United States Department of Agriculture

Forest Service

Pacific Northwest Research Station

General Technical Report PNW-GTR-718

August 2007

# A Synthesis of the Literature on the Biology, Ecology, and Management of Western Hemlock Dwarf Mistletoe

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## Cover photo

Dead western hemlock tree with numerous hemlock dwarf mistletoe infections. Tree death resulted in a canopy gap.

# Abstract

**Muir, John A.; Hennon, Paul E. 2007.** A synthesis of the literature on the biology, ecology, and management of western hemlock dwarf mistletoe. Gen. Tech. Rep. PNW-GTR-718. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 142 p.

Hemlock dwarf mistletoe (*Arceuthobium tsugense* [Rosendahl] G.N. Jones) is a small, inconspicuous parasite that has significant effects on tree growth and stand structure in coastal forest ecosystems of western North America. Most previous research focused on the effects of hemlock dwarf mistletoe on timber production. Previous clearcut harvesting of large areas that removed virtually all infected trees and forestry practices that established even-aged stands of trees effectively prevented or minimized future hemlock dwarf mistletoe impacts. Under this regime, further research on hemlock dwarf mistletoe was considered unnecessary. However, current forestry practices that restrict clearcut harvesting to small openings and retain live trees to preserve attributes of old-growth forests create conditions that appear highly favorable for enhanced seed production by hemlock dwarf mistletoe, early spread of the mistletoe to infect young trees, and, consequently, increased growth impacts to residual trees over time. More information is needed on the biology and impacts of hemlock dwarf mistletoe in coastal western hemlock retention-harvested forests in the United States of America and Canada. Further work is recommended to develop sampling and monitoring procedures to determine hemlock dwarf mistletoe spread and impacts. We also need to investigate several unusual aspects of hemlock dwarf mistletoe biology and development such as long-distance seed dispersal and persistence in old-growth forests. Detailed tree, stand, and forest-level models are needed to monitor and project hemlock dwarf mistletoe effects over a wide range of ecological conditions and management regimes in coastal forests.



Keywords: Disease management, *Arceuthobium*, selection harvest, retention harvest, disease impact.

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## Introduction

In coastal forests of western North America from northern California to southern Alaska, hemlock dwarf mistletoe (*Arceuthobium tsugense* (Rosendahl) G.N. Jones)[1] is a common but inconspicuous parasite of western hemlock and occasionally other tree species (Geils et al. 2002, Hawksworth and Wiens 1996). *Arceuthobium tsugense* consists of four subspecies that occur on and are named after their principal host tree species: western hemlock, mountain hemlock, shore pine, and Pacific silver fir (Mathiasen and Daughtery 2007, Wass and Mathiasen 2003). The western hemlock subspecies that predominates in most western hemlock coastal forests has been the subject of most of the literature on hemlock dwarf mistletoe and is the major subspecies of concern for forest management. For convenience in this review, "hemlock dwarf mistletoe" is used to designate the western hemlock subspecies unless specified otherwise, and *A. tsugense* is used to designate the whole species.

***Arceuthobium tsugense*** **is one of approximately 30 species of dwarf mistletoe in North America.**

*Arceuthobium tsugense* is one of approximately 30 species of dwarf mistletoe in North America (Geils et al. 2002, Hawksworth and Wiens 1996, Nickrent et al. 2004). Dwarf mistletoes are flowering plants that live as perennial parasites in living tree tissue. Although they produce small aerial shoots with some chlorophyll, they photosynthesize at a very low rate (Hull and Leonard 1964a, 1964b; Leonard and Hull 1965; Miller and Tocher 1975; Tocher et al. 1984) and lack phloem elements to distribute any photosynthates (Kuijt 1960; Srivastava and Esau 1961a, 1961b). Dwarf mistletoes are believed to derive most of their nutrients from parasitism of their coniferous hosts (Hawksworth and Wiens 1996; Hull and Leonard 1964a, 1964b). Dwarf mistletoes spread within trees and from tree to tree by explosively discharged seeds that are covered with a natural glue-like substance called viscin. Most seeds that hit foliage and lodge on tree bark germinate, producing a small root-like structure that penetrates into the bark. Microscopic threads of the mistletoe grow through the inner bark and sapwood. The infection produces a swelling of an infected tree branch or bole. Aerial shoots and flowers are produced from the swollen bark 2 to 3 years after infection. Berries with a single seed mature a year after pollination and forcibly discharge seed in autumn. Over periods of several decades to centuries, hemlock dwarf mistletoe can proliferate on

[1] Hereafter see appendix 1 for common and scientific names of species.

and between trees, developing large swellings and fan-shaped masses of swollen branches called witches' brooms. As trees become older and more severely infected, they experience growth reductions in annual growth of bole diameter and height of 30 to 40 percent or more.

Hemlock dwarf mistletoe is an ecologically important component of western hemlock forests from southern Oregon to southeastern Alaska. After disturbances by windstorms or wildfires, hemlock dwarf mistletoe that survives on live residual trees can spread to infect nearby regenerated trees. Patches of infected trees expand, and after several decades to centuries, severely infected trees begin to die, are windthrown, and/or break off. This creates gaps in the forest canopy that allow new trees to establish and grow, and hemlock dwarf mistletoe spreads to infect these new trees. These processes and their effects affect the growth of other tree species and the biology of associated birds, animals, and other organisms. Many of the effects of dwarf mistletoes on trees and forest stand structures are beneficial for wildlife habitat and populations (Geils et al. 2002, Hawksworth and Wiens 1996). These kinds of effects for *A. tsugense* have received limited study but could be important for some areas and wildlife species.

In contrast to several reports of herbal uses and possible medicinal properties for leafy mistletoes in Europe, dwarf mistletoes including hemlock dwarf mistletoe, have few herbal uses or medicinal properties (Hawksworth and Wiens 1996). Smith (1928) reported that First Nation people near Bella Coola, British Columbia, used the shoots of hemlock dwarf mistletoe to treat hemorrhages and tuberculosis. However, reports of medicinal properties or therapeutic uses of leafy and dwarf mistletoes have not been substantiated by clinical trials (National Cancer Institute 2006).

*Arceuthobium tsugense* has been a long-term component of the extensive western hemlock forests of western North America. Hawksworth (1978) concluded from fossil evidence that dwarf mistletoe species and western conifers in North America have coevolved since at least the Miocene period, or about 25 million years. Hemlock dwarf mistletoe pollen deposited over the last several thousand to 30,000 years ago has been reported from several coastal regions (Greenwald and Brubaker 2001; Hansen and Easterbrook 1974; Hebda 1983; Heusser 1973a, 1973b, 1974, 1977, 1978, 1983; Mathewes 1973, Mathewes and Rouse 1975; Petersen et al. 1983). Thus, *A. tsugense* has been an integral component of forest ecosystems in western coastal North America.

Despite the widespread occurrence and significant effects of *A. tsugense*, most descriptions of west coast forests and ecological processes, e.g., Franklin et al.

(2002) and MacKinnon (2005), include very little or no mention of *A. tsugense* as a significant ecological component. An analysis of forest succession based on eight old-growth forest chronosequence installations on southern Vancouver Island included a report (Garbutt and Allen 1998) that five of the eight installations in which western hemlock predominated had hemlock dwarf mistletoe in the immature to old-growth stages. However, the effects of hemlock dwarf mistletoe on succession and ecology of coastal forests were not described. Franklin et al. (2002) noted that wind, insects, and diseases were causes of tree mortality that result in canopy gaps and creation of old-growth conditions. However, the ecological role of hemlock dwarf mistletoe was only briefly described (Franklin et al. 2002) as contributing to development of decadence by creating top breakage, wood decay, and wounds in living western hemlock trees.

*Arceuthobium tsugense* is the only western mistletoe in mild, wet coastal western hemlock forests and has several unique and interesting biological features compared to other dwarf mistletoes. It has one of the most extensive latitudinal ranges of any dwarf mistletoe species (Hawksworth and Wiens 1996). Most other dwarf mistletoe species grow inland in relatively open or low-density stands of pines or other tree species in regions with continental climates. In these inland forests, soil moisture usually is a limiting factor for tree growth and dwarf mistletoe development. In extremely dense and shaded western hemlock coastal forests, light rather than rainfall is a limiting factor, particularly for growth of aerial shoots and seed production of hemlock dwarf mistletoe (Shaw and Weiss 2000). *Arceuthobium tsugense* is also notable in that its four subspecies occur in very different forest ecosystems. The western hemlock subspecies occurs in western hemlock forests in humid to hyperhumid coastal maritime climates; the subspecies in shore pine stands occurs in "rainshadow," low-rainfall coastal climates; and the mountain hemlock and pacific silver fir subspecies, in high-elevation, subalpine climates.

Most of the previous research on hemlock dwarf mistletoe focused on the effects this parasite has on tree growth and timber production, and was limited to infection of relatively small trees in clearcut areas in only a few localities. Previous clearcut harvesting removed virtually all infected and uninfected trees, and forestry practices maintained dense, even-aged stands. Under these conditions, hemlock dwarf mistletoe incidence was substantially reduced in second-growth stands, effects on tree growth were effectively prevented or minimized, and further research on hemlock dwarf mistletoe appeared unnecessary.

Recently, forestry practices have changed, often drastically. In Washington and Oregon, harvesting of old-growth western hemlock forests on federal government lands is virtually prohibited with only limited selection harvesting. In other regions such as British Columbia and southeastern Alaska, these new practices include restriction of clearcut harvesting to small openings (in some instances prohibition of clearcut harvesting), reservation of large blocks of old-growth forest, and selection and retention harvesting and silvicultural systems. These measures are intended to preserve attributes of the residual forest for wildlife and biodiversity conservation, but they often result in retention of mistletoe-infected trees. These conditions appear highly favorable for increased and earlier spread of hemlock dwarf mistletoe to young trees and ultimately, increased growth impacts. In some areas, these new forestry practices are being implemented apparently with little or no consideration of the potential effects on hemlock dwarf mistletoe. Hemlock dwarf mistletoe effects in small openings and in retention-harvested forests have not yet been determined.

**There is a wide diversity of views and opinions among forestry professionals about existing and future impacts of hemlock dwarf mistletoe under these new scenarios.**

Further, in coastal western North America, there is a wide range of forest conditions, and in many of these areas, we know relatively little about potential spread and impacts of *A. tsugense* and the effects of using these new practices. There is a wide diversity of views and opinions among forestry professionals about existing and future impacts of hemlock dwarf mistletoe under these new scenarios. The changing management needs, the relative lack of information on hemlock dwarf mistletoe behavior, and the apparently wide variability of hemlock dwarf mistletoe effects over the extensive geographic range of hemlock dwarf mistletoe prompted us to review the scientific literature and other information for hemlock dwarf mistletoe.

## Previous Studies

For this review, we identified and cited approximately 300 reports that included information directly or closely related to aspects of hemlock dwarf mistletoe ecology and management. Geils et al. (2002), Hawksworth and Wiens (1996), and Kuijt (1955) previously reviewed dwarf mistletoe literature, but a large number of published reports on hemlock dwarf mistletoe were not included or were published subsequently. Hennon et al. (2001) and Muir et al. (2004b) summarized information on hemlock dwarf mistletoe with emphasis on preventing or reducing impacts by forest management during harvesting and silvicultural treatments. Literature on hemlock dwarf mistletoe has a lengthy history beginning with early studies by Drake (1915), Rosendahl (1903), Weir (1915, 1916, 1918), and others. Hildebrand (1995) reviewed hemlock dwarf mistletoe status in old-growth forests of Washington and Oregon. At the Wind River Canopy Crane Research Facility in southern Washington, Shaw and several colleagues (Mathiasen and Shaw 1998; Meinzer et al. 2004; Shaw and Weiss 2000; Shaw et al. 2000, 2005) studied hemlock dwarf mistletoe in the upper canopy of an old-growth forest. Shaw et al. (2004) compared Australian mistletoes and western North American dwarf mistletoes, supporting a proposal by Watson (2001) that mistletoes are keystone species. A shorter report tailored to hemlock dwarf mistletoe and forest management in British Columbia (Muir et al. 2007) was based on this review.

## Objectives

This paper reviews information about *A. tsugense* and particularly hemlock dwarf mistletoe from available scientific literature, unpublished data, and observations by the authors. The information is integrated here with an emphasis on predicting the behavior of the parasite and its impact in coastal forests of northwest North America, particularly under selection or retention harvesting. In this report, we suggest how hemlock dwarf mistletoe will behave and could be managed under these new forestry management regimes. Another major objective is to review how hemlock dwarf mistletoe contributes to and is important for stand structure, biodiversity, and wildlife habitat. Recently, Shaw et al. (2004) suggested that dwarf mistletoes represent keystone species based on their similar association with many birds and other species as previously proposed for leafy mistletoes (Cooney et al. 2006, Watson 2001). Several reports reviewed here suggest that hemlock dwarf mistletoe might have a similar ecological function. We review how natural disturbances and forest management affect hemlock dwarf mistletoe populations, apparently in predictable ways that can be adapted for forest management. We identify knowledge gaps and research needs for hemlock dwarf mistletoe, particularly related to biology, ecology, and growth effects of hemlock dwarf mistletoe, and management of hemlock dwarf mistletoe under the new selection and retention harvesting regimes.

**We review how natural disturbances and forest management affect hemlock dwarf mistletoe populations, apparently in predictable ways that can be adapted for forest management.**

Forestry professionals will often find that the distribution and local incidences of hemlock dwarf mistletoe are highly variable, and at times, technical information and management guidelines are contradictory or controversial. We have attempted in this review to present the various results and opinions and suggest how they can be rationalized and possibly reconciled. We hope our approach provides information and perspectives that are valuable for interested people, researchers, and forestry professionals.

Our objectives are to (1) compile and review recent information and literature on hemlock dwarf mistletoe, (2) highlight the diversity of data and opinion on hemlock dwarf mistletoe biology and management, and (3) identify topics that require further research or study to effectively manage coastal forests with hemlock dwarf mistletoe.

# Hemlock Dwarf Mistletoe Biology

## Overview

In North America, several dwarf mistletoes and a few leafy mistletoes (*Phoradendron* spp.) are parasites of coniferous trees (Geils et al. 2002). Dwarf mistletoes are perennial, parasitic flowering plants that live in the cortex and sapwood of trees. In contrast to the leafy mistletoes, dwarf mistletoes produce aerial shoots with leaves that are reduced to small squamate scales. Shoots have a small amount of chlorophyll, but dwarf mistletoes derive most of their carbohydrates, water, and mineral nutrients directly from their coniferous hosts (Hawksworth 1978). The perennial absorptive structure of dwarf mistletoes is called the endophytic system. It is embedded in the host cortex and sapwood. Dwarf mistletoes do not have conducting tissue (phloem) that could transport nutrients from their aerial shoots to their endophytic system.

Dwarf mistletoe flowers and berries are produced on aerial shoots that develop from the endophytic system. Berries explosively discharge a single sticky seed to distances of up to 15 m. Dwarf mistletoe seeds land on the foliage of a suitable tree, lodge on the bark, and germinate in the spring. If infection occurs, a swelling, aerial shoots, and flowers develop in 3 to 5 years. Over a period of several decades, hemlock dwarf mistletoe infection produces a pronounced swelling of the infected tissues and often an extensive growth of tree branches termed witches' brooms (fig. 1). Depending on tree species, ecological conditions, and disturbances, in some instances—often over a period of several decades to centuries—dwarf mistletoes can spread extensively within tree crowns and from tree to tree. Numerous and/or large dwarf mistletoe infections can substantially reduce the growth of infected trees. In some instances, mistletoe spread is slow or limited and effects on trees appear minimal.

## Taxonomy, Subspecies and Host Tree Susceptibilities

Hawksworth and Wiens (1996) reviewed the taxonomy and nomenclature of dwarf mistletoes in detail. Rosendahl (1903) first described hemlock dwarf mistletoe as a species from a collection on Vancouver Island, British Columbia. It was named

Figure 1—Western hemlock subspecies of *Arceuthobium tsugense* caused infections (witches' brooms) throughout the crown of this mature western hemlock tree.

*Razoumofskya tsugensis*, then briefly *Arceuthobium campylopodum* forma *tsugensis* (Rosendahl) Gill (Gill 1935). Jones (1936) gave it species status again as *Arceuthobium tsugensis* (Rosendahl) G.N. Jones, the name that is still recognized. The specific epithet was changed to "tsugense" to agree with the gender of the genus as required by the Botanical Rules of the International Code of Botanical Nomenclature (Hawksworth and Wiens 1996).

The taxonomy and nomenclature of hemlock dwarf mistletoe have been controversial. Recently, Douglas et al. (2000) grouped it and the dwarf mistletoes on true fir (*A. abietinum* Engelm. ex Munz) and western larch (*A. laricis* (Piper) St. John) as "*A. campylopodium* [sic] Engelmann" on the basis that there were " …no reliable morphological differences to distinguish them." However, we prefer the taxonomy and nomenclature of hemlock dwarf mistletoe as a distinct species and subspecies as outlined by Hawksworth and Wiens (1996) and Wass and Mathiasen (2003). We believe that the subspecies designations have substantial utility for ecological studies and management of *A. tsugense* and hemlock dwarf mistletoe.

Several subspecies of *A. tsugense* have been described (Hawksworth and Wiens 1996, Hawksworth et al. 1992, Wass and Mathiasen 2003) based on small but significant differences in morphological features, phenology of flowering and seed dispersal, and differences in susceptibility of their hosts to infection. The currently described subspecies include (1) western hemlock dwarf mistletoe (fig. 2), (2) shore pine dwarf mistletoe (fig. 3), and (3) mountain hemlock dwarf mistletoe (fig. 4) (Wass and Mathiasen 2003). Another subspecies on Pacific silver fir in a limited distribution in central Oregon was recently described by Mathiasen and Daugherty (2007).

*Arceuthobium tsugense* infects several host tree species (Hawksworth and Wiens 1996, Mathiasen 1994, Mathiasen and Daugherty 2005, 2007, Wass and Mathiasen 2003). The susceptibilities of common tree species in western coastal forests associated with the three currently described subspecies of *A. tsugense* are shown in table 1.

Recent studies of susceptibility of several host tree species to hemlock dwarf mistletoe indicated that *A. tsugense* subspecies have a narrow or limited host range (Mathiasen and Daugherty 2005, Mathiasen and Hawksworth 1988, Wass and Mathiasen 2003). Mathiasen and Daugherty (2005) concluded that in stands where a high proportion of western hemlock trees are infected with the western hemlock subspecies, "…any tree species other than western hemlock can be retained without expecting severe infection to occur." Further work is needed to confirm this conclusion for other subspecies and regions, but results of experimental inoculations (Smith 1971; Smith and Wass 1976, 1979; Wass and Mathiasen 2003) indicate that this is true for all of the hemlock dwarf mistletoe subspecies.

Robert Armstrong

Figure 2—Western hemlock subspecies of *Arceuthobium tsugense*.

R.L. Mathiasen

Figure 3—Shore pine subspecies of *Arceuthobium tsugense*.

R.L. Mathiasen

Figure 4—Mountain hemlock subspecies of *Arceuthobium tsugense*.

**Table 1—Susceptibilities of common western conifers to the subspecies of *Arceuthobium tsugense***

| Common coastal tree species[a] | Susceptibility[b] to *A. tsugense* subspecies: Western hemlock[c] | Shore pine[d] | Mountain hemlock[e] | Pacific silver fir[f] |
|---|---|---|---|---|
| Western hemlock | Principal | Occasional | Rare | Occasional |
| Shore pine (var. *contorta*) | Rare | Principal | ND | ND |
| Lodgepole pine (var. *latifolia*) | ND | Occasional[g] | Rare | ND |
| Lodgepole pine (var. *murrayana*) | Immune[b] | ND | Immune | ND |
| Mountain hemlock | Occasional | ND | Principal[c] | Principal[f] |
| Pacific silver fir | Occasional | ND | Principal[c] | Principal[f] |
| Grand fir | Rare | ND | Rare | Rare |
| Subalpine fir | Rare | ND | Principal[c] | Secondary[f] |
| Noble fir | Occasional | ND | Principal[c] | Principal[f] |
| Sierra white fir | ND | ND | ND | Occasional |
| Sitka spruce | Rare | ND | ND | ND |
| Engelmann spruce | Rare[g] | ND | ND | ND |
| Douglas-fir | Rare | Immune | Immune | ND |
| Western white pine | Rare[f] | Rare | Occasional[h] | Rare[f] |
| Whitebark pine | ND | ND | Secondary[b] | ND[f] |

[a] Tree species commonly occurring within the geographic range of *A. tsugense*. Totally immune species such as western redcedar are not listed. For scientific names, see appendix 1.

[b] Based on susceptibility classification by Hawksworth and Wiens (1972) of proportion of trees infected within 6 m of a severely infected host tree: principal host is 90 or more percent infected; secondary, 50 to 90 percent; occasional, 5 to 50 percent; rare, 1 to 5 percent; immune, 0 percent. ND indicates no data or unknown.

[c] Mathiasen and Daugherty (2005)

[d] Wass and Mathiasen (2003)

[e] Hawksworth and Wiens (1996)

[f] Mathiasen and Daugherty (2007)

[g] Mathiasen (1994)

[h] Kuijt (1955), Hawksworth et al. (1992)

## Geographic Range

Hemlock dwarf mistletoe has a natural geographic range from northern California, through Oregon, Washington, and British Columbia to southeastern Alaska (fig. 5). The most southerly occurrence is in California, at approximately 38 degrees latitude (Hawksworth and Wiens 1996, Mathiasen and Marshall 1999) and the most northerly occurrence near Chilkoot Lake, Alaska, at approximately 59 degrees (Drummond and Hawksworth 1979). Hemlock dwarf mistletoe occurs farther north than any other species of *Arceuthobium* and over one of the largest latitudinal ranges.

As described by Hawksworth and Wiens (1996) and Wass and Mathiasen (2003), the western hemlock subspecies extends from a few localities in northern


Figure 5—General geographic distribution of *Arceuthobium tsugense* (from Hawksworth and Wiens 1996) from northern California to southeast Alaska.

California to southeastern Alaska (fig. 6). Only a few western hemlock trees are infected in California (Mathiasen and Marshall 1999). The shore pine subspecies occurs from a few locations on the San Juan Islands in northern Washington to approximately Campbell River, British Columbia (fig. 7) (Wass 1976, Wass and Mathiasen 2003). The mountain hemlock subspecies occurs in a few localities in northern California (Mathiasen and Marshall 1999), more commonly in Oregon, and in only a few locations in Washington and southern British Columbia (Hawksworth and Wiens 1996) (fig. 8). The recently described Pacific silver fir subspecies has a small distribution limited to central Oregon (Mathiasen and Daughtery 2007).

Generally, hemlock dwarf mistletoe is abundant on the coastal mainland and on all large and most small islands wherever western hemlock is found. In British Columbia, Alfaro (1985) estimated that 15 percent of western hemlock stands are infested by hemlock dwarf mistletoe, mostly in a band about 150 km wide along the coast. It occurs farther east in watersheds of major rivers such as the Columbia River between Washington and Oregon and the Skeena River in British Columbia. Approximately 51 percent of inventory sample plots on Vancouver Island, British


Figure 6—Geographic distribution of western hemlock subspecies of *Arceuthobium tsugense*: (a) Alaska and British Columbia; (b) Washington, Oregon, and California (from Hawksworth and Wiens 1996).


Figure 7—Geographic distribution of shore pine subspecies of *Arceuthobium tsugense* (from Hawksworth and Wiens 1996).

Figure 8—Geographic distribution of mountain hemlock subspecies of *Arceuthobium tsugense* (from Hawksworth and Wiens 1996).

Columbia, were infested by hemlock dwarf mistletoe (Beale 1985). The distribution of *A. tsugense* and several other *Arceuthobium* species in Canada were further described and mapped by Kuijt (1963), Van Sickle and Smith (1978), and Wood (1986). In southeast Alaska, vegetation plot data from an extensive 5- by 5-km grid indicated a widespread occurrence of hemlock dwarf mistletoe in the southeast but not north of Haines or farther to the northwest along the Gulf of Alaska even though western hemlock grows in these areas (fig. 9).

**Dwarf mistletoes were called "light-loving plants" by Weir (1916) because of the tendency for rapid aerial shoot growth when a stand is partially thinned.**

## Aerial Shoots and Flowering

In 1 to 2 years after infection of the host branch or bole, aerial shoots of dwarf mistletoe develop from the endophytic system in a swelling and emerge from the bark. Aerial shoots are perennial, but most usually live for only 4 to 8 years. Infections without aerial shoots can continue to grow through live host tissues for many years (Trummer et al. 1998, Weir 1916), producing large swellings and witches' brooms, and then after a disturbance, can resume production of aerial shoots.

Dwarf mistletoes were called "light-loving plants" by Weir (1916) because of the tendency for rapid aerial shoot growth when a stand is partially thinned. In contrast, Wagener (1961) suggested that partial sunlight was more favorable to the establishment of dwarf mistletoes on their hosts. With another species of dwarf mistletoe, Knutson (1984) found the greatest number of aerial shoots with the least amount of shade (i.e., maximum light) in an experiment with seedlings, suggesting that dwarf mistletoe growth is enhanced by higher light levels. Studying other species of dwarf mistletoe, Scharpf (1972) found that light also enhanced the infection process. Baranyay (1962) indicated that increased light levels, e.g., from thinning, encouraged reproduction in previously dormant infections of hemlock dwarf mistletoe.

For hemlock dwarf mistletoe, growth and persistence of aerial shoots in old-growth trees is correlated with position in the tree crown (Shaw and Weiss 2000, Smith 1969). Most of the hemlock dwarf mistletoe infections with aerial shoots are situated in the upper third of the crown (Smith 1969). In dense coastal western hemlock forests, light can be a limiting factor and shoot abundance is correlated with the intensity of incident light. At the Wind River Crane Research Facility in the state of Washington, Parker (1997) divided an old-growth Douglas-fir/western hemlock forest canopy of 65 m height into three vertical light regimes based on the proportion of incoming light. These were (1) bright zone above 40 m height with 90 percent or more available radiation, (2) transition zone where available light decreases rapidly from 90 percent at 40 m height to 10 percent at 8 m height, and

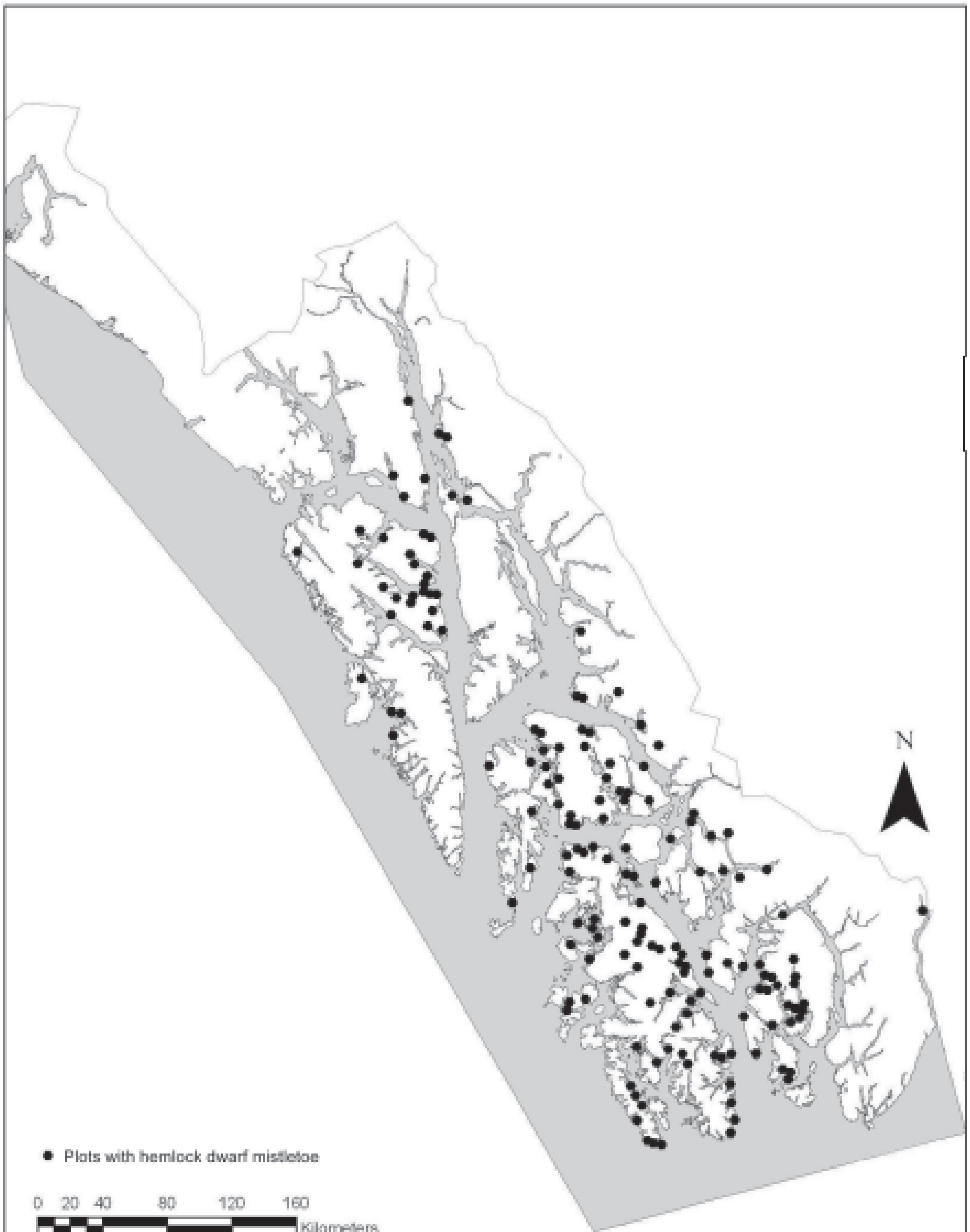


Figure 9—Occurrence of hemlock dwarf mistletoe in Alaska based on 5-km grid Forest Inventory and Analysis vegetation plots (wilderness areas not sampled).

(3) dim zone below 8 m with less than 10 percent of available light. Shaw and Weiss (2000) determined that all dwarf mistletoe infections at heights of 50 to 55 m had shoots ≥1 cm height and infections below 30 m height had no shoots. At 40 m height where 50 percent of the infections had shoots, yearly insolation was 2,200 MJ $m^{-2}$ based on hemispherical photographs taken above each infection. Shaw and Weiss (2000) noted that their results were contrary to findings from several previous studies of aerial shoot production on seedlings with hemlock dwarf mistletoe and other dwarf mistletoes, which indicated that some light was required for shoot production. Shaw and Weiss (2000) suggested that in the mid- to upper crowns of old-growth hemlock trees, the higher temperatures, photosynthetic capacity, and nitrogen content of foliage reported by several previous authors could enhance mistletoe shoot production. Light requirements for mistletoe shoot production on seedlings in experimental environments might also be anomalous compared to those for old-growth trees.

Dwarf mistletoes, including hemlock dwarf mistletoe, are dioecious, i.e., either staminate (male) or pistillate (female) flowers on separate plants (fig. 10). Staminate shoots are usually light yellow-green, and pistillate shoots are yellow-green to dark purple. In some hemlock dwarf mistletoe populations, the number of pistillate and staminate plants was reported to be unequal (Wiens et al. 1996), but this was probably attributed to the sampling method. Wiens et al. (1996) sampled plants that were within 3 m of the ground as these could easily be reached. Pistillate plants tend to survive (remain on the infected branches) longer than male plants in low light conditions, so near the ground more female infections have aerial shoots and thus are identifiable.[2] Results of a more recent study that sampled hemlock dwarf mistletoe infections over the whole tree height indicated that the sex ratio was 1:1 (Mathiasen and Shaw 1998). Male flowers are 2 to 3 mm in diameter and have sessile anthers, each containing 1,000 to 4,000 pollen grains (Hawksworth 1978). After staminate flowers open they remain open, but anthers open and close in response to changes in temperature and relative humidity (Gilbert and Punter 1990). Pollen is dispersed in clumps of 20 to 100 pollen grains. Pistillate flowers are small, approximately 1 mm in diameter, and very inconspicuous. Both staminate and pistillate flowers have nectaries, which are attractive to insects. Several studies indicate that the larger staminate flowers have more visitations by insects. Flowering occurs from June to August (Carpenter et al. 1979, Smith 1971).

[2] Mathiasen, R.L. 2006. Personal communication, Professor of Forest Ecosystem Health, School of Forestry, Northern University Arizona, Flagstaff, AZ 86011.

Figure 10—Pistillate (top left, purple-brown color) and staminate (bottom left and right, yellow) flowers of hemlock dwarf mistletoe.

## Pollination and Fruiting

The pollination process is poorly understood in hemlock dwarf mistletoe and other *Arceuthobium* species, and probably involves wind and/or insects. Flowers have characteristics suggesting both wind and insects are responsible for transferring pollen from staminate flowers to pistillate flowers. In one study of the pollination biology of lodgepole pine dwarf mistletoe Gilbert and Punter (1984) concluded that both wind and insects transported pollen. Other studies (Gregor et al. 1979, Penfield et al. 1976, Player 1979) of other dwarf mistletoes were inconclusive but described several insects that might be involved.

Following pollination, fruit maturation takes approximately 15 months. Berries contain a single seed. Up to 688 berries have been found on single infections of hemlock dwarf mistletoe that developed from inoculated seeds (Smith 1971), and several thousand berries have been observed on naturally occurring plants. During summer, pistillate plants often have both flowers and ripening fruits that will discharge seed in a few months.

## Seed Dispersal

**Dwarf mistletoes have a fascinating mechanism of seed dissemination—explosive discharge seed is forcibly ejected from each berry at an initial velocity of approximately 100 km per hour.**

With the exception of one species, all dwarf mistletoes have a fascinating mechanism of seed dissemination—explosive discharge. At maturity, a single seed is forcibly ejected from each berry at an initial velocity of approximately 100 km per hour, but seeds tumble in flight and velocity decreases rapidly (Hinds and Hawksworth 1965). Hemlock dwarf mistletoe shoots and berries are oriented so that seeds are shot off toward light sources such as patches of open sky (Thomson 1979). Thus, hemlock dwarf mistletoe seeds are mostly discharged in a trajectory upward and outward from the source tree (Bloomberg et al. 1980).

Most hemlock dwarf mistletoe seeds are dispersed in a period of approximately 3 weeks from early September to late October (Hawksworth and Wiens 1996, Smith 1973) depending on elevation and probably other factors. The number of hemlock dwarf mistletoe seeds dispersed during daylight hours is approximately three to five times the number dispersed at night (Smith 1973).

## Seed Retention and Germination

Dwarf mistletoe seeds are coated with a sticky, hygroscopic substance known as viscin (Paquet et al. 1986), which accounts for 26 to 61 percent of the seed weight (Knutson 1984) and allows seeds to adhere to objects where they land. Viscin initially absorbs water during rain or dew and becomes slippery. If the seeds land on needles, they often slide down to lodge at the base of the needle on the branch. This is the most effective location for infection. Soluble pectins in the viscin layer wash away or are absorbed by the bark, and remaining cellulose strands in the layer anchor the seed to the bark (Paquet et al. 1986).

The endosperm of dwarf mistletoe seeds is chlorophyllous and capable of small amounts of photosynthesis (Muir 1975, Tocher et al. 1984). In coastal western hemlock forests between seed dissemination in October and germination of seeds next spring, the winter is typically cold with low light intensity. Under these conditions, photosynthesis over winter, before germination, is likely minimal. However, in warmer spring weather during germination, photosynthesis of the endosperm might facilitate radicle growth and penetration.

In British Columbia, Smith (1974) hand-placed seeds of hemlock dwarf mistletoe on western hemlock foliage and followed their fate. He found that in almost snow-free winters, 96 percent of seeds were retained over one winter. In southeast Alaska, Shaw and Loopstra (1991) reported that 65 percent of hand-placed seeds remained on western hemlock foliage over one winter. Seeds placed on needles with a downward orientation had only 13 percent survival; most presumably were removed by rain or snow. Carpenter et al. (1979) found that 67 percent of seeds survived one winter on foliage in Oregon, with more seeds placed on bark retained than seeds placed on foliage.

Hemlock dwarf mistletoe seeds germinate in late winter or early spring (Smith 1971, 1985). In British Columbia, Smith (1974) found that 62 percent of hand-placed mistletoe seeds germinated in the spring. Smith reported a somewhat lower germination rate when hemlock dwarf mistletoe seeds were placed on other tree species. Carpenter et al. (1979) found that in Oregon, 45 percent of seeds germinated. In Alaska, Shaw and Loopstra (1991) found that 33 percent of mistletoe seeds germinated.

## Penetration and Infection

Germinating hemlock dwarf mistletoe seeds produce a short radicle, then a holdfast, and finally a penetration peg that mechanically penetrates into the cortex of live twigs (Hunt et al. 1996, Knutson 1984) (fig. 11). After penetration of the host cortex by the radicle, the absorptive, root-like endophytic system develops (Alosi and Calvin 1984, 1985; Srivastava and Esau 1961a, 1961b). Lateral strands of dwarf mistletoe grow in the cortex and sinkers develop in the sapwood. Sinkers develop when filaments of mistletoe contact the cambium, induce ray cells, and become embedded in extra-wide wood rays in the annual rings of sapwood.

In British Columbia, Smith (1971) found that 22 percent of seeds caused infection. Infection rate was only 8 percent in Oregon (Carpenter et al. 1979). In Alaska, 20 percent of retained seeds caused infection (Shaw and Loopstra 1991). Some infections from these artificial inoculations occurred on tree species that have never been reported as infected in nature. In inoculation experiments, infection success was enhanced with increased light levels (Knutson 1984).

By dissecting infections in young hemlock trees around residual mistletoe-infected trees at four sites in southeast Alaska, Shaw (1982) determined that hemlock tissues were between 1 and 14 years old when first infected. Fifty percent of the infections occurred on branches that were 4 years of age or younger. Only 1 to 10 percent of infections occurred on branch and bole tissues older than 10 years.

## Symptoms

The first symptom or indication of dwarf mistletoe infection of host tissue is a small swelling (fig. 12) at the point of infection (Hawksworth and Wiens 1972).


Figure 11—Hemlock dwarf mistletoe seed with radicle (arrow) and holdfast.

Figure 12—Small hemlock dwarf mistletoe infection with aerial shoots.

Hemlock dwarf mistletoe initially produces a pronouncedly swollen sapwood growth ring 1 to 2 years after infection as illustrated by Smith (1971), thus allowing determination of the approximate age of infection. As the parasite endophytic system grows within tree tissues, swellings enlarge and become fusiform-shaped as they age. Infections caused by the shore pine subspecies are typically more globose. These differences in shape are distinctive for the subspecies on other host tree species and are useful for identifying hemlock mistletoe subspecies in stands with several tree species (Smith 1971, Wass 1976, Wass and Mathiasen 2003). Many hemlock dwarf mistletoe swellings stimulate production and/or elongation of buds on swollen tissues that often develop into a profuse, dense mass of distorted branches called a “witches’ broom” (fig. 13) that continue to grow into large structures (fig. 14).

Hemlock dwarf mistletoe occasionally infects the leader of a tree, resulting in a flat broom at the top (fig. 15). With the loss of apical dominance in the broomed top, no new uninfected branch becomes a leader, and such trees do not grow any higher.

When infections occur on the bole, i.e., on the main stem or trunk of the tree, or when infections occur on branches close to the tree bole, the endophytic system grows into bole tissues resulting in a “bole infection” (see Baranyay et al. [1971] for discussion of definitions). These often become large, fusiform swellings, up to 1 m long, growing on one side of, or around, the bole. Bole infections have important detrimental effects on the health and commercial value of trees, but they appear much less important for the actual tree-to-tree spread of hemlock dwarf mistletoe than branch infections (Smith 1973). Several types or variations in bole infections occur (fig. 16). Pronounced bole infections are infrequent or absent from mistletoe-infected overstory old-growth trees in some areas such as at the Wind River Canopy Crane research area (Shaw et al. 2005).

Figure 13—Young hemlock dwarf mistletoe witches’ broom.

Figure 14—Hemlock dwarf mistletoe brooms close to the tree bole.

Figure 15—Hemlock dwarf mistletoe-caused flat treetops.

a

b

Figure 16—Hemlock dwarf mistletoe bole infections: (a) globose-shaped bole infection; (b) burl-like bole swelling with few or no shoots commonly found in infested stands.

From one to several years after a swelling develops, aerial shoots of hemlock dwarf mistletoe develop from the endophytic system and emerge from the swollen branch or bole. Aerial shoots of *A. tsugense* are confined to the basal swollen portion of branches of a witch's broom. This is termed a localized infection (Kuijt 1960). Other dwarf mistletoes such as lodgepole pine and Douglas-fir dwarf mistletoe form witches' brooms with shoots emerging in a regular pattern from non-swollen branches termed a systemic infection (Kuijt 1960).

Flowers develop 1 to 2 years after shoots emerge, with berries produced and seed dispersed in the following year. Flowering and seed dispersal usually continue on shoots for several years. Individual aerial shoots of hemlock dwarf mistletoe generally persist for 2 or 3 years with some surviving as long as 5 years (Smith 1971). The perennial endophytic system can produce repeated crops of reproductive shoots, but infections frequently do not continue to produce reproductive aerial shoots.

**Large hemlock dwarf mistletoe witches' brooms are often older than 100 years.**

The endophytic system remains alive in an infection for as long as the tree, bole, or branch lives (Smith 1985), i.e., for centuries. Large hemlock dwarf mistletoe witches' brooms are often older than 100 years (Trummer et al. 1998).

### Rate of the Reproductive Cycle

The rate of the reproductive cycle of hemlock dwarf mistletoe, i.e., time from seed dispersal to seed dispersal from new plants, is one of the factors that appear to influence hemlock dwarf mistletoe occurrence and long-term success as a parasite. The reproductive cycle of hemlock dwarf mistletoe is completed at a more rapid rate in Oregon (Carpenter et al. 1979) and British Columbia (Smith 1971) than to the north in Alaska (Shaw and Loopstra 1991). For example, in British Columbia, some hemlock dwarf mistletoe swellings are visible on branches during the first year of infection, and shoots often occur during the second year. Mature fruit is produced in the fourth or fifth year after infection. In contrast, Shaw and Loopstra (1991) found that swellings in Alaska were usually produced about 3 years after inoculation, and generally 3.5 to 4 years elapsed before shoots were produced. However, these infections died from shading before fruit production occurred; thus, the duration from infection to fruit and seed production in southeast Alaska has not been determined conclusively.

## Factors Affecting Biology and Seed Dispersal

### Local Seed Dispersal

As described below, a detailed knowledge of seed dispersal is important for predicting hemlock dwarf mistletoe spread and impacts after selection or retention harvesting. Several of these factors are included in a recent epidemiological model developed for hemlock dwarf mistletoe and other dwarf mistletoes (Robinson and Geils 2006). Factors affecting seed dispersal distances were presumed to be height in the tree of the source plant, angle of seed discharge, wind velocity, and stand density (Hawksworth 1978). Boyce (1948) suggested that hemlock dwarf mistletoe seeds disperse to a maximum distance of 12 m. In British Columbia, Smith (1966) found that over 95 percent of hemlock dwarf mistletoe seeds fell within 9 m of a severely infected residual western hemlock. Smith (1973, 1985) determined that although hemlock dwarf mistletoe seeds were dispersed up to 16 m from the bole of a source tree, most seeds landed within 2 to 4 m of the tree. Bloomberg et al. (1980) measured horizontal seed dispersal from infections positioned at three different heights. Height above the ground did not appreciably affect maximum horizontal dispersal where wind was not a factor.

In other dwarf mistletoes, wind can influence dispersal distances with the greatest distances being in the direction of prevailing winds (Scharpf and Parmeter 1971). In many coastal areas, prevailing winds during seed dispersal, i.e., September through October, are generally from the south and southeast; thus, greatest dispersal distances of hemlock dwarf mistletoe would be expected to the north and northwest of mistletoe-infected trees. However, Smith (1977) determined that on his study tree, most hemlock dwarf mistletoe infections and berries were on the south side of the tree, and most hemlock dwarf mistletoe seeds were dispersed to the south. Winds during seed dispersal in this area were usually from the south and did not significantly increase seed dispersal distance.

**Western hemlock forests with dense canopies probably reduce hemlock dwarf mistletoe dispersal distances and spread rates because seeds are frequently intercepted before they reach their maximum dispersal distance.**

The structure of the forest canopy presumably affects dispersal of hemlock dwarf mistletoe. Western hemlock forests with dense canopies probably reduce hemlock dwarf mistletoe dispersal distances and spread rates because seeds are frequently intercepted before they reach their maximum dispersal distance. This often results in seeds not escaping from the source tree to infect neighboring trees. Thus, actual dispersal distances are probably far less on average than the potential maximum distances. Shea and Stewart (1972) estimated that the spread of hemlock dwarf mistletoe is relatively slow in dense, even-aged forests, probably about 0.5 m per year. In British Columbia, Bloomberg et al. (1980) measured the mistletoe seeds that escaped from western hemlock source trees relative to the position of infections in the crown (distance to shoot tip). A maximum of 70 percent of hemlock dwarf mistletoe seeds escaped when they were produced near branch tips, i.e., at the periphery of the tree crown. However, seed escape fell to 50 percent just 40 cm from branch tips and continued to drop off to a low of about 30 percent when seeds were ejected from infections situated farther in the crown interior. When seeds escape from a source tree, they very rarely pass through an adjacent tree crown to hit the next tree, i.e., "leapfrogging" a tree (Bloomberg et al. 1980), unless the seed source is higher than the top of the adjacent tree. Thus, in a high-density, uniform-structured, even-aged western hemlock forest there is probably very slow tree-to-tree spread of hemlock dwarf mistletoe in the absence of an overhead source of hemlock dwarf mistletoe seeds, i.e., a large hemlock dwarf mistletoe-infected residual tree.

As described below in the section on stand development, vertical spread of dwarf mistletoe appears important for colonization by the parasite and eventual impacts on tree growth. For immature western hemlock stands in British Columbia, Richardson and van der Kamp (1972) estimated an upward advance of hemlock dwarf mistletoe of 30 and 65 cm per year in stands that were relatively dense or open, respectively. Hemlock dwarf mistletoe spreads vertically at about 20 cm per year in thinned young-growth stands in southeast Alaska (Shaw and Hennon 1991). These estimates were consistent with measurements made by Bloomberg et al.

(1980) on the upward trajectory of hemlock dwarf mistletoe seeds, which suggested that most infections occur less than 1 m above the source infection.

In some areas, height of hemlock dwarf mistletoe infections above ground level appears to be an important factor. Smith (1969) and Shaw and Weiss (2000) determined that in dense stands of mature trees, hemlock dwarf mistletoe infections with shoots and berries predominate in the upper one-third of the tree crown where light conditions are favorable. Generally, in retention- or selection-harvested areas, it is expected that hemlock dwarf mistletoe shoot growth and seed production will increase in the lower crown of hemlock dwarf mistletoe-infected trees. However, some well-exposed western hemlock trees appear to have very little hemlock dwarf mistletoe shoot development, possibly because of host conditions (Bickford et al. 2005) or some other factors.

Local differences in air temperature with tree height could also be important. As reported by Parker (1995) and Shaw and Weiss (2000), higher air temperatures occur in the middle to upper crown of a forest canopy. One example of a pronounced vertical temperature gradient was observed in October 2001 at the Wind River Canopy Crane Research Facility where severe frost was observed at ground level, although air temperature was well above freezing in the upper crowns of the 50- to 55-m hemlock trees at the site. In the upper crowns, hemlock dwarf mistletoe infections were dispersing seeds. Apparently in some areas, hemlock dwarf mistletoe seed production and dispersal could be limited at or near ground level by frost damage (Baranyay and Smith 1974, Kuijt 1955) but remain unaffected in the upper tree crowns of nearby trees. This could be an important factor at the upper elevation limits of hemlock dwarf mistletoe, particularly for the mountain hemlock subspecies, in mountainous areas where cold-air drainage often occurs in valleys and frost damage occurs in topographic depressions ("frost pockets"). Cold air drainage and frost damage might be important factors in these areas and where hemlock dwarf mistletoe occurs in riparian zones (Muir 2004, Swanson et al. 2006), as well as the northwest limits of the range in Alaska. Retention harvesting and recent clearcut harvesting create small openings that also could be subject to more frequent or more severe local frost occurrence and damage to hemlock dwarf mistletoe.

Hemlock dwarf mistletoe seed dispersal from tall residual trees is another important but little-known process. Our casual observations suggest that hemlock dwarf mistletoe infection of small trees is infrequent adjacent to some dense stands of tall residual trees, similar to previous observations of low incidence of lodgepole pine dwarf mistletoe adjacent to dense mature stands in Alberta (Muir 1970).

Possibly in some instances very little hemlock dwarf mistletoe seed from the upper crown of a 50-m-tall tree falls onto adjacent small regenerating hemlock trees. Another possibility is suggested by Wicker (1967), who found that for lodgepole pine, most dwarf mistletoe seeds were removed by snow, and consequently, infection of small trees less than 1 to 2 m tall was uncommon adjacent to dense, mature stands. Similarly, for hemlock dwarf mistletoe, snow loads adjacent to tall mature trees might be extremely deep, thereby reducing infection of nearby small trees. In some high-elevation and northern areas, snow makes up 50 percent or more of the annual precipitation (MacKinnon 2005, Schwartz and Miller 1983), but the actual amount of snow versus rain is highly dependent on landscape position and elevation. Heavy snow loads in northern forests could be a factor responsible for the low incidence or absence of hemlock dwarf mistletoe in some areas.

Previous results of Smith (1966, 1973, 1977), Shaw (1982), Shaw and Weiss (2000), and observations of incidence of hemlock dwarf mistletoe in young hemlock trees, e.g., Edwards (2002) and Muir (2004), indicated that seed production and dispersal are critical events in the life history and epidemiology of hemlock dwarf mistletoe. Most of the available information on seed dispersal is derived from studies of only a few trees in a few widely separated localities. Our unpublished results suggest that there is considerable tree-to-tree variation in hemlock dwarf mistletoe seed production and dispersal. This requires further study to determine variation in hemlock dwarf mistletoe seed production, dispersal, and effects of a wide range of factors including host tree features, weather, and environmental factors. These include, for example, tree height, age, hemlock dwarf mistletoe severity, position of infections in tree crowns and height above ground level, ecological zones and subzones (Meidinger and Pojar 1991), riparian zones, topographic position, latitude, and elevation.

## Long-Distance Seed Dispersal

The explosive discharge of dwarf mistletoe seeds effectively spreads the parasite over short distances. Several authors speculate that some other mechanism is responsible for long-distance dispersal from stand to stand, or in southeast Alaska and British Columbia, from island to island and across fjords, glaciers, and other barriers. Little is known about long-distance dispersal of hemlock dwarf mistletoe seeds, but several studies implicate birds as potential agents (Hawksworth 1978, Shaw et al. 2005). Most of the research on animal dispersal of dwarf mistletoe seeds has been conducted in the United States on other dwarf mistletoes (Hawksworth and Wiens 1996). Here, we summarize several results of these studies that might play a role in long-distance dispersal of hemlock dwarf mistletoe in western forests.

Anderson (1949) speculated that much of the long-range dispersal was the result of sticky seeds of dwarf mistletoe adhering to birds that were searching for food and that these seeds could later be transferred to healthy trees as the birds continued to feed. Preening and grooming by birds could deposit seeds on foliage. In general, most birds do not eat dwarf mistletoe seeds, and seeds that pass through their digestive track are not viable (Hudler et al. 1979). Hudler (1976) suggested that pH and temperature in birds' digestive tracts kill dwarf mistletoe seeds.

Geils et al. (2002) and Hawksworth and Wiens (1996) summarized the role of birds and mammals in vectoring dwarf mistletoe seeds. Mammals, especially squirrels, are known to spread dwarf mistletoe, but apparently only play a role in relatively short-range dispersal because of their small home ranges (Nicholls et al. 1984). Hudler et al. (1974) and Ostry et al. (1983) reported that flying squirrels carried seeds of eastern dwarf mistletoe in their fur. Northern flying squirrels might play a similar role in dispersing hemlock dwarf mistletoe seeds. In Alaska, Bakker and Hastings (2002) found that 54 percent of tagged northern flying squirrels made dens in mistletoe-infected western hemlock trees. In Washington, Shaw and Flick (2002) reported that the Douglas squirrel was common in the upper canopy of an old-growth Douglas-fir and western hemlock forest at the Wind River Canopy Crane Research Facility during hemlock dwarf mistletoe seed dispersal.

Birds are likely vectors for the long-range dispersal that has allowed hemlock dwarf mistletoe to become established on all islands of consequential size and nearly all mainland areas of northern portions of its range. Several studies with other dwarf mistletoes indicated that the most probable vectors for hemlock dwarf mistletoe seeds are small insectivorous birds that feed in western hemlock canopies, particularly in the fall months when dwarf mistletoe seed is dispersed. Based on previous results that indicated gray jays act as vectors of seeds for some dwarf mistletoes (Nicholls et al. 1984), Steller's jay, which is a winter resident, might be capable of vectoring hemlock dwarf mistletoe seeds. In Washington at the Wind River Canopy Crane Research Facility, Shaw et al. (2002, 2005) reported that Steller's jay, gray jay, and particularly, red crossbills are common and feed on western hemlock cones during the hemlock dwarf mistletoe seed-dispersal period. The jays are present in the upper canopy during the seed-dispersal period but do not commonly feed on seed in cones. However, the red crossbill biological species feeds exclusively on western hemlock cones and flies in large groups of 10 to 50 birds from tree to tree, remaining in the upper canopy.[3] They actively feed on hemlock seeds during the period of hemlock dwarf mistletoe seed dispersal (September to late October). These birds would be expected to travel large distances in search of cone crops and likely be responsible for long-distance spread of hemlock dwarf mistletoe seed. Shaw et al. (2005) suggested that red crossbills were responsible for establishing new mistletoe infection centers in old-growth western hemlock forests.

Marbled murrelet, which was reported to roost and nest in western hemlock trees infected by hemlock dwarf mistletoe in Washington (Nelson and Wilson 2002), might be another agent for dispersal of hemlock dwarf mistletoe seed in coastal forests, although it does not move extensively within forest canopies.

## Mortality Factors and Use of Biological Control

Most authors have assumed that hemlock dwarf mistletoe infections on nonfoliated branches were dead. Bloomberg and Smith (1982) found that the proportion of such "dead" infections on Vancouver Island, British Columbia, was substantial in the lower crown position and concluded that these infections were probably dying because of shading. Data from young western hemlock trees in British Columbia (Smith 1977, 1985), where light was probably more available, indicated 60 percent survival for infections up to 12 years of age. Shading and branch senescence are considered important mortality factors for hemlock dwarf mistletoe. This topic is explored in more detail in the section on stand development below.

Other significant damaging factors for hemlock dwarf mistletoe include hyperparasitic fungi and early frosts. Several fungi are associated with hemlock dwarf mistletoe shoots and swellings (Kope and Shamoun 2000). Several that invade and kill aerial shoots or the bark of swellings appear to be selective, persistent and effective natural biological controls (Baranyay 1966, Funk and Baranyay 1973, Funk and Smith 1981, Funk et al. 1973, Shamoun and DeWald 2002, Smith and Funk 1980). The nutritious hemlock dwarf mistletoe-infected cortical tissues, their low moisture content (Baranyay 1964) and the presence of dead phloem likely facilitate the pathogenicity and effects of the associated fungi. Recently, two fungi, *Colletotrichum gloeosporioides* and *Neonectria neomacrospora*, have been studied to determine their pathogenicity, virulence, and potential as biological control agents (Askew 2006, Reitman et al. 2005, Shamoun and DeWald 2002).

[3] Shaw, D. 2006. Personal communication, Assistant Professor, Department of Forest Sciences, Oregon State University, Corvallis, OR 97331.

Hawksworth et al. (1977) and Hawksworth and Wiens (1996) described fungal parasites that attack the shoots of the various dwarf mistletoe species in western North America. Some of these fungi occur at high incidence and appear to limit or reduce the reproduction of dwarf mistletoes. One of the most common and damaging fungal species known to occur on hemlock dwarf mistletoe aerial shoots is *C. gloeosporioides* (Kope et al. 1997, Hennon, personal observations). Usually, the incidence of native fungi on dwarf mistletoes is extremely variable from year to year, and several authors considered that the possibility of their use as biological control agents was remote (Hawksworth et al. 1977, Smith 1985). However, recent developments in enhancing effectiveness and application of biological control agents suggested that with further research and development, these fungi could be developed as effective biological control agents to reduce hemlock dwarf mistletoe spread in selection- or retention-harvested forests (Shamoun and DeWald 2002).

Stevens and Hawksworth (1984) described insects that feed on shoots or fruits of dwarf mistletoes. Larvae of Johnson's hairstreak butterfly, *Loranthomitoura johnsonii*, feed on hemlock dwarf mistletoe shoots from California to southern British Columbia (Carpenter et al. 1979, Guppy and Shepard 2001, McCorkle 1962). Mammals that feed on dwarf mistletoe are discussed below.

Occasionally, early frosts can freeze hemlock dwarf mistletoe fruits and disrupt the seed-dispersal mechanism (Baranyay and Smith 1974). Hemlock dwarf mistletoe seed dispersal in October or November is vulnerable to frost. Frost also can kill existing plants or infections (Kuijt 1955), thereby substantially reducing spread and diminishing populations of the parasite.

## Host Resistance to Infection

Smith et al. (1993) reported genetic resistance of western hemlock to infection by hemlock dwarf mistletoe. Two of 60 seedlings planted around the mistletoe–infected residual tree studied by Smith (1966, 1973, 1977) were resistant to hemlock dwarf mistletoe infection. Very few hemlock dwarf mistletoe infections developed on the trees as compared to nearby seedlings that were exposed to the same numbers of hemlock dwarf mistletoe seeds. The occurrence of two resistant trees in this small planting suggested that genetically resistant trees might occur frequently in populations of western hemlock trees. Unfortunately, the two resistant trees were the slowest growing trees in the trial,[4] but the prospects of finding other faster

[4] Wass, E.F. 2006. Personal communication. Pathologist, Canadian Forest Service, Pacific Forestry Centre, Victoria, BC V8Z 1M5.

growing, mistletoe-resistant hemlock trees appears promising. Further research is underway to determine and select genetically resistant western hemlock trees (Shamoun and DeWald 2002). Cultivation of hemlock dwarf mistletoe in vitro, which was reported by Deeks et al. (2001), is a potential screening method.

The two resistant trees that Smith et al. (1993) reported indicate that genetic resistance could be a significant factor in hemlock dwarf mistletoe spread and impacts. Western hemlock populations from different locations, elevations, latitudes and/or provenances might exhibit differences in frequency of resistance to hemlock dwarf mistletoe infection, as reported by Wu et al. (1996) for lodgepole pine resistance to stem rusts and other pathogens. Incidence of hemlock dwarf mistletoe could be low in some locations because of genetically resistant populations of western hemlock trees. Further research appears warranted to determine the frequency, nature, and extent of western hemlock genetic resistance to hemlock dwarf mistletoe.

## Effects of Dwarf Mistletoe on Individual Trees

### Tree Physiology and Form

Although hemlock dwarf mistletoe is capable of very small amounts of photosynthesis (Hull and Leonard 1964b, Miller and Tocher 1975), it draws essentially all of its nutrients from its host. This leads to growth reductions of the host tree and several physiological and pathological effects described below.

Several reactions by trees to infection by hemlock dwarf mistletoe, i.e., branch and bole swellings and witches' brooms, are believed to be induced hormonally. Dwarf mistletoe appears to alter concentrations of tree growth regulators (Knutson 1979), particularly abscisic acid, indole-3-acetic acid and zeatin riboside (Livingston et al. 1984). The most substantial evidence of hormone imbalances comes from research on eastern dwarf mistletoe infecting black spruce in Minnesota. Similar research has not been conducted on hemlock dwarf mistletoe, but it appears likely that swelling and witches' brooms are caused by hemlock dwarf mistletoe modifying concentrations of growth hormones in western hemlock.

**Several reactions by trees to infection by hemlock dwarf mistletoe, i.e., branch and bole swellings and witches' brooms, are believed to be induced hormonally.**

Hemlock dwarf mistletoe is probably affected by the physiology of its host tree, as recently demonstrated for southwestern dwarf mistletoe on ponderosa pine in Arizona (Bickford et al. 2005). The influential host factors probably include tree vigor and associated physiological characteristics such as tree age, size (tree height, diameter), crown position in canopy, crown condition (density of foliage, dieback of main stem), sapwood to foliage ratio, height to diameter ratio, and others. A more detailed knowledge of these features and their possible association with hemlock dwarf mistletoe seed production and infection could facilitate selection of hemlock dwarf mistletoe-infected trees to be retained or removed to either enhance or reduce hemlock dwarf mistletoe spread and future growth impacts.

The most important effects of dwarf mistletoe infection are growth abnormalities and their consequences, but there are other physiological effects. Using potted seedlings, Tocher et al. (1984) determined that aerial shoots of hemlock dwarf mistletoe transpire at rates approximately twice that of western hemlock tissues. Hemlock dwarf mistletoe transpired more than its western hemlock host at almost all conditions of soil moisture stress and darkness. Values as high as 62 times the transpiration rate of western hemlock tissues were recorded for hemlock dwarf mistletoe. Thus, dwarf mistletoe infections may contribute to water imbalances in trees and exacerbate droughty conditions for severely infected western hemlock trees.

The physiological effects of hemlock dwarf mistletoe on old-growth trees appear quite different. At the Wind River Canopy Crane Research Facility in southern Washington, Meinzer et al. (2004) measured hydraulic conductance, water and carbon relations on three uninfected and five severely infected 250-year-old, 55-m-tall, western hemlock trees. Uninfected trees had approximately 160 live branches, 50 percent more than severely infected trees. Uninfected trees also had 50 percent more leaf area than infected trees on branches distal to infections that were used to measure water conductance. These values were almost the reverse of observations of much younger trees where branches and foliage appear denser on infected than uninfected western hemlock trees. Daily water use was consistently and significantly greater in uninfected than in severely infected trees. The mean nitrogen content and photosynthetic capacity of foliage was less in infected than in uninfected trees. The authors concluded that with the water use of infected trees reduced by 40 percent, photosynthesis reduced by 20 percent, and foliage area reduced 40 percent, carbon accumulation was reduced 60 percent in severely infected old-growth trees. The authors further suggest that in dry seasons or weather, severely infected old-growth trees are at a disadvantage compared to nearby uninfected trees. This water-deficiency stress might explain why old, severely infected trees die prematurely in comparison to nearby similar lightly or uninfected trees.

Although the parasite occurs strictly on aboveground portions of western hemlock trees, root systems can be influenced by the parasite. Smaller root systems of trees infected by other dwarf mistletoe species have been reported (Knutson and Toevs 1972). In a forest setting, these reductions could affect the ability of an infected tree to compete with neighboring trees for soil nutrients, for water, and for light in the canopy. Debilitating effects of hemlock dwarf mistletoe infection on root systems might make infected trees more vulnerable to windthrow or more susceptible to infection by root disease fungi such as *Heterobasidion annosum*.

Hemlock dwarf mistletoe affects host-tree witches' broom formation in a manner somewhat differently than other dwarf mistletoes. Hemlock dwarf mistletoe witches' brooms are similar to normal branches in species with prolific branching but differ in that broom branches are oriented horizontally and usually in overlapping layers. Consequently, although hemlock dwarf mistletoe shoots grow upward in response to light (Thomson 1979), they often must grow through one or more dense layers of foliage to expose their berries for effective seed dispersal. Hemlock dwarf mistletoe also appears to have a more pronounced effect on growth of the distal portion of infected branches than other dwarf mistletoes and markedly increases the diameter of infected branches at the junction of the branch with the bole (Smith 1969), even on small infected branches.

The physiology of several previously unreported features of hemlock dwarf mistletoe also need to be investigated. These include physiological aspects and effects of live hemlock dwarf mistletoe-infected branches low on the bole below uninfected foliated branches. These low, infected branches have or do not have tree foliage. The unknown aspects include:

- Longevity of hemlock dwarf mistletoe-infected branches that have or do not have foliage.
- How live mistletoe-infected branches without foliage obtain their nutrients.
- How foliage on infected branches differs in shade tolerance and other features from that on uninfected branches.
- How these hemlock dwarf mistletoe-infected branches affect tree growth.

One of the most striking and interesting effects of hemlock dwarf mistletoe infection is retention of live, nonfoliated hemlock dwarf mistletoe-infected branches (fig. 17). Apparently hemlock dwarf mistletoe infections on nonfoliated branches at distances of up to 1 m or more from the bole are able to direct or draw water and nutrients from the bole in sufficient amounts to keep nonfoliated branches alive for several decades. These infected, nonfoliated branches likely contribute to overall growth loss and other effects caused by hemlock dwarf mistletoe, but their role or

Figure 17—Live hemlock dwarf mistletoe infections on nonfoliated branches of western hemlock at Harris Creek plot, Vancouver Island, British Columbia.

effects have yet to be determined. Van der Kamp[5] found that removal of these types of branches increased radial growth of boles by 5 to 15 percent, but treatment effects were not statistically significant, apparently because of large tree-to-tree variation in growth rates. Most authors have assumed that nonfoliated branches are dead, but this is not the case for many branches that have hemlock dwarf mistletoe infections.

Another interesting and potentially significant feature of hemlock dwarf mistletoe is its apparent capability to increase the shade tolerance of western hemlock foliage. Under dense canopies in coastal western hemlock forests, there is usually a heavily shaded, well-defined lower level where tree branches have no foliage (i.e., below the "live crown"). In dense hemlock stands, less than 10 percent of available light penetrates to this level (Parker 1995, 1997). However, in this extremely

[5] van der Kamp, B. J. 2004, Personal communication. Professor, Department of Forest Sciences, University of British Columbia, Vancouver, BC V6T IW4.

shaded layer, hemlock dwarf mistletoe-infected trees occasionally have mistletoe-infected branches that have retained their foliage (fig. 18). These branches occur on trees that are components of both the upper canopy and understory. Judging by the sizes of some trees, some of these infected, foliated branches are retained for several to many decades, and possibly even centuries, after noninfected branches have been shaded out and died. As with the lower live branches that appear dead, described above, these lower live foliated branches probably represent a net energy loss for these trees. The photosynthetic capacity and/or efficiency of foliage on these hemlock dwarf mistletoe-infected branches needs to be determined particularly in comparison to the foliage on shaded and exposed uninfected branches.

Retention of foliage on hemlock dwarf mistletoe-infected understory trees could enhance survival of hemlock dwarf mistletoe in dense stands by conferring a competitive advantage to mistletoe-infected understory trees. After a major disturbance to the canopy, such hemlock dwarf mistletoe-infected understory trees could grow rapidly to reach a dominant position in a regenerating forest. These trees could become major sources of hemlock dwarf mistletoe seeds for dispersal to and infection of nearby regenerating trees, similar to the tree studied by Smith (1966, 1973, 1977). Apparently, this could occur frequently, based on results of Thomson et al. (1985a, 1985b) that indicated that many of the most severely hemlock dwarf mistletoe-infected trees had an early period of suppressed growth of 60 years or more before growing rapidly after a stand disturbance. Retention of foliage on suppressed, understory hemlock dwarf mistletoe-infected trees also suggests that despite a low incidence of infection, hemlock dwarf mistletoe could persist and survive for several decades and perhaps centuries, in some areas until conditions are favorable for renewed seed production and infection of regenerating trees. Retention of foliage on hemlock dwarf mistletoe-infected trees also appears to be unusual because hemlock dwarf mistletoe infection of branches commonly results in chlorosis of foliage distal to the infection. This is apparently due to a pronounced deficiency in nitrogen associated with hemlock dwarf mistletoe infection (Meinzer et al. 2004). This type of chlorosis appears to be a frequent and often diagnostic feature of hemlock dwarf mistletoe infection (fig. 19).

**Perhaps the most important ecological and economic consequence of dwarf mistletoe infection is reduced annual tree growth. In general, annual growth reduction occurs only in moderately to severely infected trees.**

## Tree Growth

Perhaps the most important ecological and economic consequence of dwarf mistletoe infection is reduced annual tree growth. In general, annual growth reduction occurs only in moderately to severely infected trees. Height growth is more seriously affected than diameter growth for a given degree of infection (Hawksworth

Figure 18—Hemlock dwarf mistletoe-infected branch with foliage in the lower heavily shaded canopy.

Figure 19—Chlorosis of western hemlock foliage distal to hemlock dwarf mistletoe infection.

1978). In severely mistletoe-infected old-growth, tree top-kill or tree death sometimes results. Shea and Stewart (1972) claimed that excessive top-kill and mortality can reduce aesthetic values. Hawksworth (1978) reported that cone and seed crops can be reduced on severely infected trees of some dwarf mistletoes, but no quantitative information exists on these effects for hemlock dwarf mistletoe. Even if hemlock dwarf mistletoe limited tree reproduction to some degree, western hemlock reproduces so prolifically in most of its range that this probably is not an important issue. Several studies have been undertaken in various regions to quantify growth loss caused by hemlock dwarf mistletoe as described below.

## Tree Mortality

Hemlock dwarf mistletoe is associated with top-kill. Bloomberg and Smith (1982) suggested that top dieback could limit spread of the mistletoe into young stands. Buckland and Marples (1952) suggested that hemlock dwarf mistletoe influences top-kill by diverting nutrients from the tops of trees to witches' brooms lower in the crown. Excessive growth of infected tissues drains resources from other parts of the tree, and carbon allocation can be greatly affected throughout the tree. However, results of Meinzer et al. (2004) did not support this supposition. They found that the proportion of mistletoe-infested tissue was very low on their study trees.

Hemlock dwarf mistletoe is also associated with tree mortality. Tree mortality associated with hemlock dwarf mistletoe infection differs between young and old forests. In young, fast-growing forests, growth loss associated with severe dwarf mistletoe infection could debilitate trees to the extent that they lose their ability to compete with lightly or uninfected hemlock trees, or other species. Consequently, severely infected trees that are relegated to a lower crown position as relatively small trees can eventually die because of suppression. In older forests, severely infected trees in codominant and dominant canopy positions can die directly from dwarf mistletoe infection rather than from intertree competition, and their death can create canopy gaps.

**In older forests, severely infected trees in codominant and dominant canopy positions can die directly from dwarf mistletoe infection rather than from intertree competition, and their death can create canopy gaps.**

Mortality of old-growth trees (fig. 20) is often associated with numerous infections or large witches' brooms. Older, severely infected trees are weakened by the physiological effects of hemlock mistletoe infection (Meinzer et al. 2004) and consequently are likely more vulnerable to secondary insects and/or diseases. For example, western hemlock trees infected with hemlock dwarf mistletoe in British Columbia did not survive repeated defoliation during outbreaks of hemlock looper, but hemlock trees without hemlock dwarf mistletoe survived (Buckland and Marples 1952). Dead standing trees with numerous witches' brooms, apparently

Figure 20—Tree mortality of western hemlock severely infected by hemlock dwarf mistletoe.

killed by hemlock dwarf mistletoe, are a common feature of old-growth forests in southeast Alaska, and probably other areas, but the actual cause of death in this mortality has not been carefully evaluated.

In Washington near the Wind River Canopy Crane Research Facility, several long-term studies indicated a substantial amount of mortality in a 350-year-old Douglas-fir and western hemlock forest, with a large proportion of the mortality associated with hemlock dwarf mistletoe infection (DeBell and Franklin 1987, King 1961). From 1947 to 1983 gross tree growth was 22 $m^3 \cdot ha^{-1} \cdot yr^{-1}$ with 20 $m^3 \cdot ha^{-1} \cdot yr^{-1}$ mortality, essentially resulting in zero net growth (DeBell and Franklin 1987). Western hemlock accounted for one-half of the growth and 28 percent of the mortality, most of which was attributed to effects of hemlock dwarf mistletoe.

In British Columbia, Alfaro (1985) summarized data collected from seven 40- to 100-year-old western hemlock stands infected with hemlock dwarf mistletoe. An average of 4.7 stems per hectare, 0.6 percent of the total stems per hectare, were dead due to mistletoe infection. Three stands had no mortality attributed to hemlock dwarf mistletoe. Tree death not resulting from hemlock dwarf mistletoe averaged 46.7 stems per hectare or 4.9 percent of the total.

New information on tree mortality associated with hemlock dwarf mistletoe in Alaska indicates a greater annual rate of mortality associated with higher infection rates (see "Effects on Growth of Trees and Stands").

Dwarf mistletoes are associated with other mortality agents in some forest ecosystems (Geils et al. 2002, Hawksworth and Wiens 1996). Bark beetle populations can build in dwarf mistletoe-infected trees and attack other trees. However, bark beetles are usually not considered to be important in coastal forests and western hemlock does not have serious bark beetle enemies (Furniss and Carolin 1977).

## Wood Quality

Along with causing growth loss, allowing the entry of heart rot fungi, and killing trees, hemlock dwarf mistletoe affects the timber resource by reducing wood quality. Limbs that support witches' brooms form a large knot of very dense wood, a response that probably helps support the additional weight of the broom. Branches in the lower and middle portions of the crown of severely infected trees are approximately 30 percent larger in diameter than those in lightly infected trees (Smith 1969). Large knots associated with infections reduce wood quality (Shea and Stewart 1972) and adversely affect yields (Smith 1969).

Another aspect of wood quality is the dense compression wood that forms on the side of a tree that supports witches' brooms (Wellwood 1956). Resin canals are more common in infected wood (Srivastava and Esau 1961b). Infected wood tends to have a greater specific gravity (Wellwood 1956). However, when the specific gravity of whole trees was compared by infection severity, the more severely infected trees had lower specific gravity. Thus, these trees produce a more variable wood density, i.e., some wood in their boles is light and some wood is dense, and they also produce less pulp because of generally lower specific gravity. In addition, the wood in boles near witches' brooms has lower moisture content (Wellwood 1956). Hunt (1971) found higher lignin content and a doubling of concentrations of alcohol and benzene associated with hemlock dwarf mistletoe bole infections that make this wood unsuitable for use as pulp unless mixed with large amounts of uninfected wood. Microscopic examination of the dwarf mistletoe endophytic system and the cellular structure of infected wood and bark indicated that the largest effect of infection was an increase in the size of wood rays (Srivastava and Esau 1961a, 1961b).

## Wood Decay

**Bole infections and large witches' brooms on primary branches near the bole frequently harbor wood decay or heart rot fungi.**

Bole infections and large witches' brooms on primary branches near the bole frequently harbor wood decay or heart rot fungi (fig. 21a). Wood decay is one of the major losses of commercial wood volume in old-growth western hemlock forests (Farr et al. 1976, Kimmey 1956). Wood decay fungi are important ecologically because they often are associated with or cause tree death and, consequently, canopy-gap formation in old-growth forests (Hennon 1995). In Oregon and Washington, Englerth (1942) estimated that wood decay fungi that entered large witches' brooms and bole infections caused 31 percent of the heart rot in western hemlock. The same decay fungi reported by Englerth were present in southeast Alaska including *Ganoderma applanatum*, *Phellinus hartigii*, and *Ganoderma tsugense* (Holsten et al. 1985). *Phellinus hartigii* had a particularly close association with hemlock dwarf mistletoe in British Columbia and Alaska (Foster et al. 1958, Holsten et al. 1985) as a sapwood parasite (fig. 21b). Trees collapse after 25 percent of the circumference is killed (see footnote 5) creating a distinctive step-like stump as illustrated by Allen et al. (1997). Other heart rot fungi associated with hemlock dwarf mistletoe include *Echinodontium tinctorium* (Weir and Hubert 1918), *Fomitopsis pinicola* (Etheridge 1973), and *Pholiota adiposa* (Kimmey 1964). Foster et al. (1953) found that 75 percent of hemlock dwarf mistletoe bole infections were associated with wood decay in British Columbia, but in southeast Alaska bole infections are commonly but not consistently associated with heart rot (Farr et al. 1976, Kimmey 1956). Wood decay was found to be associated with hemlock dwarf mistletoe bole infections in thinned young-growth stands in Washington and Oregon (Goheen et al. 1980).

## Tree Hazards

Witches' brooms of hemlock dwarf mistletoe can eventually grow to a very large size weighing several hundred kilograms (Buckland and Marbles 1952) (fig. 22). Witches' brooms are potentially hazardous in recreation areas and around homes because they frequently have decay and often break out of trees during storms or when laden with snow (Hadfield 1977, Shea and Stewart 1972). In many hemlock dwarf mistletoe-infested stands, the forest floor is littered, sometimes densely, with witches' brooms that have broken out of trees. Wallis et al. (1980) described the potential hazard by hemlock dwarf mistletoe-infected trees in British Columbia. Russell (1966) suggested removing dead hemlock dwarf mistletoe witches' brooms from trees in recreation sites in state parks in Washington. Dead tops and snags are other potentially hazardous conditions caused by hemlock dwarf mistletoe.

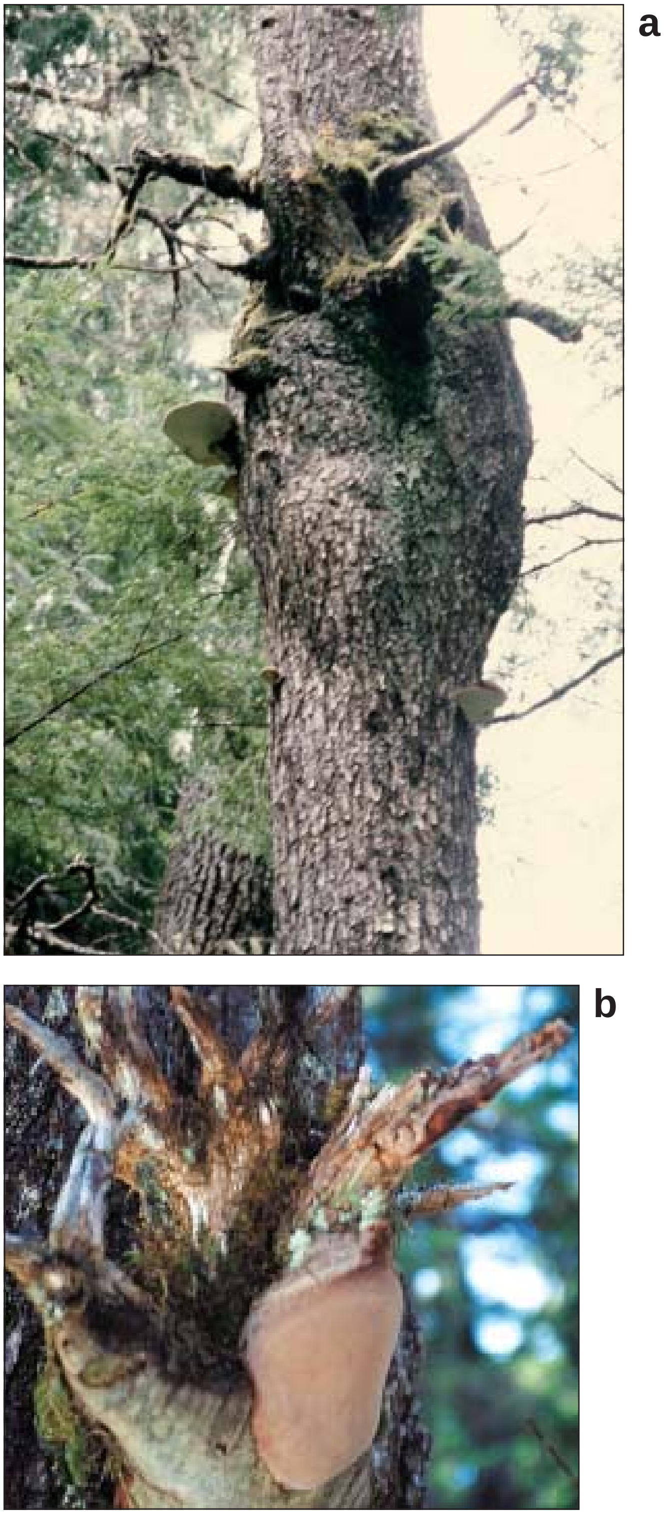

Figure 21—(a) Wood decay and decay fungi sporophores associated with hemlock dwarf mistletoe on western hemlock; (b) hemlock dwarf mistletoe broom with *Phellinus hartigii* sporophore.

Figure 22—Large hemlock dwarf mistletoe brooms on western hemlock.

## Effects on Trees, Stands, and Forests

### Infection Rating Systems

Studies on growth loss associated with hemlock dwarf mistletoe (described below) use one of several systems for rating the severity of infection. A system for quantifying dwarf mistletoe infection is necessary for evaluating effects of the disease because, hypothetically, tree responses, e.g., reduced growth, should be proportional to the amount of hemlock dwarf mistletoe infestation in a tree.

Hawksworth and Lusher (1956) and Hawksworth (1977) developed a six-class dwarf mistletoe rating (DMR), which is the most widely used system for estimating dwarf mistletoe severity. To estimate a DMR, the live crown of an infected tree is visually divided into equal vertical thirds. Each third is assigned a value: 0 for no branches infected; 1 for one-half or fewer of the branches infected; and 2 for more than half of the branches infected. The sum of the three values is the DMR, which ranges from 0 to 6. A DMR for a stand of trees is calculated by averaging all host DMRs. A stand dwarf mistletoe index (DMI) is calculated from the average of all mistletoe-infected trees for the susceptible host species (Geils and Mathiasen 1990).

The DMR was developed for open pine forests. Variations on this system have been used by other workers and for other dwarf mistletoes (Hawksworth and Wiens 1996). For example, Tinnin (1998) used an estimate of the proportion of each crown-third occupied by witches' brooms (broom volume rating, BVR), rather than the proportion of infected branches, to rate Douglas-fir infected by Douglas-fir dwarf mistletoe. In northern Arizona, Parker and Mathiasen (2004) evaluated DMR, BVR, and total broom volume, a system that they developed and recommended to rate southwestern dwarf mistletoe witches' brooms in ponderosa pine. Dooling (1978) gave an excellent tabulation of dwarf mistletoe surveys and rating systems.

Smith (1969) adapted the six-class system outlined by Baranyay et al. (1971) for a nine-point rating of mistletoe-infected western hemlock. He included large witches' brooms and bole swellings with three points per one-third interval of the whole tree height, not just the "live" foliated crown. Smith (1969) recognized that infected hemlock trees were difficult to rate because of lower dead and missing branches and upper crowns that were mostly unobservable from the ground. He recommended rating only the middle third of the tree, which was readily examined and contained the greatest number of live mistletoe infections. His rating system included ratings for bole swellings and volunteer-leader witches' brooms.

Laurent (1981) argued that the traditional six-point rating system was inappropriate in southeast Alaska. Tops of trees are often difficult to see, and the lower crown often has dead infected branches. A modification of this system, where only the middle third of the live crown is rated, has been used in other forest ecosystems with uneven-aged stands (Myers et al. 1976) and is suggested for use in southeast Alaska (Laurent 1981). If data on each third of the live crown were recorded separately during surveys, then these or other options would be available for analysis. Shaw et al. (2000) found that for hemlock dwarf mistletoe in old-growth western hemlock trees at the Wind River Canopy Crane Research Facility, 10 to 40 percent of 140 trees were accurately rated by the six-class DMR. Four of five observers correctly rated mistletoe-infected old-growth hemlock trees with an accuracy of 70 to 95 percent. Other rating systems for western hemlock dwarf mistletoe were not evaluated.

Our and previous workers' observations of live mistletoe-infected branches below what is usually considered to be the live or green crown suggest that a reevaluation of the DMR for western hemlock should be undertaken. If all of the lower infected branches were included, we suspect that a DMR rating for an infected tree would generally be higher, but a reevaluation of ratings is required to determine this. It would be useful to have one accepted rating system so that results on spread rates and tree effects of hemlock dwarf mistletoe in different regions could be compared.

**We suggest that most management plans and objectives should include a target level or threshold of acceptable or desirable dwarf mistletoe impact.**

## Effects on Growth of Trees and Stands

Information on losses owing to reduced annual growth and mortality caused by hemlock dwarf mistletoe is important for considering how to manage infested forests. We suggest that most management plans and objectives should include a target level or threshold of acceptable or desirable dwarf mistletoe impact. Some studies indicated that annual growth loss in very severely infected old-growth stands could reach 17 $m^3/ha^{-1}$ (Smith 1969), a level that might be unacceptable for any management that includes timber as an objective. However, other studies have indicated fewer or no effects.

**British Columbia—**

Several studies in British Columbia provided detailed information on growth loss and other effects to trees caused by hemlock dwarf mistletoe. Wellwood (1956) examined the effects of hemlock dwarf mistletoe infection on 10 western hemlock trees. Stem analyses were used to determine how infection affected tree growth. Trees ranged in size from 71 to 97 cm diameter at 1.2 m height and ages from 146 to 256 years. Trees were grouped into three infection classes based on the number of witches' brooms and bole infections. This early study did not use the Hawksworth and Lusher (1956) six-class DMR system. Wellwood found that growth was not significantly different between lightly and moderately infected trees. However, severely infected trees had significantly less growth. Several of the dissected trees had severe heart rot that apparently was caused by decay fungi that infected the trees through bole cankers caused by hemlock dwarf mistletoe.

Smith (1969) quantified growth loss caused by hemlock dwarf mistletoe in trees approximately 110 years old on Vancouver Island, British Columbia. For rating severity of infection, Smith used a nine-point rating system (described above) similar to the six-class system. Uninfected and lightly infected western hemlock trees had a 41 percent greater annual volume growth than severely infected dominant and codominant trees. Severely infected trees averaged 133 years age; moderately infected, 104 years; and lightly infected, 94 years.

**Uninfected and lightly infected western hemlock trees had a 41 percent greater annual volume growth than severely infected dominant and codominant trees.**

Severely infected trees were actually larger than lightly and moderately infected trees early in their lives, but by the time they were destructively sampled for stem analysis, they had significantly less volume, diameter, and height. Height/diameter ratios were less for severely infected trees. Increased taper in the lower boles of severely infected trees was also noted. Ring analysis revealed that radial growth fell off severely in 28 years prior to destructive sampling for severely infected trees, as compared to the 28-year period previous to that. A striking finding was that uninfected and lightly infected trees had 81 percent more height growth than severely infected trees toward the end of the study. For a 1.5-ha plot that encompassed the study area, annual volume loss (compared to healthy trees) was 15 to 27 percent of total tree growth, increasing to 40 percent in the last 2 years. This amounted to a reduction in growth of 17 $m^3 \cdot ha^{-1} \cdot yr^{-1}$ based on growth reductions of moderately and severely infected dominant and codominant trees.

Smith (1969) found that branches in the lower and middle portions of the crown were approximately 30 percent larger in severely infected trees than in lightly infected trees. Smith suggested that these large knots will have adverse effects on the yield and quality of forest products. Based on a sample of branches, the number of infections ranged from 23 to 1,351 per tree. The quantity and vigor of dwarf mistletoe aerial shoots increased sharply with increasing height above the ground. Smith speculated that low light intensity was responsible for reducing shoot production on infections in the lower crown.

Smith (1969) found that the difference in number of infections between lightly and severely infected trees was greatest in the middle one-third of the tree, a portion of the tree more easily observed than the top third. Volume produced by severely infected trees was found to be 37 and 43 percent less than lightly infected trees by using two different methods of rating trees, i.e., rating all three thirds and rating only the lower and middle-third, respectively. There was considerable variation in radial growth among the sample trees that could not be explained by dwarf mistletoe infection levels.

Thomson and Smith (1983) examined the growth of 22-year-old western hemlock trees that had been planted around a residual infected tree previously studied by Smith (1966, 1973, 1977). Hemlock dwarf mistletoe infection had a significant effect on height increment but not on radial growth. Radial growth was affected by microsite variables (especially growth of neighboring trees) and March to May precipitation levels (Thomson and Smith 1983).

Thomson et al. (1984, 1985b) reviewed and analyzed data from previous studies by Smith (1969) and Alfaro (1985) in British Columbia to determine growth loss associated with hemlock dwarf mistletoe. Difficulties in sampling, particularly the selection of trees to be used as controls for a comparison of growth, are discussed in their papers. They indicated that control trees—healthy or lightly infected—should ideally share all of the characteristics of age, microsite, and stand history of infected trees, but these types of trees can rarely be found near moderately or severely infected trees. Their analyses and interpretations of these data from earlier studies—described as very conservative—indicate volume reductions of 15 and 25 percent for moderately and severely infected trees compared to healthy trees for stands of up to 80 years of age (Thomson et al. 1984). They suggested that these growth reductions would likely continue in older infected stands.

**Severely infected and moderately infected trees had an average of 39 percent and 23 percent less volume growth, respectively, than uninfected or lightly infected trees.**

In another major study in British Columbia, Thomson et al. (1985a) analyzed growth of mistletoe-infected western hemlock trees in five stands on northern Vancouver Island. Infected western hemlock trees were rated for dwarf mistletoe infection severity by using the six-class system and then dissected systematically to determine growth patterns by ring analysis. Approximately 6 to 16 trees were sampled in each infection class on each of the five sites. Dissected trees ranged in age from 45 to 126 years, mostly owing to variable periods of suppressed growth before release. The authors found that growth patterns were complicated by variations in the growth history of trees before stand-opening events, presumably gap-level blowdown and mortality. They corrected for differences in suppression by comparing growth patterns after release at a selected comparison age of 45 to 80 years for each stand. Severely infected (DMR 5 or 6) and moderately infected (DMR 3 or 4) trees had an average of 39 percent and 23 percent less volume growth, respectively, than uninfected or lightly infected trees (DMR 0, 1, or 2). Lightly infected trees were pooled with uninfected trees because light infection is known to have no significant impact on growth (Hawksworth 1961, Parmeter 1978).

Thomson et al. (1985a) stated that their results reflected growth loss on an individual tree basis; their study did not examine loss on a stand basis. Because severely infected trees occupy a significant portion of the canopy and site for long periods, the authors reasoned that neighboring healthy and/or less severely infected trees probably did not compensate for very much of the growth loss. They suggested that their results can be used to estimate impacts per stand based on the proportion of the trees within each infection class.

**Washington and Oregon—**
Data from a limited study of 50- to 60-year-old stands in coastal Washington suggested that western hemlock trees severely infected with hemlock dwarf mistletoe had about 40 percent less volume than uninfected but otherwise comparable stands (Sterling 1962). This difference appeared unusually large compared to results from other studies.

In two locations in Washington, Hadfield (1980) measured trees to determine impacts of hemlock dwarf mistletoe in second-growth trees. In one unthinned area, five plots with a total of 36 infected trees averaging 43 years old were established around single, obviously infected residual trees. There were no significant differences for total tree volume or the most recent 5- or 10-year radial growth measured at a 10-cm diameter top for trees with different DMRs and distances from the residual infected trees. Possibly the variations in growth among the relatively few trees, 2 to 14 per DMR, obscured differences or differences were not pronounced at the bole height where disks were taken. Hadfield (1980) remarked that hemlock dwarf mistletoe spread appeared to be much less than expected from these residual trees in the densely stocked (1,200 trees per hectare) stand and that trees were not infected severely enough to cause significant growth reductions.

In a 75-year-old stand thinned 26 years previously, Hadfield (1980) compared growth of 40 trees in a thinned area and 40 trees in an unthinned area containing hemlock dwarf mistletoe. Trees in the thinned stand with DMR 3-6 were significantly larger and had significantly greater radial growth at stump height, but not at the height of a 10-cm diameter top, than trees with DMR 0 to 2. There were no significant differences between trees in the same DMR classes in the thinned versus unthinned areas. Hadfield reported that some of the more severely infected trees had indications of recent reduced growth but concluded that hemlock dwarf mistletoe effects on growth would not be significant because most second-growth stands managed for timber would be harvested by age 40 to 100. Hadfield also selected 42 trees in the same area to determine effects of hemlock dwarf mistletoe on log grades and found that there were no effects. He reported that infected hemlock trees had live branches below the main portion of the live crown, but did not mention any hemlock dwarf mistletoe infection on these branches. Despite finding no detrimental effects on growth of young hemlock trees, Hadfield (1980) recommended that hemlock dwarf mistletoe should not be ignored during clearcut harvesting and that control treatments were justified if large numbers of infected trees remained after harvesting.

In an extensive study of wood decay in paired, thinned and unthinned stands of 40- to 100-year-old western hemlock trees in Washington and Oregon, Goheen et al. (1980) also recorded occurrences of hemlock dwarf mistletoe-infected trees by DMR. Stands were thinned in 1959 to 1972, approximately 10 to 20 years before the study. Hemlock dwarf mistletoe occurred in six of the eight areas studied. The percentage of hemlock dwarf mistletoe-infected trees in each DMR category increased after thinning in 12 stands, decreased in 10 stands, and remained unchanged in three. In mistletoe-infested stands, trees in thinned areas were significantly larger than in unthinned areas.

**Alaska—**

New unpublished information on the association of hemlock dwarf mistletoe infection and western hemlock radial growth is available from southeast Alaska. These results were an extension of a study that evaluated the long-term spread and intensification of hemlock dwarf mistletoe following wind disturbance (Trummer et al. 1998). Wind disturbance was intended to function as a surrogate for selection harvest. Permanent plots were established in 1994 in forests that recovered from stand-replacing storm events in the 1880s. Some large and small residual trees remained after the storms and provided the inoculum for spread of hemlock dwarf mistletoe to the newly regenerated forest. Most plots were on Kuiu Island, but some additional plots on Chichagof Island were in the same forest condition and disturbance history.

Repeated diameter at breast height measurements were made over a 10-year period on western hemlock trees to determine tree growth losses associated with varying levels of hemlock dwarf mistletoe severity. Measurements of tree height were found to have large measurement error and thus this analysis was limited to diameter growth. The original plan was to contrast the diameter growth of infected trees with uninfected trees. The sample size of uninfected residual trees was too small, however. Also, for the new cohort tree class where the number of uninfected trees sampled was adequate, their growth rate was unexpectedly slower than for trees in any other infection class. This result was difficult to explain and probably indicated some difference in tree density, site quality, dominance position, or confusion in distinguishing the new cohort trees from small residuals. Because of these issues, the growth of moderately and heavily infected trees was compared with the growth of lightly infected trees (table 2). Previous research from British Columbia (Thomson et al. 1985a) demonstrated no difference in the growth between uninfected and lightly infected trees. Also, lightly infected and uninfected trees are often pooled together in evaluations of growth loss for other species of dwarf mistletoe (Hawksworth 1961, Parmeter 1978).

Radial growth rates are summarized by tree size class and hemlock dwarf mistletoe infection level in table 2. Note that no trees were growing rapidly owing to growth phase of trees in this stand age (i.e., 115 years). Analysis of variance indicated a significant difference in tree radial growth rate among dwarf mistletoe severity classes for new cohort trees and small residuals, but not for large residuals where the sample size was too small (table 2). Also, the large standard errors indicated widely variable tree growth due to other factors in these forests. As noted above, uninfected new cohort trees had the slowest growth, suggesting that some of the differences were due to variations in site quality or competition relative to infected trees. Growth rates were negatively associated with higher dwarf mistletoe levels for each of the size classes of trees, with approximately 10 percent growth loss for moderately infected trees and 34 percent growth loss for severely infected trees.

Results from an additional 308 western hemlock trees growing in similar wind-disturbed 115-year-old forests on Chichagof Island, southeast Alaska are not shown in table 2. Too few residual trees were included for analysis, but, for the new cohort size class, hemlock dwarf mistletoe severity was significantly associated with tree growth, with a 16 and 35 percent reduction in growth for moderately and heavily infected trees relative to lightly infected trees.

A second method using increment cores was employed to evaluate the effect of hemlock dwarf mistletoe infection levels on tree radial growth. Increment cores were extracted and more intensive canopy measurements were made on a subset (n = 167) of the new cohort tree class on Kuiu Island described above. Two cores were removed from each tree, mounted, and sanded. Decadal growth over the previous 10, 20, and 30 years was measured to the nearest 0.5 mm. For each tree, canopy diameter was measured in two perpendicular directions and averaged, and the degree of overtopping of the tree crown by adjacent trees was estimated. These canopy measurements were made to assess any confounding effects of intertree competition on the impact of hemlock dwarf mistletoe.

**Table 2—Annual diameter growth of western hemlock trees with different hemlock dwarf mistletoe ratings over a 10-year measurement period in 115-year-old forests of wind throw origin on Kuiu Island, southeast Alaska**

| Tree class[a]-severity rating[b] | Radial growth | | | |
|---|---|---|---|---|
| | Trees | Mean | Standard error | Growth loss[c] |
| | *Number* | *– – Millimeters per year – –* | | *Percent* |
| New cohort***: | | | | |
| None | 206 | 1.08 | 2.19 | — |
| Light | 315 | 1.73 | 2.16 | — |
| Moderate | 225 | 1.61 | 1.62 | 7.5 |
| Severe | 68 | 1.16 | 1.43 | 33.1 |
| Small residuals*: | | | | |
| None | 14 | 3.08 | 1.30 | — |
| Light | 30 | 3.00 | 1.42 | — |
| Moderate | 61 | 2.64 | 1.58 | 12.2 |
| Severe | 28 | 1.96 | 2.18 | 34.8 |
| Large residuals: | | | | |
| None | | | | |
| Light | 7 | 2.90 | 1.73 | — |
| Moderate | 18 | 2.62 | 2.01 | 9.6 |
| Severe | 41 | 2.36 | 1.80 | 18.4 |

[a] New cohort were trees that regenerated after the wind disturbance; residuals were classified as small or large if they were <20 cm or ≥20 cm diameter at breast height at the time of the disturbance (Trummer et al. 1998).

[b] Dwarf mistletoe rating (DMR) severity were none, light = 1 or 2, moderate = 3 or 4, severe = 5 or 6. Symbols *, **, and *** indicate significant differences among severity ratings for mean radial growth for each size class of trees at $\alpha$ = 0.10., 0.05, and 0.001, respectively.

[c] Growth of moderately and severely infected trees was compared to lightly infected trees because uninfected trees were underrepresented in some classes and, where adequately sampled (i.e., in the new cohort tree class), had an inexplicable lower growth rate compared to infected trees (see text).

Canopy diameters were similar among the dwarf mistletoe infection levels (mean = 5.0 to 5.7 m), except they were smaller for uninfected trees (mean = 4.4 m). The smaller crowns of uninfected trees indicated greater intertree competition and may explain the relatively poor radial growth of uninfected trees reported above. Crown overtopping was variable, ranging from none to 80 percent for all trees. Lightly infected trees had the smallest degree of overtopping (24 percent) compared to the other classes (33 to 37 percent).

Analysis of covariance was used to produce adjusted means of decadal radial tree growth (i.e., 1975-1984, 1985-1994, and 1995-2004) with canopy overtopping as the covariate. Overtopping was significantly associated with reduced tree growth for each decade. Infection levels of hemlock dwarf mistletoe were nonsignificantly ($\alpha = 0.09$), marginally ($\alpha = 0.05$), and significantly ($\alpha = 0.006$) related to radial tree growth in the each of the three successive decades, respectively (fig. 23). Moderately and severely infected trees had an approximate 12 and 30 percent reduction in growth relative to lightly infected trees. These estimated effects of hemlock dwarf mistletoe on tree growth were in general agreement with those from repeated diameter at breast height measurements from the larger pool of trees in these plots, as well as those reported from stem dissections by Thomson et al. (1985a).

Thus, we concluded that both crown competition and hemlock dwarf mistletoe are important factors in predicting radial growth. These results demonstrated the difficulty of quantifying the effect of hemlock dwarf mistletoe on western hemlock tree growth without using experimental methods. With variable-canopy structure in partially disturbed and retention-harvested forests, intertree competition is expected

**We concluded that both crown competition and hemlock dwarf mistletoe are important factors in predicting radial growth.**

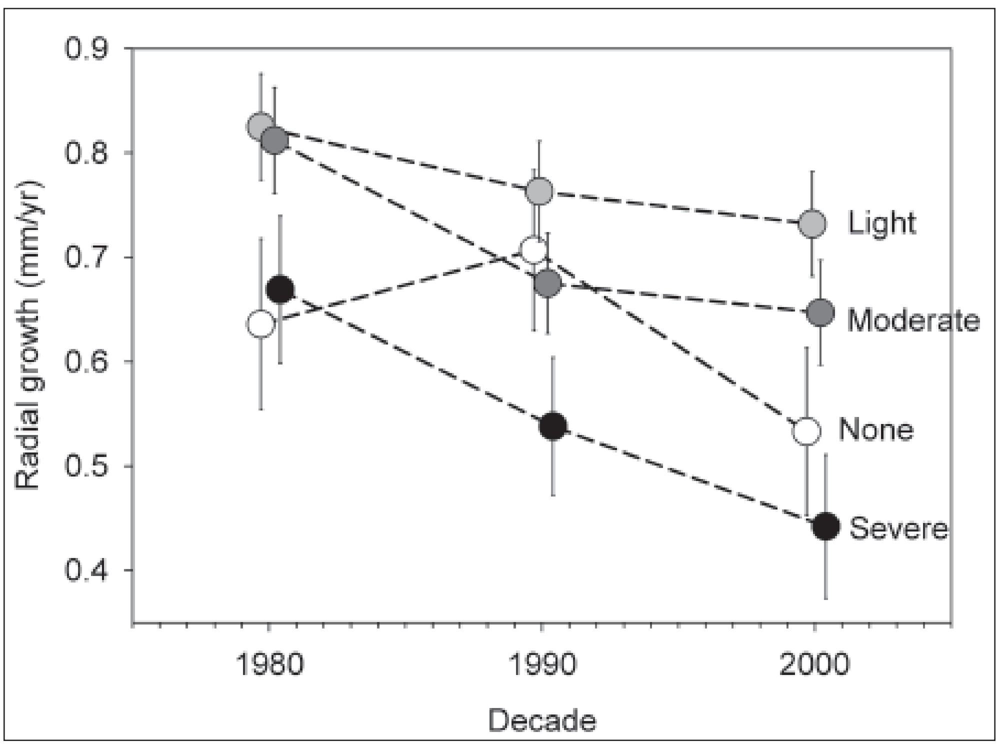


Figure 23—Mean annual radial growth in diameter at breast height (DBH) as measured in 10-year intervals from increment cores of 115-year-old new cohort western hemlock trees with varying dwarf mistletoe infection levels in wind-disturbed forests on Kuiu Island, southeast Alaska. These adjusted mean and standard error values were derived from analysis of covariance by using canopy overtopping as the covariate. Values are shown in the midpoint year for the decade covered (although they are offset slightly for clarification). Infection levels (based on dwarf mistletoe ratings [DMR]) were none, light (DMR 1 or 2), moderate (DMR 3 or 4), and severe (DMR 5 or 6).

to be a major factor in tree growth that confounds the effects of hemlock dwarf mistletoe.

The same trees on Kuiu Island, Alaska, in partial wind-disturbed stands described in the growth-loss section were monitored for mortality associated with hemlock dwarf mistletoe. Different rates and processes of mortality might be expected among the size classes of tree; thus, new cohort, small residuals, and large residuals were displayed separately in table 3. Hemlock dwarf mistletoe may slow the growth of new cohort trees and contribute to their death through suppression where intertree competition is important. For large residual trees that have already reached a codominant or dominant crown position, hemlock dwarf mistletoe may contribute more directly to their death through physiological processes associated with allocation of resources to excessive broom formation. For all of the tree size classes, greater mortality was associated with more severe infection by hemlock dwarf mistletoe with the highest mortality rates in the severe infection class. For the new cohort, which was the most extensively sampled tree size class, moderately and severely infected trees experienced approximately a 100 and 150 percent increased mortality rate, respectively, relative to lightly infected trees. As with the poor radial growth rate in uninfected new cohort trees (see section above), a relatively high mortality was found in uninfected western hemlocks. This was difficult to explain but might be related to differences in site quality or stand stagnation where residual trees did not occur. Conceivably, either the presence of residual trees or hemlock dwarf mistletoe contributes to the differentiation of trees and thereby helps avoid stagnation in this age class of forest.

**Moderately and severely infected trees experienced approximately a 100 and 150 percent increased mortality rate.**

**Summary of tree and stand-level effects—**
Hemlock dwarf mistletoe effects on tree growth have been linked to the severity of infection on a tree and tree age. Usually at least half or more of the branches on a tree must have visible hemlock dwarf mistletoe infection before significant growth reduction occurs. The six-class DMR continues to be used for rating hemlock dwarf mistletoe severity in western hemlock forests, but should be used and interpreted cautiously. The major problem is that the dense canopy in many forests obscures hemlock dwarf mistletoe infections, and the top crown intervals of tall western hemlock trees are particularly difficult to observe from the ground.

Generally, no significant growth effects occur in young trees less than approximately 20 years old, but large variations in growth of young trees due to genetic differences per tree or to microsite differences probably obscure effects of hemlock dwarf mistletoe (Thomson and Smith 1983). Small seedlings and young trees with

**Table 3—Tree mortality of western hemlock associated with hemlock dwarf mistletoe in 115-year-old wind-disturbed forests on Kuiu Island, southeast Alaska, in a 10-year measurement period**

| | Tree mortality | | |
|---|---|---|---|
| **Tree class[a]-DMR rating[b]** | **Trees sampled** | **Trees dead** | **Annual mortality rate[c]** |
| | *Number* | *Percent* | *Percent* |
| New cohort: | | | |
| None | 208 | 13.9 | 1.4 |
| Light | 308 | 6.2 | 0.6 |
| Moderate | 225 | 12.9 | 1.3 |
| Severe | 69 | 15.9 | 1.6 |
| Small residuals: | | | |
| None | 14 | 0 | 0.0 |
| Light | 30 | 0 | 0.0 |
| Moderate | 61 | 1.6 | 0.2 |
| Severe | 28 | 7.1 | 0.7 |
| Large residuals: | | | |
| None | 0 | — | — |
| Light | 7 | 0 | 0.0 |
| Moderate | 18 | 5.6 | 0.6 |
| Severe | 40 | 12.5 | 1.3 |

[a] New cohort are trees that regenerated after the wind disturbance; residuals were classified as small or large if they were <20 cm or ≥20 cm diameter at breast height at the time of the disturbance by Trummer et al. (1998).

[b] Dwarf mistletoe ratings (DMR) were none, light = 1 or 2, moderate = 3 or 4, severe = 5 or 6.

[c] Annual mortality estimated over the 10-year measurement period from 1994 to 2004.

hemlock dwarf mistletoe infection occasionally die, but it is difficult to determine if the cause of mortality was hemlock dwarf mistletoe, wood-boring moths, hyper-parasitic canker fungi, other agents, or shading.

By tree age 80 to 100, growth rates usually are significantly different between trees with DMRs 3 to 6 (moderately to severely infected) and trees with DMRs 0 to 2 (none to lightly infected). The Hadfield (1980) results described above where more severely infected trees grew faster than lightly infected trees are an anomally. However, there is a large amount of variation in tree growth rates within a local area, and trees must be selected carefully to avoid confounding effects. Often, trees with different DMRs have large differences in growth history, with severely in-fected trees often having an extended period of suppressed growth due to their understory position or to dwarf mistletoe infection before a stand disturbance (Thomson et al. 1984, 1985a, 1985b).

DeMars (1987) pointed out that a large number of factors, many interrelated, can influence tree growth, including hemlock dwarf mistletoe severity and infection history. He recommended determining hemlock dwarf mistletoe impacts by remeasuring infected and healthy trees in sets of paired, long-term plots, ideally over many decades. Uncertainty about selecting appropriate control trees or stands will continue to be a problem, however. Unfortunately, to our knowledge there have never been sufficient resources available or dedicated to establishing and remeasuring a set of plots that represent a sufficiently wide range of ecosystems, forest stands and incidence conditions for hemlock dwarf mistletoe in western forests. Several extensive long-term installations that have been remeasured over several years have produced valuable tree-growth data, including hemlock dwarf mistletoe incidence and severity as described above, but in most of these studies, the early status of hemlock dwarf mistletoe is unknown. In some instances, plots were selected to represent healthy and well-stocked stands, and we suspect that stands with severely infected trees were avoided.

A large proportion of the information on growth loss for western hemlock due to hemlock dwarf mistletoe comes from studies in British Columbia. The values reported from these studies are not identical, but they generally agree that lightly infected trees have no measurable growth loss, moderately infected trees lose about 20 percent of their current annual growth, and severely infected trees, about 40 percent. The recent information from Alaska presented above and similar results from southern Washington (Shaw et al. 2007) generally agrees with these growth loss values, suggesting that growth loss associated with various infection levels is similar throughout the natural range of hemlock dwarf mistletoe. This is in contrast to the rate of life cycle development and spread rates, which vary substantially by latitude.

With the exception of the few trees sampled by Wellwood (1956) and the information on infected residual trees in Alaska presented above, trees older than 150 years have not been sampled, and there is little information on growth loss caused by hemlock dwarf mistletoe in old-growth trees. Based on the 60 percent reduction in carbon assimilation of old-growth-infected trees reported by Meinzer et al. (2004), growth loss in old, slow-growing trees would likely exceed that of fast-growing younger trees.

Since the 1990s, forestry practices have changed dramatically with more residual and older trees now being deliberately reserved in harvested areas. Data on hemlock dwarf mistletoe growth effects in trees older that 100 years are now pertinent and highly relevant. In many regions, clearcut harvesting that removes all or most residual trees has become an exceptional rather than a common practice.

## Forest-Level Effects on Growth

Several approaches have been taken to estimate regional or forest-level losses from dwarf mistletoes, including hemlock dwarf mistletoe (Drummond 1978, Muir and Moody 2002).

Based on results of growth studies or best estimates, projections have been made for hemlock dwarf mistletoe impacts in several regions. For Oregon and Washington, both Childs and Shea (1967) and Shea and Stewart (1972) estimated that the annual growth loss was approximately 1.2 million $m^3$. In British Columbia, Van Sickle and Smith (1978) estimated that annual growth loss was 1.7 million $m^3$ per year. Their estimate was based on 4 million hectares of western hemlock forest with approximately 15 percent infested by dwarf mistletoe and a growth reduction of 4 to 5 $m^3 \cdot ha^{-1} \cdot yr^{-1}$, based on results of Smith (1969) for a 110-year-old stand.

Bolsinger (1978) summarized information in California, Oregon, and Washington for dwarf mistletoes from 17,000 inventory plots that sampled an area of approximately 20 million ha; 84 percent of the total commercial forest area of these Western States. Of 1.5 million ha of western hemlock and mountain hemlock forests in western Oregon and Washington, approximately 21 percent were infested with dwarf mistletoes, presumably either western hemlock or mountain hemlock dwarf mistletoe. On the plots that had more than 40 percent of the trees infected by dwarf mistletoe, approximately 15 percent of the infected trees had an average DMR of more than 2 and would be expected to have some reduction in tree growth. These results have to be viewed with caution because Drummond (1978) and others have noted that inventory crews usually underestimate occurrences and severity of dwarf mistletoe.

Drummond (1982), Childs and Shea (1967), and Shea and Howard (1968) estimated total growth reductions for hemlock dwarf mistletoe for Alaska, Washington, and Oregon. However, these estimates apparently were based on extrapolations of limited data.

In one of the most extensive studies and review of *A. tsugense* occurrence and effects, Hildebrand (1995) reported that hemlock dwarf mistletoe was widespread in old-growth and young western hemlock forests in Washington and Oregon. Mountain hemlock dwarf mistletoe was common in the Cascade Mountains throughout Oregon and reported in 10 to 14 percent of the inventory plots in Washington. However, the distribution in Washington was considered uncertain due to unverified identification of the mountain hemlock dwarf mistletoe in many of the reported areas. In 1994, *A. tsugense* was included in a "record of decision" because of the association of hemlock dwarf mistletoe with both the northern spotted owl and the old-growth forest stage associated with the owl. The decision stipulated that, on land managed by the U.S. Forest Service and the Bureau of Land Management in Oregon and Washington, *A. tsugense* had to be surveyed and, if present, managed to maintain the viability of the species. Hildebrand's (1995) report and supporting statements by recognized experts that viable populations of hemlock dwarf mistletoe were not threatened in this area reversed this decision.

In addition to an extensive review of the literature, Hildebrand (1995) reviewed survey data on hemlock dwarf mistletoe occurrence and presented extensive inventory plot data on western hemlock and mountain hemlock dwarf mistletoe incidence and severity. On national forests within the range of the northern spotted owl, 26 percent of 2,260 plots with western hemlock and 21 percent of 940 plots with mountain hemlock had dwarf mistletoe. Some of the forests had no *A. tsugense* on any plot. The highest occurrence was in the Olympic National Forest where 50 percent of the plots had *A. tsugense*.

It is well recognized, e.g., Muir and Geils (2002), that data on dwarf mistletoe collected by inventory crews with relatively limited experience are of variable quality and usually underestimate incidence and severity of dwarf mistletoe infection. However, detailed plot data summarized by Hildebrand (1995, see App. B, Part III, p. 44) could be used for each forest in conjunction with data on area and growth rates to estimate hemlock dwarf mistletoe growth reductions. These data indicate that on average, for all of the Washington and Oregon coastal forests, approximately 10 percent of the western hemlock trees were infected by hemlock dwarf mistletoe with 5 percent having a DMR of 3 to 6. These percentages were similar to survey data previously reported by Bolsinger (1978). These moderately to severely dwarf mistletoe-infected trees probably experience a current annual growth reduction of 15 to 40 percent. These data support estimates of substantial regional growth impacts caused by hemlock dwarf mistletoe.

Muir et al. (2004b) extrapolated Hildebrand's (1995) data to an area of 2.8 million ha of western hemlock forests in British Columbia with an estimated average productivity of 6 $m^3 \cdot ha^{-1} \cdot yr^{-1}$ to estimate a growth reduction of 0.8 million $m^3$ per year due to hemlock dwarf mistletoe.

Approximately 12 percent of forest land in southeast Alaska is infested with hemlock dwarf mistletoe (table 4). Ignoring the inaccessible wilderness not sampled, hemlock dwarf mistletoe occurs on an estimated 335 000 ha. Most of the

**Table 4—Occurrence of hemlock dwarf mistletoe on Forest Inventory and Analysis (FIA) plots in southeast Alaska**

| Stand size class[a] | Accessible forest Sampled[b] | Mistletoe occurrence | |
|---|---|---|---|
| | – – *Hectares* (thousand) – – | | *Percent* |
| Seedling/sapling | 270 | 11 | 3.9 |
| Poletimber | 171 | 4 | 2.4 |
| Young sawtimber | 283 | 56 | 19.5 |
| Old sawtimber | 1,968 | 265 | 13.5 |
| Nonstocked | 88 | 0 | 0.0 |
| All size classes | 2,780 | 335 | 12.0 |

[a] Size classes defined by plurality of stocking by live, growing stock trees. Poletimber sized trees: diameter at breast height ≥12.7 cm and < 22.9 cm; sawtimber sized trees: ≥22.9 cm for softwoods and ≥27.9 cm for hardwoods. Young sawtimber and old sawtimber are distinguished by age of sample trees.

[b] Includes all forest lands in southeast Alaska extending to the Malaspina Glacier northwest of Yakutat; does not include wilderness areas not sampled by FIA.

occurrence is in the old sawtimber classes, and both the young and old sawtimber classes have a higher proportional occurrence (19.5 and 13.5 percent, respectively) than the smaller size classes. These values are likely conservative estimates because hemlock dwarf mistletoe might not have been recorded when other damage agents were present. Also, scattered larger trees might have been present in the plots designated as smaller and younger classes. This could explain, in part, the higher level of hemlock dwarf mistletoe in the young sawtimber class.

# Ecology

## Ecological Factors and Geographic Distribution

Reasons for hemlock dwarf mistletoe absence in some western hemlock forests, such as in western hemlock north of Haines, Alaska, or in the extensive 300-km area farther west, around the Gulf of Alaska, are unknown. Parmeter (1978) pointed out that these types of absences are known for many dwarf mistletoes and likely are caused by a variety of factors. Early autumn frosts and/or short growing seasons or colder winters probably inhibit or prevent hemlock dwarf mistletoe occurrence. Gill (1957) suggested that the upper elevational limit of lodgepole pine dwarf mistletoe in the Rocky Mountains coincided with a 0 °C mean annual isotherm, suggesting that a similar temperature threshold might be determined for hemlock dwarf mistletoe. However, with recent climatic warming, it is also possible that hemlock dwarf mistletoe is migrating into these areas. Presumably during

**With recent climatic warming, it is also possible that hemlock dwarf mistletoe is migrating into these areas.**

the Pleistocene Epoch, hemlock dwarf mistletoe in southeast Alaska and/or British Columbia survived the northern continental glaciation in refugia that were not covered by continental ice. These refugia functioned as epicenters for migrating vegetation upon climatic warming and deglaciation. Dwarf mistletoes including *A. tsugense* recolonize areas slower than their hosts do (Scharpf 1984). Birds are believed to be largely responsible for stand-to-stand spread of hemlock dwarf mistletoe, but in many areas such as southeast Alaska, their migratory patterns in autumn when dwarf mistletoe seeds are produced are not in the appropriate direction to facilitate spread into noncolonized areas (Hawksworth and Wiens 1996). Regardless of the reasons for the absence of hemlock dwarf mistletoe in areas such as the entire Yakutat Ranger District and Chugach National Forest in Alaska, its absence precludes the need for hemlock dwarf mistletoe management there.

With the exception of a few limited occurrences in major river valleys, hemlock dwarf mistletoe is absent in western hemlock forests in the interior region of British Columbia east of the Cascade Mountains. However, based on results of experimental inoculations, most of these populations of western hemlock are susceptible to hemlock dwarf mistletoe (Smith 1965, 1974) and the parasite is capable of surviving in these areas (Smith and Wass 1979). Geographic barriers, autumn frosts, short growing seasons, and slow reinvasion are likely reasons for the absence of hemlock dwarf mistletoe in these interior hemlock forests.

Upper elevation limits are another interesting ecological association. Dwarf mistletoes, including *A. tsugense*, generally occur only up to a few hundred meters or more below the upper elevation occurrence of their hosts (Hawksworth and Wiens 1996). The upper elevation limits for dwarf mistletoes generally decrease from southern to northern latitudes. Mountain hemlock dwarf mistletoe occurs up to 2500 m elevation in northern California and up to 1200 m in northern Washington (Geils et al. 2002). Pacific silver fir dwarf mistletoe occurs from 1100 m to 1700 m in central Oregon (Mathiasen and Daugherty 2007). The shore pine dwarf mistletoe occurs from near sea level up to 800 m in southern British Columbia (Wass and Mathiasen 2003). The western hemlock dwarf mistletoe occurs from sea level up to approximately 1250 m elevation in southern Oregon. The upper elevation limit for the western hemlock dwarf mistletoe in southern British Columbia was stated to be 1500 m (Alfaro 1985), but we believe that this is an overestimate. The upper elevation limit in southern British Columbia appears to be near 800 m, but further surveys are needed (Muir 2004).

Drummond and Hawksworth (1979) stated that hemlock dwarf mistletoe occurred up to 150 m and rarely up to 300 m in southeast Alaska. These observations are confirmed by Forest Inventory and Analysis plot data (fig. 24). There is an apparent threshold at approximately 150 m, above which the parasite is uncommon. This occurs both in productive forests, generally closed-canopy conditions with good soil drainage, and in unproductive forests, which are more open-canopied on poorly drained soils. The principal host, western hemlock is common well above 150 m elevation, suggesting that some climatic factor limits the distribution of hemlock dwarf mistletoe at higher elevations.

Another interesting ecological feature that invites further study is a frequent association of hemlock dwarf mistletoe with riparian zones (Muir 2004, Swanson et al. 2006). Like many other dwarf mistletoe species, *A. tsugense* often is very common on poor or low-quality sites. Dwarf mistletoes usually occur more commonly on ridges or upper slope positions. However, these associations have not been quantitatively documented or tested for hemlock dwarf mistletoe. Swanson et

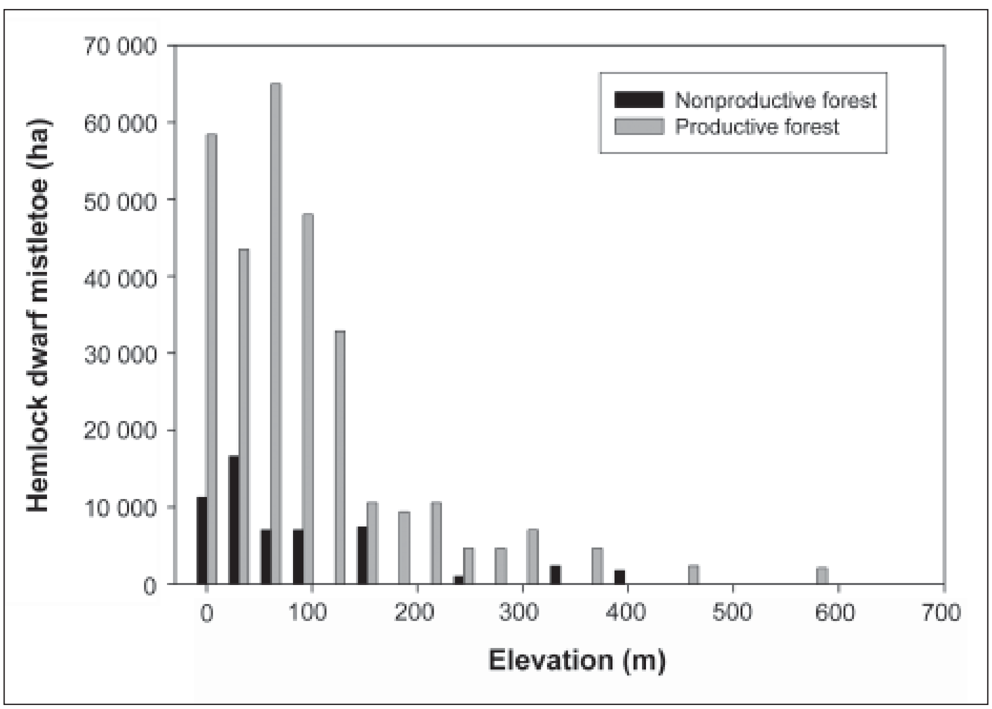


Figure 24—Occurrence of hemlock dwarf mistletoe in southeast Alaska by 30.5-m elevation classes. Data represent lands supporting either "unproductive" or "productive" (stocked and either not capable or capable of producing 1.4 $m^3 \cdot ha^{-1} \cdot yr^{-1}$ at culmination of mean annual increment, respectively). Data from Pacific Northwest Research Station, Forest Inventory and Analysis plots distributed throughout southeast Alaska except inaccessible wilderness areas and collected from 1995 to 2000.

al. (2006) found hemlock dwarf mistletoe-infected stands associated with riparian areas in 150- but not in 500-year-old Douglas-fir/western hemlock forests in southern Washington. An analysis of transects indicated statistically significant associations of mistletoe-infected hemlock trees with riparian zones. Swanson et al. (2006) attributed the occurrence of hemlock dwarf mistletoe in these riparian areas to survival of infected hemlock trees after wildfires.

Only a few dwarf mistletoes have been reported to occur in riparian areas. *A. pusillum* on eastern black spruce is common near bogs and lakes (Hawksworth and Wiens 1996). *Arceuthobium americanum* occurs on lodgepole pine in riparian zones along the Columbia and Kootenay Rivers in southeastern British Columbia. In a study of shore pine dwarf mistletoe, Wass (1976) noted that the few western hemlock dwarf mistletoe infestations near Sooke, British Columbia, occurred in valley bottoms. In contrast, the shore pine dwarf mistletoe occurred on rocky knolls, ridgetops, and mountain tops. Western spruce dwarf mistletoe also commonly occurs along stream bottoms on lower slopes of drainages on blue spruce in the Southwestern United States (see footnote 2). However, these drainages are not major river bottoms, but rather are small stream courses with or without perennial streams. These areas are subject to cold air drainage, and here blue spruce grows quite well. Western spruce dwarf mistletoe severely parasitizes blue spruce along these drainages, but it also occurs up slope on both blue and Engelmann spruce.

Muir (2004) reported several infestations of hemlock dwarf mistletoe in riparian zones in southern and eastern Vancouver Island, British Columbia. In this "rainshadow" region that corresponds to the coastal Douglas-fir biogeoclimatic zone (Meidinger and Pojar 1991), precipitation is 1250 mm or less per year. Here, western hemlock survives wildfire and competition from other tree species predominantly in riparian zones. However, Muir also observed a similar close association of hemlock dwarf mistletoe with riparian zones in northern Vancouver Island (fig. 25) in much wetter (annual precipitation greater than 1250 mm) areas of the coastal western hemlock (CWH) zone where western hemlock commonly grows across the landscape in most topographic positions.

Hemlock dwarf mistletoe shoots and seed production appear more common and prolific on trees in riparian areas probably because in these areas, stands are more open and thus trees are exposed to more sunlight. In upslope sites above riparian zones in the CWH, stands are usually very dense and light is a limiting factor for hemlock dwarf mistletoe reproduction. However, riparian zones are also subject to cold-air drainage and possible frost damage to hemlock dwarf mistletoe witches'

Figure 25—Hemlock dwarf mistletoe in a riparian zone near Port McNeill, British Columbia.

brooms (Kuijt 1960) and berries (Baranyay and Smith 1974). The local microclimate and light regimes need to be determined for these areas.

Hemlock dwarf mistletoe in riparian zones appears to be an important issue because strips or blocks of old-growth trees are usually retained or reserved from harvesting in these areas. Occurrences of hemlock dwarf mistletoe in riparian zones pose a dilemma for management: Should hemlock dwarf mistletoe-infected trees be retained to protect riparian zones if trees are a risk to increase hemlock dwarf mistletoe spread and future effects on tree growth and stability? Increased retention of hemlock dwarf mistletoe-infected trees might be desirable in some northerly localities where incidence of hemlock dwarf mistletoe has been drastically reduced by clearcut harvesting and/or extensive, severe windstorms.

The association of hemlock dwarf mistletoe with riparian zones appears less pronounced in the hypermaritime CWH subzone near Ucluelet and Tofino, British Columbia. In this subzone of extreme precipitation that extends along the coast and inland 10 to 15 km, western hemlock usually grows only on small hummocks or ridges, and western redcedar predominates on low-lying, often flooded terrain. Here, most of the older western hemlock trees appear severely infected by hemlock dwarf mistletoe. This situation is similar to southeast Alaska, where hemlock dwarf mistletoe is no more abundant in riparian areas than in upland forests. The lack of fire as a disturbance process probably explains the widespread occurrence of hemlock dwarf mistletoe in these areas.

## Disturbance Regimes

**Wildfire is the primary natural factor influencing the distribution and abundance of many dwarf mistletoes in the Western United States and Canada.**

Dwarf mistletoes influence fire behavior in several ways, and wildfires were probably the primary natural control for most dwarf mistletoe species throughout most of the Western United States (Hawksworth 1978, Parker et al. 2006). Wildfire is the primary natural factor influencing the distribution and abundance of many dwarf mistletoes in the Western United States and Canada (Hawksworth and Wiens 1996, Wright and Baily 1982) and of *A. tsugense* in the southern Cascades of Washington and Oregon (Swanson et al. 2006). However, in northern hypermaritme coastal regions, wildfire is an uncommon event and windstorms typically are the primary natural factors that influence new infestations of hemlock dwarf mistletoe (Trummer et al. 1998).

Swanson et al. (2006) indicated that hemlock dwarf mistletoe survival, spread, and subsequent impacts are largely dictated by wildfires in the southern portion of its geographic range and by windstorms in northern regions. Areas where either wildfire or windstorms are the primary disturbance regime probably overlap and depend on local climate. In areas of Washington, Oregon, and on the southeastern coast of Vancouver Island where wildfires are predominant, hemlock dwarf mistletoe-infected western hemlock trees apparently survive in more open or less vulnerable stands on poor or low production sites and in riparian zones. Generally, windstorms appear to be a more important factor than wildfires in high-rainfall areas of the west coast of Vancouver Island north to southeastern Alaska.

In more northerly, wind-affected areas, hemlock dwarf mistletoe-infected trees hypothetically occur more often in landscapes not subjected to stand-replacing windstorms, which in southeast Alaska and along the north coast British Columbia are on protected north- and northwest-facing slopes. However, as reported here, in some areas on northern Vancouver Island and possibly farther north, hemlock dwarf mistletoe appears closely associated with riparian zones. Perhaps western hemlock survives windstorms more frequently in riparian areas, or riparian areas might have ecological conditions that favor hemlock dwarf mistletoe survival and spread. These ecological associations and conditions need to be determined.

Although catastrophic windstorms are often regarded as determining factors, Hennon and McClellan (2003) found that local, more frequent and lower intensity storms, as well as other tree mortality agents, had a major influence on creating gaps and openings that encourage hemlock mistletoe spread and impacts. Even in catastrophically wind-disturbed forests, some western hemlock trees survive, enabling hemlock dwarf mistletoe spread to regenerating stands.

## Stand Structure and Species Composition

By causing changes to individual infected trees, including formation of witches' brooms, reduced height growth, top-kill, and tree mortality, hemlock dwarf mistletoe significantly alters the structure and composition of forest stands. Witches' brooms are important and unique elements that contribute to structural diversity of forest stands (Mathiasen 1996, Tinnin et al. 1982).

In mixed-species stands infested with hemlock dwarf mistletoe, trees that are less susceptible and growing near severely infected western hemlock trees can have a competitive advantage. Annual height growth of severely infected western hemlock can be reduced by up to 80 percent (Smith 1969). In Alaska, the growth and dominance of individual Sitka spruce trees appear enhanced in stands with hemlock dwarf mistletoe-infected western hemlock. Relatively slow-growing yellow-cedar trees appear able to maintain their position in the upper canopy in mixed stands on productive soils only when the growth of western hemlock is slowed by hemlock dwarf mistletoe infection. In several stands near Sitka, Alaska, yellow-cedar trees in mixed stands grow in the upper dominant and codominant crown positions with dwarf mistletoe-infected western hemlock in lower crown positions. Hemlock dwarf mistletoe infestations can enhance a greater diversity of tree species by suppressing the growth of the prolifically reproducing western hemlock.

**Hemlock dwarf mistletoe infestations can enhance a greater diversity of tree species by suppressing the growth of the prolifically reproducing western hemlock.**

Dwarf mistletoe probably alters other ecological processes in old-growth forests. Severe mistletoe infections kill trees and create canopy gaps by which old-growth forests are maintained (fig. 26). Another process contributing indirectly to canopy gap formation is that old bole swellings of hemlock mistletoe provide infection courts for heart rot fungi that result in heart rot and bole breakage (fig. 27). Both of these processes of tree mortality—snag formation and bole breakage—do not cause substantial soil disturbance or encourage reestablishment of western hemlock. Uprooting, a third major cause of canopy gap formation, causes considerable mixing of organic and inorganic layers, forms pit/mound topography, alters soil development processes, and probably leads to a different composition of understory flora and tree species. Thus, the manner in which trees die, a process in which hemlock dwarf mistletoe often participates, has a number of pronounced and complicated effects on forest structure, composition, and developmental processes.

Figure 26—Canopy gap associated with dead hemlock dwarf mistletoe infected tree.

Figure 27—Bole breakage of western hemlock and canopy gap associated with hemlock dwarf mistletoe infection.

Larger scale effects can develop in very severely infested western hemlock stands. Top-kill, tree mortality, reduced height growth, and the reduction in wood volume production can develop to such an extent that stands have a broken canopy and stunted trees. In some forest ecosystems, this results in a succession of mistletoe-resistant tree species. However, in nearly pure stands of severely infected western hemlock, western hemlock regenerates prolifically and predominates in all canopy levels. A high incidence of hemlock dwarf mistletoe develops as understory hemlock trees grow in the canopy gaps that resulted from the death of dwarf mistletoe-infected trees in the overstory. Hemlock dwarf mistletoe is able to maintain itself in the upper canopy level, and its negative effects on height growth often stunts trees. In severe cases, the entire stand eventually becomes stunted and lacks the typical vertical stand structure that develops in the absence of hemlock dwarf mistletoe. This topic is covered in more detail in the section on dwarf mistletoe "Effects of Stand Development."

The role of hemlock dwarf mistletoe in creation of canopy openings or gaps needs further study. Several dwarf mistletoe species have been reported to cause canopy gaps in forest canopies including *A. pusillum* on black spruce (Baker and French 1991) in eastern forests, *A. americanum* on jack pine (Muir and Robins 1973) in Alberta, hemlock dwarf mistletoe on western hemlock in Alaska (Hennon 1995, Hennon and McClellan 2003), and other dwarf mistletoes on other tree species (Mathiasen 1996). Gaps caused by Douglas-fir dwarf mistletoe can have positive, neutral, or negative ecological effects (Lundquist et al. 2002), but these effects have yet to be determined for hemlock dwarf mistletoe. In British Columbia, canopy gaps associated with or caused by hemlock dwarf mistletoe occur in western hemlock forests as young as 80 to 90 years (Muir 2004).

Hennon and McClellan (2003) investigated patterns of canopy gaps and tree death in 27 old-growth forests in southeast Alaska, 18 of which contained hemlock dwarf mistletoe. The annual mortality rate of codominant and dominant trees, i.e., the "gapmakers," in these 27 forests was approximately 0.4 percent through the 1900s. Most hemlock trees died standing, but approximately 20 percent each died through bole breakage and uprooting. Small canopy gaps that were formed by the death of individual dead trees and without soil disturbance (by dead standing trees or bole breakage) favored the regeneration of shade-tolerant western hemlock. Evaluating the mode of tree death in older dead trees was difficult because broken boles can result from sudden death through stem snap or from dead standing trees deteriorating to the stage where boles eventually break. By contrast, uprooting as a cause of tree death was evident long after death. Examining the more recently killed trees indicated that in these forests, most trees died standing. The incidence of these types of tree death did not differ substantially in forests where hemlock dwarf mistletoe was present or absent. Hemlock dwarf mistletoe was just one of many mortality agents of large western hemlock trees that led to canopy gaps. In forests with hemlock dwarf mistletoe, approximately 20 to 25 percent of dead western hemlock trees had evidence of infection (witches' brooms). The ecological maintenance of old-growth forests through tree death and canopy gap formation does not appear to require the occurrence of hemlock dwarf mistletoe; however, it could affect rates and types of tree death in heavily infested forests.

A key factor in gap creation appears to be death and/or bole breakage of large trees that were the source trees for the hemlock dwarf mistletoe infestation. Large old hemlock dwarf mistletoe-infected trees often have pronounced swellings on stems that are frequently extensively decayed by wood-decay fungi (e.g., Hennon 1995). However, their occurrence and deterioration are variable. In Washington, Shaw et al. (2005) found that large, severely infected trees had few, if any, bole infections, and only a few smaller understory trees had bole infections.

Canopy gaps caused by hemlock dwarf mistletoe are believed to play an important role in the ecology and development of western hemlock and western redcedar forests on northern Vancouver Island and the adjacent coastal mainland areas.[6] In windstorms or in topographic positions exposed to wind, hemlock dwarf mistletoe-infected trees often break off at large stem swellings rather than being uprooted. Many broken-off trees survive and continue as source trees for further hemlock dwarf mistletoe infection. Breakage of trees and creation of small gaps or openings encourages regeneration of western hemlock and discourages western redcedar, which requires full exposure to light and mineral soil for successful establishment (see footnote 6). Further research is needed to test these hypotheses, but it appears likely that gap creation by hemlock dwarf mistletoe encourages regeneration of its host species.

Shaw et al. (2005) studied the distribution and severity of hemlock dwarf mistletoe in an old-growth Douglas-fir and western hemlock forest at the Wind River Canopy Crane Research Facility, Washington. A 75-m-tall construction crane at the research site was used to examine hemlock dwarf mistletoe closely in tree crowns. The forest was somewhat unique in that western hemlock trees gradually replaced many of the older Douglas-fir trees over the past century (Franklin and

[6] Kimmins, J.P. Professor, 2006. Personal communication. Department of Forest Sciences, University of British Columbia, Vancouver, BC.

DeBell 1988). The forest canopy was complex with western hemlock foliage predominating from 15 to 35 m height, western hemlock and Douglas-fir codominant from 35 to 45 m, and Douglas-fir predominant from 45 to 55 m (Parker 1997).

Hemlock dwarf mistletoe infestations at the site developed in relatively discrete patches (Shaw et al. 2005). Infected western hemlock trees were larger than uninfected trees, and severely infected trees were larger than moderately or lightly infected trees. Shaw et al. (2005) suggested that the more severe infection of taller trees resulted from birds that dispersed hemlock dwarf mistletoe seeds preferentially to the taller and larger trees. Several bird species that were observed feeding in mistletoe-infected trees during dwarf mistletoe seed dispersal at Wind River Canopy Crane Research Facility are known from studies in other regions to be potential vectors for long-distance dispersal. They suggested that birds might be responsible in whole or part for establishment of mistletoe infestation centers in old-growth forests and for the common occurrence of hemlock dwarf mistletoe infections in the upper crown of severely infected trees. However, they recognized other possible scenarios for explaining the patchy occurrence of hemlock dwarf mistletoe including survival of the mistletoe on scattered trees after wildfire that grew to become some of the older and taller trees.

## Effects of Stand Development

**The abundance, reproductive success, and effects of hemlock dwarf mistletoe on trees and ecosystems are closely linked to and depend on stand development.**

The abundance, reproductive success, and effects of hemlock dwarf mistletoe on trees and ecosystems are closely linked to and depend on stand development. Oliver and Larsen (1990) developed terminology and described several developmental stages that represent the regrowth of even-aged forests after a disturbance such as wildfire, catastrophic windthrow, or clearcut harvesting. These and several other models of stand development are tabulated and compared by Franklin et al. (2002). Note that most of the models of stand development depend on a stand-replacing disturbance, either through clearcut harvesting or some natural event, and most do not apply to partial disturbance or retention harvesting. Partial disturbances or selection harvesting lead to multiaged forests with decidedly more complicated and more serious, scenarios for hemlock dwarf mistletoe spread. Details of hemlock dwarf mistletoe biology and spread that are described in previous sections are highlighted in the following stand-development scenarios presented by Franklin et al. (2002) and summarized in table 5. Depending on the climate and disturbance regimes, several differences in stand development and effects on development of hemlock dwarf mistletoe are apparent.

**Table 5—Summary of events and processes in development of coastal old-growth forests[a] in wind- or wildfire-disturbed regions and effects on hemlock dwarf mistletoe (HDM)**

| Stand-development process | Stand age (years) | Stand development effects on HDM: Wind disturbance regime | Stand development effects on HDM: Wildfire disturbance regime |
|---|---|---|---|
| Disturbance | <1 | Common in high rainfall climates where western hemlock is the predominant pioneer tree species. | Common in low rainfall climates where Douglas-fir is the predominant pioneer tree species. |
| Residual forest structure | 0 | HDM survives on residual infected trees depending on severity of disturbance, topographical features of the landscape. HDM infection affects tree vulnerability to bole breakage and uprooting in the actual disturbance event. | HDM survives on residual infected trees depending on severity of disturbance, topographical features of the landscape, particularly in moist riparian zones. HDM-infection affects tree vulnerability. Broken witches' brooms and large branches at the base of the bole increase damage. Severe HDM infection in lower crown increases vulnerability to ground fires. |
| Establishment of new cohort of trees | 1-20 (+) | Many western hemlock seedlings that were previously suppressed and survive "release" after disturbance and often achieve dominant position and numbers. HDM that survives on residual trees is stimulated to produce seeds and infect young trees. Extent of HDM infection of young trees and subsequent effects depends on the number of infected residual trees. | Mostly seedlings established from seed dispersed from residual trees after disturbance. Douglas-fir, only rarely infected by HDM, often predominates. Western hemlock survives and grows well in shady or moist microsites. HDM that survives on residual trees is stimulated to produce seeds and infect young trees. |
| Canopy closure | 25-35 (+) | HDM on lower crown branches is suppressed and loses aerial shoots but survives on bole and on nonfoliated branches of surviving trees. HDM-infected small or unthrifty trees die through competition. | HDM on lower crown branches is suppressed and loses aerial shoots but survives on bole and on nonfoliated branches of surviving trees. HDM-infected small or unthrifty trees die through competition. |
| Biomass accumulation, tree mortality, canopy gap development | 35-100 | HDM upward spread in tree crowns continues in open stands or, in dense stands, slows, is arrested, or is eradicated. Growth of severely HDM-infected trees is reduced, and infected trees can be overtaken and replaced by nonhost and/or less | HDM upward spread in tree crowns continues in open stands or, in dense stands, slows, is arrested, or is eradicated. Growth of severely HDM-infected trees is reduced, and infected trees can be overtaken and replaced by nonhost trees. In dense |

**Table 5—Summary of events and processes in development of coastal old-growth forests[a] in wind- or wildfire-disturbed regions and effects on hemlock dwarf mistletoe (HDM) (continued)**

| Stand-development process | Stand age (years) | Stand development effects on HDM | |
|---|---|---|---|
| | | Wind disturbance regime | Wildfire disturbance regime |
| | | severely infected trees. Dead HDM-infected trees and other disturbances initiate canopy gaps. Depending on gap size, western hemlock trees regenerate and are infected by HDM from nearby live trees. | stands with large numbers of Douglas-fir, HDM could be eradicated. Disturbances initiate canopy gaps. Depending on gap size, western hemlock trees regenerate and are infected by HDM from nearby live trees in moist areas or riparian zones. |
| Maturation of pioneer trees, canopy development, and loss of pioneer trees | 150+ | Western hemlock trees mature and reach maximum height at 150 years and survive to 350 to 500 years. In canopy gaps, infected trees refoliate, and suppressed infected trees grow to a codominant or dominant position. Depending on frequency and severity of disturbances, western hemlock can become extensively and severely infected and replaced by other nonsusceptible species such as western redcedar, yellow-cedar, and/or Sitka spruce. Or, in pure western hemlock stands, HDM can become so prevalent that trees become stunted with large witches' brooms with large-diameter branches developing on most trees. Old-growth infected trees commonly die, creating gaps colonized by more western hemlock. | Douglas-fir trees mature at 200 to 300 years and survive to 1,200+ years. Canopy gaps develop slowly over several hundred years with progressive invasion and replacement by shade-tolerant tree species such as western hemlock with extensive, severe HDM infection. Depending on frequency and severity of disturbances, western hemlock can become extensively and severely infected and replaced by other nonsusceptible species such as western redcedar, yellow-cedar, and/or Sitka spruce. Large witches' brooms with large-diameter branches develop on infected trees. Old-growth infected trees commonly die, creating gaps colonized by more western hemlock. |

[a] Based on Franklin et al. (2002), tables 2 and 3.

**Disturbances and establishment of seedlings and saplings—**
In northern high-rainfall areas that have very few or no wildfires and are affected mostly by windstorm disturbances, some newly developing forests predominately consist of residual trees, i.e., those that were previously established as understory trees in the preceding stand (Pearson et al. 2003). In others, there is a mixture of residual and postdisturbance regenerated trees (Shaw 1982). In areas of drier climates where wildfires are the major disturbance, newly regenerated trees that were established after a wildfire predominate. In these drier zones, mistletoe-infected and noninfected western hemlock trees survive in moist riparian zones (Muir 2004, Swanson et al. 2006).

**The type and intensity of the disturbance affects the number and distribution of residual hemlock dwarf mistletoe-infected trees. These have a major and long-term effect on the amount and extent of hemlock dwarf mistletoe.**

Many understory seedlings and saplings survive local or catastrophic disturbance. In particular, western hemlock seedlings and saplings, which are abundant on the forest floor of many old stands, survive local or large-scale windthrow events and clearcut harvesting, but almost all are killed by wildfire and landslide events. Western hemlock saplings that survive and are infected with hemlock dwarf mistletoe from the old stand are sources for the parasite to spread into the regenerating forest (fig. 28). The type and intensity of the disturbance affects the number and distribution of residual hemlock dwarf mistletoe-infected trees. These have a major and long-term effect on the amount and extent of hemlock dwarf mistletoe that develops in the resulting forest (Smith 1966, 1973, 1977; Trummer et al. 1998; see footnote 4).

On productive sites, the growth of residual saplings and newly regenerated trees is rapid because of the availability of light and nutrients. Residual saplings have a competitive advantage and usually maintain a dominant position in the new stand. Regeneration typically becomes dense, and as the stand approaches the age of about 25 to 30 years, it forms a closed continuous canopy. As trees continue their rapid height growth, many lower branches die from shading. Hemlock dwarf mistletoe can survive for several decades or more on lower shaded branches, but it must spread vertically fast enough to maintain its presence in the upper well-exposed canopy to be able to continue to produce and disperse seeds. On several sites in Alaska, the height growth of young western hemlock trees was twice the vertical spread rate of the parasite (Shaw and Hennon 1991). These results suggested that on productive sites, the rapid height growth of young western hemlock trees results in dense canopies that shade out lower branches, prevent hemlock dwarf mistletoe spread, and possibly even eliminate hemlock dwarf mistletoe from some stands. On less productive sites with young-growth stands that have more open canopy and

Figure 28—Hemlock dwarf mistletoe-infected residuals in recently harvested area at Denman Island, British Columbia.

slower growing trees, hemlock dwarf mistletoe could spread vertically fast enough to keep pace with the height growth of western hemlock and thereby retain its position in the upper canopy. Hence, a large proportion of trees could have numerous infections in the upper third of the crowns. However, hemlock dwarf mistletoe spread and intensification are likely affected by its host tree physiology as recently shown for southwestern dwarf mistletoe on ponderosa pine (Bickford et al. 2005). If so, vertical spread of hemlock dwarf mistletoe might be less on less productive sites. Some estimated rates are described below, but further information is needed on vertical spread rates of hemlock dwarf mistletoe on various sites.

**Competition and stem exclusion—**

In this phase of stand development, growing space becomes fully occupied, tree mortality increases due to intertree competition, and little to no new regeneration occurs. Tree competition for light, soil moisture and nutrients intensifies as tree crowns and roots become more crowded. Many smaller trees are disadvantaged, become suppressed, and die from increasing competition. As the rapid height growth of trees in the closed-canopy forest continues in the pole stage, hemlock dwarf mistletoe is further suppressed or even eradicated from the stand. Severely infected trees can become suppressed and die. Hemlock dwarf mistletoe can survive on lower branches or on the bole of some infected trees, but under dense shade, these infections generally cease producing reproductive shoots. This suppresses further spread at least until the next disturbance. Even if reproductive shoots were to persist, spread of mistletoe seeds from lower branch and bole infections up into the live canopy generally does not occur because of the dense foliage.

A comprehensive examination of even-aged stands in the pole stage in southeast Alaska using an existing plot system installed to evaluate the effects of thinning (DeMars 2000) indicates a nearly complete absence of hemlock dwarf mistletoe. In the few instances of occurrence, hemlock dwarf mistletoe in pole-sized trees was always associated with spread from nearby, large residual trees that had survived the initial disturbance event.

Results from several studies in British Columbia that were undertaken in mature stands to determine growth effects of hemlock dwarf mistletoe (Smith 1969; Thomson et al. 1984, 1985a, 1985b) supported this scenario but suggested another interpretation. Stands with moderate to severe hemlock dwarf mistletoe infection were typically uneven-aged, with most of the severely infected trees 20 to 80 years older than the lightly or uninfected trees. The older tree age was evidently due to periods of suppressed growth as understory trees before the disturbance. All trees grew rapidly after the disturbance, but several decades later, growth of moderately to severely infected western hemlock trees had significantly slowed compared to uninfected and lightly infected trees. Nevertheless, these older trees had an initial height advantage that enabled them to maintain a dominant position until recent years. These results indicated that substantial infestations of hemlock dwarf mistletoe could develop progressively in some western hemlock forests on good or highly productive sites and cause significant growth reductions, as long as some residual trees remained after the harvest or disturbance.

Rate of increase in hemlock dwarf mistletoe infestations appears to be correlated with survival of hemlock dwarf mistletoe-infected understory trees that are able to grow rapidly to maintain a dominant position in the new stand. Apparently in these situations, hemlock dwarf mistletoe-infected residual trees that survive in sufficient numbers enable the parasite to spread vertically, possibly by contributing to the spread of hemlock dwarf mistletoe between infected trees (Bloomberg and Smith 1982, Bloomberg et al. 1980, Knutson and Tinnin 1980). Further detailed examinations of tree growth, establishment of hemlock dwarf mistletoe, and stand development are needed.

**Transition to old growth—**

Older immature or pole-sized stands eventually begin to "break up" in transition to the next true, old-growth stage. Toppling, breakage and/or mortality of dominant and codominant trees create canopy gaps due to a variety of causal or contributing agents (Hennon 1995, Hennon and McClellan 2003). These include wind, heartwood decay, root disease, hemlock dwarf mistletoe, and insects. Trees particularly susceptible to windthrow and breakage are tall, small-diameter trees with excessive slenderness as expressed by an extreme ratio, i.e., 90 or more, of total height to diameter at breast height. In this stage of stand development, trees occupy almost all of the rooting space and carrying capacity of a site and their height growth begins to slow. In some areas, hemlock dwarf mistletoe has already been largely or completely eliminated from the stand during earlier stages. In other areas, hemlock dwarf mistletoe survives in riparian areas or on suppressed understory trees and reinvades as western hemlock regenerates. In this instance, hemlock dwarf mistletoe incidence and impacts depend on the number, size, and infection levels of residual hemlock trees that survived the disturbance that gave rise to the new stand.

Stands with hemlock dwarf mistletoe in the transition stage to old-growth are not particularly common in southeast Alaska. Casual observation of five stands approximately 150 years old suggested that hemlock dwarf mistletoe was absent at this stage in all but one stand. Hemlock dwarf mistletoe was found near Sitka, Alaska, in the Verstovia forest, which as a former Russian territory, was harvested in the 1860s. Hemlock dwarf mistletoe in the stand probably survived on some of the residual hemlock trees left during the harvest. In British Columbia, several examples of western hemlock with hemlock dwarf mistletoe in this type of transitional stage were observed in 120-year-old trees south of Beaver Cove near Naka Creek and in a 90- to100-year-old stand near Vancouver (Muir 2004).

**A small-scale disturbance regime is highly favorable for the development of hemlock dwarf mistletoe if trees with the parasite are present.**

**Old growth—**

Trees of multiple ages, various sizes, and numerous canopy levels characterize the old-growth stage. Throughout its range, hemlock dwarf mistletoe is known to thrive at this stage of stand development (Buckland and Marples 1952) (fig. 29) particularly on steep slopes (see footnote 5). Disturbance events are typically small and scattered throughout the stand where one or a few trees die through uprooting, bole breakage, or by any number of agents that leave dead trees standing. These disturbances are often described as canopy-gap or gap-phase disturbance processes. A small-scale disturbance regime is highly favorable for the development of hemlock dwarf mistletoe if trees with the parasite are present. Hemlock dwarf mistletoe

Figure 29—Hemlock dwarf mistletoe in an uneven-aged stand of western hemlock at Tow Hill, Naikoon Provincial Park, Queen Charlotte Islands (Haida Gwaii), British Columbia.

spreads efficiently over the short distance from infected large trees on the periphery of the gap to smaller hemlocks regenerating or releasing in the gap. In some instances, large fallen but only partially uprooted hemlock dwarf mistletoe-infected trees survive with hemlock dwarf mistletoe infections near ground level in proximity to regenerating trees (fig. 30). The increased availability of light in stand openings enhances aerial shoot growth and reproduction of the parasite (Shaw and Weiss 2000). Abundant hemlock dwarf mistletoe seed production in peripheral large hemlock trees leads to a greater distance of seed dispersal and increased interception of seeds by young trees.

The common occurrence of hemlock dwarf mistletoe in old-growth stands is difficult to explain in view of the scarcity of the parasite in many young and

Figure 30—Hemlock dwarf mistletoe infection on fallen, partially uprooted tree near Port McNeill, British Columbia.

immature stands. One explanation, at least in northern forest ecosystems not subjected to wildfire, could be that old-growth forests usually are only partially disturbed and rarely experience a severe stand-replacing disturbance that removes all overhead sources of hemlock mistletoe seeds. Thus, occurrence of hemlock dwarf mistletoe in a forest could be used as an indicator that there has been no relatively recent catastrophic disturbance.

In areas where hemlock dwarf mistletoe has been suppressed and/or eradicated, long-range dispersal of hemlock dwarf mistletoe seeds, thought to occur by birds or mammals inadvertently carrying seeds to the upper live canopy, might be the means by which the parasite recolonizes the stand. In a 350-year-old Douglas-fir and western hemlock forest at the Wind River Canopy Crane Research Facility in southern Washington, Shaw et al. (2005) found relatively distinct and separate hemlock dwarf mistletoe infection centers that they believed could have been established by long-distance spread of hemlock dwarf mistletoe seeds. Shaw et al. (2005) observed several animals including the Douglas squirrel and several bird species including red crossbills that were present during the hemlock dwarf mistletoe seed-dispersal period.

However, long-distance hemlock dwarf mistletoe seed dispersal appears to be an extremely rare event. Another possibility is that hemlock dwarf mistletoe infections could survive for many decades on lower branches of trees (Trummer et al.

1998). As old-growth stands break up, these infections could begin to produce aerial shoots and hemlock dwarf mistletoe seeds, which infect nearby regenerating trees.

If reintroduction of hemlock dwarf mistletoe into old-growth stands is a rare event, then it might take many centuries before hemlock dwarf mistletoe is reestablished and builds to its commonly observed, abundant levels. If so, then in some areas the practice of clearcut harvesting or possibly even severe selection cutting (Deal et al. 2002) could remove hemlock dwarf mistletoe from a site for a long time. The presence or abundance of hemlock dwarf mistletoe might indicate how long a forest has persisted in the old-growth condition.

Analyses of pollen deposits have provided several insights on development of forest vegetation and dwarf mistletoe in coastal regions, including analyses of surface pollen in different ecological zones in British Columbia (Allen et al. 1999). Dwarf mistletoe pollen records indicate local occurrences of the mistletoe because dwarf mistletoe pollen is dispersed to distances of only a few hundred meters (Hawksworth and Wiens 1996), whereas tree pollen is distributed more extensively and pollen records indicate regional occurrences (Brown and Hebda 2002). Results of several studies (Allen et al. 1999; Brown and Hebda 2002; Greenwald and Brubaker 2001; Hansen and Easterbrook 1974; Hebda 1983; Heusser 1973a, 1973b, 1974, 1977, 1978, 1983; Mathewes 1973; Mathewes and Rouse 1975; Peterson et al. 1983) suggested that although western hemlock was abundant there were lengthy periods of occurrences and absences of hemlock dwarf mistletoe in the Holocene Epoch. Although limited, these data indicated that in some areas, hemlock dwarf mistletoe incidence varied considerably over periods of several hundred years. Periods of high incidence of hemlock dwarf mistletoe often were interspersed with periods of low incidence possibly because of local extinction by wildfire and/or climatic changes and reintroduction or due to long-term persistence of infections without shoots and flowers at very low levels of incidence until conditions favor renewed flowering.

The role that dwarf mistletoe plays in either maintaining old-growth forests in a fairly sustainable equilibrium by causing scattered mortality or producing a stunted, stagnant and unproductive forest is not known. Examples of both scenarios can be found in old-growth forests. Also, well-functioning western hemlock-dominated old-growth forests can be found that lack hemlock dwarf mistletoe. Wood decay fungi, other pathogens, and other disturbance agents also lead to scattered tree mortality and diverse tree structures such as large standing snags, uprooted trees, trees with broken boles, and large cavities (Hennon 1995, Hennon and McClellan 2003). These raise questions about whether or not hemlock dwarf mistletoe represents a keystone species in these forests. Hemlock dwarf mistletoe-infested gaps likely have a variety of positive, negative, and no ecological effects as reported by Lundquist et al. (2002) for gaps associated with Douglas-fir dwarf mistletoe.

**These raise questions about whether or not hemlock dwarf mistletoe represents a keystone species in these forests.**

Ecological conditions and processes leading to a mistletoe-stunted western hemlock forest climax are largely unknown or speculative. We propose the following scenario: As hemlock dwarf mistletoe becomes common in an old-growth forest, canopy gap disturbance favors its spread and buildup. As trees become severely infected and die, hemlock dwarf mistletoe becomes one of the common mortality factors responsible for gap formation. Hemlock dwarf mistletoe infection is often associated with wood decay, which predisposes old trees to bole breakage, another cause of gap enlargement. An old-growth forest is in a dynamic equilibrium with gaps opening and closing across the landscape. Small gaps with little or no soil disturbance (i.e., trees do not die by uprooting with its associated soil mixing) lead to forest stands composed almost entirely of western hemlock, because (1) small openings inhibit establishment of nonhost trees such as Sitka spruce that reduce hemlock dwarf mistletoe spread and (2) small openings and the lack of soil disturbance enhance regeneration of western hemlock, further favoring hemlock dwarf mistletoe infection. The parasite continues to spread, eventually reaching intense levels where every hemlock is severely infected by hemlock dwarf mistletoe. As hemlock dwarf mistletoe becomes abundant in the upper canopy, infected trees experience greatly reduced height growth and top-kill, resulting in a stunting of the height development of the entire stand. In this scenario, an old-growth forest culminates in a stunted, mistletoe-infested, forest complex until the occurrence of a stand-replacing disturbance. Because of the reduced height development, these forests would be less susceptible to catastrophic windthrow events.

## Wildlife Habitat and Biodiversity

Dwarf mistletoe infestations create or are associated with gaps or openings in forest canopies that increase biodiversity of tree species, tree ages, and other vegetation (Mathiasen 1996). Trees with large witches' brooms create habitat particularly favorable for wildlife. Results of several previous studies indicate that animals and birds roost and nest in pine and Douglas-fir stands infested by dwarf mistletoe. Hawksworth and Wiens (1996) and Geils et al. (2002) summarized information on the interaction of wildlife and other dwarf mistletoe species. Currently, there is little knowledge about wildlife use of hemlock dwarf mistletoe.

**Wildlife—**

Large hemlock dwarf mistletoe witches' brooms are often flat, densely branched structures that could be suitable as nesting platforms for marbled murrelets (Lank et al. 2003). Marbled murrelet nests were found on hemlock dwarf mistletoe-infected branches of western hemlock in Washington state (Nelson and Wilson 2002), but in British Columbia, most of the few murrelet nests located were not associated with hemlock dwarf mistletoe-infected trees (Burger 2002). Further work is needed on this association.

Older hemlock dwarf mistletoe-infected trees frequently have dead tops and decayed branches that appear suitable for cavity-nesting birds and animals. In hemlock dwarf mistletoe-infested stands, large amounts of fallen, hemlock dwarf mistletoe-infected branches accumulate, and these could provide substantial cover for small animals. In Alaska, Bakker and Hastings (2002) found that northern flying squirrels made dens in hemlock dwarf mistletoe-infected western hemlock trees.

Several animals have been reported to use dwarf mistletoes for food by consuming dwarf mistletoe shoots and fruits or by chewing on the swollen bark tissue, which contains nourishing carbohydrates (Geils et al. 2002, Hawksworth and Wiens 1996, Knutson 1979). Red squirrels on Vancouver Island, British Columbia, fed on shore pine dwarf mistletoe infections on shore pine but not on western hemlock dwarf mistletoe on western hemlock (Wass 1976). Shaw and Hennon (1991) noted that a mammal, perhaps the northern flying squirrel, frequently and selectively consumed the bark of hemlock dwarf mistletoe infections in young-growth western hemlock forests on Prince of Wales Island, Alaska.

Given the abundance of hemlock dwarf mistletoe witches' brooms in western hemlock forests and the dense cover that they provide, it is possible that they are important for hiding, nesting, and feeding habitat. Animal use may be overlooked because from the ground it is difficult to inspect hemlock dwarf mistletoe witches' brooms. In some instances, it might be desirable to actively manage hemlock dwarf mistletoe-infested trees to maintain or enhance some of these features for wildlife. However, further work is needed to determine what wildlife species are using witches' brooms associated with hemlock dwarf mistletoe infection and how important this habitat is for these species.

**General biodiversity—**

Effects of hemlock dwarf mistletoe on general biodiversity are little known, but it is suspected that hemlock dwarf mistletoe infestations encourage biodiversity as was found for other dwarf mistletoes (Geils et al. 2002, Hawksworth and Wiens 1996, Mathiasen 1996). In pine forests of Colorado, the number of individual birds and bird species detected was positively correlated with the level of dwarf mistletoe, i.e., more birds and more bird species with more dwarf mistletoe (Bennetts et al. 1996). Mammals (mule deer and elk) were also more numerous, as estimated by pellet counts, in dwarf mistletoe-infested pine forests than in uninfested forests in Colorado (Bennetts et al. 1996).

Stevens and Hawksworth (1970, 1984) summarized the ecological relationships between insects and dwarf mistletoe species. There is little information on these interactions for hemlock dwarf mistletoe, but it likely plays an important part in the complex food web as do other dwarf mistletoes and leafy mistletoes. Conceivably, hemlock dwarf mistletoe witches' brooms provide a combination of hiding cover and tissue of high nutritional value that encourages a flourishing community of invertebrates. Insectivorous birds have been observed spending considerable amounts of time feeding in hemlock dwarf mistletoe witches' brooms in southeast Alaska[7] and southern Washington (Shaw et al. 2002). Perhaps a greater diversity or biomass of insects occurs in these witches' brooms.

The Johnson's hairstreak butterfly (*Loranthomitoura johnsonii*) is common in Oregon but is considered to be a rare and possibly an endangered species in British Columbia and Washington (Guppy and Shepard 2001, McCorkle 1962). In Washington, a permit is required to collect the butterfly (see footnote 3). The larvae feed exclusively on hemlock dwarf mistletoe shoots. With most of the shoots on mistletoe infections occurring high in tree crowns, the insect is rarely collected. Larvae are present on shoots in late autumn to early spring, and Muir observed a specimen on aerial shoots of hemlock mistletoe on a fallen witches' broom at Vancouver, British Columbia. Larvae are well camouflaged by their remarkable mimicry of mistletoe shoots (See Hawksworth and Wiens 1996, p. 80, for an illustration of a related species *L. spinetorum*).

In addition to the reports described above, more information on wildlife interactions with dwarf mistletoe is discussed in the section "Long-Distance Seed Dispersal."

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[7] Willson, M. 2000. Ecologist. Personal communication, 5230 Terrace Pl. Juneau, AK 99801.

## Management of Hemlock Dwarf Mistletoe-Infested Western Hemlock Forests

There is a critical need to have detailed plans for the management of coastal forests that have hemlock dwarf mistletoe infestations. Coastal forests are reserved and/or managed for a variety of purposes and resources. These include:

- Retention of natural forest ecosystem features and functions
- Maintenance of viewscapes and landscapes for visual quality objectives
- Wildlife habitat and reserves
- Watersheds and riparian zones
- Control erosion and soil stability on steep slopes
- Recreation and tourist facilities (campsites)
- Townsites and urban development
- Commercial production of timber and nontimber resources

As outlined by previous authors and/or as described in this review, hemlock dwarf mistletoe infestations can affect and/or confound management for all of the above objectives. Amaranthus et al. (1998) and Weigand (1998) reported an example of management of hemlock dwarf mistletoe for its possible effects on nontimber resources. They included treatments to reduce infestations of hemlock and lodgepole pine dwarf mistletoe in their adaptive trials in southern Oregon to enhance tree growth and promote production of valuable American matsutake (*Tricholoma magnivelare*) mushrooms.

One of the complicating factors in planning for management of mistletoe-infested stands is that hemlock dwarf mistletoe infestations are dynamic, with substantial changes to infestations, trees, and stand structures occurring within periods of one to several decades (Muir and Geils 2002). Hemlock dwarf mistletoe-infested forests therefore require detailed management plans, including what kinds of harvesting practices and silvicultural treatments will be applied to certain blocks or units at specified times. There are instances where hemlock dwarf mistletoe infestations should be prevented or reduced and possibly other instances where hemlock dwarf mistletoe should be reintroduced, encouraged to reestablish, or maintained to enhance hemlock dwarf mistletoe effects on forest ecosystems. These actions need to be specified for local forest ecosystems, depending on climate, topography, and other biophysical factors. The particular management objective for each piece of ground may help guide the establishment of desirable levels of hemlock dwarf mistletoe.

Strategies and treatments to manage hemlock dwarf mistletoe need to be based on an understanding of hemlock dwarf mistletoe spread and effects in various stages of stand development as outlined in the preceding section. In the next two sections, major harvesting/silviculture regimes are outlined for management of hemlock dwarf mistletoe-infested coastal forests: (1) clearcut harvesting of small blocks and establishment of even-aged stands and (2) selection or retention harvesting to establish and maintain uneven-aged stands. Strategies and techniques for these approaches were outlined in general for dwarf mistletoes by Muir and Geils (2002).

## Clearcut Harvesting and Even-Aged Stands

Clearcut harvesting of western hemlock forests continues to be a common harvesting practice in some areas. Currently, cutblocks or openings are usually limited to a maximum size of 15 ha on public lands in Alaska and 40 ha in coastal British Columbia. Most cutblock openings are designed to be no wider than twice the height of the residual trees at the margins of the block in British Columbia. Blocks or reserves of residual trees often are left in cutblocks to retain attributes of old-growth forests for wildlife, biodiversity, and/or protection of riparian zones. These reserves will influence the maintenance and spread of hemlock dwarf mistletoe.

Ruth and Harris (1979) described steps for silvicultural control of hemlock dwarf mistletoe in clearcut harvesting and even-aged management including detection surveys, careful layout boundaries of cutting units, sanitation cuttings, and the management of nonsusceptible species such as Sitka spruce. Shaw (1981) outlined control options, e.g., doing nothing, conversion to desirable nonhost species, clearcut harvesting, and seed tree cuts, based on stand conditions and management objectives in Alaska. These earlier recommendations were generally aimed at reducing infection levels to limit detrimental effects to the timber resource. Recommendations were outlined more recently by Hennon et al. (2001) and Muir et al. (2004b) with broader resource management objectives.

**Spread into clearcut areas—**

One frequently asked question is how rapidly and how far will hemlock dwarf mistletoe spread from residual hemlock dwarf mistletoe-infected trees at the margins of a cutblock into the young regenerating trees. Results of studies of hemlock dwarf mistletoe seed dispersal that were derived from one tree in British Columbia by Smith (1966, 1973, 1977) indicated that most initial hemlock dwarf mistletoe infection occurs within 10 m of residual mistletoe-infected trees. These results have been assumed to apply over a wide geographic area. In Washington and Oregon, Stewart (1976) determined that hemlock dwarf mistletoe had spread into young stands within 10 m of single residual infected trees to infect 5 percent of trees at age 15 and up to 70 percent at age 25 to 30. Shaw (1982) determined that dwarf mistletoe spread from single residual trees in Alaska was less frequent, amounting to 5 to 17 percent of young trees infected at ages 17 to 43 years.

Clearcut harvesting of small openings and retention of large reserves of trees in clearcut harvested areas will likely continue as preferred management practices in some areas. Frequently, in these situations, there appears to be very slow spread of hemlock dwarf mistletoe to young fast-growing trees. In several areas in Alaska (Shaw 1982) and on northern Vancouver Island, British Columbia (Bloomberg 1987), hemlock dwarf mistletoe incidence adjacent to stand margins appears to be much less than reported by Smith (1973, 1977) and Stewart (1976). Data on hemlock dwarf mistletoe spread from stand margins into adjacent young stands have not been reported for these areas, and the causes for these low incidences are unknown. Suppression of young tree growth adjacent to tall residual trees could be important for western hemlock as previously reported for lodgepole pine dwarf mistletoe (Hawksworth and Graham 1963). Possibly, as reported previously by Muir (1970, 2002) for lodgepole pine dwarf mistletoe in Alberta, hemlock dwarf mistletoe spreads more frequently and farther from single residual trees such as studied by Smith (1966, 1973, 1977) and Stewart (1976) than from infected trees at the margins of residual stands.

In some instances, severely infected hemlock trees along margins of cutblocks have been cut to reduce infection of young trees. Usually the most severely infected trees are cut, and lightly infected trees are retained. Often DMR is used to rate infection severity, but it is unknown if DMR is correlated with the amount of hemlock dwarf mistletoe seed that will be dispersed from an infected residual tree. Smith (1969) reported that hemlock dwarf mistletoe shoot growth was greater on infections in the upper crowns of more severely infected, 110-year-old trees. These trees had approximately 1,300 infections with aerial shoots, and half of these were probably pistillate infections with berries. In contrast, a nearby 15-m tall residual tree used in several studies of seed dispersal (Smith 1966, 1973, 1977) had approximately 2,200 pistillate infections with 73,000 berries (Smith 1973). Evidently, small residual infected trees can be more substantial sources of hemlock dwarf mistletoe seeds than taller and older infected trees, but further studies would be desirable to support these data.

Generally, we expect that hemlock dwarf mistletoe seed production is stimulated in infected trees recently exposed to increased light. However, in 2005 in a limited study near Ucluelet, British Columbia, at 10 years after harvesting there was little or no hemlock dwarf mistletoe seed dispersed from two hemlock dwarf mistletoe-infected residual trees (fig. 31). Apparently, host factors in addition to severity of infection influence hemlock dwarf mistletoe seed production on and dispersal from residual trees. Despite considerable searching in British Columbia, relatively few areas have been found that have residual and young regenerating, hemlock dwarf mistletoe-infected trees with prolific hemlock dwarf mistletoe shoots and berries (Muir 2004). The factors that are responsible for certain infected trees such as the tree studied by Smith (1966, 1973, 1977) becoming prolific sources of hemlock dwarf mistletoe seed have yet to be determined.

Previously in British Columbia, cutting permits for clearcut harvesting operations usually included a "3-m knockdown" rule where all trees 3 m or taller were required to be felled. This rule initially was applied for safety considerations, but recently it has been used or required to ensure that most hemlock dwarf mistletoe-infected trees are felled to reduce the potential spread of the parasite. However, the risks of spread from mistletoe-infected residual trees of various heights into young trees have not been determined. In several instances, hemlock dwarf mistletoe-infected advanced regeneration, i.e., small trees that were established in the understory of the preceding stand became virulent sources of hemlock dwarf mistletoe seeds (Smith 1966, 1973, 1977) (fig. 32). These trees appear to be more important sources for hemlock dwarf mistletoe infection of young trees than taller infected trees that were components of the upper canopy layer.

**Response by hemlock dwarf mistletoe to clearcut harvesting—**
The traditional practice of clearcut harvesting was an effective method of controlling hemlock dwarf mistletoe (Harris 1974, Hennon and Shaw 1988, Ruth and Harris 1979, Shea 1966, Taylor 1973). Hemlock dwarf mistletoe control was accomplished through removal of infected residual trees, particularly any overhead sources of hemlock dwarf mistletoe seeds. As described above, the process of stand development that follows clearcut harvesting also could reduce or eliminate hemlock dwarf mistletoe. Shea and Stewart (1972) stated that throughout the range of hemlock dwarf mistletoe, regeneration that develops after clearcut harvesting is seldom seriously infected. However, Stewart (1976) determined that the incidence of hemlock mistletoe in young trees near residual infected trees ranged from 5 percent at age 15 to 70 percent at age 25 to 30. The key factor in determining the

**Process of stand development that follows clearcut harvesting also could reduce or eliminate hemlock dwarf mistletoe.**

Figure 31—Hemlock dwarf mistletoe-infected residual tree with few hemlock dwarf mistletoe seeds dispersed as measured by seed traps in 2005 near Ucluelet, British Columbia.

Figure 32—Residual trees with large amounts of hemlock dwarf mistletoe shoots and seeds near Courtenay, British Columbia.

incidence or occurrence of hemlock dwarf mistletoe in young stands is the number and distribution of infected residual trees (Smith 1973, 1977; Trummer et al. 1998).

The primary silvicultural method of reducing hemlock dwarf mistletoe in early stages of regenerating even-aged stands was to cut most or all of the hemlock dwarf mistletoe-infected residual trees that remained after harvest. These residual trees are sometimes as large as 20 to 30 cm in diameter and are frequently found throughout harvested units. Residual trees are the primary source for introducing hemlock dwarf mistletoe into the next stand. Some trees were left in harvested units because they were considered unmerchantable, although more recently, trees have been deliberately retained for other purposes. The degree to which these trees occur in clearcut units varies considerably. Within units, residual trees may be common near unit boundaries and in reserve strips in riparian zones, but few residual trees survive around landings because nearly all of the trees left are knocked over by yarding.

Cutting residual infected trees is usually performed at the same time as precommercial thinning in southeast Alaska, at a stand age of approximately 15 years. Costs for residual control were approximately $30 per hectare when done directly following clearcut harvesting (Curtis and Swanson 1972) and are even less if conducted during a spacing or precommercial thinning, thereby avoiding a separate entry. Note that this cost value is decades old. Typically, chain saws are used to make a double cut into the lower bole of infected trees through sapwood that generally results in tree death 3 to 4 years later (Hennon and Shaw 1988). As an obligate parasite, the dwarf mistletoe dies when its host dies.

In British Columbia, a common practice is to remove residual trees including small hemlock trees (“whips”) 3 m or taller soon after harvest. Previously, when complete mistletoe control was an objective, this had the advantage of removing almost all infected trees before they could spread hemlock dwarf mistletoe seeds to young-growth western hemlock trees during the years before precommercial thinning. In many regions, spacing and/or precommercial thinning are no longer practiced due to low value of western hemlock trees, and knock-down of residuals is usually performed soon after harvesting. Laurent (1981) urged managers to perform surveys to confirm that residual trees are actually infected with hemlock dwarf mistletoe before conducting control measures. However, our impression is that mistletoe infection of residuals is difficult to determine and extremely variable. Small hemlock that were understory trees in old forests, but were left after the harvest, often have irregular branches that can be confused with hemlock dwarf mistletoe infections. We suspect that it is probably cheaper to fell all residual trees in designated areas rather than conducting a separate mistletoe survey, at least in areas where dwarf mistletoe could be present. Precommercial thinning is still a common silvicultural activity in southeast Alaska, but killing residual trees for dwarf mistletoe control usually is not included.

***Alaska—***

Perhaps the most substantial evidence of a minimal occurrence of hemlock dwarf mistletoe in even-aged stands in Alaska came from an examination of trees in a large stand density study (DeMars 2000). This plot system was designed to quantify the growth of even-aged trees in different thinning treatments. A total of 62 installations representing stand ages from approximately 15 to 115 years was selected throughout southeast Alaska. Given the abundance of hemlock dwarf mistletoe in this region, the parasite was probably present in many of the old-growth forests before the disturbance (windthrow or harvesting) that gave rise to these young, even-aged stands. However, the specific location of some plots was likely selected to avoid unusual stand conditions and damage from agents such as hemlock dwarf mistletoe. Therefore, these plots might not be a completely unbiased sample or representation of young managed forests in southeastern Alaska.

In 1990 and 1991, 59 of the 62 installations having a total of 9,279 western hemlock and 6,651 Sitka spruce trees were examined for hemlock dwarf mistletoe. Overall, only 1 percent of the western hemlock trees and no Sitka spruce trees were infected. Most of the infected western hemlock trees were lightly infected. Only 6 of the 59 stands, or 10 percent, had hemlock dwarf mistletoe. In the infested stands, an average of 15 percent of the western hemlock trees had some level of hemlock dwarf mistletoe infection.

Only one plot at Touchit Cove, Long Island, had hemlock dwarf mistletoe severe enough to reduce stand growth. An inspection revealed large residual hemlock dwarf mistletoe-infected trees in and just outside of the plot, thereby explaining the abundance of hemlock dwarf mistletoe in the young-growth stand. These trees were left after logging disturbance, which occurred about 60 years before sampling. This plot did not resemble an even-aged stand that usually results from a complete clearcut harvest or similar disturbance. Therefore, the young stand was the result of conducting what we would now consider as a selection or retention harvest of a hemlock dwarf mistletoe-infested, old-growth stand.

The low incidence of hemlock dwarf mistletoe in young western hemlock forests in southeast Alaska was further indicated by the results of Tait et al. (1985). They sampled 16, 12- to 27-year-old, even-aged, thinned or unthinned stands in the vicinity of Prince of Wales Island for the occurrence of general insect and disease activity. Although infected residuals were encountered, hemlock dwarf mistletoe was not found on any of the 160 western hemlock crop trees on the plots.

Shaw (1982) examined the distribution of hemlock dwarf mistletoe in young-growth forests age 17 to 43 years on Prince of Wales Island and neighboring islands to determine how the parasite intensified around small unmerchantable residual trees. The areas were clearcut harvested leaving unmerchantable residual trees. Shaw (1982) determined the percentage of young-growth western hemlock trees located within 9 m of single infected residual western hemlock trees (diameter at breast height 30 to 70 cm) by detailed examination and destructive sampling of 3,429 young-growth trees on 19 plots at three sites. On average, only 10 percent of trees were infected with only 1 to 2 percent of trees having two or more live infections. Western hemlock advanced regeneration was more often infected (16 percent) than western hemlock trees that regenerated after the harvest (6.5 percent). Results from this study indicated fewer infections in Alaska adjacent to source trees than reported in southern British Columbia by Smith (1977) for western hemlock trees planted around one source tree.

Shaw (1982) reported that 92 percent of the infections were alive in stands aged 17, 19, and 35 years, but only 51 percent of the infections were still alive in the stand aged 43 years. This initiated the hypothesis that hemlock dwarf mistletoe begins to die out during crown closure in even-aged stands. However, in some areas in British Columbia, many of these "dead" infections are actually alive despite their occurrence on lower branches that lack foliage, leading to an alternate hypothesis of long-term persistence.

Shaw and Hennon (1991) investigated hemlock dwarf mistletoe development in two young (15 years old at the study onset) thinned stands of western hemlock near Thorne Bay, Prince of Wales Island, Alaska. Plots were established around unmerchantable, severely infected trees, 25 to 30 cm diameter at breast height, to determine the pattern of dwarf mistletoe colonization of the surrounding young hemlock trees. In total, 206 young trees on 11 plots were examined systematically every 2 years from 1981 to 1987. These trees were not destructively sampled so that hemlock dwarf mistletoe development could be monitored through time. Each branch of every tree was searched carefully for any evidence of infection by hemlock dwarf mistletoe. Tree heights and crown dimensions were measured every 2 years to compare the height growth of hemlock trees to the vertical spread of the parasite in infected trees. The plots were thinned before the first measurement and, to conform to current practices, residual trees were girdled to kill them. One site was developed into a demonstration area to inform foresters, students, and others of the biology and management options for hemlock dwarf mistletoe (Hennon and Shaw 1988).

Shaw and Hennon (1991) found that the percentage of infected trees increased during their study, reaching 79 percent during the last sampling year when trees were 21 years old. All plots except one had at least one infected young-growth western hemlock tree. Although most of the trees were infected, few trees had 3 or more infections and only eight trees had 10 or more infections. Most infections were small swellings, but a few had developed small witches' brooms. The numbers of infections were insufficient to measurably reduce tree growth or to cause mortality. There was no significant orientation by distance or direction of infected trees from the infected residual trees. Infections were significantly more common in the lower and inner portions of the crowns than elsewhere in the infected trees. From 1981 to 1987, the height growth of hemlock trees on these plots was approximately double the vertical advancement of hemlock dwarf mistletoe. Infected trees grew about 21 cm per year more in height than the parasite spread vertically.

**Infected trees grew about 21 cm per year more in height than the parasite spread vertically.**

As suggested by Drummond and Hawksworth (1979), hemlock dwarf mistletoe develops more slowly in Alaska than farther south on Vancouver Island, Washington, and Oregon. The potentially detrimental effects of hemlock dwarf mistletoe with even-aged management in Alaska were overemphasized in the past due to reliance on research results from British Columbia (Drummond and Hawksworth 1979).

There are several possible explanations for the lower infection rates of hemlock dwarf mistletoe in Alaska. Disease of hemlock dwarf mistletoe caused by hyperparasites, early fall frost damage of berries, ineffective pollination due to weather or reduced insect pollinator activity, abortion of fertilized embryos, and seeds being dislodged by snow or rain during winter before they can germinate are some of the possible factors. Bloomberg (1987) suggested that differences in infection levels of hemlock dwarf mistletoe in various portions of its range might be due to effects of weather on seed production and spread, stand composition and growth rate, and hemlock dwarf mistletoe biotypes, i.e., genetically different populations of hemlock dwarf mistletoe. Regardless of causal mechanisms, these differences emphasize the need to gather more information on intensification and spread by regions and to exercise caution in extrapolating research results to large geographic areas.

In Alaska, Drummond and Hawksworth (1979) and Shaw and Hennon (1991) concluded that intensive control efforts are not necessary for hemlock dwarf mistletoe in clearcut harvested, "residual-free," even-aged managed stands. In these even-aged forests in Alaska and possibly other areas, hemlock dwarf mistletoe is reduced in incidence and might even die out because of stand developmental processes, i.e., shading and the inability of the parasite to spread vertically, on sites with average and above-average productivity. Hemlock dwarf mistletoe effects on tree mortality and growth loss will probably be negligible in these situations. On these sites under clearcut harvesting and even-age silvicultural regimes, hemlock dwarf mistletoe effects will likely be minimal as long as short rotations are used.

In Alaska in recent years, clearcut harvesting has rarely removed all of the residual structure from the previous forest. Often, infected seedlings, saplings, small trees, and even large trees remain. Utilization standards have changed frequently, with the result that codominant and dominant old-growth trees 20 to 30 cm diameter have been left because of excessive internal defect, i.e., wood decay. These harvest practices no longer resemble clearcut harvesting and, with regard to spread and intensification of hemlock dwarf mistletoe, should be considered to be more similar to retention harvests discussed below.

***British Columbia, Washington, and Oregon—***

As in Alaska, forest managers in British Columbia, Washington, and Oregon have been concerned about the spread of hemlock dwarf mistletoe from residual trees that remain in clearcut areas. Much of the applied research on hemlock dwarf mistletoe has focused on intensification of the parasite in the presence of these small residual trees. In one survey in British Columbia, Morris and Wood (1978) found that approximately half of the residual hemlock trees left after harvesting were infected with hemlock dwarf mistletoe. In Washington and Oregon, leaving residual trees resulted in 70 percent infection of nearby young trees at 25 to 30 years after harvesting (Stewart 1976). In British Columbia, Tripp et al. (1979) suggested that treatment of residuals at the time of precommercial thinning is too late; 98 percent of selected crop trees were already infected with an average of 20 infections (range 1 to 170) per tree. Morris and Wood (1978) and Muir (1985) recommended using the 3-m knockdown clause to reduce the spread of hemlock dwarf mistletoe in British Columbia. To further reduce hemlock dwarf mistletoe incidence, Muir (1985) recommended laying out harvest boundaries for clearcutting to minimize infected trees along the perimeter of units, thinning out infected young-growth trees during spacing activities, and leaving infected young hemlock stands on very poor sites unspaced. More recent recommendations were outlined by Hennon et al. (2001) and Muir et al. (2004a). In recent years, few young hemlock stands have been spaced or precommercially thinned in British Columbia, but this practice continues in Alaska. In many areas, removal of larger infected trees as important sources of hemlock dwarf mistletoe infection is still recommended, but the biological basis for the practice has yet to be established.

Bloomberg and Smith (1982) investigated infection levels of hemlock dwarf mistletoe in seven western hemlock stands that had a mix of residual and young-growth trees on southern Vancouver Island, British Columbia. The number of infections per tree varied considerably, from 373 to 4,058 on residual trees and from 3 to 455 on young-growth trees. Taller and larger diameter young-growth trees had more infections, presumably because they were older, were exposed to infection for longer periods, and were larger targets for intercepting mistletoe seeds from the residual trees. The authors recorded dead infections and found that these were significantly related to crown position; more dead infections were found in the lower crowns. Severity of infection of the young-growth trees was directly proportional to the number of residual hemlock trees and inversely proportional to the number of nonhost trees, e.g., Douglas-fir, Pacific silver fir, and Sitka spruce. The authors concluded that the primary factors affecting hemlock dwarf mistletoe infection levels in young trees were number of residuals, stand composition (proportion of different species), growth rates, and stand density. The data verified results from using a previously developed hemlock dwarf mistletoe model (Bloomberg et al. 1980) to predict spread and infection of hemlock dwarf mistletoe in the young trees.

Alfaro et al. (1985) reported data on occurrence and infection by hemlock dwarf mistletoe from seven western hemlock stands in British Columbia. The stands were selected from inventory maps to represent even-aged stands. Average tree age ranged from 40 to 100 years per stand with total volumes of 120 to 750 $m^3 \cdot ha^{-1}$. At three of the locations, approximately 45 trees were felled and growth increments measured. Growth reductions caused by hemlock dwarf mistletoe were variable depending on tree size, age, and position within each stand. Reductions in annual growth rates in moderately and severely infected trees at age 80 were estimated at 15 and 25 percent, respectively.

In western Washington and Oregon, Stewart (1976) developed an equation to estimate the percentage of infected western hemlock in young trees within a 10-m distance of infected residual trees. The percentage of infected trees increased exponentially up to the oldest stand sampled (25 to 30 years old) at which time 70 percent of young hemlock trees were infected.

In British Columbia, for clearcut-harvested units, Smith (1977) estimated that 86 evenly spaced residual infected trees per hectare similar to the one he studied would be sufficient to severely infect every young-growth hemlock. In an earlier report, Smith (1966) stated that only 25 evenly spaced residual trees per hectare would be needed, but the discrepancy between these two predictions was due to a difference in the numbers of hemlock dwarf mistletoe seeds dispersed from the same tree reported in 1966 and 1977. Based on these studies, intensification of hemlock dwarf mistletoe in southern British Columbia is faster than reported by Shaw (1982) in Alaska. However, the studies involved different conditions that are not necessarily equivalent. In British Columbia, trees were planted around one infected residual tree at 30+ years after harvest, and in Alaska, naturally regenerated trees around infected residual trees were examined 17 to 43 years after harvest.

Van der Kamp and Wilford (1981) examined the intensification of hemlock dwarf mistletoe in two western hemlock stands in British Columbia. They found that the number of infections doubled every 2 years during the early stage of stand development. They predicted that intensification would slow considerably as the stand developed, primarily through mortality of the infections by branch senescence at the base of tree crowns. They suggested that high levels of hemlock dwarf mistletoe that are visible at an early stand stage do not necessarily translate into high, or damaging hemlock dwarf mistletoe levels later in stand development.

In two young stands in British Columbia, Richardson and van der Kamp (1972) found that vertical spread of hemlock dwarf mistletoe was faster (65 ± 4 cm per year) on trees that were widely spaced than on trees that were growing in a dense stand (30 ± 4 cm per year). The height growth of trees in the widely spaced and dense stands was 58 and 33 cm per year, respectively. However, in southeast Alaska, Shaw and Hennon (1991) reported a 20-cm-per-year vertical spread rate for dwarf mistletoe and a 40-cm-per-year hemlock height growth. In British Columbia, Wass (see footnote 4) remeasured height growth and vertical spread of hemlock dwarf mistletoe in 28, 45-year-old trees that were planted and survived in the experimental trial established by Smith (1966, 1973, 1977). On average, lightly infected (DMR 0, 1, 2) trees grew 64 cm per year in height with a vertical spread of 20 cm per year for the parasite; moderately infected (DMR 3, 4) trees grew 55 cm per year with a vertical spread rate of hemlock dwarf mistletoe of 25 cm per year.

Van der Kamp (1987) suggested that site quality is important in determining the effects of hemlock dwarf mistletoe in even-aged managed stands. In dense stands on productive sites with rapid height growth, hemlock dwarf mistletoe is relegated to the lower crown. On poor sites, the mistletoe is able to spread vertically at the same rate as the height growth of western hemlock trees and therefore is able to spread into the upper canopy as the stand develops. Thus, hemlock dwarf mistletoe is expected to continue to be a factor in hemlocks growing on poor sites. However, the hypothesis of differences of hemlock dwarf mistletoe spread rates between good and poor sites has yet to be tested in a randomized, replicated study across a representative range of sites with different densities, numbers, and distributions of residual, infected trees.

Hadfield (1980) concluded that crown closure and rapid height growth of western hemlock stands in Washington were factors that minimized hemlock dwarf mistletoe damage in 40- to 80-year-old even-aged stands. Hadfield urged managers to consider no residual removal after clearcut harvesting unless the number of residual trees was "excessive," but he did not specify a number. Hadfield also recommended that managers consider stand thinning, a technique that they were hesitant to use because of the anticipated increase in dwarf mistletoe seed dispersal. Thinning, he argued, increased the height growth of the remaining trees, which restricted dwarf mistletoe occurrence to the lower crown. Concern was so high about light and stand opening increasing the spread of hemlock dwarf mistletoe (Morris and Wood 1978) that Russell (1978) suggested that severely infected western hemlock stands should not be thinned in Washington. It is generally expected that thinning will increase the abundance of hemlock dwarf mistletoe, probably for a short time, by increasing seed production and reducing barriers to dispersal. However, in some stands, there was a decrease or no effect of thinning on mistletoe abundance (Goheen et al. 1980). On productive sites, fast-growing, released trees could outgrow the vertical spread of the parasite, which would probably reduce its impact on growth rates of infected trees as they matured. This scenario is expected particularly where there is a large difference between the height growth of western hemlock trees and the upward spread of hemlock dwarf mistletoe (Shaw and Hennon 1991).

## Selection or Retention Harvesting and Uneven-Aged Stands

As discussed by Muir and Geils (2002), previous experience and reports indicated that selection harvesting or partial cutting initially decreased, but eventually increased hemlock dwarf mistletoe incidence or severity. Initially, removal of infected trees reduces dwarf mistletoe incidence and severity, but the more open stand conditions are believed to enhance dwarf mistletoe seed production and dispersal, so that in a few years, dwarf mistletoe incidence and severity could be higher in the treated stand.

**The best strategy to manage dwarf mistletoe-infested stands is to apply an appropriate silviculture treatment that will enhance tree growth.**

The often-dramatic increase in hemlock dwarf mistletoe in some thinned stands has persuaded some workers to recommend that stands infected by dwarf mistletoe should not be thinned. However, 10- to 20-year data for thinned, infested-western hemlock stands demonstrated that hemlock dwarf mistletoe severity increased in some stands, decreased in some stands, and did not change in others when compared to nearby unthinned stands (Goheen et al. 1980). Regardless of mistletoe incidence, tree volumes were greater in thinned than unthinned stands. These data supported the contention that the best strategy to manage dwarf mistletoe-infested stands is to apply an appropriate silviculture treatment that will enhance tree growth (Muir and Geils 2002). When thinning infected stands, incidence and severity of hemlock dwarf mistletoe will undoubtedly increase, and tree growth will be affected. However, the overall increase in tree growth in thinned hemlock dwarf mistletoe-infested stands could justify the costs of thinning even though the growth rate in infested stands was less than in uninfested stands.

With selection harvesting, there are opportunities to maintain overall tree health and stand productivity by periodically cutting severely infected trees. For a discussion of various strategies for treatments and related references, see Muir and Geils (2002). Tree growth rates are usually not significantly reduced until 50 percent or more of the live branches are visibly infected. This is equivalent to a dwarf mistletoe rating (DMR) of 3 or more. Usually DMR increases by a maximum of one class per decade so that entries for sanitation cutting and thinning should be made at approximately 20-year intervals. In recreation and high-use sites, tree health can be maintained by pruning infected branches and large witches' brooms. Not more than 50 percent of the live crown should be removed. These approaches should be effective for maintaining hemlock dwarf mistletoe-infected trees, but experimental data are needed for confirmation.

**Factors that influence intensification in uneven-aged stands—**
Several factors described below will most likely have a major influence on the amounts and impacts of hemlock dwarf mistletoe that develop in uneven-aged stands that grow following selection or retention harvesting.

***Presence and severity of dwarf mistletoe in residual trees—***
If hemlock dwarf mistletoe is absent in a stand before harvest, then introduction is unlikely in the short term and management need not be concerned about it. For example, stands at higher elevations, e.g., above 150 to 300 m in Alaska, are often completely free of hemlock dwarf mistletoe and will probably remain so. If hemlock dwarf mistletoe is present but only a few trees are infected, then infected or

uninfected trees could be selected and harvested to achieve the desired proportion of infected to uninfected trees after logging. This option is not possible in some western hemlock stands where every tree is infected. Hemlock dwarf mistletoe incidence and severity data are needed to plan appropriate management activities.

***Species composition—***

In mixed-species stands, selection and/or retention of western hemlock trees could modify the incidence of hemlock dwarf mistletoe. Less susceptible or immune tree species such as Sitka spruce, Pacific silver fir, mountain hemlock, western redcedar, and yellow-cedar, could provide partial barriers for mistletoe spread if they are tall enough to block dispersing mistletoe seeds from infected western hemlock trees. However, because many of these species are more valuable than western hemlock, selective harvesting might favor their removal. Many old-growth stands are dominated by western hemlock trees to an extent that there are few other species available for retention. Several methods of selection or retention harvesting, especially those that produce soil disturbances and larger stand openings, could favor the regeneration of Sitka spruce and other species instead of western hemlock. This could result in a more diverse understory with a higher proportion of trees less susceptible to hemlock dwarf mistletoe. Planting species other than western hemlock after harvesting is another common mistletoe-reduction strategy in many areas. However, in some forests where maintenance of biodiversity is a major objective, extensive planting of less susceptible tree species might significantly reduce the occurrence of western hemlock below acceptable levels (Edwards 2002).

***Heights of infected trees and vertical position of infections—***

Hypothetically, hemlock dwarf mistletoe infections located in small trees or confined to the lower crowns of large trees should not have the same potential for spread and impact in a stand as higher positioned infections. Infections high in the crowns of large trees are overhead sources of hemlock dwarf mistletoe seeds that could infect adjacent, younger trees for decades to possibly centuries. Nearby western hemlock trees could be exposed to hemlock dwarf mistletoe seeds lodging in their upper crowns for a typical harvest rotation of 80 to 100 years and perhaps for their entire lifespan of 300 to 400 years. Hemlock dwarf mistletoe seed sources in lower crown positions, i.e., on infected small residuals and lower branch infections on large residuals, will likely be overtopped and suppressed by regenerating and releasing western hemlock trees, particularly if harvest patterns allow for adequate light to encourage fast height growth. The leaders of some of the regenerating western hemlock trees will become infected, resulting in witches' broom formation and permanent stunting. Without an overhead source of hemlock dwarf mistletoe seeds, many infected small residuals will respond to release following selection harvest by fast height growth; the result is mistletoe-free upper crown, because the height growth of the residuals should exceed the vertical spread of the parasite. However, small, infected trees in a cutblock often appear important. These residual infected trees can become prolific sources of hemlock mistletoe seeds (Smith 1966, 1973, 1977), producing more seeds than nearby overstory old-growth trees (Smith 1969). Due to their initial taller height than regenerating younger trees, their rapid height growth after a disturbance, and their frequent large numbers, they are potential sources for rapid horizontal and vertical spread, presumably because of intertree, reciprocal seed dispersal and infection (Bloomberg and Smith 1982). More research is needed on this topic of the amount of inoculum produced and then disseminated from trees of different heights.

***Size and horizontal distribution of harvested canopy openings—***
The size and pattern of openings and the number and distribution of retained infected trees determine the amount and distribution of hemlock dwarf mistletoe in the developing western hemlock forest. However, predicting hemlock dwarf mistletoe abundance is complicated by the manner in which important ecological parameters are affected by the size of openings. There is little direct information from which to predict responses by hemlock dwarf mistletoe other than the knowledge that minimal hemlock dwarf mistletoe levels develop in very large clearcut openings. With our current understanding of the biology of hemlock dwarf mistletoe, some qualitative speculation can be made on how dwarf mistletoe will respond to different harvesting patterns.

Harvesting that creates numerous, small openings such as individual tree selection or small group selection will remove fewer hemlock dwarf mistletoe-infected trees, result in slower hemlock tree growth, and favor the short-range dispersal of hemlock dwarf mistletoe seeds. These factors will probably maintain or increase hemlock dwarf mistletoe incidence and severity. Conceivably, small openings might not provide adequate light to increase hemlock dwarf mistletoe seed production (Baranyay 1962) enough to lead to a potentially large population increase.

The actual size and spatial distribution of openings will likely have a pronounced effect on the amount of infection by hemlock dwarf mistletoe. The number of hemlock dwarf mistletoe seeds produced and distance that seeds disperse dictate how far hemlock dwarf mistletoe spreads into openings as they regenerate to western hemlock. Secondary spread of mistletoe among young-growth trees is likely to be quite slow (Alfaro et al. 1985) and of less consequence. Because most mistletoe seeds fall within about 5 to 10 m from their source, openings with a diameter larger than 10 m (0.03 ha) are likely to have an interior zone with trees relatively free of hemlock dwarf mistletoe. Conversely, in openings with a diameter smaller than 10 m, all trees probably are exposed to hemlock dwarf mistletoe seeds from infected trees on the periphery. Openings with a diameter of 100 m (0.8 ha) would have a central portion of about 78 percent of the area not exposed to infection from the margins of the opening.

***Numbers and sizes of residual trees—***

As described above, Smith (1966, 1973, 1977) studied hemlock dwarf mistletoe seed dispersal from one small residual tree on southern Vancouver Island, British Columbia, and predicted that 86 hemlock dwarf mistletoe-infected residual trees per hectare would result in almost 100 percent infection of regenerating young trees.

In southeast Alaska, Trummer et al. (1998) determined mistletoe severity for 10 western hemlock stands of 1.5 to 20 ha that were affected by near-catastrophic windstorms in the late 1880s. They expected that their results would be similar to those expected from selection harvesting that leaves large, old-growth trees. Wind damage varied considerably within each site. Some portions of the stands had no surviving residual trees and other portions had few to many surviving trees. Plots were selected and results grouped for areas having 0, 1-32, and 33 or more residual trees in each stand. Trummer et al. (1998) determined that the number and basal area of large and small residual trees could be used to predict the severity of infection in a stand, in this case the mean DMR for a stand. The size, number, and infection levels of residual trees were highly correlated with infection severity in western hemlock that regenerated after each disturbance. Mean DMRs in the wind-damaged stands were less than expected based on the results of Smith (1966, 1973, 1977) in British Columbia. Trummer et al. (1998) also determined that large mistletoe infections on the lower bole and branches were up to 200 years old. A linear relationship was found between the estimated age of infection for a bole infection and the diameter of the bole swelling: infection age was equal to approximately 35 plus five times the swelling diameter in centimeters.

***Other factors—***

Other factors that affect the amount of hemlock dwarf mistletoe after selection harvesting include slope and aspect of the site. Hemlock dwarf mistletoe is expected to spread faster and farther from uphill sources to downhill targets. Uphill spread is reduced with increasing slope gradient (Bloomberg et al. 1980). Greater shoot and seed production occurred on the southwest portion of an infected western hemlock tree in British Columbia (Smith 1977). Smith (1977) found differences by quadrant in the number of hemlock dwarf mistletoe infections on one residual tree and on the young-growth trees surrounding the hemlock dwarf mistletoe seed source. Approximate percentages of infections per southwest, northwest, northeast, and southeast quadrants were 48, 22, 16, and 14 percent, respectively. These results supported the supposition that spread of hemlock dwarf mistletoe would be greatest downhill on sites with a southwest aspect, but seed dispersal has to be determined on different slopes and exposures before any predictions can be made confidently.

**Response by hemlock dwarf mistletoe to selection or retention harvesting—** Although a substantial reduction of hemlock dwarf mistletoe can be expected by clearcut harvesting followed by the development of even-aged stands, selection harvesting in old-growth forests is expected to dramatically increase the incidence of hemlock dwarf mistletoe. Any harvesting system that leaves dwarf mistletoe-infected western hemlock trees and encourages regeneration of western hemlock is expected to result in intensification of the hemlock dwarf mistletoe. By contrast, Deal et al. (2002) found that any level of selection harvesting reduced dwarf mistletoe levels over those found in adjacent unharvested old-growth stands. Apparently, removing any infected trees during harvest reduced dwarf mistletoe to a greater extent than it could spread and intensify. Reconstructive methods were used; thus, a long-term experimental approach is needed to resolve this question in Alaska. Generally, leaving tall infected trees guarantees parasite seed sources high in the canopy from which spread to regenerating or understory trees can occur for long periods. In these situations, hemlock dwarf mistletoe will probably spread extensively to young trees and intensify rapidly within tree crowns.

There are numerous possible harvesting patterns that could be considered as selection or retention harvesting. To the degree that each prescribed system leaves large, infected residuals and creates canopy openings, hemlock dwarf mistletoe will likely be affected in some way. Malot (1991) argued that the previous view of forest management conducting a “battle” with hemlock dwarf mistletoe must be abandoned now that conservation of biodiversity is a central goal of forest management planning and that selection harvesting of old-growth forests will become the tool to achieve that end. However, in our view, a selection harvesting and silvicultural approach that ignores hemlock dwarf mistletoe is too simplistic because a specific prescription could result in large variations in the severity of infection over a rotation and even over a single cutting cycle. Potentially, selection harvesting gives flexibility in achieving various amounts of mistletoe in managed forests, but the end results will often differ widely depending on the site, number, and distribution of infected residuals, and their severity of infection.

Buckland and Marples (1952) observed the spread of hemlock dwarf mistletoe on Turnour Island in British Columbia (latitude 50 degrees) following three harvesting techniques. These included (1) clearcut harvesting; (2) harvesting with retention of small blocks of residual trees; and (3) selective thinning or high-grading of large overstory trees, which left a large number of scattered nonmerchantable trees. Their conclusions were based on general observations rather than rigorous data collection and analysis. Sites were logged operationally, and it was not known if site or stand factors differed among the three harvesting techniques before logging. Hemlock dwarf mistletoe was present in only widely spaced locations in the even-aged stand that regenerated in the clearcut units. Buckland and Marples (1952) assumed that birds or other animals had introduced hemlock dwarf mistletoe into the clearcut units through seed vectoring. Hemlock dwarf mistletoe had not spread far from the residual blocks, but was abundant in the areas colonized. Hemlock dwarf mistletoe was both abundant and well distributed throughout units after selective cutting (high-grading) of overstory trees. They concluded that the practice of leaving some western hemlock trees as seed sources for regeneration exacerbated hemlock dwarf mistletoe infestation. Buckland and Marples (1952) argued that the practice of leaving smaller and poorer quality trees encouraged slower growing trees with greater susceptibility to hemlock dwarf mistletoe. They suggested that any form of selective (high-grading) or selection harvesting will maintain or increase hemlock dwarf mistletoe incidence and severity.

**Potentially, selection harvesting gives flexibility in achieving various amounts of mistletoe in managed forests, but the end results will often differ widely depending on the site, number, and distribution of infected residuals, and their severity of infection.**

In southeast Alaska, Hennon established four large stem-mapped plots to determine the distribution and severity of infection of hemlock dwarf mistletoe under selection or retention management. Two plots were located in stands that were selectively harvested about 60 years before sampling and two were in stands that had extensive windthrow that mimicked selective harvesting about 110 years before sampling. Figure 33 shows the distribution of residual and young-growth trees in the two plots disturbed by wind. Infection severity was classified as absent, DMR 0; light, DMR 1 or 2; moderate, DMR 3 or 4; and severe, DMR 5 or 6.

The infected young-growth trees were closely associated with infected residual trees, as was particularly evident in the Halleck Harbor No.1 plot, which had only two infected residuals. In the other plots, a larger number of infected residual trees allowed hemlock dwarf mistletoe to occupy most of the plot. About 80 percent of

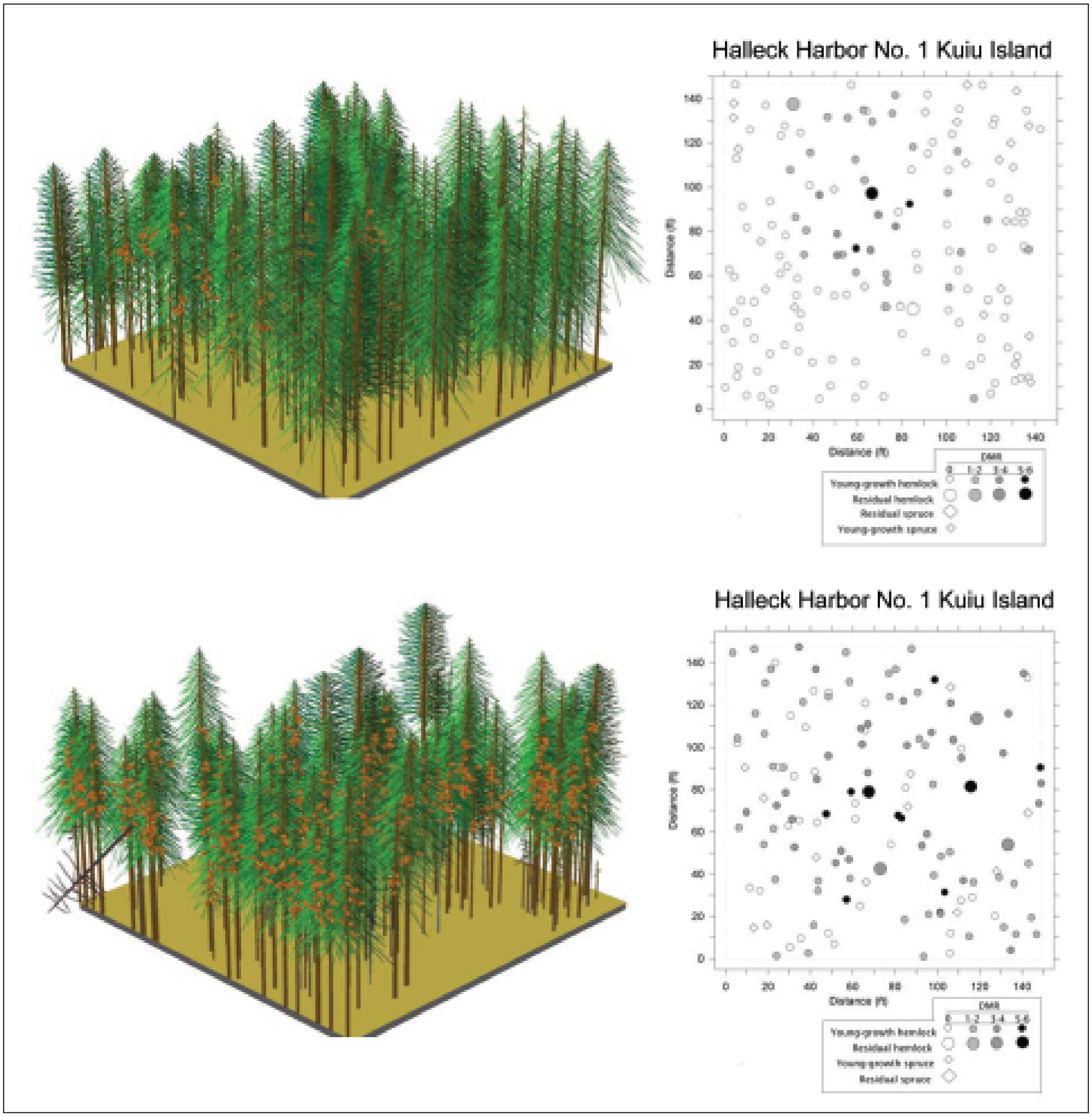


Figure 33—Stand Visualization Software (SVS) images of Halleck Harbor plots 1 (above) and 2 (below), Kuiu, Alaska, depicting the spread of hemlock dwarf mistletoe from two and five infected residual trees, respectively, to surrounding young-growth trees. Stem maps show the number, infection level, and location of residual trees that represented the inoculum for eventual spread. DMR = dwarf mistletoe rating. See Trummer et al. (2007) for developing SVS images that depict dwarf mistletoe.

the western hemlock trees were infected on these plots. Although the incidence of infection was high, the severities of infection (DMRs) were low in these three plots. Growth loss and mortality are substantial only for severely infected trees, which represented only about 10 percent of the infected trees.

A 10-percent growth loss of moderately infected trees and 40 percent growth loss of severely infected trees were applied to the proportion of young-growth hemlock trees in each DMR to calculate an average growth reduction by hemlock dwarf mistletoe per plot for young-growth hemlock trees. The residual trees were of various sizes and infection levels, but only infected residuals were included in table 6. Information from these plots suggested only a modest amount of mortality and growth loss resulting from hemlock dwarf mistletoe 60 years after selective harvesting and 110 years after a windstorm. Four plots did not adequately sample the range of conditions needed to provide information on different silvicultural approaches to selection harvesting. However, they indicated that leaving some residual trees does not necessarily result in substantial levels of hemlock dwarf mistletoe in southeast Alaska.

Short-term effects of hemlock dwarf mistletoe under selection harvesting is being investigated in a large multidisciplinary ecosystem management study jointly conducted by the Pacific Northwest Research Station and Alaska Region of the U.S. Forest Service. The study, called "Alternatives to Clearcutting," involves different patterns of selection harvesting in old-growth forests within an experimental design and randomized assignment of treatments (McClellan et al. 2000). Hemlock dwarf mistletoe intensification after harvest treatment is one part of this study. In addition, the role of hemlock dwarf mistletoe as a mortality agent and the cause of gaps in old-growth western hemlock unmanaged forests was measured before treatments at all sites (Hennon and McClellan 2003). The third and last block was harvested in 2005; early results on short-term intensification after harvest will be available following the first 5-year measurement cycle.

Another approach in the "Alernatives to Clearcutting" study is to examine forests that had been partially harvested in the early 1900s, attempt to reconstruct how much of the stand had been removed, and describe subsequent development (Deal et al. 2002). Eighteen stands were studied, mostly near shorelines, with plots installed in different parts of the stand that had received different harvest intensities. A control plot was placed in an adjacent unharvested area at each site.

Preliminary results from the study indicated that dwarf mistletoe severity was generally light in the selected stands. There was a tendency for lighter severity with more intense harvests, suggesting that hemlock dwarf mistletoe levels were reduced

**Table 6—Incidence of hemlock dwarf mistletoe and estimated growth loss based on the severity of infection of western hemlock trees in four plots in southeast Alaska**

| Site | Age | Residuals | Estimated growth loss |
|---|---|---|---|
| | *Years* | *No./ha* | *Percent* |
| Halleck No. 1 | 110 | 10 | 1.0 |
| Halleck No. 2 | 110 | 25 | 6.0 |
| Todd | 60 | 65 | 4.0 |
| Touchit | 60 | 40 | 3.5 |

by removing infected trees during the harvest. Selective harvesting maintained hemlock dwarf mistletoe but did not lead to greater severity of infection in residual western hemlock trees. Caution should be used in interpreting results from this reconstructive study, however, because hemlock dwarf mistletoe severity at the time of harvest was unknown and because of the variable spatial distribution of hemlock dwarf mistletoe in stands. In addition, plots placed in adjacent unharvested stands might not serve as appropriate controls.

Additional research is needed to provide information on how much hemlock dwarf mistletoe will result from different selection harvesting schemes and what impact different severities of hemlock dwarf mistletoe infection will have on the residual forest development. The most reliable information will come from repeatedly measured permanent plots. Along with blowdown and tree wounding, intensification of hemlock dwarf mistletoe is a concern with partial harvesting in western hemlock forests (Beese et al. 2003, Jaeck et al. 1984, McClellan et al. 2000). Considerable divergence of opinion among forest managers and scientists will continue until new information demonstrates the amount or extent of hemlock dwarf mistletoe growth losses and other effects under the various types of selection or retention harvesting.

Results of previous studies and available information on hemlock dwarf mistletoe spread and effects in selection- or retention-harvested areas are summarized below.

***Individual tree selection—***

Theoretically, individual tree selection is similar to natural small-scale disturbance in old-growth stands where individual trees die leaving small gaps in the canopy. In some instances where overstory trees are cut, crowns of neighboring canopy-level trees grow into the canopy space and a new codominant or dominant tree does not develop (Deal et al. 2002). If a subcanopy tree grows into the small vacant space, typically, the tree is fully exposed to hemlock dwarf mistletoe seeds from neighboring trees. Hemlock dwarf mistletoe could intensify in the old-growth trees due to the effects of stand opening. A small-size disturbance generally favors the spread of hemlock dwarf mistletoe and leads to severe infestations in old-growth stands. However, a small opening might not provide enough additional light to increase spread and intensification of hemlock dwarf mistletoe.

With this exception, individual tree selection is believed to enhance nearly all factors that lead to higher severity of hemlock dwarf mistletoe. However, there are exceptions to this view. In Alaska, a reconstructive study of western hemlock stands selectively harvested in the early 1900s indicated that hemlock dwarf mistletoe was maintained but severity did not increase significantly in these stands (Deal et al. 2002). In this case, trees infected by hemlock dwarf mistletoe were probably removed during the harvest, and spread and intensification presumably did not return dwarf mistletoe levels to the preharvest condition.

***Dispersed residual trees—***

The density, distribution, size, and infection severity of residual trees will influence the pattern of hemlock dwarf mistletoe that results from this silvicultural treatment. If individual infected residual trees were widely spaced, then dwarf mistletoe will be aggregated in discrete infection centers of young-growth trees around these residuals with uninfected or lightly infected young-growth trees between. If a supply of infested trees and witches' brooms were important for wildlife, such a pattern of dwarf mistletoe might enhance some aspects of wildlife habitat while still maintaining timber productivity. However, there are concerns about the wind firmness of these exposed residual trees. Most windthrow occurs within the first few years following harvest, but it is difficult to predict which trees will be wind-thrown. Thus, spread of hemlock dwarf mistletoe may be of short duration from some of these retained trees.

***Small group selections—***

The size of the opening created and occurrence of infected trees on the perimeters will influence the amount of resulting hemlock dwarf mistletoe in small group selections. Openings smaller than a 10-m radius (0.03 ha) could be fully colonized by hemlock dwarf mistletoe if the parasite were present in the perimeter trees. Hemlock dwarf mistletoe can intensify in the perimeter old-growth trees due to

**The size of the opening created and occurrence of infected trees on the perimeters will influence the amount of resulting hemlock dwarf mistletoe in small group selections.**

the effects of stand opening. Small openings will likely regenerate primarily with western hemlock. Openings larger than 0.03 ha will likely develop with a central portion free of hemlock dwarf mistletoe and could regenerate a higher proportion of less susceptible tree species.

***Thinning from above (diameter-limit harvest)—***
Some silvicultural prescriptions remove large trees and retain smaller ones. Such systems remove the tallest trees, and therefore, the highest sources of hemlock dwarf mistletoe. Considerable infection may often occur in the smaller trees that remain. Hemlock dwarf mistletoe may intensify immediately after the stand treatment as conditions favor reproduction and seed dispersal. On productive sites, however, these same conditions favor fast height growth of western hemlock trees. If all or most high sources of hemlock dwarf mistletoe seeds are removed, then most infected trees are anticipated to outgrow the vertical spread of the parasite. Under this scenario, they would develop upper crowns that are free of dwarf mistletoe and probably not experience any large reductions in annual growth due to infection. Trees could have brooms or bole infections in the lower crown, however, which may reduce wood quality.

**Monitoring programs for certification and forest-level effects—**
Recently, many private, corporate, and government forestry organizations that harvest and manage private or publicly owned forest land have registered with one or more institutions that certify the long-term sustainability of forest management plans and practices. In many areas, including British Columbia, certification is a statutory requirement for forest harvesting licenses and agreements. Generally, certification requires a forestry organization to provide periodic reports with data that demonstrate acceptable and effective results of their practices. In Canada these data are often based on a set of criteria and indicators developed by the Canadian Council of Resource and Environmental Ministers. These indicators include a measure of the area of forest damaged by forest insects and diseases. However, these data are too general to adequately characterize many of the effects of most forest insects and diseases, particularly the effects of hemlock dwarf mistletoe (Muir et al. 2004a).

Monitoring is needed to determine incidence and severity of hemlock dwarf mistletoe in harvested blocks over an extensive forest land base to adequately characterize hemlock dwarf mistletoe infestations and measure (or estimate) current or future impacts. Monitoring is required in most coastal forest areas because of variable ecological conditions, incidence, severity, and development of hemlock dwarf mistletoe infestations.

Recently we began developing more detailed measurements for monitoring hemlock dwarf mistletoe effects in young trees and retention-harvested stands (Muir 2005), but further work is required. Criteria to be measured include tree numbers, sizes, dwarf mistletoe ratings, and spatial distributions of infected trees. Trees on the same plots should be remeasured over a period of several decades after harvest or disturbance. Ideally, monitoring plots for hemlock dwarf mistletoe should be integrated with the overall monitoring procedure used for certification. However, with the generally low incidence of mistletoe-infected trees, a two-stage sampling design will be needed to efficiently select an unbiased set of plots with infected trees.

**Modelling spread and impacts of hemlock dwarf mistletoe—**
One approach to integrating information and available data on biology, ecology and management of hemlock dwarf mistletoe (and other insects and pathogens) has been to construct models. Various modelling approaches have been developed for dwarf mistletoes including hemlock dwarf mistletoe (Bloomberg et al. 1980, Geils et al. 2002, Hawksworth and Wiens 1996, Robinson and Geils 2006, Robinson et al. 2002). A general overview of modeling and development of forest models is presented by Amaro et al. (2005).

Bloomberg et al. (1980) produced a model to predict the development of hemlock dwarf mistletoe in British Columbia from infected residuals left after clearcut harvesting. The experimental basis for the model involved only a few residual trees up to 15 m in height. Where stand conditions include small residuals, the model is very useful because it integrates results from several studies of spread and intensification of hemlock dwarf mistletoe.

The Bloomberg et al. (1980) hemlock mistletoe model includes a number of factors. These include distribution of dwarf mistletoe infections in residual source trees, seed production, escape from crown and dispersal, interception of seeds by neighboring trees, distribution of seeds within crowns, development of infections, mortality of dwarf mistletoe plants, and tree crown growth. The model accurately predicted hemlock dwarf mistletoe intensification within trees and spread over a 10-year period at several locations (Bloomberg and Smith 1982). Most of the assumptions used by the model were from data collected on southern Vancouver Island, British Columbia. The model has not been verified for use in other regions or for conditions where large residual trees occur. Recently, Robinson et al. (2002) and Robinson and Geils (2006) incorporated many of the relationships and data of the Bloomberg and Smith (1982) model into a more detailed model that was modified for hemlock dwarf mistletoe and other dwarf mistletoes.

In response to the well-recognized lack of data on "healthy" tree growth in most areas, detailed tree growth models such as the Tree and Stand Simulator (TASS) have been developed in British Columbia and used to project western hemlock tree growth under various conditions, including retention-harvested stands (Goudie and DiLucca 2004). Although based on detailed measurements of tree growth, TASS and most other tree growth models have deliberately excluded effects of most insects and diseases, including hemlock dwarf mistletoe (Muir et al. 2004a). To rectify this limitation, a modeling project was initiated (Muir 2003) to develop a hemlock dwarf mistletoe component for TASS. The TASS/ hemlock dwarf mistletoe model incorporates the detailed dwarf mistletoe model initially developed for hemlock dwarf mistletoe by Bloomberg et al. (1980) and further developed by Robinson et al. (2002). However, data collection and analyses for the new model have yet to be completed, pending further funding. More model development will be required before a prototype TASS/hemlock dwarf mistletoe model is available for testing.

In southeastern Alaska, Trummer et al. (1998) developed a set of regression equations to predict the spread and intensification of hemlock dwarf mistletoe in wind-disturbed hemlock stands that mimic selection harvests. They intend to link the model to the SEAPROG variant of the forest vegetation simulator (FVS) used for southeast Alaska (McClellan and Biles 2003) to project effects of hemlock dwarf mistletoe in infested stands. However, the base model requires further development before it is acceptable for use in uneven-aged stands in Alaska (McClellan and Biles 2003).

J.P. Kimmins and associates at the University of British Columbia are developing a hemlock dwarf mistletoe component for their forest level and ecosystem models (see footnote 6). Hemlock dwarf mistletoe plays a significant role in the development and succession of western hemlock and western redcedar forests on northern Vancouver Island and the adjacent mainland, and therefore, must be included in landscape-level models.

## Needs for Further Research

Although there is a large body of research on the biology and impacts of dwarf mistletoes (Geils et al. 2002, Hawksworth and Wiens 1996), several controversies and major gaps in our knowledge need to be addressed to improve the understanding and management of hemlock dwarf mistletoe. Over the extensive geographic range of hemlock dwarf mistletoe, incidence and severity of the parasite vary greatly, resulting in a wide diversity of effects on forest trees and ecosystems. These in turn have resulted in a diversity of scientific data and controversial opinions on hemlock dwarf mistletoe impacts and significance.

**Over the extensive geographic range of hemlock dwarf mistletoe, incidence and severity of the parasite vary greatly, resulting in a wide diversity of effects on forest trees and ecosystems.**

As noted by Trummer at al. (1998) and others, most of the information on hemlock dwarf mistletoe reported from the 1960s to 1990s was based on or directed towards effects of the parasite on tree growth and silvicultural treatments, particularly in conjunction with clearcut harvesting and even-age management. More recent changes in forestry practices have emphasized selection harvesting, reduced sizes of openings, and retention of scattered or blocks of old-growth trees. These new practices create conditions that potentially favor rapid spread and more severe impacts of hemlock dwarf mistletoe, but in many areas, actual data on hemlock dwarf mistletoe spread and effects under these situations are limited or lacking.

In British Columbia, hemlock dwarf mistletoe is severe in some second-growth hemlock forests (Muir 2004) and partially cut areas (Buckland and Marples 1952) that resemble retention-harvested areas. Apparently, conditions that enhance or suppress hemlock dwarf mistletoe seed production, spread, and eventual impacts on tree growth are highly variable. Hemlock dwarf mistletoe impacts could become severe in many retention- or selection-harvested stands, but perhaps remain inconsequential in others. We urgently need more detailed studies of hemlock dwarf mistletoe spread and impacts in retention- or selection-harvested forests to clarify and quantify regional and local variations in hemlock dwarf mistletoe spread and impacts. The limited and often controversial data and opinions on management of hemlock dwarf mistletoe-infested forests under these new regimes prompted our review of available literature and information on hemlock dwarf mistletoe.

If the intensification by hemlock dwarf mistletoe and impacts that it causes under selection harvesting in old-growth forests can be quantified, the results should be combined with growth loss estimates from studies in various regions and developed into subroutines for stand and tree growth models. These models include FVS for Washington and Oregon, PROGNOSIS $^{BC}$ stand model and TASS for British Columbia, and for southeast Alaska, FVS (McClellan and Biles 2003).

Several basic features of reproductive biology are still not well understood. For example, the methods of pollination for hemlock dwarf mistletoe, whether by insects, wind, or both is unclear. The factor or stage in hemlock dwarf mistletoe reproduction that limits spread and intensification needs to be determined in a wide range of environmental conditions. Currently, we do not know how stand disturbances, e.g., selection harvesting, will influence hemlock dwarf mistletoe shoot, fruit, and seed production; although we do know that they are greatly enhanced for other dwarf mistletoes. Responses to selection harvesting by hemlock dwarf mistletoe appear extremely variable but are probably to be expected under the wide range of environmental conditions and management regimes in coastal forests. These topics require further research for a better understanding and prediction of how the parasite responds to different forest management practices.

Very little is known about wildlife associations with and use of hemlock dwarf mistletoe. If wildlife-hemlock dwarf mistletoe interactions are as important as for other dwarf mistletoes in other regions, then this type of information is needed to determine and ensure levels of hemlock dwarf mistletoe that are beneficial for wildlife management objectives. Maintaining particular levels of hemlock dwarf mistletoe for wildlife habitat could be accomplished by using harvesting systems. Clearcut harvesting appears to largely eliminate hemlock dwarf mistletoe from many sites for a long time. Some form of selection harvesting could be used to extract timber but maintain hemlock dwarf mistletoe at a favorable level for wildlife or other objectives. Thus, research on wildlife use of hemlock dwarf mistletoe as food and as sites for resting, perching, and nesting should be con-ducted so that managers can judge what tree, stand, and ecosystem effects are gained or lost by retaining or encouraging different levels of hemlock dwarf mistletoe.

**Some form of selection harvesting could be used to extract timber but maintain hemlock dwarf mistletoe at a favorable level for wildlife or other objectives.**

Several other more specific topics of needed research are listed in appendix 2.

## Diverse Opinions on Hemlock Dwarf Mistletoe Impacts

Several studies of spread and effects of hemlock dwarf mistletoe have produced contradictory results, controversial opinions, and considerable uncertainty about future impacts of the parasite. Opinions regarding the potential impacts of hemlock dwarf mistletoe and management practices often are divergent. We have encountered three prominent opinions:

- Hemlock dwarf mistletoe has severe impacts on tree growth and should be eradicated or reduced as much as possible to protect timber values
- Hemlock dwarf mistletoe is an important ecological agent that contributes to stands structure, biological diversity, and wildlife habitat and should be maintained
- Hemlock dwarf mistletoe has insignificant impacts and can be ignored

The first view that hemlock dwarf mistletoe has severe effects on tree growth and should be reduced in occurrence as much as possible is derived from several early reports and studies beginning with Drake (1915), Weir (1915, 1916, 1918), and others who reported severe infestations of hemlock dwarf mistletoe. Drake (1915), who worked as a forest examiner, first reported hemlock dwarf mistletoe from southeast Alaska near Tenakee and later at a number of other locations. Drake stated that in many areas of the Tongass National Forest, typically 30 to 80 percent of western hemlock trees were infected. These reports and views that hemlock dwarf mistletoe infestations are damaging were reinforced by more recent authors who examined hemlock dwarf mistletoe impacts in recently harvested areas and recommended harvesting and silvicultural treatments for management of hemlock dwarf mistletoe-infested stands (Buckland and Marples 1952, Shea 1966). Many of the earliest reports were made before a DMR system was developed and before any quantified estimates of impact were available. Also, these views were developed during an era of resource management that was predominantly focused on harvesting and timber productivity.

The second view is that hemlock dwarf mistletoe has ecological value, or is even a keystone species, and should be maintained in managed forests. Desirable levels of hemlock dwarf mistletoe to help meet specific wildlife or other objective are rarely established, however. Thus, there are no target values to apply in attempts to manipulate hemlock dwarf mistletoe. Another related perspective on hemlock dwarf mistletoe is the degree to which selection harvests can be conducted in a manner in which hemlock dwarf mistletoe is maintained, but not at levels that are devastating to timber values or other resources. In this case, hemlock dwarf mistletoe is not the primary focus of forest management, but there is concern that certain types of timber harvesting may exacerbate the disease. This situation applies to forests managed for multiple resource objectives and scenarios where there are reasons to consider harvesting methods other than clearcutting.

The third view apparently derives from either a lack of understanding about the importance of the parasite or a belief that the parasite spreads too slowly to cause significant impacts. As we have outlined here, there are many studies that indicate that hemlock dwarf mistletoe has distinct effects on both the timber resource and a range of ecological factors, including stand structure and disturbance. Perhaps hemlock dwarf mistletoe can be ignored in unmanaged forests where natural processes are allowed to run their course, but in forests with any level of management, actions that may increase or decrease the parasite should be evaluated.

The viewpoint that hemlock dwarf mistletoe can be ignored because it spreads slowly is true for some areas. Examples of low rates of spread include several studies from Alaska (Deal et al. 2002, Hennon et al. 2001, Shaw 1982, Shaw and Hennon 1991, Trummer et al. 1998) and in British Columbia, the high-elevation Montane Alternative Silviculture Systems (MASS) project site (Nevill and Wood 1995). However, the authors of these studies do not recommend that hemlock dwarf mistletoe be ignored, but rather that certain selection harvest scenarios result in only limited negative impacts of the disease. We suspect that much of the perception of low impacts of hemlock dwarf mistletoe is based on the fact that the parasite develops relatively slowly in young trees. Often, 10 to 20 years after harvesting are required before infection of young trees becomes obvious to casual observers. It is important to realize that hemlock dwarf mistletoe in southeast Alaska extends from sea level to an elevation of approximately 150 to 300 m. In Alaska, hemlock dwarf mistletoe probably spreads relatively slowly because of some environmental factor associated with these higher elevations at this latitude. Similarly, the MASS site in British Columbia at 750 m is near the upper elevation limit of hemlock dwarf mistletoe in southern British Columbia. Low incidence and low rates of spread of hemlock dwarf mistletoe could be expected there. Several authors including Baranyay and Smith (1974) and Hennon et al. (2001) suggested that cold temperatures limit hemlock dwarf mistletoe seed production and dispersal. Snow could be a factor in the overwintering survival of seeds in higher elevation stands and in more northerly populations of western hemlock.

We believe that the wide range in hemlock dwarf mistletoe behavior, including differing spread rates in the southern and northern portions of its range, has contributed to the divergent views about increasing or decreasing its occurrence. Differing views about the goals of resource management, which often have an underlying philosophical basis, also have a strong influence in shaping these opposing opinions. The challenge is to determine what management approaches are most appropriate for a particular ecological condition or resource management objective, with different severities and incidences of hemlock dwarf mistletoe infestation. Widespread implementation of selection- or retention-harvesting practices in coastal forests could exacerbate effects of hemlock dwarf mistletoe and thereby negatively affect the long-term productivity and sustainability of managed forests. Alternatively, hemlock dwarf mistletoe could be substantially eradicated by some practices, particularly clearcut harvesting, with potentially substantial effects on stand structure, wildlife habitat, and biodiversity of forest ecosystems. Fortunately, the relatively predictable nature of the spread and impact of hemlock dwarf mistletoe facilitates the management of this important forest parasite.

**Fortunately, the relatively predictable nature of the spread and impact of hemlock dwarf mistletoe facilitates the management of this important forest parasite.**

## Conclusions

In some regions, maintenance of current levels of hemlock dwarf mistletoe might not be a desirable strategy. In southeastern Alaska, several surveys indicate an almost complete eradication of hemlock dwarf mistletoe due to clearcut harvesting and the resulting development of even-aged stands. In the past, when timber was the predominant management objective, reduction of hemlock dwarf mistletoe was viewed as highly desirable. Management objectives now include a broader objective of maintaining forest ecosystems. Attributes of a healthy forest include biological diversity, structural diversity, essential functional components, and processes. In this context, particular levels of hemlock dwarf mistletoe may enhance forest health.

The challenge for forestry professionals is to adapt, but not rigidly apply, general guidelines for managing hemlock dwarf mistletoe to local or specific stands. Specific management actions will probably not be directly aimed at hemlock dwarf mistletoe, but the consequences of management on the parasite should be considered. Every location in the extensive western hemlock coastal forests probably has a unique complex of environmental, biotic, climatic, and historical factors that must be considered in determining suitable or appropriate management regimes and silvicultural treatments. Hemlock dwarf mistletoe is inconspicuous, but its presence and impacts are far easier to evaluate and predict than infestations by forest insects and pathogens such as root diseases or wood decay fungi. Hemlock dwarf mistletoe seed production, dispersal, infection, and effects on tree growth are relatively easier to measure and predict. Tree- and forest-level models need to be developed to estimate hemlock dwarf mistletoe spread and impacts for particular situations. However, spread rates and impacts of hemlock dwarf mistletoe also need to be measured and monitored over a wide range of ecological conditions as a basis for sustainable forest management.

The differences in results of studies on the biology and impacts of hemlock dwarf mistletoe are striking particularly between those in Alaska and British Columbia. We suspect that a large part of the difference in results and opinions derives from the types of stands and trees selected for study. A second-growth, immature stand of western hemlock with no or few residual trees from the previous forest will likely have a low incidence of hemlock dwarf mistletoe. An older, second-growth stand with hemlock dwarf mistletoe infection ranging from light to severe will likely include several residual trees from the previous stand that became sources of mistletoe spread into the young stand. The incidence and impacts of hemlock dwarf mistletoe are closely related to the number of residual infected trees. Our review suggests that the two types of stands can be found in most regions, but it is not known how frequently each scenario occurs.

We suggest that to resolve these differences and controversies, an extensive, nonbiased sampling procedure is needed in each region to determine hemlock dwarf mistletoe incidence and effects, and to form a basis for designed experimental studies. An inventory-based sample of hemlock dwarf mistletoe is available for Washington and Oregon (Hildebrand 1995) and for nonwilderness areas of Alaska (described in this report). Inventory plots or subsamples will likely have to be remeasured to ensure accuracy of records on mistletoe incidence and severity (see references in Muir and Moody 2002).

Many, if not most, of the studies on biology and effects have been based on selected, infected trees or stands of trees with varying attributes. Because of the methods of selection in many previous studies, personal bias in the selection process cannot be excluded. An extensive, stratified, random sampling method with a two- (or more) stage procedure will be needed to select infested stands and infected trees, but costs for implementing such a sampling design could be prohibitive. Until this type of a sampling design can be established, the extent and significance of the effects of hemlock dwarf mistletoe in many areas will likely remain uncertain or controversial.

Management of coastal western hemlock forests will not focus solely on hemlock dwarf mistletoe, but will include many other factors. However, our review indicates that if hemlock dwarf mistletoe influences on stand structure and productivity are ignored, all harvesting and management regimes could produce unintended and undesirable results.

## Acknowledgments

Much of the information on hemlock dwarf mistletoe is unpublished, and we have drawn on several of these sources for information and ideas. We are indebted to several researchers and workers who have shared their opinions and information with us.

In compiling this report, we made extensive use of the dwarf mistletoe literature database, which is maintained at the USDA Forest Service, Rocky Mountain

Research Station in Flagstaff, Arizona. We deeply appreciate the efforts of the late Frank Hawksworth and Brian Geils who initiated and maintained this invaluable literature database over five decades. In addition, we thank Brian Geils and Terry Shaw for searches of the database and citations of the literature.

We appreciate the help of Bill van Hees of the Forest Inventory and Analysis staff in Anchorage who provided summaries of hemlock dwarf mistletoe occurrence in Alaska.

We are very grateful for the substantial efforts of Diane Hildebrand, Robert Mathiasen, David Shaw, Dick Smith, and Lori Trummer who reviewed our extensive draft manuscripts and provided many helpful suggestions for improvement.

We are also grateful to U.S. Forest Service, Forest Health Protection, Pest Trend Impact Plot System program, the Forest Investment Account, and International Forest Products Ltd., British Columbia, for funds that supported the preparation of this report. We thank Warren Warttig, International Forest Products Ltd., and Roderick Negrave, British Columbia Ministry of Forests and Range, Nanaimo, for their support in preparing the shortened version of this review for British Columbia.

## English Equivalents

| When you know: | Multiply by: | To find: |
|---|---|---|
| Millimeters | 0.039 | Inches |
| Centimeters (cm) | .4 | Inches |
| Meters (m) | 3.3 | Feet |
| Kilometers (km) | .6 | Miles |
| Hectares (ha) | 2.5 | Acres |
| Kilograms (kg) | 2.2 | Pounds |
| Cubic meters ($m^3$) | 35.3 | Cubic feet |
| Cubic meters | .0283 | Cubic feet ($ft^3$) |
| Cubic meters per hectare ($m^3$/ha) | 14.3 | Cubic feet per acre |
| Trees per hectare | .4 | Trees per acre |
| Degrees Celsius (°C) | 1.8 (and then add 32) | Degrees Fahrenheit |
| Cubic meters per hectare | .07 | Cubic feet per acre ($ft^3$ acre) |
| Kilometers per hour | .621 | Miles per hour |

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# Appendix 1: Common and Scientific Names

| Common name | Scientific name |
|---|---|
| Trees: | |
| Black spruce | *Picea mariana* (Mill.) B.S.P. |
| Blue spruce | *Picea pungens* Engelm. |
| Douglas-fir | *Pseudostuga menziesii* (Mirb.) Franco |
| Engelmann spruce | *Picea engelmannii* Parry ex Engelm. |
| Grand fir | *Abies grandis* (Douglas ex D. Don) Lindl. |
| Jack pine | *Pinus banksiana* Lamb. |
| Lodgepole pine | *Pinus contorta* Dougl. ex Loud var. *latifolia* Engelm. ex Wats. |
| | *Pinus contorta* Dougl. ex Loud var. *murrayana* Engelm. ex Wats. |
| Mountain hemlock | *Tsuga mertensiana* (Bong.) Carr. |
| Noble fir | *Abies procera* Rehd. |
| Pacific silver fir | *Abies amabilis* (Dougl.) Forbes |
| Ponderosa pine | *Pinus ponderosa* Dougl. ex Laws. |
| Shore pine | *Pinus contorta* Dougl. ex Loud. var. *contorta* |
| Sierra white fir | *Abies lowiana* (Gordon) A. Murray |
| Sitka spruce | *Picea sitchensis* (Bong.) Carr. |
| Subalpine fir | *Abies lasiocarpa* (Hook.) Nutt. |
| Western hemlock | *Tsuga heterophylla* (Raf.) Bong. |
| Western larch | *Larix occidentalis* Nutt. |
| Western redcedar | *Thuja plicata* Donn ex D. Don |
| Western white pine | *Pinus monticola* Dougl. ex D. Don |
| Whitebark pine | *Pinus albicaulis* Engelm. |
| Yellow-cedar | *Chamaecyparis nootkatensis* (D. Don) Spach |
| Mistletoes: | |
| Douglas-fir dwarf mistletoe | *Arceuthobium douglasii* Engelm. |
| Eastern dwarf mistletoe | *Arceuthobium pusillum* Pk. |
| Fir dwarf mistletoe | *Arceuthobium abietinum* Engelm. ex Munz |
| Hemlock dwarf mistletoe | *Arceuthobium tsugense* (Rosendahl) G.N. Jones |
| Subspecies: | |
| Mountain hemlock dwarf mistletoe | *A. tsugense* (Rosendahl) G.N. Jones subsp. *mertensianae* Hawksworth & Nickrent |
| Shore pine dwarf mistletoe | *A. tsugense* (Rosendahl) G.N. Jones subsp. *contortae* Wass & Mathiasen |
| Pacific silver fir dwarf mistletoe | *A. tsugense* (Rosendahl) G.N. Jones subsp. *amabilae* Mathiasen & C. Daugherty |

| Common name | Scientific name |
|---|---|
| Western hemlock dwarf mistletoe | *A. tsugense* (Rosendahl) G.N. Jones subsp. *tsugense* |
| Lodgepole pine dwarf mistletoe | *Arceuthobium americanum* Nutt.:Engelm. |
| Southwestern dwarf mistletoe | *Arceuthobium vaginatum* (Willd.) Prsl. subsp. *cryptopodum* (Engelm.) Hawksw. & Wiens |
| Western dwarf mistletoe | *Arceuthobium campylopodum* Engelm. |
| Western larch dwarf mistletoe | *Arceuthobium laricis* (Piper) St. John |
| Western spruce dwarf mistletoe | *Arceuthobium microcarpum* (Engelm.) Hawksw. & Wiens |
| Leafy (true) mistletoes | *Phoradendron, Viscum* spp. |
| Fungi: | |
| American matsutake | *Tricholoma magniverlare* (S. Ito & S. Imai) Singer |
| Colletotrichum canker | *Colletotrichum gloeosporioides* (Penz.) Penz & Sacc. |
| Neonectria canker | *Neonectria neomacrospora* (Booth & Samuels) Mantiri & Samuels |
| Annosus root disease | *Heterobasidium annosum* (Fr.) Bref. |
| Artist's conk | *Ganoderma applanatum* (Pers.: Wallr.) Pat. |
| Hartig's conk | *Phellinus hartigii* (Allsch. & Schnabl.) Bond. |
| Paint fungus | *Echinodontium tinctorium* (Ell. & Ev.) Ell. & Ev. |
| Pinicola conk | *Fomitopsis pinicola* (Swartz ex Fr.) Karst. |
| Yellow cap fungus | *Pholiota adiposa* (Batsch) P. Kumm. |
| Insects: | |
| Hemlock looper | *Lambdina fiscellaria* |
| Johnson's hairstreak butterfly | *Loranthomitoura johnsonii* |
| Blue mistletoe hairstreak | *Loranthomitoura spinetorum* |
| Birds: | |
| blue grouse | *Dendragapus obscurus* |
| brown creeper | *Certhia americana* |
| chippping sparrows | *Spizella passerina* |
| dark-eyed junco | *Junco hyemalis* |
| goshawk | *Accipiter gentilis* |
| gray jay | *Perisoreus canadensis* |
| great gray owl | *Strix nebulosa* |
| hermit thrush | *Catharus guttatus* |
| house wren | *Troglodytes aedon* |
| long-eared owl | *Asio otus* |
| marbled murrelet | *Brachyramphus marmoratus* |

| Common name | Scientific name |
|---|---|
| mountain chickadee | *Parus gambeli* |
| northern spotted owl | *Strix occidentalis* |
| pine siskin | *Carduelis pinus* |
| red crossbill | *Loxia curvirostra* |
| red-breasted nuthatch | *Sitta canadensis* |
| sharp-shinned hawk | *Accipiter striatus* |
| Steller's jay | *Cyanocitta stelleri* |
| western tanager | *Piranga ludoviciana* |
| Mammals: | |
| Douglas squirrel | *Tamiasciurus douglasii* |
| Elk | *Cervus elaphus* |
| Marten | *Martes americana* |
| Mule deer | *Odocoileus hemionus* |
| Northern flying squirrel | *Glaucomys sabrinus* |
| Red squirrel | *Tamiasciurus hudsonicus* |

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# Appendix 2: Hemlock Dwarf Mistletoe Research Topics or Needs for Further Study

| Subject and/or research | References |
|---|---|
| Medicinal uses | Smith 1928 |
| Host specificity of subspecies | Mathiasen and Daugherty 2005 |
| Temperature thresholds for geographic and upper elevation occurrences | Gill 1957 |
| Association with riparian zones | Muir 2004, Swanson et al. 2006 |
| Disturbance regimes | Hennon and McClellan 2003 |
| Aerial shoot production in young stands | Shaw and Weiss 2000 |
| Seed production and dispersal from old-growth trees | Smith 1966, 1973, 1977 |
| Replicated studies of life cycle in different regions | Carpenter et al. 1979, Smith 1974, Smith and Wass 1979, Shaw and Loopstra 1991 |
| Lack or variability of bole swelling | Shaw et al. 2005 |
| Animal and bird vectors of mistletoe seeds | Shaw et al. 2002, 2005 |
| Tree-to-tree variation in hemlock dwarf mistletoe seed production and dispersal | Smith 1966, 1973, 1977 |
| Biocontrol agents | Shamoun and DeWald 2002 |
| Survival and effects of infection on lower foliated and unfoliated branches | |
| Genetically resistant western hemlock | Shamoun and DeWald 2002 |
| Physiological effects on trees | Bickford et al. 2005, Meinzer et al. 2004 |
| Reevaluation of dwarf mistletoe rating for hemlock | Shaw et al. 2000 |
| Regional forest-level growth impacts | Hildebrand 1995 |
| Top-kill and whole tree mortality | Hennon and McClellan 2003 |
| Role in canopy gap formation | Hennon 1995, Hennon and McClellan 2003 |
| Wildlife habitat and biodiversity | Geils et al. 2002, Mathiasen 1996 |
| Stand development and residual infected trees | Trummer et al. 1998 |
| How much hemlock dwarf mistletoe will result from different harvesting schemes | |
| Criteria, indicators, and monitoring | Muir et al. 2004a |
| Models for spread and impact | Robinson and Geils 2006 |

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