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Hemlock Dwarf Mistletoe

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Hemlock dwarf mistletoe, Arceuthobium tsugense (Rosendahl) G.N. Jones, causes a serious disease of western hemlock and several other tree species along the Pacific Coast of North America. This small, seed-bearing plant lives exclusively as a parasite on living trees.

Throughout its range, hemlock dwarf mistletoe occurs in patch-like patterns in the forests. Some forests are severely infected, some sparsely, and some not at all. The incidence and severity of the parasite are greatly influenced by stand structure and disturbance history.

Severe infections of trees can cause growth loss, topkill and tree death. Dwarf mistletoe infections also produce densely branched structures called witches' brooms that are used by wildlife.

The disease can be managed to various levels depending upon land management objectives. One challenge for management may be to maintain the disease in some areas or some parts of stands to maintain wildlife habitat, but to avoid producing severe dwarf mistletoe infections where timber or other resources are impaired.

Hosts

There are two subspecies of hemlock dwarf mistletoe, western hemlock dwarf mistletoe and mountain hemlock dwarf

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Table 1. Host susceptibility to the two subspecies of hemlock dwarf mistletoe.

Common name	Western hemlock dwarf mistletoe	Mountain hemlock dwarf mistletoe
Scientific name	*A.tsugenese* subsp. *tsugense*	*A.tsugense* subsp. *mertensianae*
Primary host trees	Western hemlock Noble fir Pacific silver fir Subalpine fir Shore pine	Mountian hemlock Pacific silver fir Subalpine fir Noble fir
Secondary hosts		Whitebark pine
Occasional hosts	Grand fir Mountain hemlock	Western white pine
Rare hosts	Engelmann spruce Sitka spruce Douglas-fir Western larch Western white pine	Brewer's spruce Lodgepole pine Western hemlock

mistletoe, each having different host tree preferences (Table 1.)

Distribution

Hemlock dwarf mistletoe occurs further north than any other dwarf mistletoe. The natural distribution for hemlock dwarf mistletoe is shown in Figure 1. The western hemlock dwarf mistletoe subspecies is found near Haines, Alaska, south through coastal British Columbia, on the west side of the Cascade Mountain Range in Oregon and Washington, to near Mendocino in northern California. The mountain hemlock subspecies does not occur as far north; it grows from near Vancouver Island in British Columbia, through the Cascade Mountains in Oregon and Washington, and south to the central Sierra Nevada Mountains in Alpine County, California. A population of mountain hemlock dwarf mistletoe occurs in the Olympic Mountains.

Climate may be responsible for limiting the distribution of hemlock dwarf mistletoe. The parasite is not found along the Gulf of Alaska in the northwest portions of western hemlock's natural range. Hemlock dwarf mistletoe is also uncommon at higher elevations throughout its range. Observations by several scientists suggest that fruits of dwarf mistletoe sometimes freeze in the fall, killing seeds before they can disseminate. It is possible that the parasite cannot complete its life cycle in these northern and high-elevation areas where growing seasons are short.

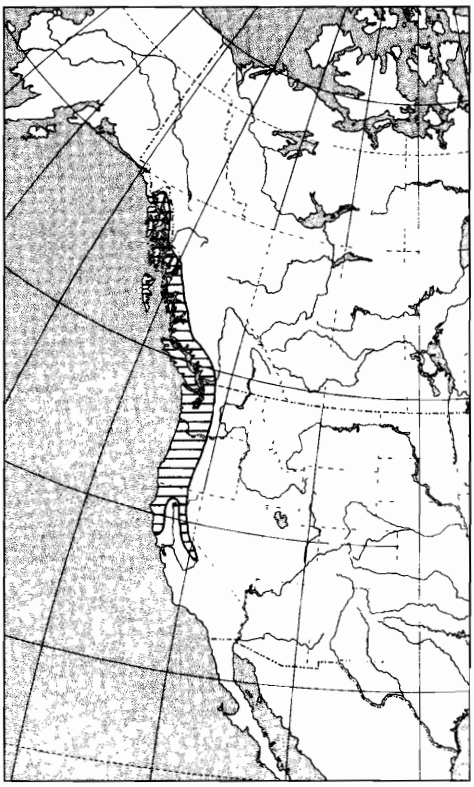

Fig. 1. The natural distribution of hemlock dwarf mistletoe (adapted from Hawksworth and Wiens 1996).

Studies on the rate of western hemlock dwarf mistletoe spread indicate differences by latitude with a slower rate of spread in the northern portions of the range. Several mechanisms may be responsible for these differences: dwarf mistletoe seeds removed by snow sloughing during winter, varying reproductive success during pollination, fruits freezing during early fall frosts.

Life History

Hemlock dwarf mistletoe is a small, leafless flowering plant consisting of an endophytic system and aerial shoots. The dwarf mistletoes are obligate parasites, requiring a living conifer host for their survival. The endophytic system (modified "roots") functions as feeding structures imbedded in the cambium and sapwood of host tree twigs, branches, or boles. The aerial shoots are the visible portion and are produced solely for the purpose of reproduction. Female and male flowers occur on different dwarf mistletoe plants (Figure 2). Hemlock dwarf mistletoe shoots vary from greenish to reddish, and can be from 3 to 13 cm long, averaging about 7 cm.

Fig. 2. Aerial shoots of hemlock dwarf mistletoe: female plants with berries on the left, male plants on the right. Photo taken by Kenelm Russell, Washington State Department of Natural Resources.

The fruit is a berry that usually contains one seed. When ripe, hydrostatic pressure builds up in the fruit until it ruptures at the base, forcibly discharging the seed occasionally over 15 m. However, most hemlock dwarf mistletoe seeds fall within 6 m of their source. The initial velocity of a dwarf mistletoe seed's explosive discharge has been measured at 27 m/sec! Seeds are discharged from late summer to early November.

Dwarf mistletoe seeds are coated with viscin, a sticky, hygroscopic substance. Many seeds hit and adhere to host foliage. Precipitation lubricates the viscin, and the seed eventually slides down the needle and sticks to the twig, or falls to the ground. Seeds overwinter and germinate early the next spring. The elongating radicle of the germinating seed grows along the surface of a twig until it meets an obstruction or break in the bark, usually the base of a needle. The tip of the radicle then forms a disc-like holdfast from which an infection peg penetrates bark tissues.

A small, spindle shaped swelling is the first symptom of dwarf mistletoe infection, and appears one or two years after infection. After another one or two years, dwarf mistletoe shoots emerge from the enlarged swelling and produce either male or female flowers by late summer. Pollination occurs sometime in July, August, or September for both subspecies of hemlock dwarf mistletoe. Fruits mature in the fall of the year following pollination. Thus, infections of hemlock dwarf mistletoe can spread to new hosts in as few as four years. In some instances, infections may remain in the host tissues

for years before aerial shoots appear. During this time, swellings are the only evidence of these latent infections. Inoculation studies in Alaska suggest that the life cycle may take longer to complete there than further south. The endophytic system of a dwarf mistletoe infection remains viable for many years and may produce large swellings and many successive crops of aerial shoots and fruits.

Symptoms and Signs of Infection

The aerial shoots are the most positive diagnostic characteristic of hemlock dwarf mistletoe. The shoots are sparse and poorly developed in dense stands, older infections, and lower branches. They reach maximum size on open-grown trees or

and frequently become spindle-shaped (elongated with the axis of the branch). With time, infected tissues begin to develop a proliferation of branches known as witches' brooms (Figure 3b). These brooms are the most conspicuous symptom of dwarf mistletoe infection and can

Fig. 3. Swelling and witches' brooms of hemlock dwarf mistletoe: (a) indicate young infections which grow into young brooms (b) and finally large brooms (c).

where infected branches are exposed to sunlight. When aerial shoots drop off, the basal cups often are present on the spindle-shaped swellings of infected branches. The basal cups remain for many years after aerial shoots have disappeared.

Dwarf mistletoe infection interferes with tree growth regulators causing increased growth in the tree tissues that are infected. This results in twig and branch swellings (Figure 3a). These slowly enlarge in size,

often be seen easily from the ground (Figure 3c). Brooms are even more obvious on dead trees. Witches' brooms vary from small, palm-like structures in young infections to large masses of branches weighing several hundred pounds. Brooms can grow to very large size and survive for 100 years or more. Infections can occur in the main stem of trees, some of which originate in side branches and grow into

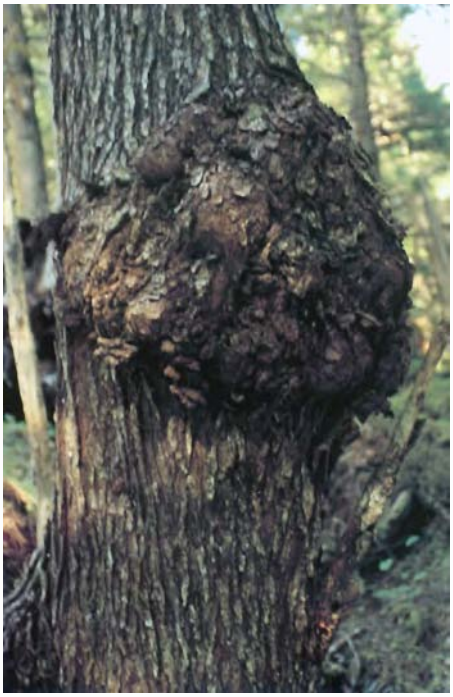

Fig. 4. Old bole infections resembling large burls develop from hemlock dwarf mistletoe infections that grow into the bole from the tree's leader or branches.

the bole. These bole infections sometimes lose all branches and develop into large burl-like structures (Figure 4).

Spread, Intensification, and Influence of Disturbance

Hemlock dwarf mistletoe spreads to nearby hosts and intensifies within the crown of the same host by means of the forcibly discharged seeds. Spread is most rapid in forests with multiple size classes of host trees. Small understory trees are continuously exposed to dwarf mistletoe seed from infected overstory trees. After overstory trees die or are harvested, they are replaced by the infected understory trees, and the cycle of infection continues.

Hemlock dwarf mistletoe is favored by small-scale disturbance (i.e., gap formation) that occurs in older forests where mistletoe seeds produced in large trees can infect new trees that regenerate in small openings. The dispersal mechanism of seeds discharging sometimes over 15 meters allows the parasite to penetrate into most areas where one or a few trees have died or blown over. Regeneration that develops after complete harvest or stand destruction is seldom infested. Catastrophic, stand-replacing events, such as fires or windstorms can eliminate hemlock dwarf mistletoe.

In even-age forests, spread of dwarf mistletoe is much slower than in multiple-aged forests. In dense even-aged forests, lateral spread is probably less than 50 cm per year, because the thick foliage reduces light intensity necessary for prolific seed production, and intercepts the discharged seed. In open-grown, thinned stands, dwarf mistletoe may spread faster because increased light favors seed production and the seeds are discharged for greater distances.

Birds and, to a lesser degree, mammals are responsible for long-range dispersal of hemlock dwarf mistletoe over large areas where it can expand its range or colonize forests after catastrophic disturbance. Dwarf mistletoe seeds do not survive the digestive systems of animals. Seeds adhere to the feathers, fur, or feet of birds or mammals who remove them during preening, often wiping them on twigs. Birds perch in treetops and preen, and the tops of conifers contain a high proportion of young tissues susceptible to infection. Dwarf mistletoe infection in the upper

crown has the greatest potential for spread to surrounding trees.

Effects of Infection

Witches' brooms and swellings divert the tree's resources to these points of infection. This can adversely affect tree height and diameter growth, reduce tree vigor, and make infected trees more susceptible to insects and other diseases. The degree of growth loss is directly correlated to the intensity of infection (the number and size of infections). Lightly infected trees have no measurable growth loss, but severely infected trees can lose up to 40% of their potential growth. When a major portion of the live crown consists of infections and brooms, the tree weakens and dies prematurely (Figure 5). Mortality occurs as a direct result of the infection or from attacks by other diseases and insects on the already weakened tree. Bole infections and broken branch stubs from large brooms frequently provide infection courts for wood decay fungi, leading to significant heart rot.

Fig. 5. Western hemlock tree mortality from severe infection with hemlock dwarf mistletoe.

In forests with several tree species, hemlock dwarf mistletoe may favor the development of succession of secondary hosts or non-susceptible species.

Brooms that develop from dwarf mistletoe infections provide additional structures in the forest. Birds and mammals may use dwarf mistletoe brooms as habitat for nesting, resting or foraging. Brooms vary greatly in their size, distance from the bole, and shape. Some can support a platform nest. Arboreal mammals (e.g., squirrels) are known to selectively feed on the swollen nutritious tissues of hemlock dwarf mistletoe infections, especially in southeast Alaska. Sometimes this feeding results in a biological control of the disease as branches are girdled and their infections die.

Dwarf mistletoe infections affect the quality and usable volume of wood. The presence of the endophytic system in wood alters its physical and chemical properties, reducing its quality. The large knots associated with brooms reduce timber values. Decay increases the amount of unusable (cull) wood. In recreational areas, large witches' brooms can create hazardous conditions because of their potential to break and fall. Increased decay in old infected trees greatly reduces structural strength, increasing the danger from falling trees. In scenic areas, accelerated mortality and numerous dead tops may be considered unsightly. Severely infested stands increase opportunities for catastrophic outbreaks of insects, diseases, and fire.

Management

The management of hemlock dwarf mistletoe should consider the resource objectives for the stand and the value of the dwarf mistletoe, as a disturbance agent and as food and habitat for other species. In stands where timber production or intensive recreation use are major considerations, control of dwarf mistletoe may be necessary to meet management objectives. In other areas, allowing dwarf mistletoe populations to remain and even increase may be appropriate.

Complete harvest of infected stands is the most effective control for dwarf mistletoe. As an obligate parasite, dwarf mistletoe is killed and will not reproduce on slash or downed logs. Infected residual trees (left after logging), advanced reproduction, and large trees growing adjacent to the clearcut boundary are sources of inoculum for spread to young-growth forests. Reinvasion of harvested areas can be prevented by taking advantage of natural barriers such as roads, ridge tops, and changes in forest type as cutting boundaries. After usable trees are harvested, the recommendation is to destroy any remaining host trees over 1 meter tall. Even those without visible infections are likely to harbor latent infections, if the overstory was more than moderately infected. It takes only 25 evenly spaced infected trees remaining per hectare to re-infest the entire new stand.

However, where a young stand can be kept growing vigorously, the trees may put on height growth faster than infections can intensify upward. In Alaska, the height growth of hemlock is frequently twice as great as the upward advance of the parasite. In these cases, the dwarf mistletoe may eventually die out as stands reach 40 years of age or so and infected lower branches die. However, as the stand ages and tree growth slows, residual dwarf mistletoe can eventually reach tree crowns.

When complete harvest of infested stands is not appropriate, shelterwood or seed tree methods of regeneration harvest are good alternatives. Remove as many infected overstory trees as possible at the initial harvest. When regeneration is established, but before trees are 1 meter tall or 6 years old, remove or kill all remaining infected overstory trees. Infection in the new stand should then be sufficiently low to cause little loss during the rotation. During all subsequent cultural treatments, select against any infected trees.

Partial harvests of old, infected forests can greatly increase dwarf mistletoe infection levels because dwarf mistletoe can spread from the mid and upper crown of large trees to infect the tops of other trees. Partial cutting results in varying amounts of dwarf mistletoe, with the amount dependent upon 1) the number of large hosts that remain, 2) their infection level, and 3) their spatial distribution. Where a clump of dwarf mistletoe is desirable, natural barriers including non-host vegetation and bare ground are useful in limiting spread.

Non-susceptible or occasional and rare hosts can be favored to decrease disease levels in a forest. Besides being uninfected or lightly infected, these trees sometimes act as a barrier to spread among the more susceptible species.

In forested recreation sites with hemlock dwarf mistletoe infestations, sanitation treatments that favor non-susceptible hosts, or removal of infected overstory trees may be appropriate. In areas where trees have high individual values such as developed recreation sites, pruning of large brooms can be effective in reducing hazard from falling branches and improving tree vigor and longevity. Trees with brooms and branch infections in the lower crown would benefit most from pruning.

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