeast Alaska, although research has been conducted in western Canada (Buckland and Marples 1952, Bloomberg et al. 1980, Bloomberg and Smith 1982). In British Columbia, observation of dwarf mistletoe spread within areas selectively logged indicated that the pathogen was present, but not quantified, throughout the developing stand (Buckland and Marples 1952). The authors warned that the continuation of logging practices that establish uneven-aged stands would result in a high incidence of dwarf mistletoe infection and in subsequent low timber yields. Presently there is little evidence from southeast Alaska to dispute the authors' observations, although studies have indicated that the parasite may have a two- or three-fold longer life cycle in southeast Alaska than in more southern parts of its distribution (Shaw and Loopstra 1991). A prolonged life cycle suggests that the pathogen may require a substantially longer time to develop to high levels and for subsequent high growth loss to occur in host trees.

A model that predicts hemlock dwarf mistletoe spread and intensification originating from unmerchantable residual trees that remain in a stand up to 30 years after clear-cut harvesting was developed in western Canada (Bloomberg et al. 1980). This model is not applicable for young stands on productive sites developing after clear-cut harvesting in Alaska since research has indicated considerably less parasite spread and intensification in Alaska than in comparable stands in western Canada (Shaw 1982a, Shaw and Hennon 1991). The model may have limited applicability to explain pathogen behavior for young-growth trees growing on poor quality sites (Shaw and Hennon 1991) or for hemlock trees that developed in the presence of infected overstory trees. Since the applicability of the western Canada hemlock dwarf mistletoe model in southeast Alaska is uncertain, development of a model specific to long-term parasite behavior in mature uneven-aged forests in southeast Alaska is warranted.

This study is the first to examine hemlock dwarf mistletoe spread and intensification in mature uneven-aged western hemlock-Sitka spruce (*Picea sitchensis* (Bong.) Carr.) forests in southeast Alaska. In central southeast Alaska, post-disturbance hemlock trees, trees that regenerated naturally soon after windthrow of the previous forest in the late 1800's, were examined for incidence and severity of dwarf mistletoe. The post-disturbance hemlock trees developed in the presence of zero, one, or more than one dwarf mistletoe infected residual trees within 10 m, which represented 0, 32, or > 64 residual trees/ha. A residual tree was defined as an infected hemlock tree that survived the late 1800's wind event and was large at the time of the storm. Additionally, plots contained from 0 to 7 dwarf mistletoe infected advanced regeneration hemlocks which represented from 0 to 224 advanced regeneration trees/ha. An advanced regeneration tree was defined as an infected hemlock tree that survived the storm but was small at that time.

Correlations among disease incidence, the density of infected residual and advanced regeneration trees, and various plot, site, and tree factors were used to develop a model that predicts the mean dwarf mistletoe rating (DMR) of mature post-disturbance hemlock trees within a plot in eight stands on Kuiu Island. Two stands on Chichagof Island were examined for preliminary verification of the model.

Two subspecies and two host races of *Arceuthobium tsugense* have been described: subspecies *tsugense* (western hemlock race and shore pine (*Pinus contorta* (Dougl. ex Loud.) var *contorta*) race), and subspecies *mertensiana* (Nickrent and Stell 1990, Hawksworth et al. 1992). The western hemlock race appears to be the only dwarf mistletoe present in southeast Alaska. For simplicity, in this thesis the pathogen *Arceuthobium tsugense* subsp. *tsugense* (western hemlock race) is referred to simply as *Arceuthobium tsugense*.

Although *A. tsugense* is most abundant in old-growth uneven-aged forests in southeast Alaska (Laurent 1974), the pathogen may occur in each stage of natural forest succession: seedling/sapling, pole, mature even-aged, and old-growth uneven-aged (Hennon, unpublished). Dwarf mistletoe may be abundant in early successional stages. Infected understory hemlock seedlings and saplings that survive catastrophic disturbance may become the source of pathogen introduction to smaller developing trees. On productive sites the height growth of hemlocks may outpace the vertical spread of the parasite, relegating the dwarf mistletoe to lower branches which typically die from shading (Shaw and Hennon 1991). On unproductive sites or where height growth of young trees is suppressed by the presence of overstory trees, the vertical spread of dwarf mistletoe may outpace young hemlock growth, resulting in maintenance of the parasite in the live crown of young hemlock trees.

The rapid height growth of hemlocks continues through the closed-canopy pole stage (Alaback 1982). Dwarf mistletoe may be greatly reduced and sometimes eradicated on individual trees through branch shading and the death of lower infected limbs. A comprehensive survey of even-aged pole stage stands in southeast Alaska indicated almost complete absence of the parasite (Hennon and Farr, unpublished data). Pole stage stands on unproductive sites or sites that contain scattered infected overstory trees likely maintain the parasite at some level. Surveys of uneven-aged pole stage stands that contain scattered residual trees within and just outside the site indicated that the pathogen was present at low levels (Hennon and Farr, unpublished data).

Mature even-aged western hemlock stand development is characterized by "break-up" of the closed-canopy through mortality of dominant and co-dominant trees likely caused by decay fungi, wind, and, occasionally, defoliating insects. Height growth of trees has slowed, but dwarf mistletoe is frequently absent during this stage because of its elimination during earlier stages. The pathogen may be re-introduced into the upper canopy by birds or mammals, although the frequency of introduction events has not been quantified. Once introduced, dwarf mistletoe may slowly recolonize the stand. In mature uneven-aged forests, the parasite may be common since it has persisted from earlier successional stages.

The old-growth stage is characterized by multiple canopy levels composed of trees with a broad range of age, height, and diameter (Alabeck 1984). Small canopy gaps created from scattered tree mortality are common in the old-growth stage. Regeneration within these gaps is primarily western hemlock likely due to the shade tolerance of the species and the lack of soil disturbance. Sitka spruce regeneration is not shade tolerant and may be favored by site disturbance because of increases in nitrate nitrogen associated with soil warming and an increase in organic decomposition (Taylor 1929, Harris and Farr 1974, Deal and Farr 1994). Dwarf mistletoe may be present in the old-growth stage either because it was present in previous successional stages or it was introduced by birds or mammals. In either case, the old-growth stand structure and composition, multi-storied and almost entirely western hemlock, is ideal for the perpetuation of dwarf mistletoe. Reduced height growth of old-growth hemlocks allows vertical intensification of the parasite within the live crown of individual trees. Infected overstory trees readily spread dwarf mistletoe to lower canopy levels, perpetuating both horizontal and vertical pathogen expansion in hemlock trees. The lack of non-host trees reduces a barrier to disease spread. Dwarf mistletoe may eventually heavily infect all hemlocks in a stand.

The forests of southeast Alaska comprise approximately 46 percent of the land area (Hutchinson and LaBau 1975) and are primarily in an old-growth condition because of the low frequency of stand replacing natural disturbance and intensive logging has only occurred since the 1950's. Western hemlock and Sitka spruce account for 89 percent of the coastal forest canopy (Hutchinson and LaBau 1975). Western hemlock, the dominant species on nearly two-thirds of the commercial forest land, is the only species severely parasitized by hemlock dwarf mistletoe in southeast Alaska. Sitka spruce comprises 30-50 percent of the stand volume on one third of the commercial forest land. Mountain hemlock (*Tsuga mertensiana* (Bong.) Carr.) is found on less than 4 percent of the land area in southeast Alaska (Harris and Farr 1974).

Windstorms are the most widespread cause of natural forest disturbance in southeast Alaska (Harris 1989). Gale-force windstorms occur frequently throughout the region uprooting and breaking healthy trees as well as knocking over some trees that contain root or stem decay. As a result gaps are created in the forest canopy, ranging from single trees to hundreds of hectares and containing a mixture of trees that sustained little or no damage, have broken boles, or were uprooted (Harris 1989). Historical records from "The Alaskan", a Sitka, Alaska newspaper, documented eleven gale-force storms in southeast Alaska between 1867 and 1904 (Anonymous 1886a, Anonymous 1886b, Anonymous 1889, Anonymous 1893, Anonymous 1894, Anonymous 1895, Anonymous 1899, Anonymous 1903, Anonymous 1904). The forests on Kuiu and Chichagof Island apparently experienced catastrophic windthrow from those storms.

Stands that were windthrown at the turn of the century provided an ideal opportunity to perform a retrospective study on long-term pathogen spread and intensification on Kuiu and Chichagof Island. Windthrown stands chosen for study were several hectares in size, greater than 100 years old, primarily regenerated with western hemlock, and contained hemlock dwarf mistletoe. Old partially harvested stands could not be used as study sites because few exist across southeast Alaska, and those few stands are typically less than one hectare and younger than 80 years old. Windthrown stands that contain surviving trees have a similar forest structure to partially harvested stands that retain canopy-level trees. The major difference between windthrown and partially harvested stands is whether the downed wood is removed from the site. Since hemlock dwarf mistletoe is an aerial parasite that requires a living host, parasite behavior should be similar in both circumstances. Thus, parasite behavior in windthrown stands is a plausible mimic for behavior in partially harvested stands.

Removal of all merchantable trees in a single entry, or clear-cut harvesting, has been considered the only practical means of harvest and regeneration of southeast Alaska western hemlock-Sitka spruce forests (Harris and Farr 1974). Clear-cut harvesting was also an effective silvicultural treatment for the control of hemlock dwarf mistletoe. Harvesting practices other than clear-cut harvesting that remove single trees or groups of trees at periodic intervals have not been used in the Alaska region. A key difference between clear-cut harvesting and other harvesting practices is that the former removes all overstory trees, while the latter retains some of the overstory canopy. If the retained overstory trees contain hemlock dwarf mistletoe, pathogen spread to and intensification within a developing stand may increase dramatically (Russell 1976).

THESIS OBJECTIVES

This thesis explores long-term spread and intensification of hemlock dwarf mistletoe in mature uneven-aged stands through description of field measurements on Kuiu and Chichagof Island in southeast Alaska. The goal of this thesis was to simulate hemlock dwarf mistletoe spread and intensification following partial harvest of the overstory canopy. The following objectives are addressed in this thesis:

1. Characterize the forest structure of stands that developed after stand replacing wind storms in the late 1800's. Measure and characterize the past and present dwarf mistletoe incidence and severity on western hemlock trees that developed soon after the catastrophic wind disturbance.

2. Test stand and site factors including density of infected residual and advanced regeneration hemlock trees, density of Sitka spruce, distance from post-disturbance hemlocks to pathogen inoculum sources, elevation, aspect, percent slope, plant

association, and site index, for influence on the dwarf mistletoe rating of post-disturbance hemlock trees.

3. Develop and validate a model that predicts the dwarf mistletoe rating of mature post-disturbance hemlock trees in partially disturbed stands after a century of pathogen exposure.

REVIEW OF SELECTED TOPICS

Hosts

A. tsugense infects a broad range of commercially important conifers in the Pacific Northwest (Mathiason 1994). The principal hosts are western hemlock, Pacific silver fir (*Abies amabilis* (Dougl.) Forbes), subalpine fir (*Abies lasiocarpa* (Hook.) Nutt. var. *lasiocarpa*), and noble fir (*Abies procera* Rehd.). Occasional hosts include grand fir (*Abies grandis* (Dougl.) Lindl.), and lodgepole pine (*Pinus contorta* Dougl. ex Loud. subsp. *latifolia* (Engelm. ex Wats.)). Rare hosts include western larch (*Larix occidentalis* Nutt.), Engelmann spruce (*Picea engelmannii* Parry), Sitka spruce, western white pine (*Pinus monticola* Dougl.), mountain hemlock, and Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii*).

In southeast Alaska, the primary host of hemlock dwarf mistletoe and the only tree species severely affected by the pathogen is western hemlock (Laurent 1974). Occasional infections reported on mountain hemlock (Shaw 1982b) and Sitka spruce (Laurent 1966) confirm the rare host status for these species (Mathiason 1994). Sitka spruce infection has been observed on three islands in southeast Alaska where intensive surveys have been completed (Hennon unpublished data). Mathiason (1994) reported that both Pacific silver fir and subalpine fir are principal hosts, however, the pathogen has not been observed in Alaska on either species. Hemlock dwarf mistletoe has also not been observed on shore pine, western redcedar (*Thuja plicata* Donn ex D. Don), or Alaska yellow-cedar (*Chamaecyparis nootkatensis* (D. Don) Spach) in Alaska.

Distribution

The range of hemlock dwarf mistletoe includes the coastal western hemlock-Sitka spruce forests of northern California, Oregon, Washington, British Columbia, and southeast Alaska (Hawksworth and Wiens 1972). The parasite is also found in parts of interior California and on the westside of the Cascade Mountains in Oregon and Washington. Although the range of western hemlock, the primary host, extends from northern California to southcentral Alaska and east into interior British Columbia, hemlock dwarf mistletoe does not occur in southcentral Alaska or interior British Columbia (Baranyay and Smith 1972, Drummond and Hawksworth 1979). Interruption of the mistletoe life cycle by abiotic factors may partly explain the observed distribution limits.

A region-wide elevation gradient appears to occur for the pathogen. In the central Sierra Nevada of California the pathogen occurs to about 2,470 m (Hawksworth and Wiens 1972). In British Columbia the pathogen occurs from sea level to about 1,500 m (Alfaro 1985) while in southeast Alaska the pathogen is most common from sea level to 150 m and rarely observed above 300 m (Drake 1915, Loomis and Hofacker 1981).

Pathogen distribution at the landscape level is uneven, with extensive areas lacking the pathogen. Surveys estimate 15 and 21 percent of coastal forest land contains the pathogen in British Columbia and Washington/Oregon, respectively (Bolsinger 1978, Alfaro 1985). In southeast Alaska the pathogen has been considered ubiquitous in old-growth forests but the actual distribution has not been determined (Laurent 1974).

Pathogen distribution at the stand level may be even or uneven depending on seed dispersal patterns (Smith 1973), the number and distribution of overhead inoculum sources within a stand (Stewart 1976, Smith 1977, Alfaro 1985), stand composition, stand density, and growth rate (Bloomberg and Smith 1982). Early reports of dwarf mistletoe in southeast Alaska noted that parasite infection in a stand varied from 30 to 80 percent (Drake 1915).

Signs and Symptoms of Infection

Hemlock dwarf mistletoe is a perennial parasitic vascular plant in the family Viscaceae dependent upon a living host for water and nutrition (Weir 1916, Hawksworth and Wiens 1972). The dwarf mistletoe plant is composed of two parts: a "root-like" system embedded in the host tissue, and small, dioecious, leafless, aerial reproductive shoots. The function of the endophytic "root" system is absorption and transfer of water and nutrients obtained from the host. The basally meristematic aerial shoots vary in length from 5 to 13 cm and in color from yellow-green to purple (Hawksworth and Wiens 1972). Female shoots produce fruits 3 mm in length and seeds 1 to 2 mm long, while male shoots produce clusters of spined pollen in a small flower (Hawksworth and Wiens 1972). After aerial shoot death, basal cups, remnants of the shoot meristematic tissue, may remain at the infection site for many years (Shea and Stewart 1972).

The most conspicuous symptoms of dwarf mistletoe infection are spindle shaped branch or twig swellings and palmate branch proliferations, or brooms, which occur at the infection site. Brooms can vary in size from several centimeters to over a meter in diameter and weigh several hundred kilograms. Dwarf mistletoe infection on the tree trunk or bole typically results in localized abnormal burl-like growth of the bole. The bole invasion site may serve as an entrance point for decay-causing fungi, and accelerate tree breakage and mortality (Shea and Stewart 1972).

Pathogen Life Cycle

The life cycle of hemlock dwarf mistletoe is initiated in late fall by explosive expulsion of seeds to a distance of 9 m from the source tree (Smith 1966). Seeds have been trapped up to 16 m away, but such distances are rare (Smith 1985). The seed, coated with sticky viscin cells, is intercepted most commonly by foliage or less commonly by twigs or branches. The transfer of seeds from needles to susceptible branch tissue is likely accomplished by rain wash. Throughout the winter, seeds adhere tightly to the branch until germination in spring. Germination is indicated by the emergence of a root-like structure called a radicle. The radicle elongates and forms a holdfast structure from which filaments develop, penetrate the host, and begin the infection process (Hawksworth and Wiens 1972). The parasite's endophytic system developing within the host consists of longitudinal strands in the cortex and phloem and radially-oriented sinker "roots" in the xylem (Alosi and Calvin 1984). The sinker "roots" do not actively penetrate wood but instead are embedded by successive layers of xylem tissue. Both the cortical strands and sinker "roots" serve as anchor and absorptive structures for the parasite.

Spindle shaped branch swellings occur at the infection site one to two years following infection. Aerial shoots, both male and female, appear in the third year. Pollination and fertilization occurs the fourth year, and mature fruit is discharged the fifth year. The life cycle of hemlock dwarf mistletoe, infection to initial seed production, can be as short as 4 years, but typically extends to 5 or 6 years (Baranyay and Smith 1972). Inoculation studies in southeast Alaska noted shoot production in a similar time span but seed production did not take place even after 12 years, suggesting a considerably longer life cycle in this region (Shaw and Loopstra 1991).

Dwarf mistletoes have features characteristic of both insect- and wind-pollinated plants (Hawksworth and Wiens, 1972). Research on the pollination biology of *A. americanum* (Nutt. ex Engelm.), *A. pusillum* (Peck), *A. vaginatum* subsp. *cryptopodum* (Engelm.), *A. cyanocarpum* (A. Nels.), *A. douglasii* (Engelm.), and *A. strictum* (Hawks. ex Wiens) indicated that both insects and wind contribute to pollination success, although not equally (Gregor et al. 1974, Penfield et al. 1976, Player 1979, Gilbert and Punter

1984, Baker et al. 1985). Nectar produced by the female flowers is likely a strong insect pollinator attractant (Brewer et al. 1974).

Minimal research has been conducted on the pollination biology of *A. tsugense*. In southeast Alaska, pollen is typically released in June and July (Hennon unpublished), and has also been observed in August. Pollen release appears to be associated with warm, dry weather. It is not known whether wind, insects, or a combination of the two are responsible for pollination of the female flowers. Casual observation suggested that, in southeast Alaska, flies in the family Anthomyiidae visit female flowers while carrying a few grains of pollen, and these events may contribute to the annual pollination success. Similar flies have been implicated as likely pollinators for *A. americanum* in the Rocky Mountains (Gregor et al. 1974, Penfield et al. 1976). Further study will help determine the importance of insects and wind for pollination of *A. tsugense* in southeast Alaska.

Host Resistance

Resistance to dwarf mistletoe infection is primarily expressed as reduced host susceptibility (Scharpf 1984). Determining resistance, however, has been a difficult task compounded by large geographic areas that contain uninfected susceptible host species. For example, western hemlock on the Pacific coast is heavily parasitized by *A. tsugense* while populations in southcentral Alaska or interior Canada remain free of the pathogen (Baranyay and Smith 1972, Drummond and Hawksworth 1979). Climatic factors that limit reproduction may play an important role in determining pathogen distribution at the landscape level.

Individual trees or groups of trees within a stand often escape infection, giving the appearance of resistance. In many cases, escape from infection can be explained by the lack of adequate levels of inoculum or the lack of a suitable target (Scharpf 1984). Many variables can reduce inoculum levels on a site including poor pollination rates, low temperature damage to fruits, and unusual seed distribution patterns (Smith 1973, Baranyay and Smith 1974). The lack of a suitable host target may occur through screening of the susceptible host by non-hosts or because the host target is too small. Non-host species in close proximity to infected trees can impede seed distribution by blocking spread to adjacent host trees (Parameter 1978). The likelihood that a seedling less than one meter tall will be hit by a dwarf mistletoe seed is extremely low (Wicker and Shaw 1967).

Evidence of resistance in western hemlock clones to hemlock dwarf mistletoe infection was found, although the mechanism was not determined (Smith et al. 1993). Resistance, observed as early death of the penetrating structure, appeared to be from a mechanism operating within, rather than outside, the host branch.

Host Impacts: Growth Loss and Mortality

Mistletoe infection in the upper tree crown has a greater impact on tree growth than infections lower in the crown (Richardson and van der Kamp 1972). On productive clear-cut sites in southeast Alaska, height growth of young hemlock trees can outpace dwarf mistletoe upward advance by a ratio of 2:1 (Shaw and Hennon 1991). Thus, little height or volume loss due to the pathogen occurs in these young thrifty stands. In contrast, hemlock trees that have reached their maximum height or hemlock trees growing beneath infected overstory trees are unable to outpace upward advance of dwarf mistletoe and may contain substantial numbers of dwarf mistletoe infections. Severe growth loss, mortality, and reduced wood quality have been shown to occur on heavily infected trees (Buckland and Marples 1952, Wellwood 1956, Smith 1969, Thompson et al. 1984, Alfaro et al. 1985).

Heavy dwarf mistletoe infection alters the specific gravity and moisture content of host tissue, and results in volume loss of mature trees (Wellwood 1956). Stem analysis of 110 year old hemlocks in western Canada indicated that lightly infected trees had 41 percent greater volume growth and 84 percent greater height growth as compared to heavily infected trees (Smith 1969). A second stem analysis study in the same region estimated volume losses in moderately and severely infected 45-80 year old hemlocks at

23 and 39 percent, respectively, as compared to healthy trees (Thompson et al. 1985). Although a large number of infections are needed to cause a significant impact on tree growth, up to 4,000 infections have been measured on a single hemlock (Bloomberg and Smith 1982). Cumulative mortality from dwarf mistletoe in western hemlock stands in south coast British Columbia ranged from 0-1.8 percent, averaging 0.6 percent per stand (Alfaro et al. 1985). Neither growth loss nor mortality estimates due to mistletoe infection have been calculated for western hemlock stands in southeast Alaska. Growth loss estimates on moderate and severely infected trees from stem analysis studies in western Canada (Smith 1969, Thompson et al. 1985) are generally accepted as appropriate for use in southeast Alaska.

Pathogen Spread and Intensification

Spread and intensification of hemlock dwarf mistletoe is complex and dependent on a number of factors including proximity of host tree to an inoculum source, vertical growth of host trees, and stand composition (Richardson and van der Kamp 1972, Bloomberg and Smith 1982, Smith 1985). The fate of dispersed seeds is determined by the location of the infection and the proximity of interception trees (Smith 1985). Infections located at the outer edge of the crown disperse approximately 70 percent of the seeds outward and 30 percent inward (Smith 1985). Successful seed escape for those dispersed outward occurs approximately 40 percent of the time. Any tree, host or non-host, within two or three meters of the source will intercept the majority of dispersed seeds. If the interception tree is a hemlock, reciprocal dispersal will likely occur between the trees. If the interception tree is a non-host species, spread will be prevented to adjacent trees.

Simulation models for the spread and intensification of dwarf mistletoe have been developed for *A. americanum* on lodgepole pine (Myers et al. 1971), *A. douglasii* (Engelm.) on Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) (Geils and Mathiason 1990), *A. vaginatum* subsp. *cryptopodum* on ponderosa pine (*Pinus ponderosa* Laws.)

(Dixon and Hawksworth 1979), *A. campylodum* (Engelm.) on ponderosa pine (Strand and Roth 1976), *A. tsugense* on western hemlock (Bloomberg et al. 1980). The models for species other than western hemlock were not considered suitable for use in this study due to host and pathogen differences.

The hemlock dwarf mistletoe spread and intensification model developed in western Canada may have limited applicability in this study. The western Canada model predicted that dwarf mistletoe infection level on second growth trees was proportional to the number of unmerchantable residual trees that remain on a site up to 30 years after clear-cut harvesting and inversely proportional to the percent of non-host species, density of second-growth trees, and growth rate of second-growth trees (Bloomberg and Smith 1982). It is possible and worth testing whether similar variables are important in the long-term spread and intensification of the pathogen in southeast Alaska. It is also likely, however, that differences in pathogen reproductive behavior between regions (Shaw and Loopstra 1991), differences in period of time since disturbance, and differences in model objectives will preclude use of the western Canada model for accurately predicting long-term pathogen behavior in partially disturbed stands in southeast Alaska.

Hemlock dwarf mistletoe research in Washington, Oregon, and British Columbia indicates aggressive spread and intensification of the pathogen from infected residual trees to young-growth hemlock trees. Dwarf mistletoe infections on a host species may double approximately every four years and advance at an upward rate of slightly less than one meter per year (Richardson and van der Kamp 1972). Eighty percent of the regeneration beneath a heavily infected hemlock tree may contain the pathogen after 25 years of exposure (Stewart 1976). Additionally, in British Columbia heavy infection of all regenerating hemlock trees on a hectare is predicted to occur from 86 evenly scattered heavily infected overstory trees (Smith 1977).

In southeast Alaska, research indicates slower spread rates and less pathogen intensification following clear-cut harvest operations. Dwarf mistletoe spreads horizontally from infected non-merchantable hemlocks left in a stand after harvest operations. The vertical spread, or upward advance, of the dwarf mistletoe is usually slower than the growth of hemlock regeneration (Shaw 1982a, Shaw and Hennon 1991).

Over time, the parasite becomes relegated to the lower one-third of the live tree crown. As canopy closure continues, lower branches of the live crown and the dwarf mistletoe infections become shaded and die. Parasite introductions from trees remaining on clear-cut edges or introductions from birds or mammals are not expected to be substantial over a forest rotation (Shaw and Hennon 1991).

Research in southeast Alaska indicates substantially less spread and intensification of hemlock dwarf mistletoe following clear-cut harvesting operations than encountered in other parts of the Pacific Northwest and little likelihood that the pathogen will intensify to damaging levels over a 90-120 year forest rotation period (Shaw 1982a, Shaw and Hennon 1991). No information is currently available on the long-term spread and intensification of dwarf mistletoe in uneven-aged forests in southeast Alaska. Long-term pathogen spread and intensification information is critical for forest managers who need to make decisions on the number and condition of retained trees in managed stands.

Pathogen Management

Dwarf mistletoes have been easy to control and often eliminate from young-growth stands because of limited seed dispersal distance, living host specificity, and easy detection of the parasite. In Washington, Oregon, and British Columbia dwarf mistletoe control has been accomplished through removal of infected overstory trees during clear-cut harvesting and, when necessary, by a separate stand entry within 5 years after logging to girdle or remove infected unmerchantable hemlocks remaining in a stand (Baranyay and Smith 1972). Removal of all trees greater than 3 m in height during harvesting operations and laying out unit boundaries so as to minimize the number of infected trees along the stand perimeter is standard dwarf mistletoe control practice in western Canada (Muir 1985).

In the past, Region 10-Alaska Forest Pest Management (FPM) Guidelines have recommended hemlock dwarf mistletoe control through clear-cut harvesting and by removal of infected unmerchantable residual hemlock trees and favoring Sitka spruce during pre-commercial thinning operations which occur 12-20 years following stand establishment (USDA, 1984). The most recent Forest Plan for the Tongass National Forest dictates that 2,500 ha/year of young-growth stands receive pre-commercial thinning (USDA, 1979). If the lands received thinning as scheduled, approximately 50,000 ha have been thinned and infected residual hemlocks killed in young-growth stands since 1980. Region 10-Alaska FPM Guidelines have recently been updated to allow retention of dwarf mistletoe infected hemlock trees as needed to meet management goals (Paul Hennon, pers. comm. 1996).

Dwarf Mistletoe Effects on Community Ecology

The ecological importance of dwarf mistletoes in a forest is primarily attributed to the formation of large branch proliferations, or brooms (Tinnin et al. 1982). Broom formation may alter structure and function of individual host trees and change forest community dynamics by destabilizing host stands through increased host tree mortality (Tinnin et al. 1982, Tinnin 1984). Many species of wildlife take advantage of dwarf mistletoe brooms as nesting or resting sites (Tinnin et al. 1982, Bull and Henjum 1990, Bennetts 1991) and utilize the plant as a food source (Beer 1943, Baranyay 1968, Tinnin et al. 1982, Linhart et al. 1989). Although little is known regarding the ecological importance of hemlock dwarf mistletoe in southeast Alaska, it is assumed to be a contributor to wildlife nesting sites, bird and mammal food, and enhanced forest structural diversity as is reported for other dwarf mistletoe species in the Pacific Northwest (Beer 1943, Baranyay 1968, Tinnin et al. 1982, Tinnin 1984, Linhart et al. 1989, Bull and Henjum 1990, Bennetts 1991).

Resource managers have historically sought elimination of dwarf mistletoe from areas managed for timber production because of the concern that the parasite would cause unacceptable forest production losses. Severe growth loss, host mortality, and decreased wood quality have been documented in heavily infected trees in the Pacific Northwest (Buckland and Marples 1952, Wellwood 1956, Smith 1969). In southeast Alaska, however, parasite behavior appears less aggressive (Drummond and Hawksworth 1979, Shaw 1982a, Shaw and Hennon 1991), allowing increased opportunity for alternative pathogen management strategies. Although the desired level of the parasite within managed forests is dependent on management goals, moderate to low parasite levels may enhance structural and biological diversity and minimize growth loss in developing trees.

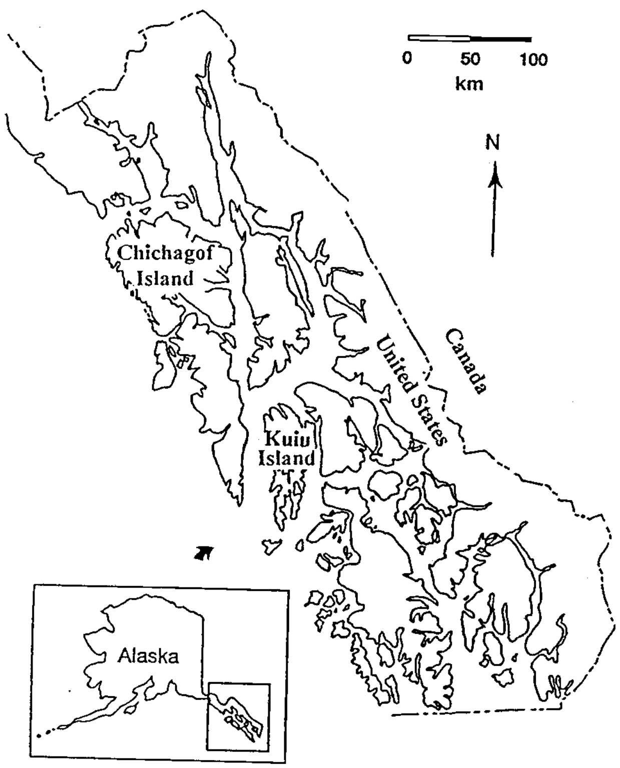
Chapter 2. Methods

EXPERIMENTAL DESIGN

Stand Selection

In June-September of 1994 and 1995, field plots were established on two islands in southeast Alaska, Kuiu and Chichagof (Figure 1). These islands were chosen for study because wind disturbed stands of multiple ages and sizes had been located through aerial photo analysis and entered into the USDA Forest Service Geographic Information System (GIS) database. GIS maps detailing hundreds of wind disturbed stands of multiple ages and sizes on both islands greatly assisted preliminary stand reconnaissance.

Figure 1. Location of Kuiu and Chichagof Island in southeast Alaska



Stands that experienced extensive windthrown in the past on Kuiu and Chichagof Island were selected for study based on the following criteria: 1. contained hemlock dwarf mistletoe, 2. were disturbed by wind 90-120 years ago, 3. could be stratified into areas of partial and complete disturbance, and 4. were at least one hectare in size. Eight stands ranging from 1.5 to 20.5 ha were selected on Kuiu Island; two stands approximately 5.0 ha were selected on Chichagof Island (Table 1).

Table 1. Legal description, area, estimated year of wind disturbance, and number of plots in each residual tree category (0, 1, >1) for eight stands on Kuiu Island (1-8) and two stands (9-10) on Chichagof Island.

		Area	Estimated	Number of Plots[1]		
Stand	**Legal Description**	**(ha)**	**disturbance yr.**	**0**	**1**	**>1**
Kuiu Is.						
1	T58S, R71E, S22	20.5	1885	3	3	5
2	T59S, R72E, S2	4.0	1884	3	3	3
3	T58S, R72E, S26	1.5	1886	3	3	3
4	T59S, R72E, S9	7.3	1881	3	3	3
5	T60S, R71E, S3	3.6	1880	3	3	4
6	T59S, R71E, S28	3.6	1888	3	3	3
7	T59S, R72E, S11	5.3	1884	3	3	3
8	T59S, R72E, S11	4.5	1883	3	4	3
Chichagof Is.						
9	T45S, R62E, S16	4.9	1876	3	3	3
10	T46S, R63E, S2	5.0	1878	3	3	3

[1] Plots were stratified by the number of residual trees that survived the storm: 0 = no surviving residual trees, 1 = one residual tree per plot, >1 = 2 to 5 residual trees per plot.

The year of catastrophic windthrow for each stand was estimated through analysis of increment cores from at least five trees per stand. Increment cores were examined for evidence of a release pattern or wide annual rings in the late 1880's which were preceeded by a series of tight annual rings. For each tree, the year prior to release was estimated as the most likely year of catastrophic disturbance. Since a narrow range of apparent release dates occurred, the mode of dates within each stand was used to estimate the year of catastrophic wind disturbance. For example, increment cored trees in Stand 1 on Kuiu Island exhibited clear release patterns from 1873 to 1897, the mode of the release dates was 1886, and the year of catastrophic wind disturbance was estimated as 1885.

Plot Selection

At least nine 10-m radius circular plots, 1/32 hectare, were located in each stand. Three plots in each stand contained zero residual trees, at least three contained one residual tree, and at least three contained two to five residual trees. Herein, these plots will be referred to as zero residual (0R), one residual (1R), and greater than one residual (>1R) plots with the "R" referring to residual trees. Residual trees were defined as trees that survived the catastrophic wind disturbance, were at least 20.0 cm diameter at that time, and contained past and/or present evidence of hemlock dwarf mistletoe infections.

Stands on both islands were stratified in an initial walk-through into areas where zero, a low density, and a high density of residual trees survived the late 1800's catastrophic windstorm. Within each stratum plots that contained the desired density of residual trees were located by blindly tossing a flagged stick to establish plot center and measuring a 10 m radius from center. Plots were not located in areas that had sustained more recent wind disturbance and, where possible, were located at least 40 meters apart.

Increment core analysis assisted in identifying residual trees and thus, in determining plot type. Since it was not feasible to bore all trees on a plot, those with the largest diameters and all trees with diameter at breast height (DBH) greater than 60 cm were assumed to be residual trees and were bored for verification. Trees were bored one meter above root crown using a manual increment borer; cores were briefly examined, sealed in a straw, labeled, and analyzed in the laboratory at a later date. During laboratory analysis, cores were measured for tree diameter at the year of catastrophic wind disturbance. Core analysis revealed more residual trees than expected, resulting in more than three plots in some stands for the 1R and >1R plot types and fewer than three plots in the 0R plot type. Since at least three plots of each type were desired, four extra plots, each containing the desired number of residuals, were located within the appropriate stand and added to the data set (Table 1).

DATA COLLECTION

Tree Characterization

All plot trees with a current DBH greater than 10 cm were labeled with a metal tree tag and sketch mapped for use in future growth loss and mortality studies. Trees with a DBH less than 10 cm were ignored because they were likely post-disturbance hemlock trees less than 90 years old, too young to be included in the study. Data recorded for plot trees included: species, DBH, estimated height (nearest m), age and diameter at time of catastrophic windthrow (for trees that were increment bored), and a tree classification of residual, advanced regeneration, or post-disturbance (Appendix Table 3).

A residual tree was defined as a tree that survived the catastrophic wind disturbance, was at least 20.0 cm diameter at that time, and contained past and/or present evidence of hemlock dwarf mistletoe infections. An advanced regeneration tree was defined as tree that survived the catastrophic wind disturbance, was 1.0 to 19.9 cm diameter at that time, and contained past and/or present evidence of hemlock dwarf mistletoe infections. A post-disturbance tree was defined as a tree that established soon after the catastrophic wind disturbance or was less than 1.0 cm diameter at that time. A post-disturbance tree may or may not have contained evidence of past or present hemlock dwarf mistletoe infection.

A preliminary tree classification of residual, advanced regeneration, or post-disturbance was made in the field based on tree size and appearance. All trees with a current DBH greater than 60 cm or suspected to be residual trees were increment cored at one m above root crown for confirmation. Since it was not feasible to increment core all other trees on a plot, the plot center tree and 1-5 of the largest diameter trees were cored to determine plot age-diameter relationships for advanced regeneration and post-disturbance hemlock trees.

On Kuiu Island a total of ninety-four residual trees, ninety-six advanced regeneration trees, and ninety-eight post-disturbance hemlock trees were bored and cores were retained. Cores were briefly examined in the field and tree classification assignments were made for the bored trees. Cores were sealed in straws and retained for further lab analysis at a future date. Assignment of tree classification to non-bored trees was accomplished through development of plot DBH ranges of bored post-disturbance hemlock and advanced regeneration trees. The non-bored trees were assigned a tree classification according to whichever DBH range they best fit. In general, residual trees had the largest diameters (>60 cm), post-disturbance hemlock trees had the smallest (<45 cm), and advanced regeneration were intermediate (45 to 60 cm).

Residual and advanced regeneration trees within 10 m of the plot boundary that contained visible dwarf mistletoe infections were counted and measured. Data recorded for these trees included: DBH, estimated height, tree classification (residual or advanced regeneration), and distance to plot center. Each of these trees was increment cored to facilitate tree classification.

Dwarf Mistletoe Characterization

The dwarf mistletoe component of trees within a plot and residual and advanced regeneration trees outside a plot was measured through assignment of a live crown dwarf mistletoe rating and a dwarf mistletoe below-live-crown rating, estimation of height to lowest dwarf mistletoe infection, and estimation of height to dwarf mistletoe bole infections (Appendix Table 3). Additionally, distance from plot center to nearest dwarf mistletoe inoculum source within the plot was estimated from the plot sketch map (Appendix Table 2).

Dwarf mistletoe rating (DMR) followed the 6-point system (Hawksworth 1977) which assigns a 0, 1, or 2 rating to each third of the live crown based on the number of visible dwarf mistletoe infections: 0 = no infections on any branches, 1 = less than 50 percent of the branches have infections, 2 = more than 50 percent of the branches have infections. For each plot tree, live crown ratings were recorded separately for each crown third and summed for a tree rating.

A single dwarf mistletoe rating (0-2) was also assigned to live and dead branches below the live crown. For this study, the live crown extended from the height of the lowest two live branches to the top of the tree. All branches below the live crown were assessed as a unit: 0 = no infections on any branches, 1 = less than 50 percent of the branches contained evidence of past or present dwarf mistletoe infection (branch swellings or brooms), 2 = more than 50 percent of the branches contained evidence of past or present dwarf mistletoe infections.

Site Characterization

Site data collected for each plot included elevation (measured with an altimeter), aspect, percent slope, plant association series, and site index (Appendix Table 2). Plant association classification followed the series keys developed by the Stikine Area, Tongass National Forest (Pawuk and Kissinger 1989) which determined the dominant overstory and understory plants. The three plant associations that occurred in stands on Kuiu and Chichagof Island were coded as follows: 1 = western hemlock-blueberry series, 2 = western hemlock-blueberry-devils club series, and 3 = western hemlock-blueberry-shield fern series. Site index was defined as the height of a 100 year old Sitka spruce tree (Farr and Harris 1979). For plots that lacked a 100 year old Sitka spruce tree, site index was determined from the plant association series key which estimated site index (Pawuk and Kissinger 1989).

The aspect data were converted to a measure of heatload based on a 9-point scale that related aspect to soil moisture status (Whittaker 1960, Muir and Lotan 1985). The scale was not symmetrical north to south because it was adjusted for the portion of the day that direct solar radiation was received. North-northeast was ranked the most mesic site and south-southwest was ranked the most xeric site. In general, northern aspects were considered mesic while southern aspects were considered xeric. The complete ranking from mesic (1) to xeric (9) was as follows: 1 = NNE; 2 = NE, N; 3 = ENE, NNW; 4 = E, NW; 5 = ESE, WNW; 6 = SE, W; 7 = SSE, WSW; 8 = S, SW; 9 = SSW.

DATA ANALYSIS

Stand Characterization

Tree Core Analysis

Increment cores from trees on Kuiu Island were briefly analyzed in the field, sealed in straws, labeled, and transported to Corvallis, Oregon for further analysis. In the laboratory, cores were removed from the straws, wetted with distilled water in order to make ring patterns visible, and rings counted using a dissecting microscope. One ring was counted as one year of tree age because neither western hemlock nor Sitka spruce commonly develop more than one annual ring per year or do not develop an annual ring (William Wilson, pers. comm. 1994). Increment cores from trees on Chichagof Island were measured in the field.

Analysis of tree cores from both islands allowed determination of tree diameter at the time of disturbance and total tree age. Cores were examined for age and the presence of a ring release pattern approximately 110 years ago. The release pattern was a reliable visual cue for quickly distinguishing whether a tree was present prior to the catastrophic disturbance. Post-disturbance hemlock trees did not contain the release pattern because they established after the late 1800's windthrow events.

The release pattern appeared approximately 110 years ago as a series of tight annual rings, denoting slow diameter growth, immediately followed by a series of annual rings at least twice as wide, denoting faster diameter growth. This pattern suggested that prior to wind disturbance the canopy was closed, competition for light and nutrients among trees was keen, and annual tree diameter growth was slow. Catastrophic windthrow occurred, creating large canopy gaps with uprooted or damaged trees. Reduced competition for resources, including light and nutrients, allowed residual and advanced regeneration trees that survived the storm to rapidly increase height and diameter growth. Canopy closure within the gap did not recur for many years, evidenced by a long period of more rapid growth, an average of 61 years for residual trees and 66 years for advanced regeneration trees (Table 5).

Tree diameter at the time of catastrophic windthrow was recorded as twice the distance from the pith to the onset of release. If a core missed the pith but a concentric ring pattern was present, the pith was assumed to be the mid-point of the concentric rings. If a core did not reach the pith because of rot, disturbance diameter was reconstructed by subtracting the diameter measurement of growth since wind disturbance from current tree diameter.

Total tree age was useful for distinguishing advanced regeneration trees that did not contain a release pattern from post-disturbance hemlock trees and to determine plot site index. An auxiliary study on six recently dead and down hemlock trees helped to determine how many rings were missed by coring at one meter above root crown. For each tree, cores were taken at 30 cm intervals from the base of the tree up to one meter. Results indicated that estimates of tree age required a minor correction of approximately four years.

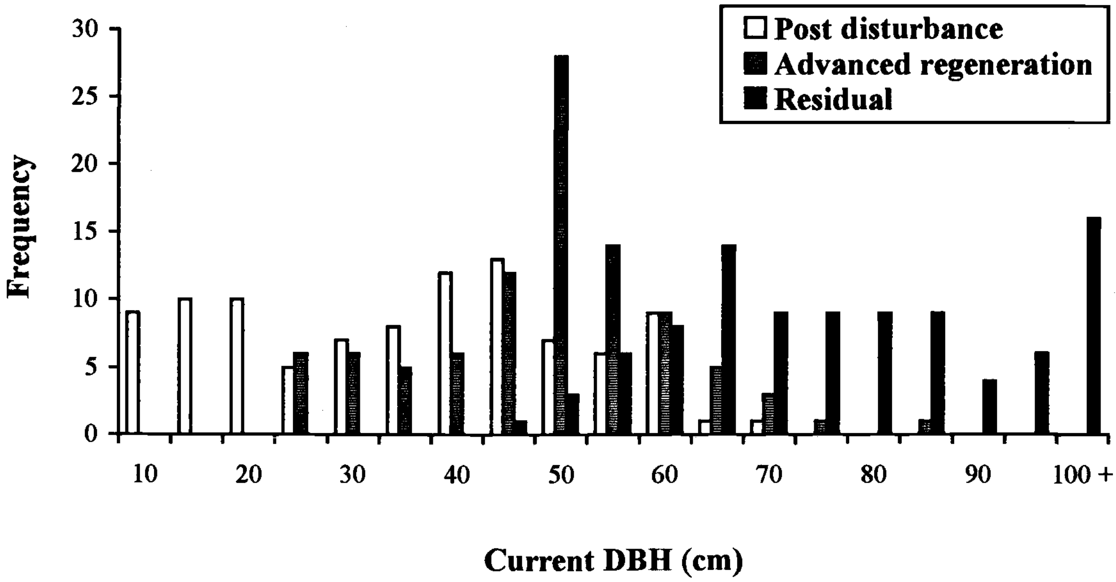
Final Assignment of Tree Classification

Laboratory increment core analysis for trees on Kuiu Island revealed that some field assignments of bored trees were wrong, indicating that some assignments of non-bored trees were also wrong. As a result, tree classification assignments for each plot tree were re-examined. In the re-examination 66 of 1,279 hemlock trees, ranging in current DBH from 39.5 to 53.5, could not be confidently classified as either advanced regeneration or post-disturbance because the current DBH ranges of both tree classifications overlapped. Post-disturbance hemlock tree current DBH ranged from 10 to 70 cm, while advanced regeneration tree current DBH ranged from 25 to 85 cm.

While the 66 hemlock trees with questionable classifications represented only 6 percent of the total post-disturbance hemlock tree population, they represented 56 percent of the total advanced regeneration tree population. Since proper assignment of tree classification was crucial to modeling spread of the pathogen from infection sources to post-disturbance hemlock trees, three analyses were used to determine final tree classification for the hemlock trees with a questionable classification on Kuiu Island. The three analyses were current DBH comparisons, bole infection comparisons, dwarf mistletoe below-live-crown rating comparisons.

A frequency graph of current DBH for all bored hemlock trees on Kuiu Island was developed to establish age-diameter relationships for post-disturbance and advanced regeneration trees (Figure 2). Residual trees are included in the graph for comparison. Trees with current DBH > 50 cm were four times more likely to be advanced regeneration than post-disturbance (Figure 2). Therefore, all hemlock trees with a questionable classification that had a current DBH > 50 cm were classified as advanced regeneration. No consistent age-diameter relationships occurred for hemlock trees with current DBH 35-50 cm (Figure 2).

Figure 2. Frequency distribution of current DBH (cm) for increment bored residual, advanced regeneration, and post-disturbance hemlock trees on Kuiu Island.



A comparison of the frequency of dwarf mistletoe bole infections between tree classifications revealed that advanced regeneration were four times more likely to have bole infections than post-disturbance hemlock trees (Table 2). Thus, hemlock trees with a questionable classification that had a current DBH < 50 cm and contained bole infections were classified as advanced regeneration trees.

Finally, a comparison of dwarf mistletoe below-live-crown ratings between tree classifications revealed that advanced regeneration trees were two times more likely to have a rating of 2 than post-disturbance hemlock trees (Table 2). Thus, hemlock trees with a questionable classification that had a current DBH < 50 cm and had a rating of 2 on branches below-live-crown were classified as advanced regeneration trees. The remainder of the hemlock trees with a questionable classification were considered post-disturbance hemlock trees. The final classification of the 66 hemlock trees with a questionable classification was 37 advanced regeneration and 29 post-disturbance hemlock trees.

Table 2. Percent of hemlock trees with bole infections and with 0, 1, or 2 dwarf mistletoe below-live-crown rating for increment bored residual, advanced regeneration, and post-disturbance trees, and hemlock trees with a questionable classification on Kuiu Island.

Tree classification	Bole infections	Dwarf mistletoe below-live-crown rating: 0	1	2
Residual	21	18	7	75
Adv. regeneration	26	18	31	51
Post-disturbance	7	38	40	22
Questionable	23	23	38	39

Dwarf Mistletoe Component

The live crown DMR for all post-disturbance hemlock trees with a DBH >10 cm in a plot was calculated as a plot mean and used as the dependent variable for multiple linear regression model development and to graphically display dwarf mistletoe spread to and intensification on post-disturbance hemlock trees.

The dwarf mistletoe below-live-crown rating for residual and advanced regeneration trees was used as a rough estimate of dwarf mistletoe infection level on these trees in the late 1800's. Since infections are usually initiated on young tissue less than 5 years old (Baranyay and Smith 1972), infections noted below the live crown developed when that section of the tree contained needles and was part of the live crown. Although the number of branches that have fallen off over the last century can not be quantified, it is reasonable to assume that if the remaining branches contain numerous old infections the tree was likely heavily infected 100 years ago (live crown DMR = 5 or 6). Likewise, few old infections may equate to moderate infection levels (live crown DMR = 3 or 4), and no visible infections may equate to light or no infection 100 years ago (live crown DMR = 0, 1, or 2).

Model Development

Selection of Variables

Multiple linear regression was used to develop a mathematical model that predicted the mean DMR of post-disturbance hemlock trees within a plot based on plot, site, and tree variables on Kuiu Island. Generality of the model was tested with data from plots on Chichagof Island.

The response or dependent variable for the model was the mean DMR of post-disturbance hemlock trees within a plot. The explanatory or independent variables tested for inclusion in the model included plot, site, and tree variables (Table 3). All tree variables, except for number of stems, were calculated as plot means.

Forward and backward variable selection procedures were used to develop a pool of preliminary models. In both selection procedures an iterative scheme tested whether the coefficient for explanatory variables was significantly different from zero through the calculation of an F-statistic. An F-statistic of 4.0 was pre-chosen as significant because this value roughly corresponds to two-sided $P = 0.05$, and an α value of 0.05 was chosen as the significance level. All reported P-values are two-sided. Since forward and backward selection may yield different models, both procedures were utilized during preliminary model development.

Preliminary Model Development

Forward and backward stepwise regression indicated that measures of residual and advanced regeneration density (basal area, percent, and number per plot) had significant explanatory power. Residual and advanced regeneration DMR also had significant explanatory power and these two variables alone explained most of the variation in mean DMR of post-disturbance hemlock trees within a plot. Elimination of density variables,

Table 3. Notation and description of plot, site, and tree explanatory variables.

Explanatory Variable	Description
Plot	
Distance.residual	distance from plot center to nearest infected residual tree (m)
Distance.advregen	distance from plot center to nearest infected adv. regeneration tree (m)
Distance.anyinoc	distance from plot center to nearest inoculum source, residual or advanced regeneration (m)
Site	
Elevation	elevation (m)
Htload	aspect (ranked 1-9)[2]
Slope	percent slope (%)
PAssoc	plant association series (ranked 1-3)[3]
SIndex	site index (ft)
Tree	
BA.residual	mean basal area of residual trees (m^2/plot)
BA.advregen	mean basal area of adv. regeneration trees (m^2/plot)
BA.spruce	mean basal area of Sitka spruce trees (m^2/plot)
BA.post	mean basal area of post-disturbance hemlock trees (m^2/plot)
Pct.residual	mean percent of residual trees (% of plot trees classified as residual)
Pct.advregen	mean percent of advanced regeneration trees (% of plot trees classified as advanced regeneration)
Pct.spruce	mean percent of Sitka spruce trees (% of plot trees classified as spruce)
Pct.post	mean percent of post-disturbance hemlock trees (% of plot trees classified as post-disturbance)
Stems.residual	number of residual trees (#/plot)
Stems.advregen	number of advanced regeneration trees (#/plot)
Stems.spruce	number of Sitka spruce trees (#/plot)
Stems.post	number of post-disturbance hemlock trees (#/plot)
DMR.residual	mean current live crown DMR of residual trees (rated 0.0-6.0)
DMR.advregen	mean current live crown DMR of advanced regeneration trees (rated 0.0-6.0)

[1] Dwarf mistletoe ratings (DMR) followed the 6-point system (Hawksworth 1977).
[2] Aspect rankings followed the 9-point scale for heatload status (Whittaker 1960, Muir and Lotan 1985).
[3] Plant association rating followed series keys (Pawuk and Kissinger 1989).

however, weakened the applicability of the model for managers interested in understanding how retention of various densities of inoculum sources will affect pathogen spread and intensification. To address this problem, explanatory variables were created that multiplied the density and DMR for residual and advanced regeneration trees within a plot.

Three preliminary models (A, B, and C) were developed that utilized the combined explanatory variables as a foundation (Table 4). Each model contained two variables, one that described residual tree density and DMR and one that described advanced regeneration tree density and DMR. Explanatory variables for residual and advanced regeneration trees were described as the number per plot in Model A (Stems.residuals * DMR.residuals and Stems.advregen * DMR.advregen), as the basal area per plot in Model B (BA.residuals * DMR.residuals and BA.advregen * DMR.advregen), and as the percent of plot trees in Model C (Pct.residuals * DMR.residuals and Pct.advregen * DMR.advregen) (Table 4).

Table 4. Significance levels (*P*) for explanatory variables and explained variation in mean DMR of post-disturbance hemlock trees within a plot (R^2) for three preliminary multiple linear regression models A, B, and C.

Model Description	*P*	R^2
A. Stems.residuals * DMR.residuals	<0.001	0.48
Stems.advregen * DMR.advregen	<0.001	
B. BA.residuals * DMR.residuals	<0.001	0.41
BA.advregen * DMR.advregen	<0.001	
C. Pct.residuals * DMR.residuals	<0.001	0.41
Pct.advregen * DMR.advregen	<0.001	

Since sampling was nested, plots occurred within stands, Models A, B, and C were tested for stand effects with an indicator variable "STAND" to ensure that relationships were consistent among stands. Stand effects are a violation of sample unit independence, which is an assumption of the multiple linear regression model. In the presence of stand effects, explanatory variable estimates are considered unreliable because variable relationships can not be generalized across stands. As a result, plots from one stand may be more similar to each other than to plots from another stand, requiring separate models to be developed for each stand. The lack of plot independence may be essentially ignored if stand effects do not occur.

Stand effects did not occur in Model A (STAND $P = 0.206$), but did occur for Models B and C (Model B STAND $P = 0.026$, Model C STAND $P = 0.035$). Since stand effects occurred for Models B and C, variable estimates were considered unreliable and neither model was given further consideration. Model development continued with Model A only.

Refinement of Preliminary Model

Additional explanatory variables that were added to Model A were checked for significance, model contribution, and stand effects using a conditional sum of squares analysis of variance (CSS ANOVA), component effects plots, and extra sum of squares F-tests (ESS F-test). The CSS ANOVA table displayed the amount of explained variation and significance level for model explanatory variables in the order fitted. Explanatory variables may be eliminated from a model if a variable is non-significant in the CSS ANOVA table (Ramsey and Schafer 1995). Explanatory variables were checked for stand effects with the indicator variable STAND, as described above. If stand effects occur, the explanatory variable may be eliminated from a model (Ramsey and Schafer 1995). The component effects plot approximates the response variable as a separate linear function of each explanatory variable. Explanatory variables may be eliminated from the model if the component effects plot indicates little or spurious explanatory power (Ramsey and Schafer 1995). The ESS F-test determines whether an explanatory variable adds significantly to the variation explained by the model. An ESS F-test $P > 0.05$ indicates that the variable does not contribute significant explanatory power to the model and may be eliminated (Ramsey and Schafer 1995).

Model Validity

The validity of a multiple linear regression model is dependent on the variables meeting four assumptions: linearity, homogeneity of variance, normality, and sample independence. A linear equation was adequate to express the model relationship (ANOVA $P = <0.001$) (Table 12). In scatterplots, the spread of the response variable was roughly the same across the X-axis without outlying observations, indicating homogeneity of variance. Populations of explanatory variables were roughly normally distributed in frequency distributions and the model residual plot also appeared normal. Correlations among explanatory variables were low, hence multicollinearity was not a problem.

Sample independence, however, was not met because plots were nested within stands, and therefore not independent of one another. The lack of plot independence may be effectively ignored if stand effects did not occur. Preliminary analysis indicated that stand effects did not occur and data from the Kuiu Island stands were combined to create a single model rather than eight separate stand models (STAND $P > 0.05$, extra-sum-of-squares F-test). Stand effects did not occur in final model (STAND $P = 0.206$). The lack of true sample independence, however, dictates that model coefficients and their confidence intervals should be interpreted with caution.

Data from 18 plots in two stands on Chichagof Island served as a check on the generality of the hemlock dwarf mistletoe model developed on Kuiu Island. Stand effects occurred on Chichagof Island (STAND $P = 0.003$) hence, fit of the variables from the Kuiu model was tested separately for each stand on Chichagof Island (Tables 13 and 14).

Chapter 3. Results

STAND CHARACTERIZATION

Stand Condition Before Catastrophic Windthrow

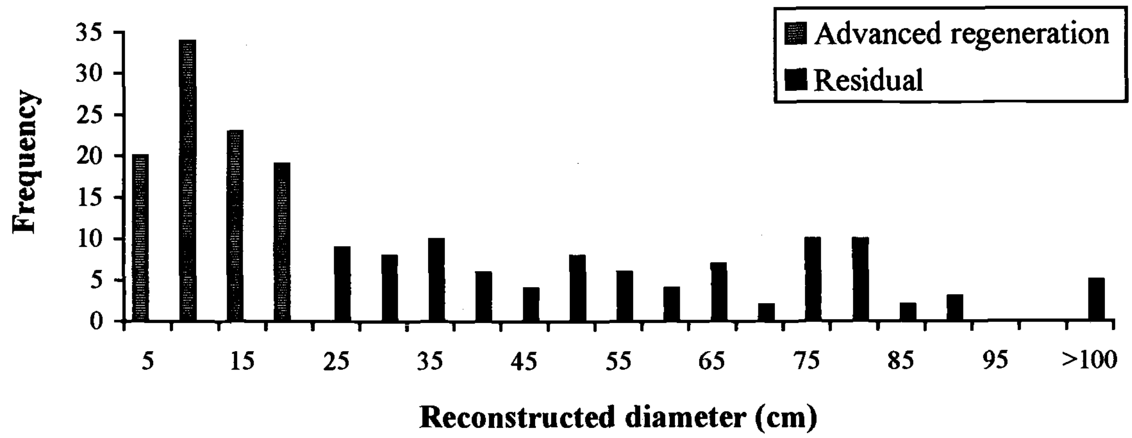
Prior to the major storm events in the late 1800's, stands on Kuiu Island were likely old-growth forests as evidenced by age, diameter, and height ranges of the oldest live hemlock trees (Appendix Table 1). The observed wide range of age (308 to 451 years old), diameter (41.6 to 123 cm), and height (28 to 48 m) for the oldest hemlocks was likely as dramatic 110 years ago and is indicative of old-growth forest structure (Appendix Table 1) (Alaback 1982). Additionally, short release patterns from 1670-1873 observed in increment cores from the oldest live hemlock trees suggested that small openings periodically occurred in the overstory canopy, a pattern also indicative of old-growth forest structure (Appendix Table 1) (Alaback 1982).

Stand Condition After Catastrophic Windthrow

All stands on both islands experienced catastrophic windthrow from severe storms in the late 1800's. As a result, each stand contained areas where no residual trees survived and areas where some density of residual trees survived. In the former case, the area presently contains post-disturbance hemlock trees and may contain some advanced regeneration trees. In the latter case, the area presently contains post-disturbance hemlock and residual trees and may contain some advanced regeneration trees.

Although the distributions of residual and advanced regeneration tree diameter in the late 1800's appeared continuous (Figure 3), substantial differences in mean diameter at disturbance and predicted height between tree classifications suggested that each could be tested separately to determine their contribution to the mean DMR of post-disturbance hemlock trees within a plot. On Kuiu Island, residual and advanced regeneration tree average diameter in the late 1800's was 55 cm and 10 cm, respectively, while on Chichagof Island they were 50 cm and 18 cm, respectively (Table 5). Diameter/height yield tables (Barnes 1962) predicted residual tree height at disturbance on both islands was 37 m while predicted advanced regeneration disturbance height was 10 m on Kuiu and 17 m on Chichagof Island.

Figure 3. Reconstructed diameter distributions at the time of wind disturbance (1880-1886) for 94 residual and 96 advanced regeneration trees in eight stands on Kuiu Island.



All plot types on Kuiu Island contained a greater number of dwarf mistletoe source trees/ha (including both residual and advanced regeneration trees) than plots on Chichagof Island. The mean number of inoculum sources trees in the 0R, 1R, and >1R plots on Kuiu Island was equitable to 47, 92, and 149 inoculum source trees/ha, respectively (Table 6). The mean number of inoculum source trees in the 0R, 1R, and >1R plots on Chichagof Island was equitable to 0, 43, and 69 inoculum source trees/ha, respectively (Table 6). Differences in the number of inoculum source trees/ha between islands can largely be accounted by the presence of advanced regeneration trees in all plot types on Kuiu Island.

On Chichagof Island, advanced regeneration trees were only found in the 1R plot type. The lack of advanced regeneration trees in plots on Chichagof Island may be due to differences in disturbance intensity or disturbance history in stands on both islands.

Table 5. Estimated date of catastrophic windthrow, diameter of surviving trees at release (range in parentheses), and duration of release growth for residual and advanced regeneration trees in eight stands (1-8) on Kuiu Island and two stands (9-10) on Chichagof Island.

Stand	Tree classification	n	Year of windthrow	Diameter (cm) at release (range)	Duration of release (yrs)
1	residual	13	1885	46 (22-123)	39
	adv regeneration	14	1885	8 (3-18)	59
2	residual	11	1883	55 (20-128)	87
	adv regeneration	32	1884	12 (4-19)	47
3	residual	12	1894	52 (26-78)	72
	adv regeneration	10	1887	10 (3-16)	36
4	residual	12	1889	51 (23-103)	44
	adv regeneration	20	1886	9 (2-19)	80
5	residual	15	1890	57 (22-117)	91
	adv regeneration	18	1881	8 (1-17)	70
6	residual	12	1891	43 (23-81)	81
	adv regeneration	19	1888	14 (7-19)	96
7	residual	9	1889	68 (49-88)	59
	adv regeneration	19	1889	9 (3-18)	75
8	residual	11	1889	61 (28-79)	15
	adv regeneration	22	1886	8 (3-19)	66
9	residual	10	1876	53 (26-86)	n/a[2]
	adv regeneration	0	-[1]	-	n/a
10	residual	9	1878	47 (22-76)	n/a
	adv regeneration	2	1878	18 (18-19)	n/a
Means Kuiu	residual			55	61
	adv regeneration			10	66
Means Chichagof	residual			50	n/a
	adv regeneration			18	n/a

[1] No advanced regeneration trees were examined in Stand 9.

[2] The number of years released was not collected for trees on Chichagof Island.

The mean number of post-disturbance hemlock trees/ha was greater in all plot types on Chichagof than on Kuiu Island (Table 6). Opposing trends appeared to occur on each island for establishment of post-disturbance hemlocks in the presence of overstory remnant trees. On Chichagof Island, the number of post-disturbance hemlock trees/ha was similar across all plot types while on Kuiu Island, the mean number of post-disturbance hemlock trees/ha was highest in plots that lacked residual trees and lowest in plots that contained the greatest number of residual trees (Table 6).

Table 6. Mean number and standard deviation (in parentheses) of trees/ha for residual, advanced regeneration, and post-disturbance hemlock trees, Sitka spruce trees, and total trees by plot type across all stands on Kuiu and Chichagof Island.

Location	Plot type	Residual/ha	Advanced regen./ha	Post disturbance/ha	Sitka spruce/ha	Total trees/ha
Kuiu Island	0	0 (0)	47 (59)	507 (247)	108 (112)	662 (250)
	1	32 (0)	60 (62)	492 (233)	87 (84)	671 (226)
	>1	83 (27)	66 (57)	315 (165)	23 (36)	487 (159)
Chichagof Island	0	0 (0)	0 (0)	672 (140)	75 (80)	747 (101)
	1	32 (0)	11 (26)	640 (166)	53 (52)	736 (211)
	>1	69 (13)	0 (0)	715 (273)	48 (27)	832 (275)

Both islands appeared to exhibit similar trends with the mean number of Sitka spruce trees/ha where it occurred, highest in plots that lacked residual trees, and lowest in plots with the greatest number of residual trees (Table 6). On average Sitka spruce trees comprised 16, 13, and 5 percent on Kuiu Island and 10, 7, and 6 percent on Chichagof Island of the total trees/ha for 0R, 1R, and >1R plots, respectively (Table 6). Although mean percentage of spruce/ha was less than 20 in all plot types on both islands, 14 plots on Kuiu and 2 plots on Chichagof Island contained more than 20 percent spruce trees.

Present Condition of Tree Classifications

The average residual tree was generally similar in stature and dwarf mistletoe component in all plots on both islands, except in the 1R plots on Chichagof Island where the average residual tree was slightly smaller in height and diameter, contained a lower live crown DMR, and contained a higher dwarf mistletoe below-live-crown rating (Table 7). Advanced regeneration trees occurred in all stands and plot types on Kuiu Island but were absent from most plot types on Chichagof Island (Table 7). On Kuiu Island, in general, advanced regeneration tree stature decreased and their dwarf mistletoe component increased as the number of residual trees per plot increased (Table 7). On Kuiu Island, the total number of inoculum source trees/plot (including both residual and advanced regeneration trees) ranged from 0 to 12 while on Chichagof Island the range was from 0 to 3.

In general, on both islands post-disturbance hemlock tree stature decreased and the dwarf mistletoe component increased as the number of residual trees/plot increased (Table 7). Sitka spruce trees in all plot types on both islands were generally similar in stature and dwarf mistletoe component (Table 7). Low incidence of dwarf mistletoe infection was detected in spruce trees on both islands. On Kuiu Island, 12 of 169 (7%) spruce trees contained infections in the live crown and 3 of 169 (2%) trees contained infections below the live crown. On Chichagof Island, 3 of 33 (9%) of spruce trees contained infections in the live crown, no infections were noted below the live crown. All infected spruce trees on both islands had a DMR of 1.

Table 7. Mean number and standard deviation (in parentheses) of trees/plot for residual, advanced regeneration, and post-disturbance hemlock trees, and Sitka spruce trees and their present DBH, height, live crown dwarf mistletoe rating (DMR), and dwarf mistletoe below-live-crown rating by plot type on Kuiu and Chichagof Island.

Tree type and Island	Plot type	n/plot	DBH (cm)	Height (m)	Live crown DMR (0-6)	Below-live-crown rating (0-2)
Residual						
Kuiu	0	0.0 (0.0)	-[1]	-	-	-
Island	1	1.0 (0.0)	80.8 (18.6)	36 (7)	4.6 (1.5)	1.6 (0.8)
	>1	2.6 (0.8)	80.8 (18.6)	34 (10)	4.8 (1.4)	1.5 (0.8)
Chichagof	0	0.0 (0.0)	-	-	-	-
Island	1	1.0 (0.0)	69.1 (10.4)	33 (3)	4.2 (1.5)	2.0 (0.0)
	>1	2.2 (0.4)	78.3 (18.4)	32 (8)	4.5 (1.4)	1.5 (0.8)
Advanced Regeneration						
Kuiu	0	1.5 (1.8)	52.3 (8.6)	34 (4)	2.4 (1.8)	1.1 (0.8)
Island	1	1.9 (1.9)	50.8 (10.7)	33 (6)	3.4 (1.5)	1.5 (0.7)
	>1	2.1 (1.8)	45.4 (9.3)	31 (6)	3.8 (1.4)	1.6 (0.6)
Chichagof	0	0.0 (0.0)	-	-	-	-
Island	1	0.3 (0.8)	41.6 (1.1)	21 (0.7)	3.5 (0.7)	1.0 (1.4)
	>1	0.0 (0.0)	-	-	-	-
Post-disturbance						
Kuiu	0	15.8 (7.4)	30.0 (11.4)	26 (7)	1.2 (1.4)	0.6 (0.7)
Island	1	15.6 (7.3)	26.2 (9.7)	23 (7)	2.5 (1.6)	1.0 (0.7)
	>1	10.0 (5.5)	25.9 (10.3)	22 (7)	2.9 (1.6)	1.0 (0.8)
Chichagof	0	21.0 (4.4)	35.9 (11.1)	29 (7)	0.3 (0.6)	0.2 (0.4)
Island	1	20.0 (5.2)	28.1 (10.8)	24 (7)	1.7 (1.2)	0.7 (0.7)
	>1	22.3 (8.5)	27.5 (9.6)	23 (7)	2.2 (1.4)	0.7 (0.7)
Sitka spruce						
Kuiu	0	3.4 (3.4)	40.2 (16.9)	32 (7)	0.06 (0.2)	0.00 (0.0)
Island	1	2.7 (2.6)	36.6 (12.7)	30 (7)	0.07 (0.3)	0.04 (0.2)
	>1	0.7 (1.1)	48.2 (27.1)	32 (9)	0.11 (0.3)	0.00 (0.0)
Chichagof	0	2.3 (2.5)	41.1 (13.6)	32 (6)	0.0 (0.0)	0.0 (0.0)
Island	1	1.7 (1.6)	40.2 (18.5)	31 (9)	0.2 (0.4)	0.2 (0.4)
	>1	1.5 (0.8)	39.2 (19.2)	30 (9)	0.1 (0.3)	0.0 (0.0)

[1] No trees of a classification present within a plot type.

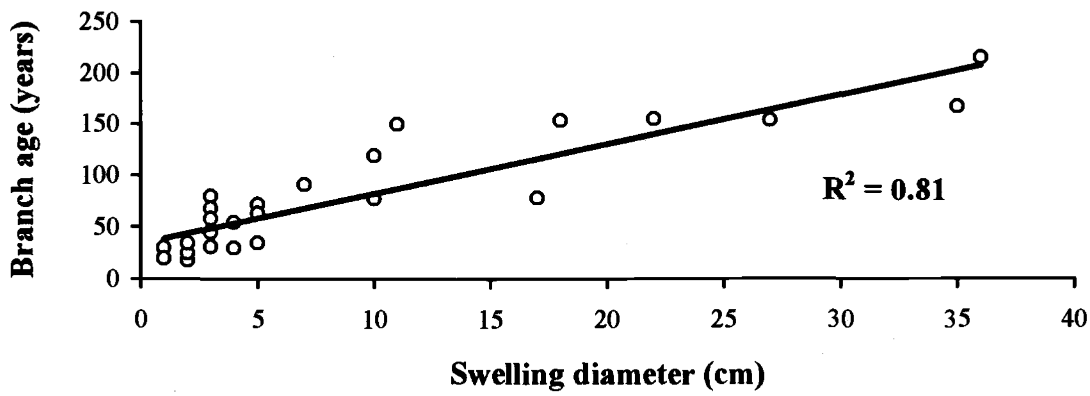
DWARF MISTLETOE COMPONENT

Before Catastrophic Windthrow

Hemlock dwarf mistletoe occurred in each stand prior to the late 1800's and, considering a potentially long pathogen life cycle (Shaw and Loopstra 1991) and slow rates of spread and intensification (Shaw and Hennon 1991), has likely been a component of these stands for several centuries. All old hemlocks, 300-400 years old, contained visible dwarf mistletoe brooms in the live crown and 87 percent contained evidence of infections below the live crown, suggesting that dwarf mistletoe was not recently introduced to these trees (Appendix Table 1).

Additionally, casual observation suggested that many of the oldest hemlock trees contained enormous dwarf mistletoe swellings and brooms that comprised the majority of the live crown. I hypothesized these infections were centuries old, attaining a large size after many years of growth. An auxiliary study was undertaken to determine the relationship between branch age and swelling diameter by dissecting and aging 26 swellings from downed trees on Kuiu Island. Results of a regression analysis indicated that infection age increased with an increase in swelling diameter; the youngest, smallest branch infection measured 1.7 cm diameter and was 18 years old while the oldest, largest branch infection measured 36 cm diameter and was 215 years old (Figure 4). The linear regression model for the relationship was: $Y = 34.427 + 4.833X_1$, where Y was the branch age and X_1 was the swelling diameter. The standard error for the constant was 6.622 and for the coefficient of X_1 was 0.486. The model of the relationship between branch age and swelling diameter indicated that the very large dwarf mistletoe swellings and brooms observed in the 300-400 year old hemlock trees were likely growing for several centuries and thus, were present before the wind disturbance in the late 1800's.

Figure 4. Branch age vs. swelling diameter for 26 dwarf mistletoe infections.



Pathogen Spread

Residual trees within a plot were hypothesized to be the primary inoculum source for pathogen spread to post-disturbance hemlock trees. Since residual trees did not occur in 0R plots, the pathogen was not expected to occur on post-disturbance hemlock trees in this plot type. Hemlock dwarf mistletoe, however, occurred in low amounts in post-disturbance hemlock trees in 0R plots on both Kuiu and Chichagof Island (Table 7). On Kuiu Island, dwarf mistletoe infections in 0R plots likely resulted from infected advanced regeneration trees within a plot (Table 7) and infected advanced regeneration and residual trees outside a plot (Table 8a).

Table 8a. Mean number of trees, live crown dwarf mistletoe rating (DMR), and dwarf mistletoe below-live-crown rating for infected residual and advanced regeneration trees growing within 10 m of 0R plot type boundaries for eight stands (1-8) on Kuiu and two stands (9-10) on Chichagof Island.

Stand	Tree classification	Trees within 10 m outside of plot	Live crown DMR (0-6)	Below-live-crown rating (0-2)
1	residual	1.0 (1.0)	4.3 (1.5)	2.0 (0.0)
	adv regeneration	0.7 (1.2)	0.3 (0.5)	1.4 (0.5)
2	residual	1.3 (1.5)	3.5 (1.7)	1.3 (0.5)
	adv regeneration	5.0 (1.7)	1.6 (1.5)	1.1 (0.6)
3	residual	2.7 (1.2)	4.1 (1.4)	1.5 (0.8)
	adv regeneration	0.3 (0.6)	2.0 (0.0)	1.0 (0.6)
4	residual	0.7 (1.2)	2.0 (1.4)	1.5 (0.7)
	adv regeneration	1.7 (2.9)	1.9 (2.1)	1.8 (0.5)
5	residual	0.3 (0.6)	0.0 (0.0)	2.0 (0.0)
	adv regeneration	2.0 (1.7)	2.3 (1.6)	1.7 (0.8)
6	residual	2.0 (2.6)	5.3 (1.3)	1.8 (0.4)
	adv regeneration	4.0 (4.6)	2.3 (1.1)	2.0 (0.0)
7	residual	0.7 (1.2)	4.0 (1.4)	1.5 (0.7)
	adv regeneration	2.7 (3.8)	2.4 (1.1)	1.8 (0.5)
8	residual	2.7 (1.5)	5.4 (1.1)	2.0 (0.0)
	adv regeneration	6.0 (1.7)	3.2 (1.2)	1.6 (0.5)
9	residual	0.3 (0.6)	5.0 (0.0)	1.0 (0.0)
	adv regeneration	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
10	residual	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
	adv regeneration	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)

Although infected residuals were located outside of plot boundaries in some 0R plots on Chichagof Island (Table 8a), none of the post-disturbance hemlock trees with dwarf mistletoe infections occurred on those plots. Thus, the origin of dwarf mistletoe infections in post-disturbance hemlock trees in 0R plots on Chichagof Island remains unexplained. Possible explanations include: 1. spread from advanced regeneration or residual trees within the plot that have died and decayed beyond recognition since the catastrophic windthrow; 2. spread from nearby post-disturbance hemlock trees; and 3. spread from introduction by birds and/or small mammals. None of these explanations can be evaluated with the current data.

Infected residual and advanced regeneration trees occurred within 10 m of 1R and >1R plots for the majority of stands on both islands, likely contributing dwarf mistletoe to post-disturbance hemlock trees within a plot (Table 8b and 8c). The relative dwarf mistletoe contributions of inoculum sources, both within and outside a plot, to the mean DMR of post-disturbance hemlock trees within a plot are provided in the Model Development section of this chapter.

Table 8b. Mean number of trees, live crown dwarf mistletoe rating (DMR), and dwarf mistletoe below-live-crown rating for infected residual and advanced regeneration trees growing within 10 m of 1R plot type boundaries for eight stands (1-8) on Kuiu and two stands (9-10) on Chichagof Island.

Stand	Tree classification	Trees within 10 m outside of plot	Live crown DMR (0-6)	Below-live-crown rating (0-2)
1	residual	2.0 (1.7)	2.7 (1.2)	0.8 (0.8)
	adv regeneration	1.0 (1.7)	4.3 (1.2)	1.3 (1.2)
2	residual	3.3 (2.1)	4.2 (1.3)	1.5 (0.5)
	adv regeneration	3.7 (3.8)	3.0 (1.2)	1.2 (0.9)
3	residual	4.7 (3.1)	5.2 (1.1)	1.7 (0.7)
	adv regeneration	4.3 (3.2)	3.2 (0.9)	1.8 (0.4)
4	residual	4.0 (3.6)	3.5 (1.3)	1.9 (0.3)
	adv regeneration	2.7 (2.3)	2.9 (0.6)	2.0 (0.0)
5	residual	2.3 (2.1)	5.4 (0.8)	1.4 (1.0)
	adv regeneration	0.7 (0.6)	3.5 (0.7)	1.5 (0.7)
6	residual	5.0 (3.6)	4.9 (1.2)	2.0 (0.0)
	adv regeneration	4.3 (1.5)	4.0 (1.2)	2.0 (0.0)
7	residual	2.0 (1.0)	4.7 (2.2)	1.8 (0.4)
	adv regeneration	6.3 (0.6)	2.5 (1.5)	1.5 (0.5)
8	residual	2.0 (0.8)	4.9 (1.4)	2.0 (0.0)
	adv regeneration	4.2 (2.2)	2.9 (1.2)	1.8 (0.4)
9	residual	0.3 (0.6)	5.0 (0.0)	2.0 (0.0)
	adv regeneration	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
10	residual	0.7 (1.2)	4.5 (0.7)	1.0 (1.4)
	adv regeneration	0.7 (1.2)	2.0 (0.0)	1.5 (0.7)

Table 8c. Mean number of trees, live crown dwarf mistletoe rating (DMR), and dwarf mistletoe below-live-crown rating for infected residual and advanced regeneration trees growing within 10 m of >1R plot type boundaries for eight stands (1-8) on Kuiu and two stands (9-10) on Chichagof Island.

Stand	Tree classification	Trees within 10 m outside of plot	Live crown DMR (0-6)	Below-live-crown rating (0-2)
1	residual	2.6 (1.8)	3.2 (2.0)	1.3 (0.7)
	adv regeneration	2.4 (1.3)	1.7 (1.1)	1.3 (0.4)
2	residual	3.3 (1.5)	3.8 (1.3)	1.5 (0.7)
	adv regeneration	2.3 (3.2)	4.7 (1.1)	1.7 (0.5)
3	residual	5.3 (3.8)	5.1 (1.1)	1.0 (1.0)
	adv regeneration	1.0 (1.0)	4.6 (1.5)	1.7 (0.6)
4	residual	5.3 (2.5)	4.1 (1.7)	1.8 (0.4)
	adv regeneration	3.3 (4.0)	3.6 (1.6)	1.4 (0.7)
5	residual	3.0 (2.6)	4.7 (1.2)	1.8 (0.6)
	adv regeneration	1.5 (1.0)	3.0 (2.1)	1.9 (0.4)
6	residual	6.7 (3.8)	5.4 (0.9)	2.0 (0.0)
	adv regeneration	3.0 (1.7)	5.1 (1.2)	2.0 (0.0)
7	residual	2.7 (0.6)	4.6 (1.5)	1.8 (0.5)
	adv regeneration	5.7 (3.1)	2.7 (1.6)	1.6 (0.5)
8	residual	5.0 (4.4)	4.3 (1.4)	1.7 (0.7)
	adv regeneration	2.7 (0.6)	1.8 (1.9)	1.1 (0.3)
9	residual	4.0 (2.0)	5.1 (1.2)	1.9 (0.3)
	adv regeneration	1.7 (2.9)	3.4 (0.5)	2.0 (0.0)
10	residual	0.3 (0.6)	4.0 (0.0)	2.0 (0.0)
	adv regeneration	0.7 (1.2)	3.0 (0.0)	0.0 (0.0)

On Kuiu Island, the range of mean DMR of post-disturbance hemlock trees within a plot was from 0.0 to 5.3 while on Chichagof Island the range was from 0.0 to 2.9. On both islands, the percent of trees with no dwarf mistletoe decreased as the mean DMR of post-disturbance hemlock trees within a plot increased (Figures 5 and 6). Both islands showed strikingly similar trends, approximately 50 percent of post-disturbance hemlock trees contained the pathogen when mean DMR of post-disturbance hemlock trees within a plot was 0.7; and when above 2.0, nearly 100 percent infection of post-disturbance hemlock trees consistently occurred (Figures 5 and 6). The trendlines in Figures 5 and 6 were computer generated as fourth-order polynomials.

Figure 5. Proportion of post-disturbance hemlock trees with DMR of 0 vs. mean DMR of post-disturbance hemlock trees for 76 plots on Kuiu Island.

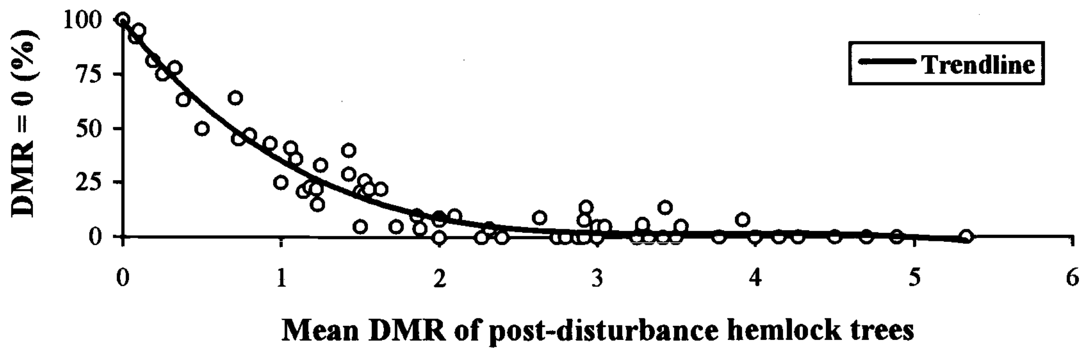
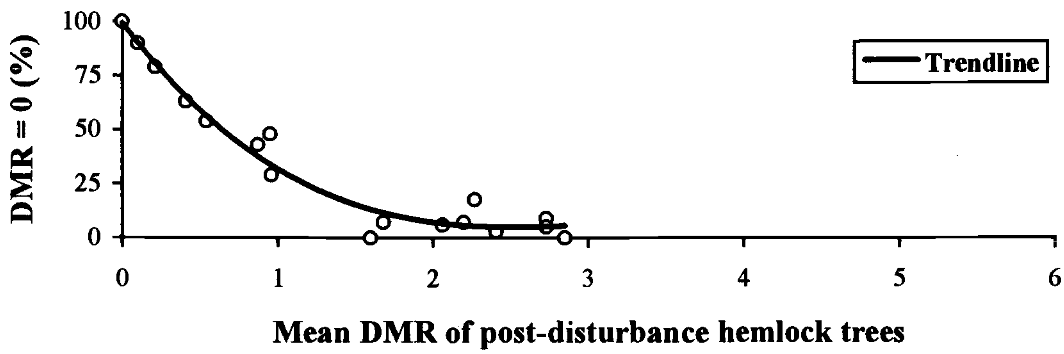


Figure 6. Proportion of post-disturbance hemlock trees with DMR of 0 vs. mean DMR of post-disturbance hemlock trees for 18 plots on Chichagof Island.



Pathogen Intensification

Crown Location

Dwarf mistletoe infection in the upper tree crown has a greater impact on tree growth than infections lower in the crown (Richardson and van der Kamp 1972). Since dwarf mistletoe requires at least half a decade to complete a life cycle, host tree growth may outpace advance to the upper crown third even when there is constant seed rain from overhead inoculum sources. Unless the leader branch of a young tree becomes infected with dwarf mistletoe, the upper live crown third typically contains fewer infections than the middle or lower crown thirds.

In this study, dwarf mistletoe infection in post-disturbance hemlock trees resulted from seed rain from overstory inoculum sources and from within tree intensification, although these two factors can not be analyzed separately with the current data. Similar intensification trends occurred on both islands; as the number of residual trees per plot increased, the proportion of post-disturbance hemlock trees with dwarf mistletoe in the upper third of the live crown increased (Table 9). The proportion of post-disturbance hemlock trees with no dwarf mistletoe decreased correspondingly.

Table 9. Mean percentage and standard deviation (in parentheses) of post-disturbance hemlock trees without dwarf mistletoe, or with dwarf mistletoe in the lower, mid, or upper live crown third by plot type on Kuiu and Chichagof Island.

	Dwarf mistletoe crown location (% of trees):			
Plot type	None in any crown 1/3	Low 1/3 only	Low and Mid 1/3 only	Low, Mid, and Up 1/3
Kuiu Island				
0	41 (35)	20 (18)	24 (23)	16 (17)
1	13 (20)	14 (13)	35 (14)	38 (25)
>1	6 (10)	10 (13)	46 (24)	38 (27)
Chichagof Island				
0	77 (27)	18 (17)	5 (12)	0 (0)
1	20 (24)	29 (11)	36 (20)	16 (13)
>1	13 (16)	19 (13)	43 (24)	24 (18)

Infection Classes

In British Columbia, a substantial diameter and height growth loss of 40 percent can occur in trees that contain heavy dwarf mistletoe infection levels (DMR = 5 or 6), 23 percent loss can occur in trees with moderate infection levels (DMR = 3 or 4), and an unmeasurable growth loss can occur in trees with light infection levels (DMR = 1 or 2) (Smith 1969, Thompson et al. 1985). In this study, the proportion of trees with DMR >3 generally increased as the number of residual trees per plot increased (Table 10). The proportion of trees with DMR < 3 decreased correspondingly.

Although similar intensification trends occurred on both islands, Kuiu Island plots consistently contained a higher proportion of post-disturbance hemlock trees with dwarf mistletoe ratings >3 in all plot types (Table 10).

Table 10. Mean percentage and standard deviation (in parentheses) of post-disturbance hemlock trees in four dwarf mistletoe classes (0, 1 or 2, 3 or 4, 5 or 6) by plot type on Kuiu and Chichagof Island.

Location	Plot type	Dwarf mistletoe class (% of trees):			
		0	1 or 2	3 or 4	5 or 6
Kuiu Island	0	42 (29)	40 (18)	14 (14)	4 (6)
	1	15 (14)	37 (19)	38 (14)	11 (11)
	>1	7 (7)	31 (14)	43 (13)	19 (14)
Chichagof Island	0	77 (24)	23 (24)	0 (0)	0 (0)
	1	19 (18)	59 (0)	20 (15)	3 (4)
	>1	14 (16)	45 (3)	35 (16)	7 (2)

Although the range of mean DMR of post-disturbance hemlock trees within a plot was smaller on Chichagof Island (0.0 to 2.9) than on Kuiu Island (0.0 to 5.3), both islands showed strikingly similar intensification trends up to 2.9, the maximum mean DMR of post-disturbance hemlock trees within a plot observed on Chichagof Island. For example, approximately 50 percent of post-disturbance hemlock trees with DMR of 3 or 4 occurred when mean DMR of post-disturbance hemlock trees within a plot was 2.5 on Kuiu Island and 2.8 on Chichagof Island (Figures 7a and 8a). Also, for both islands, less than 25 percent of post-disturbance hemlock trees had DMR of 5 or 6 when mean DMR of post-disturbance hemlock trees within a plot was below 3.0 (Figures 7b and 8b). The trendlines in Figures 7a-b and 8a-b were computer generated as fourth-order polynomials.

On Kuiu Island, the proportion of post-disturbance hemlock trees with DMR of 3 or 4 increased as mean DMR of post-disturbance hemlock trees within a plot approached 3.5 and decreased thereafter (Figure 7a). The decrease was due to the increase in trees with DMR of 5 or 6 (Figure 7b). Also, the proportion of post-disturbance hemlock trees with DMR of 5 or 6 increased dramatically when mean DMR of post-disturbance hemlock trees within a plot was above 3.0 and, when above 5.0, more than 75 percent of post-disturbance hemlock trees had DMR of 5 or 6 (Figure 7b). These trends could not be verified on Chichagof Island because the maximum mean DMR of post-disturbance hemlock trees within a plot was less than 3.0.

Figure 7a. Proportion of post-disturbance hemlock trees with DMR of 3 or 4 vs. mean DMR of post-disturbance hemlock trees for 76 plots on Kuiu Island.

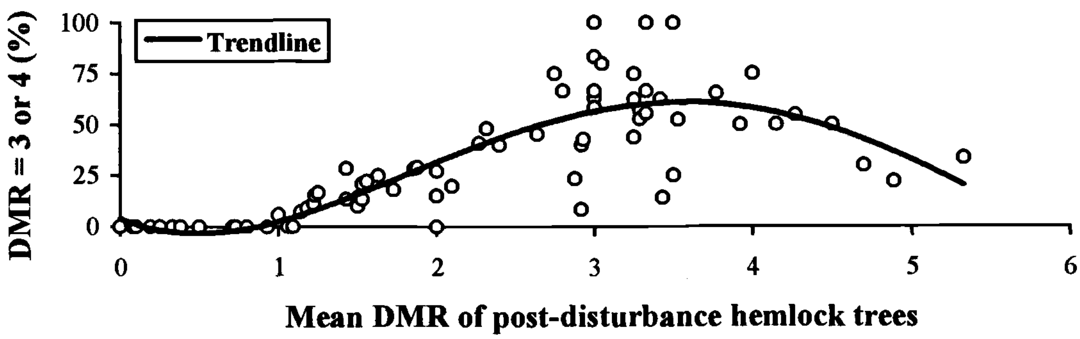


Figure 7b. Proportion of post-disturbance hemlock trees with DMR of 5 or 6 vs. mean DMR of post-disturbance hemlock trees for 76 plots on Kuiu Island.

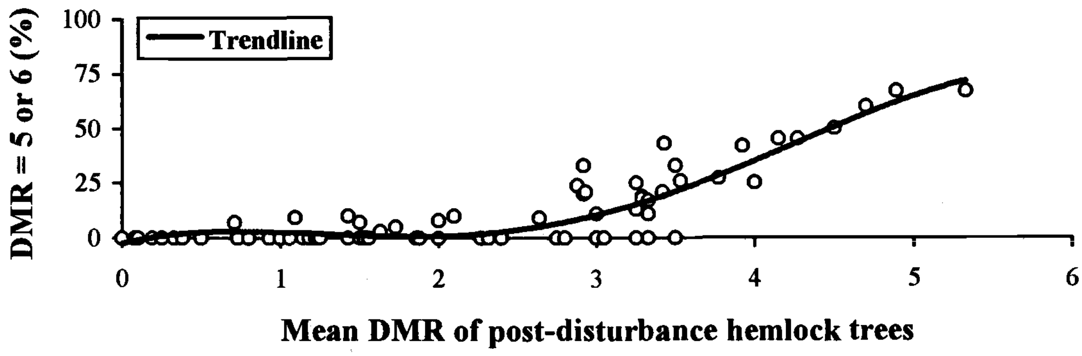


Figure 8a. Proportion of post-disturbance hemlock trees with DMR of 3 or 4 vs. mean DMR of post-disturbance hemlock trees for 18 plots on Chichagof Island.

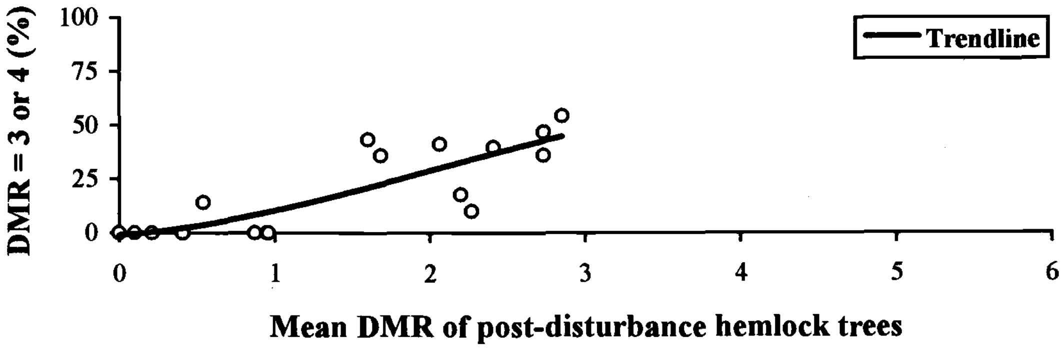
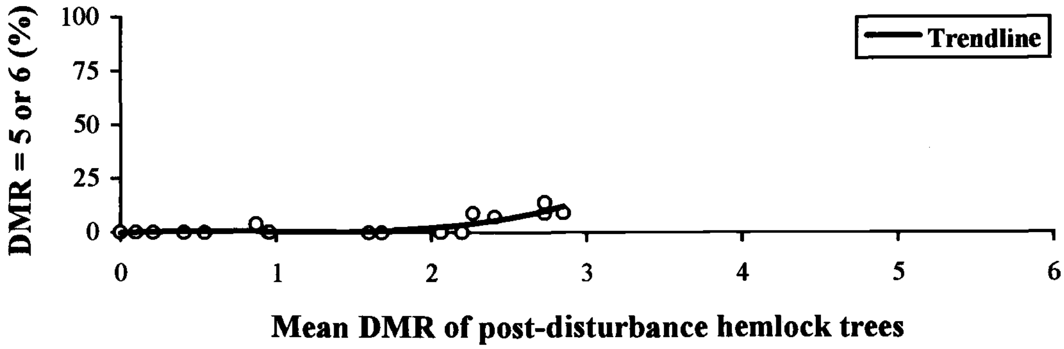


Figure 8b. Proportion of post-disturbance hemlock trees with DMR of 5 or 6 vs. mean DMR of post-disturbance hemlock trees for 18 plots on Chichagof Island.



MODEL DEVELOPMENT

Refinement of Preliminary Model

Explanatory plot, site, and tree variables were tested for contributions to Model A, a preliminary model that explained the mean DMR of post-disturbance hemlock trees within a plot with two variables, the number of residual trees per plot and their mean DMR (Stems.residual *DMR.residual) and the number of advanced regeneration trees per plot and their mean DMR (Stems.advregen*DMR.advregen). None of the additional explanatory variables tested, except the distance to nearest residual tree (Distance.residual $P = 0.017$), distance to nearest inoculum source (Distance.anyinoc $P = 0.025$) and aspect (Htload $P = 0.040$), contributed significant explanatory power to Model A (all $P > 0.05$) (Table 11). The percent of spruce trees/plot (Pct.spruce $P = 0.061$) and the percent of post-disturbance hemlock trees/plot (Pct.post $P = 0.066$) were marginally non-significant explanatory variables (Table 11).

Table 11. Significance levels (*P*) for explanatory variables added to preliminary Model A (See Table 3 for definitions).

Explanatory Variable	*P*
Distance.advregen	0.288
Distance.residual	0.017
Distance.anyinoc	0.025
Elevation	0.430
SIndex	0.215
Slope	0.339
Htload	0.040
PAssoc	0.074
BA.spruce	0.489
Pct.spruce	0.061
Stems.spruce	0.161
BA.post	0.859
Pct.post	0.066
Stems.post	0.144

The three variables Htload, Distance.residual, and Distance.anyinoc, were further analyzed to determine whether they should be included in a final Kuiu Island hemlock dwarf mistletoe model. A component effects plot of Htload vs. the response variable (mean DMR of post-disturbance hemlock trees within a plot) revealed no discernible relationship. Thus, Htload was interpreted as having spurious explanatory power and was not included in the model. Extra sum of squares F-tests with Distance.residual and Distance.anyinoc revealed that each variable added only minor explanatory power (P >0.05 and P >0.05, extra sum of squares F-test), too little to merit inclusion of either variable in the model.

In the final model, which was the same as initial Model A, the mean DMR of post-disturbance hemlock trees within a plot on Kuiu Island was positively related to the number of residual trees and their dwarf mistletoe rating and the number of advanced regeneration trees and their dwarf mistletoe rating (Table 12). The relationship was: $Y = 1.23 + 0.114X_1 + 0.061X_2$, where Y was the mean DMR of post-disturbance hemlock trees within a plot (DMR.post), X_1 was the number of residual trees and their dwarf mistletoe rating (Stems.residuals * DMR.residuals), and X_2 was the number of advanced regeneration trees and their dwarf mistletoe rating (Stems.advregen * DMR.advregen) (Table 12). The 95 % confidence intervals for the estimates were 0.895 to 1.571 for the constant, 0.077 to 0.152 for the coefficient of X_1, and 0.030 to 0.093 for the coefficient of X_2. This model explained approximately 48 percent of the variation in the mean DMR of post-disturbance hemlock trees within a plot (Table 12).

Table 12. Multiple linear regression and ANOVA tables for the Kuiu Island hemlock dwarf mistletoe model.

Source of Variation	Coefficient	Standard Error	t	P
Constant	1.233	0.169	7.28	<0.001
Stems.residuals * DMR.residuals	0.114	0.019	6.11	<0.001
Stems.advregen * DMR.advregen	0.061	0.016	3.84	<0.001

$R^2 = 0.48$ (adjusted for degrees of freedom)

Source of variation	DF	Sum of squares	Mean square	F	P
Model	2	65.57	32.78	35.63	<0.001
Error	73	67.17	0.92		
Corrected total	75	132.734			

The importance of pathogen spread from inoculum sources outside a plot to post-disturbance hemlock trees within a plot was tested because infected residual and advanced regeneration trees occurred within 10 m of the boundary on nearly every plot (Tables 8a-c). I hypothesized that these trees may have spread significant amounts of the pathogen into the plots over the last century.

To test this hypothesis two explanatory variables, Out.stems.residual * Out.dmr.residual and Out.stems.advregen*Out.dmr.advregen, were added to the Kuiu Island hemlock dwarf mistletoe model. The variable Out.stems residual was the number of residual trees within 10 m of a plot boundary and Out.dmr.residual was the mean current DMR of those residual trees. The variable Out.stems.advregen was the number of advanced regeneration trees within 10 m of a plot boundary and Out.dmr.advregen was the mean current DMR of those advanced regeneration trees.

Both variables which represented inoculum source trees outside a plot were significant for explaining the mean DMR of post-disturbance hemlock trees within a plot ($P < 0.003$ for each variable) and their addition improved the explanatory power of the model ($P < 0.05$, extra sum of squares F-test). A model which included inoculum sources outside a plot explained approximately 60 percent of the variation in mean DMR of post-disturbance hemlock trees within a plot ($R^2 = 0.603$), hence increased considerably the explanatory value of the Kuiu Island model which did not include inoculum sources outside a plot ($R^2 = 0.48$). Thus, future refinement of the Kuiu Island hemlock dwarf mistletoe model should incorporate explanatory variables representing inoculum source trees outside a plot.

<u>**Kuiu Model Validation on Chichagof Island**</u>

Data from two stands on Chichagof Island were tested with significant independent variables from the Kuiu Island hemlock dwarf mistletoe model to determine if similar qualitative trends occurred on both islands. The mean DMR of post-disturbance hemlock trees within a plot in Stand 9 on Chichagof Island increased with increasing numbers of residual trees and their dwarf mistletoe rating within a plot (Table 13). Advanced regeneration trees were not found in Stand 9, thus this variable was not included in the Stand 9 model. The relationship was: $Y = 0.241 + 0.154X_1$, where Y was the mean DMR of post-disturbance hemlock trees within a plot (DMR.post), X_1 was the number of residual trees and their dwarf mistletoe rating (Stems.residuals * DMR.residuals) (Table 13). The 95 % confidence intervals for the estimates were -0.081 to 0.562 for the constant, and 0.108 to 0.201 for the coefficient of X_1. This model accounted for approximately 88 percent of the variation in the mean DMR of post-disturbance hemlock trees within a plot (Table 13). Inoculum source trees outside a plot did not contribute significantly to the explanatory power of the model ($P > 0.05$, extra sum of squares F-test).

Table 13. Multiple linear regression and ANOVA tables for Kuiu model variables tested in Stand 9 on Chichagof Island.

Source of Variation		Coefficient	Standard Error	t	*P*
Constant		0.241	0.136	1.77	0.120
Stems.residuals * DMR.residuals		0.154	0.019	7.87	0.000
$R^2 = 0.884$ (adjusted for degrees of freedom)					
Source of variation	DF	Sum of squares	Mean square	F	*P*
Model	1	5.62	5.62	61.87	0.000
Error	7	0.64	0.09		
Corrected total	8	6.26			

The mean DMR of post-disturbance hemlock trees within a plot in Stand 10 on Chichagof Island increased with increasing numbers of residual trees and their dwarf mistletoe rating within a plot (Table 14). Although a small number of advanced regeneration trees were found in Stand 10, this variable was not significant ($P = 0.762$) and was not included in the Stand 10 model. The relationship was: $Y = 0.772 + 0.229X_1$, where Y was the mean DMR of post-disturbance hemlock trees within a plot (DMR.post), X_1 was the number of residual trees and their dwarf mistletoe rating (Stems.residuals * DMR.residuals) (Table 13). The 95 % confidence intervals for the estimates were -0.015 to 1.460 for the constant, and 0.109 to 0.349 for the coefficient of X_1. This model accounted for approximately 71 percent of the variation in the mean DMR of post-disturbance hemlock trees within a plot (Table 14). Inoculum source trees outside a plot did not contribute significantly to the explanatory power of the model ($P > 0.05$, extra sum of squares F-test).

Table 14. Multiple linear regression and ANOVA tables for Kuiu model variables tested in Stand 10 on Chichagof Island.

Source of Variation		Coefficient	Standard Error	t	*P*
Constant		0.722	0.301	2.40	0.054
Stems.residuals * DMR.residuals		0.229	0.049	4.68	0.003
$R^2 = 0.713$ (adjusted for degrees of freedom)					
Source of variation	DF	Sum of squares	Mean square	F	*P*
Model	2	6.93	3.46	10.95	0.010
Error	6	1.90	0.32		
Corrected total	8	8.83			

Chapter 4. Discussion

Retention of overstory canopy dwarf mistletoe infected hemlock trees in southeast Alaska forests will result in pathogen spread to and intensification on developing hemlock trees after approximately 110 years but not to the devastating levels predicted by research in coastal British Columbia, Washington, or Oregon (Richardson and van der Kamp 1972, Stewart 1976, Smith 1977). Smith (1977) suggested that 86 evenly scattered, heavily infected hemlock trees/ha would be sufficient to heavily infect all intervening regeneration. By contrast, results from this study on Kuiu Island suggested that in plots with an average of 3 heavily infected residual trees (83 residual trees/ha) an average of 19 percent of post-disturbance hemlock trees would have heavy infection levels (DMR of 5 or 6) and 43 percent would have moderate infection levels (DMR of 3 or 4) (Table 10). Results on Chichagof Island suggested that in plots with an average of 2 heavily infected residual trees (64 residual trees/ha), an average of 7 percent of post-disturbance hemlock trees would have heavy infection levels and 35 percent would have moderate infection levels (Table 10). On both islands, a low mean percentage of post-disturbance hemlock trees per plot contained the highest dwarf mistletoe ratings despite the additional presence of infected advanced regeneration trees within a plot and residual and advanced trees within 10 m of most plot boundaries.

A model for long-term hemlock dwarf mistletoe spread and intensification on Kuiu Island suggested that the mean DMR of post-disturbance hemlock trees within a plot increased with increasing numbers and DMR of residual and advanced regeneration trees within a plot. The two explanatory variables, number and DMR of residual trees and the number and DMR of advanced regeneration trees, accounted for nearly 50 percent of the variation in mean DMR of post-disturbance hemlock trees within a plot. The effects of residual tree number and DMR were nearly twice that of advanced regeneration tree number and DMR. Pathogen spread did not appear to be affected by any of the site factors examined. Measures of density for post-disturbance hemlock trees and Sitka spruce trees were marginally non-significant in the model. Both number and DMR of advanced regeneration and residual trees outside a plot boundary appeared to contribute significantly to the mean DMR of post-disturbance hemlock trees within a plot, thus further model refinement should include variables representing inoculum source trees outside a plot. Kuiu Island model estimates were based on the plot level and further model refinement will yield estimates for the number of inoculum source trees on a per hectare basis.

Preliminary testing of the same predictors used in the Kuiu Island model for two stands on Chichagof Island revealed generally similar trends but also several important differences. Since advanced regeneration trees did not occur in one stand and only two occurred in the other stand on Chichagof Island, verification of the importance of inoculum from advanced regeneration trees was not possible. Models for both stands on Chichagof Island revealed that infected overstory residual trees within a plot were important pathogen contributors, accounting for 88 percent of the variation in mean DMR of post-disturbance hemlock trees within a plot in Stand 9, and 71 percent in Stand 10. Inoculum sources outside of plot boundaries did not contribute significantly to mean DMR of post-disturbance hemlock trees within a plot, likely because such a large amount of the variation was explained by inoculum sources within the plot.

A hemlock dwarf mistletoe spread and intensification model developed in British Columbia also suggested that the infection level in second-growth trees increased with the number of residual trees (Bloomberg et al. 1980, Bloomberg and Smith 1982). The Canadian model further suggested that infection level in second-growth trees decreased with an increase in percent of Sitka spruce trees, an increase in density of second-growth trees, and an increase in growth rate of second-growth trees, although most of these factors were marginally non-significant in Kuiu Island model. Post-disturbance tree growth rate was not measured and, therefore, not tested in the Kuiu Island model.

The Canadian hemlock dwarf mistletoe model predicted a decrease in host infection levels with as low as 20 percent spruce trees (Bloomberg et al. 1980), implying that spruce trees act as barriers to dwarf mistletoe seed dispersal, although the lack of field plots that contained a high proportion of spruce prevented a direct test of the model. In the coastal forests of British Columbia a "significant" decrease in host infection levels could be expected with 30 percent spruce trees (Richard Smith pers. comm. 1995). The "barrier" effect of a spruce trees was not confirmed by the Kuiu Island model, however, the percent of spruce trees/plot was only marginally non-significant ($P = 0.061$) and had a negative coefficient. The negative coefficient implied that as the percent of spruce trees/plot increased, the mean DMR of post-disturbance hemlock trees decreased. On both islands less than 10 percent of all Sitka spruce trees contained hemlock dwarf mistletoe infections and, of those infected, all had a dwarf mistletoe rating of one. This suggests that spruce trees on Kuiu and Chichagof Island did not contribute to spread of the pathogen but may contribute to the impediment of spread, occasionally becoming infected in the process. Further analysis of only those plots that contain more than 20 percent spruce trees may reveal a "barrier" effect from Sitka spruce trees.

Differences in hemlock dwarf mistletoe behavior between Alaska and coastal forests further south are real and yet poorly understood. Modest hemlock dwarf mistletoe intensification rates on post-disturbance hemlock trees, as noted in this study, have been previously reported by researchers in southeast Alaska (Drummond and Hawksworth 1979, Shaw 1982a, Shaw and Hennon 1991). Although previous studies noted pathogen behavior around small unmerchantable residual trees left standing following clear-cut harvesting operations, the same trend of lower pathogen intensification was shown as compared to similar stands in the Pacific Northwest and Canada.

Lower intensification rates in southeast Alaska may be due to a slower pathogen life cycle, reduced seed dispersal distance, or increased resistance of host trees. Dwarf mistletoe inoculation trials in southeast Alaska indicated the lack of seed production in infections after twelve years of observation (Shaw and Loopstra 1991). An increase in the length of the pathogen life cycle would extend the time needed for heavy infection levels to occur on all regeneration. Damage to dwarf mistletoe fruits from freezing temperatures has been shown to reduce the capacity of seed dispersal by 95 percent (Baranyay and Smith 1974). Early frosts may occur in scattered microsites across southeast Alaska, reducing local seed dispersal.

Evidence of genetic resistance, observed as post penetration incompatibility, has been shown in western hemlock clones, although the mechanism is not understood (Smith et al. 1993). Dwarf mistletoe resistance in western hemlocks in southeast Alaska has not been studied. In this study, an average of 7 percent of post-disturbance hemlock trees in plots on Kuiu Island that contained an average of 3 heavily infected residual trees did not appear to contain dwarf mistletoe infection, suggesting these trees may have escaped infection or may be resistant to infection. Host trees may escape infection for many reasons including low levels of dispersed seeds, unequal seed dispersal patterns from a source tree, interception of seed by spruce trees, or clumped distribution of source trees (Scharpf 1984, Alfaro et al. 1985). Evaluation of plots on Kuiu Island for total seed dispersed and dispersal patterns will help determine whether the post-disturbance hemlock trees that appeared to lack dwarf mistletoe infection have escaped the pathogen. Evaluation for evidence of resistance, such as interception of seeds by host trees but inability of the seed to penetrate the host or post penetration incompatibility, will help determine whether genetic resistance to dwarf mistletoe occurs in western hemlock trees in southeast Alaska.

This retrospective observational study was conducted in stands that sustained extensive windthrow in the past and was designed as a simulation for stand structure and disease conditions expected after use of silvicultural systems that retain overstory canopy trees in a managed forest. The simulation is plausible despite differences of stand conditions following extensive windthrow and partial canopy harvest. Since hemlock dwarf mistletoe is an obligate parasite on aerial living branches, unable to survive or proliferate on fallen branches or boles, the pathogen will be maintained only on live branches in either disturbance regime. Thus, wind disturbed and partially harvested stands that retain similar amounts of infected live hemlock trees from the previous overstory canopy should have commensurate pathogen spread to and intensification on developing hemlock trees.

An important limitation of our simulation, however, is the lack of measurement of dwarf mistletoe on surviving trees immediately after disturbance. In this study, the level of dwarf mistletoe on infected inoculum sources was measured approximately 110 years after extensive wind disturbance. A crude estimate of dwarf mistletoe level in residual and advanced regeneration at the time of catastrophic windthrow was obtained through assessment of dwarf mistletoe infections in branches within and below the live crown. In this study, evidence of heavy dwarf mistletoe infection below-live-crown and large brooms and swellings within the live crown of residual trees suggested that these trees contained heavy infection levels in the past. Advanced regeneration trees contained evidence of moderate to heavy dwarf mistletoe infection below-live-crown, suggesting that these trees contained moderate to heavy infection levels in the past. It is plausible, therefore, to use this study as a simulation of long-term parasite behavior after partial harvest of the overstory canopy when there is retention of heavily infected residual trees and moderate to heavily infected advanced regeneration trees.

Similar post-disturbance hemlock dwarf mistletoe intensification trends occurred on both Kuiu and Chichagof Island. On both islands, nearly all of the post-disturbance hemlock trees on a plot contained some dwarf mistletoe when the mean DMR of post-disturbance hemlock trees within a plot was 2.0. On Kuiu Island mean DMR of post-disturbance hemlock trees within a plot ranged from 0.0 to 5.3 with 0 to 12 inoculum sources per plot, while on Chichagof Island the range was from 0.0 to 2.9 with 0 to 3 inoculum sources per plot. Intensification trends between islands were similar up to 2.9, the maximum mean DMR of post-disturbance hemlock trees within a plot observed on Chichagof Island. This suggested that dwarf mistletoe behavior was similar on both islands and that the trends on Chichagof Island were simply a truncated version of that observed on Kuiu Island. Further study on Chichagof Island in plots that contain up to 12 inoculum sources will assist in confirming the observed trends.

Intensification of the parasite on post-disturbance hemlock trees will likely continue in the future as the pathogen spreads to and intensifies in the top live crown third. On Kuiu Island in plots with an average of 3 residual trees, nearly half of the post-disturbance hemlock trees contained infections in the top live crown third. On Chichagof Island in plots with 2 residual trees, one-fourth of the post-disturbance hemlock trees contained infections in the top live crown third.

Although future intensification rates are not known, past dwarf mistletoe intensification rates on post-disturbance hemlock trees can be estimated by assuming that increases in single dwarf mistletoe classes are linear and that the trees have attained their highest rating very recently. For post-disturbance hemlock trees that currently contain a DMR of 6, an increase in one DMR class may have occurred approximately every 18 years. If the estimated past intensification rate continues, post-disturbance hemlock trees that currently contain moderate infection levels will contain heavy infection levels in 18-36 years. However, increases in single dwarf mistletoe classes are likely not linear and future dwarf mistletoe intensification rates are likely faster than estimates of past rates. Also, post-disturbance hemlock trees have nearly reached maximum height, allowing upward advance of the pathogen to exceed host height growth. Further study is needed to confirm intensification rates in stands older than 110 years.

In British Columbia, a growth loss of 40 percent was estimated on trees with heavy dwarf mistletoe infection (DMR of 5 or 6), and growth loss of 23 percent was estimated on trees with moderate dwarf mistletoe infection (DMR of 3 or 4) (Smith 1969, Thompson et al. 1985). Similar growth loss estimates can be expected for trees with heavy and moderate dwarf mistletoe infection in southeast Alaska. On Kuiu Island retention of an average of 3 heavily infected residual trees/plot (83 residual trees/ha) resulted in an average of 19 percent post-disturbance hemlock trees with heavy infection and 43 percent with moderate infection. Thus, a severe growth loss (40 percent) due to pathogen infection may occur in an average of less than one-fifth of the hemlock trees and moderate growth loss (23 percent) may occur in an average of less than one-half of the hemlock trees developing for at least 110 years in the presence of overstory trees infected with hemlock dwarf mistletoe.

This study showed conflicting results for the natural regeneration of western hemlock in the presence of large overstory hemlock trees. On Kuiu Island, western hemlock reproduction appeared to be reduced in plots that contained an average of 3 residual trees/plot, yet this trend did not occur on Chichagof Island. Considering that western hemlock is shade-tolerant, the shade provided by overstory trees should not preclude natural regeneration, however, increased competition from the overstory trees for scarce resources may hamper development of young trees. Further study will help determine whether development of western hemlock trees is indeed hampered by the presence of overstory trees. On Kuiu Island, Sitka spruce trees naturally regenerated in modest numbers, 10 percent of plot trees, in the presence of up to 7 overstory trees/plot (224 overstory trees/ha). Although spruce is considered relatively intolerant of shade during establishment, the tree will apparently regenerate in small amounts in partially disturbed stands (Farr and Harris 1971).

The following conclusions summarize the major results of this study.

1. Retention of overstory canopy dwarf mistletoe infected hemlock trees in southeast Alaska forests will result in pathogen spread to and intensification on developing hemlock trees for at least 110 years, but not to the devastating levels predicted by research in coastal forests south of Alaska.

2. On Kuiu Island, the retention of an average of 3 heavily infected residual trees/plot (83 residual trees/ha) resulted in nearly 100 percent infection of post-disturbance hemlock trees. Of those trees infected, less than one-fifth had a DMR of 5 or 6, and thus may have severe growth loss. Approximately one-half of the infected trees had a DMR of 3 or 4, and thus may have moderate growth loss.

3. On Chichagof Island, the retention of an average of 2 heavily infected residual trees/plot (69 residual trees/ha) resulted in nearly 100 percent infection of post-disturbance hemlock trees. Of those trees infected, less than ten percent had a DMR of 5 or 6, and thus may have severe growth loss. Approximately one-third of the infected trees had a DMR of 3 or 4, and thus may have moderate growth loss.

4. A model to long-term hemlock dwarf mistletoe spread suggested that mean DMR of post-disturbance hemlock trees within a plot increased with increasing number and dwarf mistletoe rating of residual trees and number and dwarf mistletoe rating of advanced regeneration trees within a plot. The effect of residual trees was nearly twice that of advanced regeneration trees. No other site or tree factors in plots appeared important in the model.

5. A test of Kuiu Island model predictors on Chichagof Island revealed that mean DMR of post-disturbance hemlock trees within a plot increased with increasing number and dwarf mistletoe rating of residual trees within a plot. Advanced regeneration trees did not occur within plots in sufficient numbers on Chichagof Island to test their influence on mean DMR of post-disturbance hemlock trees within a plot. Neither residual nor advanced regeneration tree number and DMR appeared to influence mean DMR of post-disturbance hemlock trees within a plot.

6. Sitka spruce trees, though rare hosts of hemlock dwarf mistletoe, did not appear to increase the mean DMR of post-disturbance hemlock trees within a plot. When present in sufficient numbers, spruce trees may act as barriers to pathogen spread, occasionally becoming infected in the process, though this needs further analysis.

7. Despite limitations, retrospective studies in southeast Alaska may be the best approach for obtaining reliable estimates for the long-term hemlock dwarf mistletoe spread to and intensification on mature western hemlock trees in uneven-aged forests.

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APPENDICES

Appendix Table 1. Current age, DBH, height, live crown dwarf mistletoe rating (DMR), dwarf mistletoe below-live-crown rating, estimated dates of windstorms prior to 1875 that resulted in released growth patterns of surviving trees, and duration of release pattern for live 300-400 year old trees that survived windstorms from 1670-1873 in eight stands on Kuiu Island.

Stand	Age (years)	DBH (cm)	Height (m)	Live crown DMR	Rating (below-live-crown)	Estimated year of windstorm	Duration of release pattern
1	308	61.0	35	4	2	1844	45
	320	73.4	~35[1]	6	2	-[2]	-
	328	55.4	35	3	2	1840	154
	334	104.2	38	3	1	1755	128
	340	95.0	43	4	2	-	-
	340	66.1	37	2	2	-	-
	417	59.6	~29	6	0	1717	63
	422	53.5	38	3	1	-	-
	443	91.2	35	4	0	-	-
	451	88.4	34	3	0	1817	6
						1845	6
2	325	75.4	38	4	0	-	-
	370	94.9	34	6	2	1687	22
3	321	69.9	35	6	2	-	-
	321	123.0	48	3	2	1687	48
	324	66.8	30	6	2	-	-
	342	56.5	30	6	2	-	-
	364	86.5	47	5	0	1711	58
						1784	25
						1825	8
						1873	68
4	313	63.2	28	6	2	-	-
	313	52.0	34	4	2	-	-
	322*[3]	81.4	41	3	2	-	-
	376	69.5	36	5	2	-	-
	378	78.4	37	6	2	1714	16
						1784	25
	404	71.2	~25	6	2	1799	32
						1858	19
5	331	66.9	43	3	2	-	-
	379	62.6	38	3	2	-	-
6	311	60.2	37	3	2	-	-
	314*	100.8	~36	4	2	-	-
	320	41.6	30	4	2	-	-
	324	64.5	37	6	2	1853	27

Appendix Table 1, continued.

Stand	Age (years)	DBH (cm)	Height (m)	Live crown DMR	Rating (below-live-crown)	Estimated year of windstorm	Duration of release pattern
7	334	88.1	40	4	2	-	-
	383	84.4	41	6	2	-	-
	411	77.9	41	6	2	-	-
	424	87.5	43	5	2	-	-
8	329	72.8	~30	6	2	1771	98
	342	77.2	43	5	2	1826	48
	347*	98.7	46	5	2	-	-
	375	58.4	~30	6	2	-	-
	394*	71.0	~33	6	2	-	-
	408*	90.4	46	5	2	1769	36
						1835	28

[1] Represents a minimum tree height due to a broken top.
[2] Represents the lack of a distinct release pattern.
[3] Represents a minimum tree age due to the lack of a pith in the core.

Appendix Table 2. Site variables for 76 plots on Kuiu Island.

Stand	Plot	Elevation (m)	Heatload (rank 1-9)	Slope (%)	Plant Assoc. (rank 1-3)	Site Index (ft)	Distance (m) to nearest adv. regen	Distance(m) to nearest residual	Distance (m) to nearest inoc. source
1	1	125	8	15	1	75	6	2	2
1	2	140	8	18	2	96	11	2	2
1	3	150	8	24	1	75	6	13	6
1	4	165	7	20	1	75	3	-	3
1	5	165	7	26	1	75	-	13	13
1	6	175	8	29	1	75	3	8	8
1	7	160	8	20	1	75	8	6	6
1	8	125	8	18	1	75	11	8	8
1	9	130	8	15	1	75	6	8	6
1	9.1	120	8	16	1	75	9	2	2
1	9.2	150	5	19	1	75	-	9	9
2	10	20	6	14	1	108	5	5	5
2	11	25	6	4	1	125	7	-	7
2	12	25	2	30	1	75	6	17	6
2	13	35	6	15	1	75	4	11	4
2	14	40	8	20	1	75	2	9	2
2	15	35	2	22	1	75	4	5	4
2	16	30	2	14	1	75	8	9	8
2	17	30	4	10	1	75	6	5	5
2	18	30	4	35	1	75	6	5	5
3	19	65	8	26	1	75	11	5	5
3	20	80	8	28	1	75	13	6	6
3	21	105	8	5	1	75	6	7	6
3	22	95	6	21	1	75	9	14	9
3	23	85	6	24	1	75	8	9	8
3	24	80	6	32	1	125	10	13	10
3	25	65	6	25	1	75	5	6	5
3	26	80	6	2	1	75	-	6	6
3	27	85	6	35	1	75	19	18	18
4	28	40	8	15	1	75	9	8	8
4	29	35	8	4	1	75	4	9	4
4	30	45	8	8	1	75	4	4	4
4	31	60	8	20	3	100	3	3	3
4	32	85	8	28	3	100	7	6	6
4	34	70	8	24	1	75	4	18	4
4	35	65	8	34	1	75	11	-	11
4	36	55	4	19	3	100	-	-	-
4	37	45	4	28	3	100	-	9	9
5	38	20	8	6	1	121	13	-	13
5	39	15	8	10	1	75	9	4	4
5	40	25	6	9	1	75	10	5	5
5	41	15	9	11	1	131	20	9	9
5	42	20	6	7	3	100	15	13	13
5	43	10	8	6	3	100	7	6	6

Appendix Table 2, continued.

Stand	Plot	Elevation (m)	Heatload (rank 1-9)	Slope (%)	Plant Assoc. (rank 1-3)	Site Index (ft)	Distance (m) to nearest adv. regen	Distance(m) to nearest residual	Distance (m) to nearest inoc. source
5	44	10	6	12	1	75	7	9	7
5	45	10	6	6	1	75	18	6	6
5	46	25	6	8	3	100	8	-	8
5	46.1	20	6	8	3	100	19	9	9
6	47	75	8	13	1	75	9	7	7
6	48	90	8	30	1	75	2	8	2
6	49	95	8	8	1	105	16	9	9
6	50	90	8	24	3	100	7	14	7
6	51	105	9	14	3	100	13	8	8
6	52	110	9	7	1	75	2	8	2
6	53	105	9	9	1	75	5	-	5
6	54	105	6	16	1	141	14	20	14
6	55	105	6	11	1	75	3	8	3
7	56	30	6	13	1	75	7	9	7
7	57	35	6	20	1	75	10	8	8
7	58	35	2	8	3	131	19	-	19
7	59	20	4	28	3	138	7	5	5
7	60	20	4	19	2	96	-	-	-
7	61	20	2	32	2	96	3	8	3
7	62	20	2	32	2	96	3	7	3
7	63	20	2	22	2	96	4	5	4
7	64	20	2	13	1	75	4	12	4
8	65	45	6	26	2	96	4	6	4
8	66	20	2	38	2	96	4	8	4
8	67	40	2	24	3	100	4	5	4
8	68	50	2	4	1	75	2	8	2
8	69	60	2	12	1	75	6	8	6
8	70	65	4	25	3	100	5	12	5
8	71	55	4	25	1	75	2	8	2
8	72	50	8	6	3	125	7	9	7
8	73	50	8	40	1	75	4	10	4
8	73.1	60	5	16	1	75	18	-	18