Dwarf Mistletoes

Ecology and Management in the Rocky Mountain Region

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1. INTRODUCTION

The genus *Arceuthobium* (Santalales: Viscaceae) is a group of small plants that are exclusively parasitic on conifers and can strongly influence forest structure and dynamics. There are about 42 species, mostly in North and Central America, where they occur only on members of the family Pinaceae. Eight species occur in Eurasia and Africa, where some are also parasitic on junipers (family Cupressaceae). *Arceuthobium* species tend to be fairly host-specific.

Five species occur in the Rocky Mountain Region (Table 1). Most of our abundant tree species (piñon, lodgepole and ponderosa pines, and Douglas-fir) are commonly infected in at least parts of their ranges. Common conifer species that are not, or only rarely, hosts of mistletoes in the Region include all spruces and true firs.

Table 1. Dwarf mistletoes and their hosts in the Rocky Mountain Region (Hawksworth & Wiens 1996, Mathiasen *et al.* 2005).

	Hosts [a]	
Arceuthobium species	Principal	Other
A. americanum	Lodgepole pine	Secondary: ponderosa pine Occasional: whitebark and limber pines; Rare: Engelmann and blue spruces, bristlecone pine
A. cyanocarpum	Limber, whitebark and bristlecone pines	Rare: ponderosa and lodgepole pines
A. divaricatum	Piñon	
A. douglasii	Douglas-fir	Rare: subalpine fir, blue and Engelmann spruces
A. vaginatum subsp. *cryptopodum*	Ponderosa pine	Occasional: bristlecone pine, lodgepole pine; Rare: limber and southwestern white pines, blue spruce

[a] Hosts are in the following categories:
Principal: More than 90% infection when close to heavily infected trees.
Secondary: Frequently attacked (50–90% infection) when close to heavily infected principal hosts.
Occasional: Occasionally attacked (5–50% infection) when close to heavily infected principal hosts.
Rare: Rarely attacked (≤ 5% infection), even when close to heavily infected principal hosts.

2. LIFE CYCLE

Let's begin with a dwarf mistletoe seed clinging to the bark of a young twig. After germination, the young radicle contacts the host bark and forms a disk-like holdfast that enlarges and grips the bark tightly. From it, a wedge develops and penetrates the bark. Penetration continues to the cambium and stops. From this penetration peg, cortical strands begin to grow in the bark toward the shoot tip, away from the shoot tip, and around the circumference.

As the cortical strands extend through the bark, they periodically send additional pegs radially to the cambium like the first penetration peg. These each form a meristem that is continuous with the host cambium. Whenever the cambium grows, adding wood and phloem, the mistletoe meristems grow as well, producing tissue in the newly formed wood and keeping up with growth so it is not torn apart. As the years go by, these "sinkers" are embedded radially in the wood and in fact are integrated into the wood rays. They do not actively penetrate existing wood, instead they cleverly incorporate themselves into the wood as it grows. Together, the cortical strands and sinkers are called the endophytic system and provide anchorage and absorption of nutrients and water for the dwarf mistletoe.

Infection generally occurs in host shoots that are one to five years old. That is because such shoots are most likely to have needles that intercept flying seeds, but also because the bark is thin enough to be penetrated before the germinating seed depletes its resources.

There are two types of infections by dwarf mistletoes:

– **Systemic infection**: The endophytic system grows to the tip of the shoot and may even invade the bud. It keeps pace with shoot growth and may invade all branches subsequently produced from it. Dwarf mistletoe shoots may be produced anywhere along the systemically infected branch system or at annual bud scars. In our area, systemic infections are produced by lodgepole pine dwarf mistletoe and by Douglas-fir dwarf mistletoe.

– **Local infection**: The endophytic system does not advance far towards the shoot tip. Mistletoe shoots are produced only near the original site of infection. This is typical of southwestern, limber pine and piñon dwarf mistletoes. Lodgepole pine dwarf mistletoe may occasionally produce local infections, especially in the early stages of disease development.

About 3–5 years after infection, after the endophytic system is developed, the mistletoe plant produces shoots. Shoots are generally less than 8 in (20 cm) tall. The smallest species in our area is Douglas-fir dwarf mistletoe, with shoots only 0.8 in (2 cm) tall and 0.04 in (1 mm) in diameter, and the largest is southwestern dwarf mistletoe, typically 4 in (10 cm) tall and 0.12 in (3 mm) diameter. Shoots are yellow to olive green or orange to reddish brown. They have small, scale-like leaves in pairs at each node. The leaf bases tend to fuse together during development, forming a small cup around the node. Plants are dioecious (only one gender in a given plant); male and female plants may differ in color and/or form. Shoots are segmented at the nodes. Shoots typically live for 5 to 7 years and may produce several crops of flowers before they die and dehisce. The plant stays alive inside the host, however, and typically produces new shoots repeatedly for many years.

Time of flowering varies among the species. The species in Region 2 that occur on the most economically important hosts (*A. americanum*, *A. vaginatum* ssp. *cryptopodum*, and *A. douglasii*) flower in spring or early summer (Table 2). The other two species flower in late summer or fall. Seed is typically dispersed in late summer or fall of the year after flowering. The time from flowering (pollination) to fruit maturation thus varies from about 12 to 17 months in our species.

Table 2. Phenology of flowering and seed dispersal in the *Arceuthobium* species of the Rocky Mountain Region (Hawksworth & Wiens 1996).

	Flowering	Seed dispersal
A. americanum	early April – early June	mid-May – late Sept.
A. cyanocarpum	mid-July – early Sept.	mid-Aug. – late Sept.
A. divaricatum	early Aug. – late Sept.	early Sept. – late Oct.
A. douglasii	May	late Aug. – late Sept.
A. vaginatum ssp. *cryptopodum*	mid-May – June	late July – early Aug.

Both wind and insects are likely involved in pollination. Insect pollinators may include a variety of flies, thrips, bees, and ants (Stevens & Hawksworth 1984).

The mature fruit contains a single seed that is explosively discharged by one of the most effective hydrostatic mechanisms among flowering plants. During maturation, the fruit pedicel bends so that the seed is discharged at about 30 degrees above the horizontal (Hawksworth 1961b, data for southwestern dwarf mistletoe), an angle that maximizes lateral distance for targets within 35 vertical feet below the source, and also allows the possibility of climbing. The initial velocity of the seed is about 27 m sec^{-1} (60 mph). Maximum dispersal distance is about 52 ft, but most seeds fall within 33 ft. The seed is coated with a mucilaginous substance (viscin), so it adheres to needles that it strikes. It remains on the needle until rain wets the viscin, whereupon the lubricated seed slides down the needle and, if the needle is upright, makes contact with the bark and needle base. Seeds that fall from downward-pointing needles may be intercepted by lower branches. Seeds germinate

in spring or early summer of the year following dispersal, except for *A. vaginatum* ssp. *cryptopodum*, whose seeds germinate in August or September immediately after dispersal.

The entire life cycle, from infection to fruit maturation and dispersal, takes 6 years or more for lodgepole pine dwarf mistletoe and 7 or 8 years for southwestern dwarf mistletoe.

2.1 Vectors of dwarf mistletoes

Nicholls *et al.* (1984) provided a detailed review of the literature on vectoring of dwarf mistletoe seeds by animals. A more recent summary was provided by Hawksworth & Geils (1996).

Although dwarf mistletoe seed is primarily dispersed by explosive discharge of the sticky seed from fruits, numerous birds and mammals have been implicated as potential vectors that could have a role in occasional long-distance dispersal. The primary candidates are passerine birds and squirrels. Direct proof and quantitative measurement of effective vectoring (i.e., resulting in establishment of a new infection center) would be difficult or impossible to obtain. Evidence generally consists of capturing animals with attached seeds of dwarf mistletoe and the existence of isolated, "satellite" infection centers. Satellite centers could result from animal vectoring or from survival of small, residual infected trees from a previous stand or larger residuals that subsequently died or were removed.

Successful establishment of new infection centers by vectoring almost certainly occurs, but its frequency and ecological importance are unclear. Dispersal over very long distance (beyond the common distance for pollen dispersal, which is unknown) is unlikely to result in successful establishment because dwarf mistletoes are dioecious, so both male and female plants are required for seed production. Although vectoring may be important in considering biogeography and dispersal over a time scale of centuries and millennia, it is generally considered to be relatively unimportant to the epidemiology of the disease from a management perspective.

An apparent exception is limber pine dwarf mistletoe, *Arceuthobium cyanocarpum* on limber pine, *Pinus flexilis*, in the Rocky Mountains. Infections often occur in isolated trees or in the tops of otherwise uninfected trees, and birds are therefore thought to be important in dispersal in this case (Hawksworth & Geils 1996, citing unpublished 1968 data of Urban).

Red squirrels and flying squirrels have been trapped in infested stands of *Picea mariana* in Minnesota with seeds of *Arceuthobium pusillum* stuck to their fur (Hudler *et al.* 1974, Ostry *et al.* 1983). In *Pinus ponderosa* heavily infested with *A. campylopodum* in Oregon, up to 50% of squirrels carried one or more seeds (Lemons 1978). Squirrels up to 150 m away from infected trees were found with seeds. However, Lemons doubted they were important for establishment of new and distant infection centers because squirrels groom seeds from their fur soon after they become attached.

In lodgepole pine in Colorado, seeds of *Arceuthobium americanum* were found occasionally on least chipmunk, golden-mantled ground squirrel, red squirrel and American marten (Nicholls *et al.* 1989, Nicholls *et al.* 1986). Although chipmunks and ground squirrels carried seeds more frequently than the others, they were thought to be unlikely vectors because they spend most of their time near the ground. Red squirrels may carry seeds to appropriate infection courts more often because they reside in tree crowns, but they have a small home range and are thus unlikely to result in long-distance dispersal.

Birds are more likely than mammals to result in long-distance dispersal because many frequent tree crowns and may travel over relatively large areas. When isolated infections occur in the tops of tall, otherwise uninfected trees, vectoring by birds is a likely explanation. Numerous species have been trapped with seeds stuck to their feathers or other surfaces (Hawksworth & Geils 1996,

Nicholls *et al.* 1984). For *A. americanum* in lodgepole pine, during peak time for seed dispersal, 22% of captured birds had seeds (Nicholls *et al.* 1984); over all time periods 6.3% carried seeds (Nicholls *et al.* 1986). The most important bird species were gray jay, mountain chickadee, Steller's jay (Figure 1), gray-headed junco, and Audubon's warbler. In Colorado ponderosa pine forests, *A. vaginatum* ssp. *cryptopodum* was found on 4% of 411 birds, including pygmy nuthatch, mountain chickadee, gray-headed junco, chipping sparrow, and Williamson's sapsucker (Hudler *et al.* 1979).

In two studies, birds were observed to deposit seeds from their external surfaces onto susceptible hosts. Birds with artificially acquired seeds, caged with potted black spruce, deposited several seeds on spruce foliage during preening (Ostry *et al.* 1983). In ponderosa pine stands in Colorado, chickadees with naturally acquired seeds transferred seeds to pine needles in five instances (Hudler *et al.* 1979).

Figure 1. Frank Hawksworth (1926-1993), a foremost authority on dwarf mistletoes, and a Steller's jay, a foremost potential vector of lodgepole pine dwarf mistletoe. Photo courtesy of Tom Nicholls.

3. DWARF MISTLETOES OF THE ROCKY MOUNTAIN REGION

3.1 Lodgepole pine dwarf mistletoe – *A. americanum*

Lodgepole pine dwarf mistletoe (sometimes called American dwarf mistletoe) is the most widely distributed, one of the most damaging, and the best studied dwarf mistletoes in North America. Shoots are yellowish to olive green, 2–3.5 in (5–9 cm) long (maximum 12 in) and up to 0.04–0.12 in (1–3 mm) diameter, with verticillate branching (in whorls). The distribution generally follows the distribution of its principal host, lodgepole pine, in the Rocky Mountain Region (Figure 2).

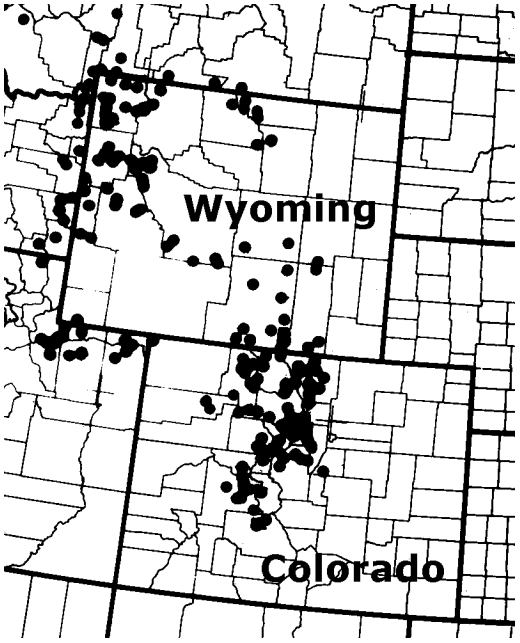


Figure 2. Distribution of American dwarf mistletoe, *A. americanum*, in the Rocky Mountain Region (from Hawksworth & Wiens 1996).

Arceuthobium americanum infects systemically, sometimes causing large witches' brooms with elongated, pendulous branches.

An interesting feature of this species, potentially useful in management, is that the upper elevational limit is usually 185–200 m (about 600–650 feet) below the upper elevational limit of lodgepole pine for a given latitude (Figure 3). Experiments have shown that the mistletoe can survive at higher elevations, but it cannot reproduce because the fruit is killed by early autumn frosts before it can fully mature (Hawksworth & Wiens 1996).

As noted in *Table 1*, ponderosa pine is considered a secondary host of this species. However, *A. americanum* can sustain itself and even be aggressive in pure stands of Rocky Mountain ponderosa pine in northern Colorado and southern Wyoming, sometimes a mile or more away from infected lodgepole pine (Hawksworth & Wiens 1996). This generally occurs in areas outside the range of ponderosa pine's usual parasite, southwestern dwarf mistletoe.

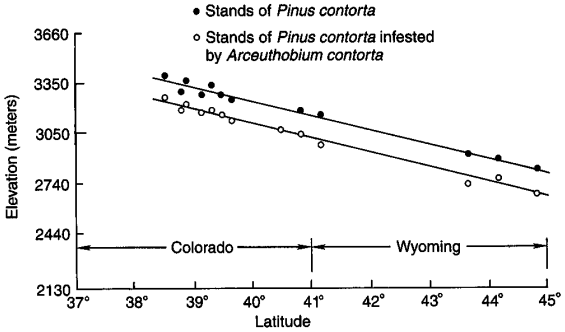


Figure 3. Upper elevation limits of American dwarf mistletoe and stands dominated by its host, lodgepole pine, in Colorado and Wyoming (Hawksworth 1956, Hawksworth & Wiens 1996).

Spread rate in even-aged stands can be about 1.7 ft per year in open stands and 1.2 ft per year in dense stands (Hawksworth & Johnson 1989).

Intensification (increase in number of infections over time) occurs most quickly in stands 15–60 years old in Colorado. During that time dwarf mistletoe rating (DMR) increased one class in 14 years (Hawksworth & Johnson 1989).

A Forest Insect and Disease Leaflet is available for this disease (Hawksworth & Dooling 1984).

3.2 Limber pine dwarf mistletoe – *A. cyanocarpum*

All of the high-elevation white pines in the Rocky Mountain Region, including limber, whitebark, and Rocky Mountain bristlecone pine, are primary hosts of limber pine dwarf mistletoe (see *Table 1* for definitions of host categories). The only endemic white pine that is not a host in nature is southwestern white pine. Shoots are yellow green, 1.2–2.8 in (3–7 cm) long and up to 0.08 in (2 mm) diameter. Branching is flabellate (fan-shaped) and shoots are densely clustered. It is generally distributed along the Continental Divide in our area, but also occurs in other mountain ranges (Taylor & Mathiasen 1999).

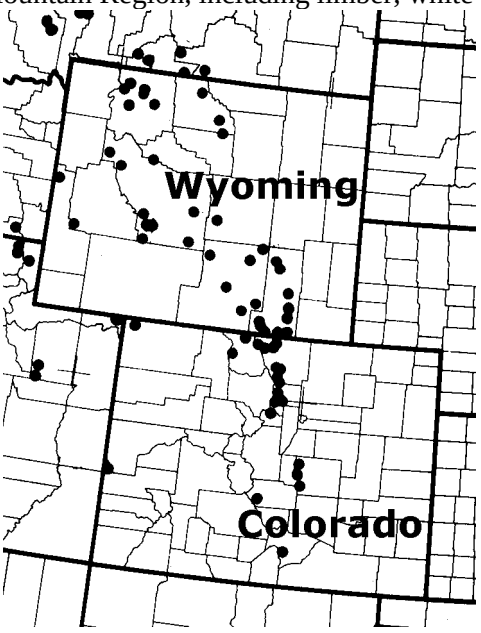


Figure 4. Distribution of limber pine dwarf mistletoe, *A. cyanocarpum*, in the Rocky Mountain Region (from Hawksworth & Wiens 1996).

Arceuthobium cyanocarpum causes small, tightly clustered witches' brooms. It causes extensive mortality of limber pine in many parts of the Rocky Mountains and can also cause mortality in other hosts when severe. It is the most important native disease of high-elevation white pines in the West; only white pine blister rust is more damaging. The potential for damage from white pine blister rust must be considered while planning any management in white pine stands.

Some animals depend on seeds of white pines at certain times of year. For instance, limber pine seeds can be an important part of the diet of black and grizzly bears (McCutcheon 1996), Clark's nutcracker (Tomback & Kramer 1980), and red squirrels (Hutchins & Lanner 1982). Whitebark pine seeds may play an even more critical role in the diet of grizzly bears (Baskin 1998, Mattson & Reinhart 1994). The large reduction in seed production in severely infested stands may have a consequent impact on populations of these animals.

Lateral spread in single-storied stands is estimated to be 1.5–2 ft per year. A Forest Insect and Disease Leaflet is available for this disease (Taylor & Mathiasen 1999).

3.3 Piñon dwarf mistletoe – *A. divaricatum*

Piñon dwarf mistletoe infects only piñons. Shoots are olive green to brown, about 3–5 in (8–13 cm) long and up to 0.16 in (4 mm) diameter. Shoots often have a long, thin and spreading appearance. Branching is flabellate (fan-shaped). In our area *A. divaricatum* occurs only in Colorado west of the Continental Divide (Figure 5).

This dwarf mistletoe may not result in well-developed witches' brooms, and those that do develop are usually small. However, growth loss and mortality can be high when infection is severe (DMR 5 or 6).

Southwestern dwarf mistletoe greatly affects seed production of ponderosa pine (see 4.2, Forest dynamics), but mistletoe effects on piñon are unknown. This may be a particularly important effect in piñon because the nuts are collected for food by humans in many areas and are used by wildlife, as well as being necessary for reproduction.

A Forest Insect and Disease Leaflet is available for piñon dwarf mistletoe (Mathiasen *et al.* 2002).

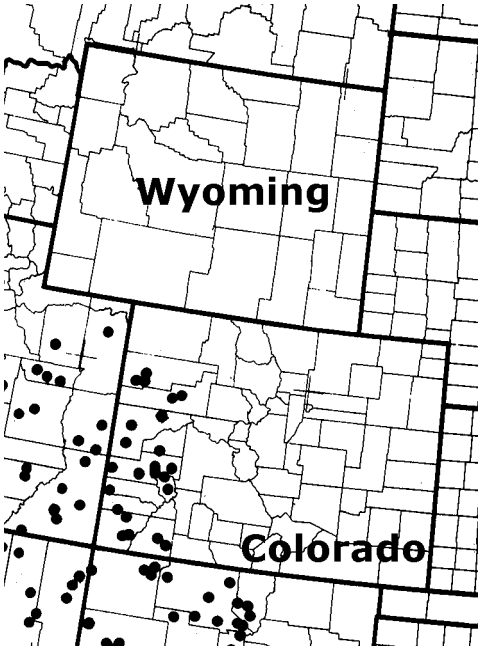


Figure 5. Distribution of piñon dwarf mistletoe, *A. divaricatum*, in the Rocky Mountain Region (from Hawksworth & Wiens 1996).

Another mistletoe also occurs in the piñon-juniper cover type, *Phoradendron juniperinum* on junipers (Geils *et al.* 2002). Although it is practically leafless, it is a true (American) mistletoe rather than a dwarf mistletoe. In the Rocky Mountain Region it occurs only in western Colorado. A Forest Insect and Disease Leaflet is available for *Phoradendron* spp. on conifers (Hawksworth & Scharpf 1981).

3.4 Douglas-fir dwarf mistletoe – *A. douglasii*

Douglas-fir dwarf mistletoe has the smallest shoots of all mistletoes in our area, but it can cause formation of the largest witches' brooms. It primarily infects its namesake, although several true firs and spruces are occasional or rare hosts in some circumstances (see *Table 1* for host categories). Shoots are olive green, average 0.8 in (2 cm) long (maximum 3 in or 8 cm) and 0.04–0.06 in (1–1.5 mm) diameter, with flabellate branching. The pathogen occurs throughout the range of Douglas-fir in the central and southern mountains of Colorado, but it is absent from northern Colorado (except for the extreme northwest) as well as the portion of Wyoming in the Rocky Mountain Region (Figure 6).

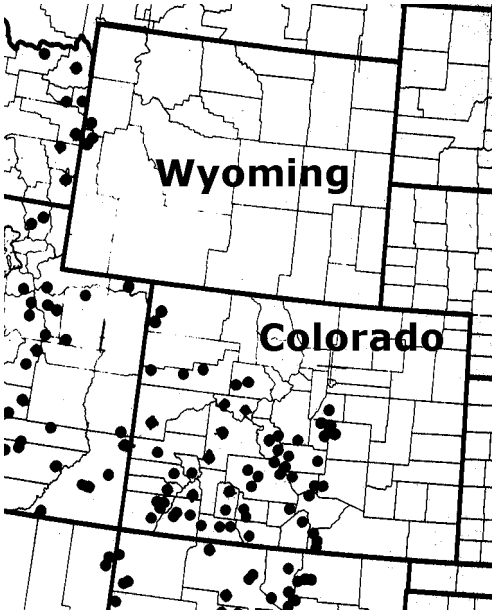


Figure 6. Distribution of Douglas-fir dwarf mistletoe, *A. douglasii*, in the Rocky Mountain Region (from Hawksworth & Wiens 1996)

Arceuthobium douglasii infects systemically. Mistletoe shoots may be spread along young host branches or be aggregated at the annual bud scar zones. Because shoots are so small, they are normally detectable only in branches close to the ground, and witches' brooms are used for detection and rating. Witches' brooms become noticeable about 10 years after infection and develop best in direct sunlight (Hadfield *et al.* 2000). They occur mostly in the lower half of tree crowns. They can weigh hundreds of pounds, can break off the tree, and are considered hazards in developed sites.

Where it occurs in the Region, dwarf mistletoe is generally the most important disease of Douglas-fir. It has reportedly increased in abundance since the late 1800s (Hadfield *et al.* 2000). At least in the northern Idaho and western Montana, Douglas-fir stands have become more widespread due to fire suppression, a history of selective harvesting that removed pines and encouraged shade-tolerant and less valuable species, and white pine blister rust, which largely eliminated western white pine.

Data on growth effects from western Montana indicate that light, medium and severe infections caused decreases in basal area growth rate of 14, 41 and 69%, respectively (Hadfield *et al.* 2000). Effects on height growth were similar.

Horizontal spread in single-storied stands is estimated at 1.5–2 ft per year. Upward spread in crowns is about 4–6 in (10–15 cm) per year. A Forest Insect and Disease Leaflet is available for this disease (Hadfield *et al.* 2000).

3.5 Southwestern dwarf mistletoe – *A. vaginatum* ssp. *cryptopodum*

Southwestern dwarf mistletoe primarily infects the Rocky Mountain variety of ponderosa pine in the four-corner states (Colorado, Utah, Arizona and New Mexico, with a small distribution in west Texas) and is distinct from western dwarf mistletoe (*A. campylopodum*), which infects the Pacific coast variety of ponderosa pine from southern California to northern Washington and western Idaho. Within the Rocky Mountain Region, southwestern dwarf mistletoe is confined to southern Colorado on the Western Slope and extends into northern Colorado on the Front Range (Figure 7). Damage is usually greater in the Front Range than in southwestern Colorado (Hawksworth & Wiens 1996). No dwarf mistletoe occurs in the Black Hills National Forest, where ponderosa pine is most productive in the Region.

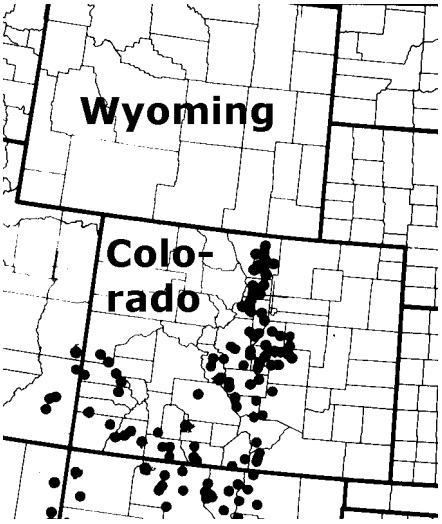


Figure 7. Distribution of Southwestern dwarf mistletoe, *A.vaginatum* subspecies *cryptopodum*, in the Rocky Mountain Region (from Hawksworth & Wiens 1996)

Both witches' brooms and swellings are common symptoms. Development of witches' brooms can be weak, but large and robust brooms with thick, distorted branches are common in older infestations. Shoots vary in color from orange to reddish brown to almost black. Shoots are the largest of our dwarf mistletoes, approximately 4 in (10 cm) long (maximum 11 in or 27 cm) with a basal diameter of 0.08–0.4 in (2–10 mm). The species is unusual among dwarf mistletoes in temperate areas in that seed germination occurs immediately after dispersal in the fall, rather than the following year. This unusual life cycle trait and the robust size of this dwarf mistletoe reflect the fact that this is the extreme northern distribution of a tropical/subtropical species (B. Geils, pers. comm.).

Mortality due to southwestern dwarf mistletoe was quantified in a 32-year study at Grand Canyon National Park (Hawksworth & Geils 1990). Ninety percent of uninfected or lightly infected (DMR 0–1 at the start) trees survived the entire study period. Of heavily infected trees (DMR 6), only 5% over 9″ DBH survived, and none survived in the 4–9″ size class. Intermediate infection levels were associated with intermediate mortality levels. Infection intensified during the study, so that most trees that died were in DMR class 6 by the time of death. Based on the data, the authors estimated the half-life of trees (time in which half the trees are expected to die) by DMR class (Table 3).

Table 3. Expected half-life (time in years for half the trees to die) of ponderosa pine infected with Southwestern dwarf mistletoe at Grand Canyon National Park (Hawksworth & Geils 1990).

	Half-life	
Initial DMR	4-9″ DBH	>9″ DBH
0-1	ND [a]	ND [a]
2-3	30	57
4-5	17	25
6	7	10

[a] No decrease in longevity detected; half-life too long to estimate

Estimates of spread rate in single-storied stands vary. Recent estimates clock it as one of the faster dwarf mistletoes at 2–3 ft per year (Beatty & Mathiasen 2003). An earlier estimate is about 1.3 ft per year in open stands and 0.9 ft per year in dense stands (Hawksworth 1961b, calculated from slopes in his Fig. 32). Spread from overstory to understory is faster in ponderosa than in lodgepole pine.

Two Forest Insect and Disease Leaflets are available for this disease (Beatty & Mathiasen 2003, Lightle & Weiss 1974).

4. IMPACTS OF DWARF MISTLETOES ON TREES AND FORESTS

4.1 Tree growth and longevity

Dwarf mistletoes can have large impacts on trees when infection is severe. Effects have traditionally been quantified as loss of timber productivity. The total annual loss (reduced growth increment and mortality) caused by dwarf mistletoes in the United States was estimated at 418,000,000 cubic feet or 3,000,000,000 board feet (Drummond 1982). At $472 per thousand board feet (average ponderosa pine sawlog price in western Montana, Anonymous 2004b), that loss is more than $1.4 billion per year. Growth in height and diameter is decreased, so that immature lodgepole pine trees infected at an early age have only 23% of the cubic-foot volume of healthy trees after 70 years (based on stands up to 147 years old, Hawksworth & Hinds 1964). When mortality is included, merchantable volume is only 12.4% of that of healthy stands (Figure 8). In severely infested stands, all economic value of wood products from the stand is often lost.

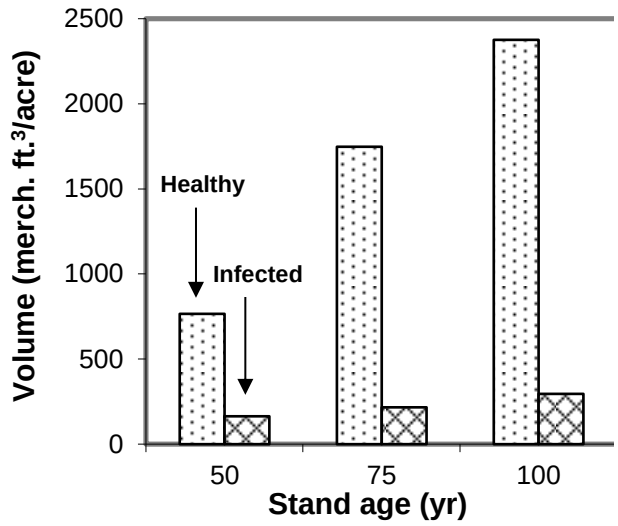


Figure 8. Effect of infection of lodgepole pine by dwarf mistletoe at an early age on volume (which integrates effects on height growth, diameter growth, and mortality). Data from Hawksworth & Hinds (1964).

Dwarf mistletoes typically increase mortality rates when DMR is > 4. Certain dwarf mistletoes are considered to be especially lethal (Hawksworth & Wiens 1996), and four of the five in the Rocky Mountain Region have that distinction (Table 4). Mortality due to dwarf mistletoe is difficult to quantify because tree growth is less in infested than in uninfested stands, so a lower proportion of the mortality is due to competition. Therefore, mortality due to dwarf mistletoe is underestimated when subtracting mortality in uninfested stands from that in infested stands.

Table 4. Dwarf mistletoe-host combinations in Colorado and Wyoming that have particularly high mortality rates (Hawksworth & Wiens 1996).

Pathogen	Host
A. americanum	lodgepole pine
A. cyanocarpum	limber and whitebark pines
A. douglasii	Douglas-fir
A. vaginatum	ponderosa pine

Using averages from multiple studies, the increase in 10-year mortality rates caused by dwarf mistletoes has been quantified (Table 5). However, mortality is affected by many variables. Mortality due to dwarf mistletoe is greater on dry than on wet sites (Baranyay & Safranyik 1970) and also during or following a drought (Geils & Hawksworth 2002). When heavily infected, large trees survive longer than small trees. Heavily infected (DMR 6) ponderosa pines > 9 inches dbh have an expected half-life of 10 years; smaller trees have a half-life expectancy of only 7 years (Table 3). Even large, mature ponderosa pines can be killed by dwarf mistletoes (Roth 2001).

In lodgepole pine stands infested for 80 years, 15% of the standing basal area was killed by dwarf mistletoe (determined by subtracting standing mortality in similar but uninfested stands, Hawksworth & Hinds 1964). However, most of the snags in that study were quite small.

Mechanisms of tree damage are related in part to allocation of resources. The biomass of the mistletoe plant itself may be a minor drain to the tree (although the endophytic systems of systemically infecting mistletoes can be much larger than the shoots); disruption of tree physiology may be a bigger effect. High hormone levels in the mistletoe (primarily cytokinins and indole-acetic acid) cause photosynthate and other nutrients to be shunted to infected branches (Livingston *et al.* 1984). Although host tissues near the infection may receive much of this bounty, the tree is damaged because nutrients do not go to the growing top and roots where they are needed most. Witches' brooms develop luxuriantly while the upper crown thins and dies. It is not uncommon to observe that infected branches are the last part of the crown to die.

Table 5. Increase in 10-year mortality rate in stands infested with *Arceuthobium* sp., relative to uninfested stands.

		Additional ten-year mortality due to disease (% of trees) by stand DMR					
		DMR					
Pathogen	Host	1	2	3	4	5	6
A. abietinum	white fir	1[a]	3	6	10	15	21
A. americanum	lodgepole pine	2	4	5	6	7	8
A. douglasii	Douglas-fir	1	2	4	9	15	23
A. vaginatum	ponderosa pine	1	4	8	15	23	34

[a] The percent of trees dying per decade was estimated for each stand. The value for uninfested control stands was subtracted from the corresponding infested stands, and the average of those values from multiple stands and studies is reported here. From Hawksworth *et al.* (1996, 1992).

An additional mechanism of damage relates to water relations. Dwarf mistletoes are typically less efficient at water use and transpire at a rate several times that of their host, with even greater differential under conditions of water stress (Hawksworth & Wiens 1996). During a drought, this additional water demand may result in decreased growth or even death of other parts of the tree.

Dwarf mistletoes frequently increase susceptibility to attack by bark beetles (Hawksworth & Wiens 1996, Stevens & Hawksworth 1984). In Colorado, dwarf mistletoe increases susceptibility of ponderosa pine to mountain pine beetle (MPB, *Dendroctonus ponderosae*) and western pine beetle, *D. brevicomis* (Frye & Landis 1975, Fuller 1983, Johnson *et al.* 1976, McCambridge *et al.* 1982, Ziegler 1978). Ponderosa pine may also have increased susceptibility to attack by *Ips* spp. when infected by dwarf mistletoe. Recent evidence from a 2002 outbreak in in Arizona indicated that severely infected trees of intermediate crown class are at greatest risk during outbreaks and are selectively killed by *Ips* spp. (Kenaley 2004). Ponderosa pines killed by *Ips* spp. had significantly higher dwarf mistletoe ratings than paired live trees, and the authors suggested that severely infested stands have greater probability of attack (Kenaley *et al.* 2006).

A similar effect is seen in piñon. In an outbreak of *Ips confusus* on piñon in Arizona, regression analysis showed that dwarf mistletoe infection and tree diameter were good predictors of individual tree attack by the beetle (Negron & Wilson 2003). Beetle-infested trees and plots had significantly more dwarf mistletoe than did uninfested trees and plots. This supports earlier observations that dwarf mistletoe predisposes piñon to attack by ips (Wilson & Tkacz 1992).

In the case of *D. pseudotsugae* and Douglas-fir, dwarf mistletoe may have little effect on bark beetle susceptibility (Furniss *et al.* 1981). However, such predisposition has been suggested for northern Idaho (Weir 1916a).

Lodgepole pine dwarf mistletoe apparently *decreases* susceptibility of lodgepole pine to MPB (McGregor 1978, Roe & Amman 1970, Ziegler 1978). However, data from the Shoshone National Forest, Wyoming, and Sawtooth N.F., Idaho, showed no significant difference in DMR or number of brooms between attacked and unattacked trees, though the high incidence of mistletoe may have clouded the results (Rasmussen 1987). Hawksworth & Johnson (1989) suggested that also in Colorado dwarf mistletoe has little or no effect on MPB susceptibility in lodgepole pine. Decreased susceptibility, where it occurs, is probably due to smaller diameter and thinner phloem caused by dwarf mistletoe (Roe & Amman 1970). However, stem infections, which often have thicker bark than the rest of the tree, may be selectively attacked by MPB (McGregor 1978).

4.2 Forest dynamics

Dwarf mistletoes are closely related to the fire regime in many of our forest types. Fire has been the most important single factor governing the distribution and abundance of dwarf mistletoes (Alexander & Hawksworth 1975). Because they are obligate parasites, dwarf mistletoes die when trees are killed by fire. In most cases, trees recolonize the site much more quickly than does the dwarf mistletoe. Even scorching of lower branches from a surface fire can substantially reduce the abundance of dwarf mistletoe in a surviving overstory (Conklin & Armstrong 2001, Koonce & Roth 1980).

Although a stand-destroying fire removes dwarf mistletoe over a large area, infected trees that survive the fire can reinfest a portion of the stand, explaining in large part the continued survival of dwarf mistletoe in ecosystems with infrequent, stand-replacing fire regimes.

Because dwarf mistletoe is often eradicated locally or at least reduced by fire, it may seem strange that dwarf mistletoes would increase the likelihood of such a fire. But they do. Infected trees often have large witches' brooms in the lower crown, persisting after the lower branches of healthy trees become shaded and die. These brooms, full of resin and dense accumulations of live and dead needles, act as fuel ladders that increase the opportunity for a surface fire to torch or become a crown fire. Numerous observers have noted selective torching of infected trees during a surface fire. In general, infested stands have greater total fuel loading than uninfested stands (Hawksworth & Wiens 1996, Hoffman *et al.* 2007, Koonce & Roth 1985).

Dwarf mistletoe abundance therefore increases the likelihood of severe fire, and can be viewed as contributing to the feedback loop that regulates the frequency and severity of fire. When such fires occur, dwarf mistletoe abundance decreases. This was demonstrated in a study in lodgepole pine: the current abundance of dwarf mistletoe was inversely related to fire frequency during the period from the late 1800's to the 1980's (Zimmerman & Laven 1984). The feedback loop can thus be viewed from the other side: fire regulates the abundance and distribution of dwarf mistletoe on the landscape.

Other effects of dwarf mistletoes on stand dynamics are less well studied, but logically predictable and easy to observe. Because dwarf mistletoes selectively reduce growth and increase mortality of their hosts in mixed stands, they can increase the likelihood and rate of succession when infecting seral species, or maintain early seral species when infecting late seral or climax species (Hagle *et al.* 2000). For example, growth reduction and mortality of lodgepole pine caused by *A. americanum* can be spectacular, encouraging succession to Engelmann spruce and subalpine fir, which are largely immune to indigenous mistletoes in our Region. On the other hand, the role of dwarf mistletoes in facilitating crown fires can have just the opposite effect. When fire destroys a mixed stand of mature lodgepole pine with invading spruce and fir, lodgepole pine readily recolonizes the site in pure stands, due in large part to its serotinous cones. Thus, dwarf mistletoes can either hasten succession or reset it, enhancing the persistence of seral forest types.

The latter effect may explain the conundrum hinted at earlier: what possible advantage could there be for dwarf mistletoes to enhance the likelihood of severe fire? Although dwarf mistletoe contributes to its local demise in the immediate future, over the longer term it may help to perpetuate its seral host, increasing opportunities for infection in the future.

Dwarf mistletoe infection also reduces the number and viability of seeds produced by ponderosa pine (Hawksworth & Wiens 1996) and presumably other hosts. Seed production was not affected by light infection, but moderate infection reduced it to 42% of healthy trees (by weight); severe infection reduced it to 29% of healthy trees (Korstian & Long 1922). When viability is considered, the effect is somewhat greater. Consequences on forest regeneration are considered in management but have not been explicitly studied.

5. IMPACTS OF DWARF MISTLETOES ON ANIMALS

Birds and mammals may be influenced, directly or indirectly, positively or negatively, by dwarf mistletoes. Among the features and effects of dwarf mistletoe that may influence animals are:

- Shoots of the dwarf mistletoe plant, which may be used as a food source.
- Witches' brooms, which may be used by some animals for nesting, denning, hiding, caching, or foraging.
- Decrease in number and size of seeds produced by the host tree, which may affect animals that use the seeds for food.
- An increase in mortality of host trees, which may influence animals through a change in the dynamics or size of snags.
- Through growth inhibition and mortality of the host species, the vegetation type may gradually change, influencing animals in various ways.

5.1 Diversity and abundance of vertebrates

5.1.1 Dwarf mistletoes as a food source for vertebrates

Numerous birds and mammals have been reported to feed on dwarf mistletoe shoots and/or fruits, though in most cases it is not a significant part of their diet. They may also feed on bark of tree shoots that are swollen and otherwise modified by dwarf mistletoe. A recent list of 21 species recorded as feeding on dwarf mistletoes was provided by Shaw *et al.* (2004). Birds that feed on dwarf mistletoes usually use it as a small part of their diet except for the euphonia in the Dominican Republic and the gray silky-flycatcher in Mexico (Hawksworth & Geils 1996). Among dwarf mistletoe herbivores in the United States are blue grouse, for which Douglas-fir dwarf mistletoe forms 2-8% of the diet in eastern Arizona, and Abert's squirrel, which feeds occasionally on dwarf mistletoe shoots and grazes on infected bark of ponderosa pine. Red squirrel in lodgepole pine forests often feed on pine shoots 6-13 mm in diameter; a preference for mistletoe-infected shoots has been observed (Hawksworth & Geils 1996). Bark of mistletoe cankers on various hosts is frequently gnawed, mostly by squirrels. In ponderosa pine forests of Colorado and the southwest, there are indications that dwarf mistletoe shoots may make up to 25% of the diet of porcupines at certain times of year, although individual porcupines apparently vary in this regard (Hawksworth & Geils 1996). In general, feeding by animals on dwarf mistletoes primarily occurs during winter when other food sources are unavailable. Dependence by any vertebrate has not been reported.

Urness (1969) conducted nutritional analyses of Southwestern dwarf mistletoe (*A. vaginatum* ssp. *cryptopodum*) in comparison with five species of true mistletoes in the genus *Phoradendron*, which are more heavily used for food by wildlife. The dwarf mistletoe had much higher levels of acid-detergent fiber (inversely related to digestibility) than all the *Phoradendron* spp. Crude protein was among the lowest levels of the species tested. The dwarf mistletoe had moderate levels of phosphorus but low levels of calcium. When exposed to rumen contents of deer, digestion of the dwarf mistletoe was lower than that of all the true mistletoes and comparable to that of available shrubs.

5.1.2 Ponderosa pine and southwestern dwarf mistletoe

Perhaps the most widely cited work on effects of dwarf mistletoe on wildlife diversity is a paper by Bennetts *et al.* (1996) on bird diversity. Eight ponderosa pine stands with varying levels of southwestern dwarf mistletoe (*Arceuthobium vaginatum* ssp. *campylopodum*) in two Front Range locations in Colorado were studied. Average dwarf mistletoe ratings (see 7.2, Bennetts *et al.* used a nonstandard approach of a mean of cell means within the stand, rather than a mean of all individual trees) were about 0.0, 0.6, 2.1 and 3.6 for the Cheesman Reservoir location and 0.0, 2.5, 2.5 and 4.6 for the Florissant location.

Although the abstract reports that abundances of 24 of 28 bird species were positively correlated with dwarf mistletoe, this proportion misrepresents the actual results. The number 24 in the abstract includes those for which the positive relationship was not significant at any tested level of α, and the number 28 excludes those with insufficient observations to estimate slope. As noted by a subsequent researcher, "Bennetts *et al.*'s (1996) study is frequently misinterpreted because regression coefficients for insignificant equations are reported. . . . Conclusions from [the] study can be somewhat misleading" (Parker 2001).

The abundance of 4 species was positively correlated with DMR and had a slope significantly different from 0 at $\alpha = 0.05$. When α was relaxed to 0.10, 5 additional bird species had a positive correlation and slope significantly different from 0. The remainder either had insufficient detections to estimate slope (19 species), had positive slopes that did not differ significantly from 0 (16 or 21 species, depending on α), or had negative correlation (4 species, slopes were not significantly different from 0). Thus, in contrast with the abstract, only 4 of 47 species detected on the plots were significantly associated with dwarf mistletoe using usually accepted statistical criteria.

DMR was positively correlated with the number of bird species detected per stand. The trend was apparent overall as well as within each location. DMR was not associated with species evenness.

Snag abundance was correlated with DMR, and the authors suggested that dwarf mistletoe caused an increase in mortality in the study areas. Since many of the bird species may have been favored by snags because of increased foraging or cavity-nesting opportunities they presented, it is not clear to what extent the positive associations of bird abundance with DMR is an effect of snags vs. a direct effect of dwarf mistletoe shoots and witches' brooms.

The authors opine that all dwarf mistletoe control should be abandoned except where timber production is the sole management goal (Bennetts *et al.* 1996). On public lands, no areas have exclusive management goals, so this is a recommendation to completely abandon dwarf mistletoe management on public lands.

The question was revisited more recently (Parker 2001). In 19 stands in northern Arizona, with DMR ranging from 0 to 3.7, the abundance of four species was positively and significantly correlated with measures of dwarf mistletoe, five species were negatively and significantly correlated,

and seven were unrelated. The total number of species observed was not given (>25), but 16 species were abundant enough to be analyzed in detail. The number of species observed was not correlated with DMR.

As in the previous study (Bennetts *et al.* 1996), snag abundance was positively correlated with dwarf mistletoe severity (Parker 2001). Three of the four species that were positively correlated with dwarf mistletoe were cavity-nesting birds.

Garnett *et al.* (2004) compared wildlife use of broomed vs. nonbroomed trees in 12 stands in northern Arizona. All study stands had DMR ≥ 1. Broomed trees were used significantly more than nonbroomed trees for wildlife activities (mean over all sites was 25% use of broomed trees and 2% use of nonbroomed trees), including foraging/caching, nesting, and roosting/resting. Animals observed in brooms included Abert's squirrel, porcupine, and passerine birds. Of 226 brooms examined, 23% had evidence of wildlife use, 75% of which was Abert's squirrel. Of the 39 brooms with Abert's squirrel evidence, 8 were nesting and 31 were caching/foraging. Only 10 of the 226 brooms were used by birds, 2 for nesting and 8 for roosting/resting.

5.1.2.1 Abert's squirrel

Abert's squirrel (Figure 9; also known as tassel-eared squirrel) is endemic to the Southern Rockies, the Colorado Plateau, and the northern Sierra Madre Mountains of Mexico. In the United States, it occurs primarily in Colorado, New Mexico, Arizona, and in a small part of Utah, but the distribution has expanded into southern Wyoming in recent decades (Keith 2003). Although many local subspecies have been named, they do not conform to phylogenetic variation in mitochondrial DNA (Lamb *et al.* 1997).

Although it is often stated that Abert's squirrel depends on ponderosa pine for food, cover and nest sites, the squirrel was introduced to and established successful populations in mixed-conifer and spruce-fir forests with little to no ponderosa pine in the Pinaleño Mountains of Arizona (Edelman & Koprowski 2005). The populations used similar food items as in ponderosa pine forests (see below), but the conifers used most frequently were Douglas-fir and southwestern white pine. Cavity nests were more common in this introduced population (10% of nests found) than in native populations, and large aspen with stem decay were favored sites for cavity nests (Edelman & Koprowski 2006). Abert's squirrel has been noted in many other habitats aside from ponderosa pine forests (see references in Edelman & Koprowski 2005).

Large nests are typically built in pine trees, especially on crotches against the bole (Burt & Grossenheider 1976, Keith 2003). Nests are constructed of fine twigs, usually 2-10 cm in length. Nests are 30 to 100 cm (1.0 to 3.3 feet) in diameter (Keith 2003). Witches' brooms may be incorporated into or support Abert's squirrel nests (Anonymous 2003). Of 226 brooms examined in northern Arizona, 8 were used by Abert's squirrel for nesting and 31 for caching/foraging (Garnett *et al.* 2004). Brooms

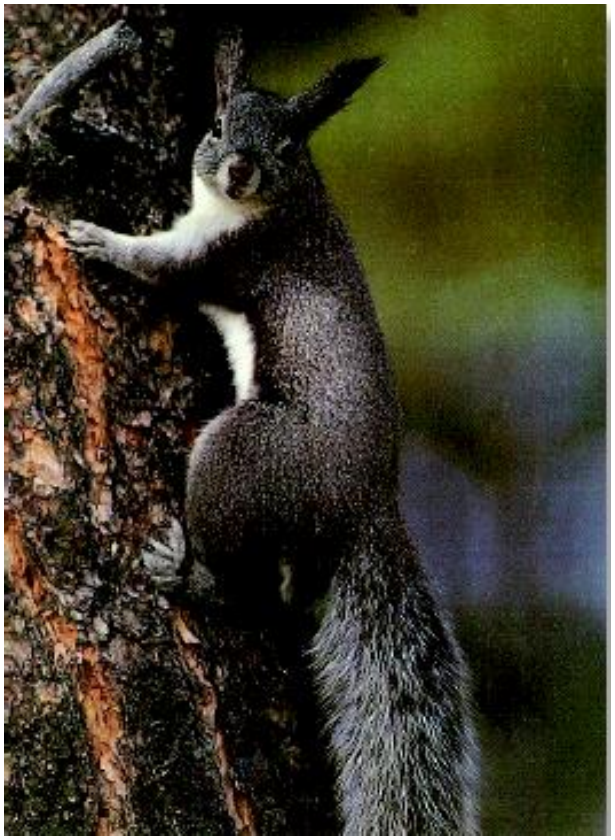


Figure 9. Abert's squirrel, *Sciurus aberti*. Photo from Keith (2003).

that were used for caching and foraging tended to have more branches and be on taller trees than unused brooms, leading to the recommendation that ponderosa pines >18 m tall having brooms with >7 branches be retained for squirrel use (Garnett *et al.* 2006). Too few nests were found in brooms for statistical analysis. No information was given on nesting or caching/foraging outside of brooms. Of 40 nests identified at a site in Colorado, 10 were built in witches' brooms (Farentinos 1972a), but in this case brooms were rare and all large brooms were occupied.

The diet of Abert's squirrel is varied. Preferred foods are seeds of ponderosa pine and mushrooms. Mushrooms (especially hypogeous fungi such as truffles) are an important food in late summer and early fall and "provide an important source of moisture in the diet of these squirrels, for in many areas where they live they must derive most of their water from their food" (Hoffmeister 1986). Squirrels also feed on the cambium and phloem of young shoots, needles, terminals, and flowers of ponderosa pine (Burt & Grossenheider 1976, Hoffmeister 1986). Bark grazing on larger branches, though not a major form of feeding, is confined to mistletoe-infected branches (Allred & Gaud 1994). Acorns of Gambel oak, insects, carrion, and occasionally pieces of shrub and grasses may also be consumed. There is evidence that shoots of dwarf mistletoe may also be a minor food source (Keith 2003).

An important effect of dwarf mistletoe infection is reduced seed production (see 4.2, Forest dynamics). Since Abert's squirrel sometimes depends on ponderosa pine seed as a food source, and indeed the populations of the squirrel vary notably with the pine cone crop (Farentinos 1972b), it is likely that moderate to heavy dwarf mistletoe infestations decrease food availability for squirrel populations and may negatively impact carrying capacity. However, these effects on the squirrel have apparently not been studied.

It is not clear that dwarf mistletoe is important to the squirrel, and no work has shown an effect of mistletoe on Abert's squirrel population size, positive or negative. In a 62-page assessment of the status of the squirrel in the Rocky Mountain Region by an authority on Abert's squirrel, no dependence or association with dwarf mistletoe was mentioned other than minor feeding on mistletoe shoots (Keith 2003).

The Natural Heritage Program gives Abert's squirrel a rating of "demonstrably secure" globally and in Colorado (Anonymous 2004c). It is not on the Rocky Mountain Region sensitive species list nor any federal or state list of threatened or endangered species. Populations in Colorado are considered secure and several southwestern states, including Colorado, Arizona and New Mexico, classify it as a game animal and administer a hunting season for Abert's squirrel (Anonymous 2004d). The squirrel has expanded its range in Colorado and crossed the border into southern Wyoming in the latter part of the 20th century (Keith 2003).

However, it is a management indicator species (MIS) in several National Forests of Colorado. A number of projects, such as the Missionary Ridge Fire Salvage, have been stopped by appellants or litigants, who have pointed out that population data are missing for the squirrel and other MIS (Draper 2004).

5.1.3 Lodgepole pine and lodgepole pine dwarf mistletoe

Witches' brooms caused by *Arceuthobium americanum* in lodgepole pine are often used as nest sites by red squirrel and American marten (Hawksworth & Geils 1996). The animals are not dependent on the presence of brooms as nesting habitat, but it is not clear to what extent brooms are preferred or enhance survival or reproductive success. Apparently no studies have tested the effect of dwarf mistletoe intensity on wildlife diversity in lodgepole pine.

Although an emphasis is placed on witches' brooms as nesting sites of arboreal squirrels by some workers, the consensus seems to be that populations of northern flying squirrel and other squirrels are limited more often by food abundance rather than nesting and hiding sites (Ransome *et al.* 2004, Ransome & Sullivan 2004, Waters & Zabel 1995). Arboreal squirrels like northern flying squirrel often use witches' brooms when they are available, but they successfully use constructed nests and cavities in the absence of brooms (see literature cited in Ransome & Sullivan 2004). Although they did not study the role of dwarf mistletoe, Ransome *et al.* (2004) found that young lodgepole pine (29-39 yr old) thinned 12 years earlier had populations of northern flying squirrel and red squirrel at levels recorded in old-growth forests over three years of measurements. Diversity of small ground mammals in a related study was also found to be similar in young, thinned and old-growth lodgepole pine stands (Sullivan *et al.* 2005).

5.1.4 Douglas-fir and *Arceuthobium douglasii*

A variety of owls and accipiters have been reported to nest in the large, dense witches' brooms often caused by Douglas-fir dwarf mistletoe (Hawksworth & Geils 1996). Some of these raptors apparently prefer brooms as nesting sites. However, in a study designed to assess the role of brooms as wildlife habitat in Douglas-fir (Parks *et al.* 1999a, discussed in detail below), only two avian nests were found, both in nonbroomed trees.

Porcupines in northeastern Oregon often use brooms in Douglas-fir for shelter (Smith 1982). Flying squirrels and red squirrels also may use the brooms for cover, caching and nesting (Hawksworth & Geils 1996, Shaw *et al.* 2004).

Parks *et al.* (1999a) inspected 117 trees with witches' brooms and 42 nonbroomed trees for evidence of wildlife use in northeastern Oregon. Evidence of mammalian nesting and resting was found only in broomed trees (18%). Evidence of mammalian foraging was found in 51% of broomed trees and 29% of nonbroomed trees. On the other hand, evidence of foraging was found on the ground beneath 36% of broomed and >62% of nonbroomed trees. Few avian nests were found (2), and they were only in nonbroomed trees.

Although the results suggest that brooming may influence certain kinds of wildlife use, no statistical analysis was provided that compared wildlife use of broomed vs. nonbroomed trees. A sampling issue also makes it difficult to draw conclusions: half (22) of the nonbroomed trees were in uninfested stands where there was no comparable sample of broomed trees, suggesting that stand differences were not controlled and may not have been comparable between broomed and nonbroomed trees. No comparison of use of nonbroomed trees in infested vs. uninfested stands was provided.

More recently, Bull *et al.* (2004) reported a study on the effects of dwarf mistletoe treatment on red squirrel and northern flying squirrel. Two treatments were tested: (1) thin from below, selectively removing broomed trees, but leaving untreated, infested islands up to 0.5 ha in size – one island occurred in about every 3.7 ha; (2) removing all trees with brooms >25 cm diameter. Squirrels were live-trapped one or two years before treatment and again both one and two years after treatment. Trapped squirrels were anesthetized, and received ear tags and radio collars in all but the last year of the study.

In general, red squirrel trapping went up after the treatment, and northern flying squirrel trapping decreased (Bull *et al.* 2004). However, it is difficult to interpret the results and support the conclusions of the authors for the following reasons:

a) There were no untreated control stands. Trapping was only done for one year before treatment vs. two years after treatment, and the data were variable, so it is not clear that

the data would be consistent in the absence of treatment. Other studies have shown that populations of northern flying squirrel may vary significantly from year to year in the absence of treatment (Carey 1995, Ransome & Sullivan 2003).

b) No statistical analysis of these data was presented, although other results in the study were thoroughly analyzed. I analyzed data provided by the author (Table 6). The island treatment had no significant effect on flying squirrel numbers at all, but it increased numbers of red squirrel significantly the first year (not the second year or overall). The total removal treatment had no significant effect on flying squirrel in either year, but when both years are combined the decrease was marginally significant. Total removal caused highly significant increase in red squirrel in both years and overall. These results do not support some of the conclusions presented in the paper (Bull *et al.* 2004), which stated that both treatments negatively affected northern flying squirrel numbers, and de-emphasized the increase in red squirrel numbers in discussing management implications of the study.

c) The potentially negative effect of trapping, anesthesia and radio collars on flying squirrel survival was not discussed. This potential makes an untreated control all the more important.

d) Each treatment was done in only two stands, and the variability between stands was not reported or analyzed.

Table 6. Statistical analysis of abundance of red squirrels and northern flying squirrels (percent of trap/nights with squirrels) before and after two treatments for dwarf mistletoe control in northeastern Oregon. Raw data for analysis provided by E. Bull (personal communication) based on the study by Bull et al. (2004).

Treatment	Red squirrel			Northern flying squirrel		
	Percent	P[a]		Percent	P[a]	
Island						
Pretreatment	1.40			0.21		
Posttreatment 2001	2.75	0.011	} ns	0.25	ns	} ns
Posttreatment 2002	1.28	ns		0.07	ns	
Total removal						
Pretreatment	0.69			0.64		
Posttreatment 2001	1.53	0.022	} <0.001	0.29	ns	} 0.04
Posttreatment 2002	3.14	<0.001		0.21	ns	

[a] Comparison of counts of positive and negative trap/nights between pretreatment and posttreatment measurement years and with posttreatment years combined, by chi-square analysis. ns = not significant at $\alpha = 0.05$

Hedwall *et al.* (2006) compared the use of different types of witches' brooms in Douglas-fir by red squirrels. They found that brooms resulting from infections within 1 m of the stem and those on the stem itself had more evidence of nesting, caching and foraging than brooms farther out on branches. Unbroomed trees were examined but apparently had little evidence of use (Hedwall, personal communication). Evidence of use is more likely to be caught and retained in brooms, particularly large, dense ones with platforms, than in unbroomed branches, and it is difficult to separate this difference from differences in actual use by animals.

5.1.5 Five-needle pines and *Arceuthobium cyanocarpum*

Some animals depend on seeds of white pines at certain times of year. For instance, limber pine seeds can be an important part of the diet of black and grizzly bears (McCutcheon 1996), Clark's

nutcracker (Tomback & Kramer 1980), and red squirrels (Hutchins & Lanner 1982). In whitebark pine areas, seeds of that species may play an even more critical role in the diet of grizzly bears (Baskin 1998, Mattson & Reinhart 1994). The large reduction in seed production in stands severely infested by *A. cyanocarpum* may have a consequent impact on populations of these animals.

5.2 Effect of mistletoe-caused snags on vertebrates

The effect of dwarf mistletoes on mortality, resulting in snags, is discussed in section 4.1, Tree growth and longevity. Snags may also be created during management projects by girdling or burning to reduce dwarf mistletoe incidence while providing wildlife habitat (Parks *et al.* 1999b).

Snags and, in a broader view, coarse woody debris contribute to wildlife habitat in a variety of ways (Bull *et al.* 1997). Snags and downed logs provide sites for nesting, roosting, denning, foraging, resting and hiding for a variety of wildlife species. The diversity of organisms for which there is less active concern, such as fungi and insects, can also be associated with coarse woody debris (Bader *et al.* 1995, Nilsson & Baranowski 1997, Rydin *et al.* 1997). Decaying wood is an important site for nitrogen fixation, a reservoir for soil moisture and nutrients, and is a favored habitat for mycorrhizal roots, especially on dry sites (Harvey *et al.* 1987, Jurgensen *et al.* 1989). Managers have been encouraged over the past decade to increase coarse woody debris, including snags, in managed forests (Hagan & Grove 1999).

The literature cited in the previous section (4.1, Tree growth and longevity) indicates that, in the short term, mistletoe-infested stands often have more snags than otherwise comparable, uninfested stands. In the long term, however, snag habitat may be more abundant and of higher quality in the absence of dwarf mistletoe because of effects on snag size and potential for occurrence of internal decay.

Since trees grow faster and survive longer without dwarf mistletoe, they are larger when they do die. Larger snags remain standing for a longer period and provide higher quality wildlife habitat. Subsequently, as coarse woody debris, this larger material also provides more habitat for a wider variety of wildlife species (Bull *et al.* 1997).

Trees that survive longer are more likely to develop internal stem decay ("heart rot") which develops only in living trees over a long period and greatly enhances nesting and denning opportunities in living trees (Figure 10), as well as in the resulting snags and coarse woody debris (Parks & Shaw 1996). For instance, primary cavity nesters often detect and select living trees with internal decay for excavation (Conner *et al.* 1976, Hooper *et al.* 1991), and that habitat feature persists after tree death. Large diameter greatly enhances the value of hollow trees, snags and logs to a variety of wildlife, including primary cavity nesters, secondary cavity nesters, American marten, bears, etc. (Bull *et al.* 1997, Fan *et al.* 2003).

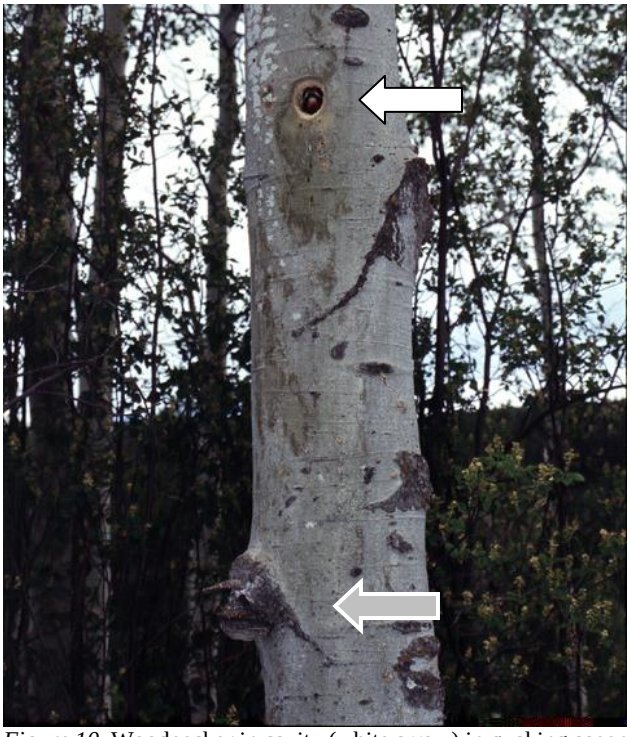


Figure 10. Woodpecker in cavity (white arrow) in quaking aspen (*Populus tremuloides*) with conk of the stem-decay fungus, *Phellinus tremulae*, about a meter below (gray arrow).

5.3 Effects of dwarf mistletoes on insects

Several insects are known to feed on dwarf mistletoes (Stevens & Hawksworth 1984). The best known are two species of *Mitoura*, the hairstreak butterflies (Lepidoptera: Lycaenidae), whose larvae are obligate dwarf mistletoe herbivores and the adults of which are prized by butterfly collectors. *Mitoura johnsonii*, a candidate for listing as a threatened species in Washington state (http://wdfw.wa.gov/hab/phsinvrt.htm) but not federally, is found on several species of *Arceuthobium*, but most commonly on *A. tsugense* (hemlock dwarf mistletoe). *Mitoura* (*Callophrys*) *spinetorum*, the thicket hairstreak (Figure 11), occurs from southern British Columbia to central Mexico on *Arceuthobium* spp. It is relatively common and has no federal listing status. The Natural Heritage Program lists it as "demonstrably secure" globally and in Colorado (Anonymous 2004c). It is not clear if these butterflies have a significant impact on dwarf mistletoe populations.

Other lepidopterans that feed on dwarf mistletoes and are said to be more damaging than the *Mitoura* spp. are *Dasypyga alternosquamella* (Pyralidae, the snout moths) and *Filatima natalis* (Gelechidae, the twirler moths) (Hawksworth & Geils 1996). The larvae of both species mine large shoots and consume small shoots. These insects destroyed complete crops of dwarf mistletoe shoots in local areas, but, because plants are not killed when the shoots are consumed, it is not known how much or how often they affect population increase of the mistletoe. Spittlebugs are often seen on dwarf mistletoe in the Southwest, especially *Clastoptera distincta*.

Figure 11. Thicket hairstreak butterfly, *Mitoura spinetorum* (male). The larvae are obligate dwarf mistletoe herbivores. Photo from (Anonymous 2004a).

5.4 Dwarf mistletoes and animals: Conclusions

Clearly many wildlife species make use of dwarf mistletoes, associated witches' brooms, and affected forests. In most cases this use appears to be incidental. A wide variety of animals has been observed feeding on dwarf mistletoe shoots, but it is a small part of their diet. There is little or no evidence that the success or abundance of animals is affected by the presence of witches' brooms, and no indication that any mammal or bird in the United States depends on dwarf mistletoe.

In one study, the number of bird species and abundance of certain species were positively correlated with mistletoe abundance (Bennetts *et al.* 1996); in another study bird diversity was not correlated with mistletoe and abundance of other species was inversely correlated with DMR (Parker 2001).

Evidence suggests that the most likely effect on animals, particularly birds, is indirect. By decreasing the longevity of trees, dwarf mistletoes tend to increase the number of snags in young to middle-aged stands. Snags are important to many animals, particularly those that nest in cavities in dead trees. Evidence suggests that larger snags are the best habitat overall, because they are suitable for the largest number of species and persist for a long time (Bull *et al.* 1997). Because every tree that lives will eventually die, it must be considered that the small snags made available now due to dwarf mistletoe means there will be fewer large snags at a later time. Trees that are infected but not killed by dwarf mistletoe will be smaller than uninfected trees due to the growth effects. From a management perspective, one must weigh the potential advantages and disadvantages of small snags early in stand development vs. large snags later.

Research regarding wildlife and dwarf mistletoe must be evaluated carefully, as some statistical analyses, data and conclusions selectively emphasize certain findings. There are a number of complexities in the relationships between dwarf mistletoe and species abundance, diversity and richness, such that a simple trend with increasing mistletoe may not be expected:

1. Competitive interactions among wildlife species may cause populations of some to decrease as others increase.
2. Nest predators such as Steller's jay and Abert's squirrel (Craig 1998) may nest in witches' brooms, although their abundance is not always correlated with DMR (Parker 2001). Reproductive success of some songbirds could then be lower where predator nest sites are common.
3. Similarly, severe dwarf mistletoe infestation and associated mortality can create a competitive advantage for other plant species. As plant species diversity increases, wildlife diversity may increase. Again, this is not a unique feature of mistletoe-infested stands.
4. Effects of dwarf mistletoe on a given species likely have an optimum level of mistletoe for such an effect. For instance, if a species benefits from a certain level of dwarf mistletoe, there may be no further benefit or even a net detriment above that level as the stand eventually deteriorates because of disease severity.
5. Because dwarf mistletoes increase tree mortality, they often increase snag density. Because this is not a unique feature of mistletoe-infested stands, a strict correlation of abundance or richness with DMR may be confounded if other causes of mortality are present.
6. Viewed over the long term, dwarf mistletoe infestation may reduce the value of snags and coarse woody debris as wildlife habitat because the snags are smaller (due to both reduced growth rate and early mortality) and are less likely to have internal stem decay (heart rot).

6. FACTORS AFFECTING DWARF MISTLETOES

6.1 Fire

Fire is the most important factor affecting the distribution and abundance of dwarf mistletoes in most forest types of the western United States. The mutual interaction of dwarf mistletoes and fire is described in detail in section 4.2, Forest dynamics.

Fire that kills infected trees reduces the population of dwarf mistletoe, at least in the short term. Large, continuous, stand-replacing fires substantially reduce dwarf mistletoe populations across the landscape over long periods and may eliminate local populations and result in new stands that are disease-free to maturity. Patchy burns also reduce dwarf mistletoe populations, but scattered, infected residuals may provide inoculum for early infection of new regeneration (Alexander & Hawksworth 1975).

6.2 Stand structure and composition

Size structure. Size structure of forest stands has a strong effect on the rate of mistletoe spread. This relationship has been well documented (literature summarized by Parmeter 1978). Because of the nature of seed dispersal, trees under an infected overstory are more likely to be hit by seeds than are trees in a single-storied stand (*Figure 12*). Because of their trajectory, seeds from an infested overstory are also dispersed a greater distance before they strike the understory than is the case between trees of equal size, so spread rate is greater in two-storied or multi-storied stands. Trees in the understory can be infected anywhere in the crown, whereas trees in single-storied stands are most likely to be infected in the lower crown where the infection has less effect and can spread less effectively. Finally, trees infected at a young age suffer much greater damage than trees infected when they are old.

Very small and young trees are unlikely to be infected. This is not because of resistance, but because they have been exposed to inoculum for a relatively short time and because they present a

small target for randomly dispersed seeds to strike. Generally, trees less than 1 m tall or less than 10 years old (whichever comes first) are unlikely to be infected (Wicker 1967, Wicker & Shaw 1967).

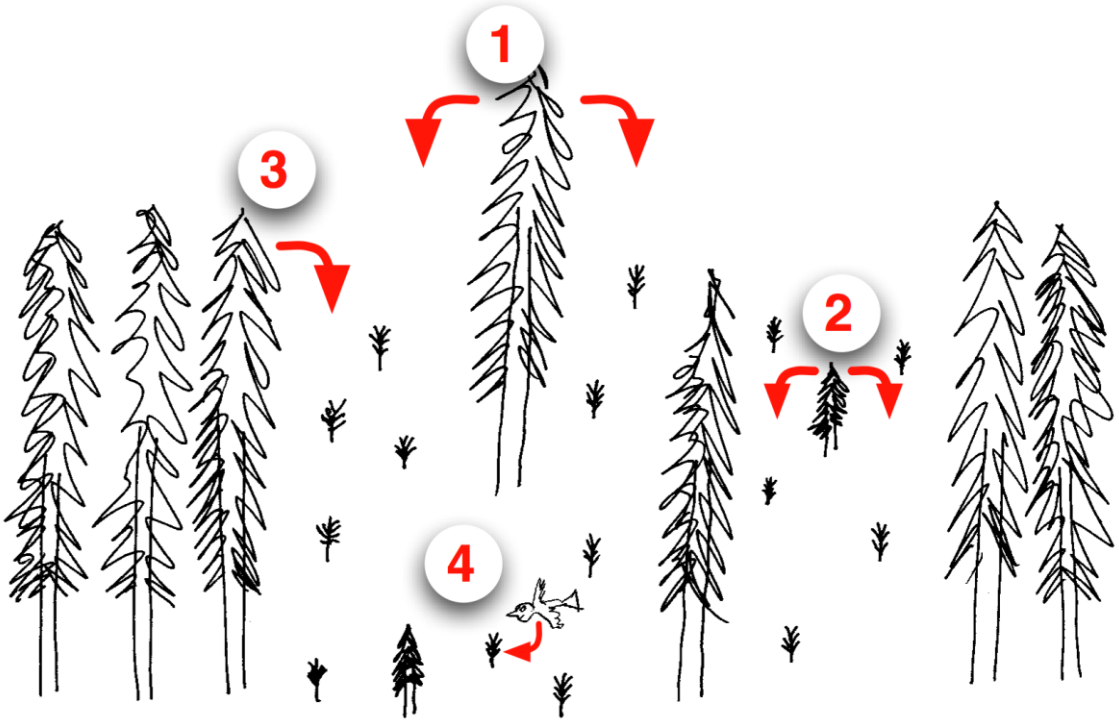


Figure 12. Sources of dwarf mistletoe infection for a young stand, in order of importance. In the scenario used for illustration, a shelterwood has been established in a larger infested area, but a similar pattern could be established by mixed-severity wildfire. Sources of infection are: 1) residual overstory trees after seedling establishment; 2) pre-existing (advanced) regeneration that is infected; 3) spread from infected trees at the border of the treated area, and; 4) vectoring of seed by wildlife. The first is critically important, the last is usually considered unimportant from a disease management perspective.

Density. Tree density can have a strong influence on spread rate (distance through the stand over time) at the extremes of density. Obviously, spacing beyond the maximum dispersal distance (about 52 ft) will result in little or no spread (Figure 13). As density increases, more seeds will successfully make the jump and spread rate increases. However, as density increases further, seeds are intercepted before they get very far, so spread rate decreases again (Hawksworth 1961b). As a practical matter, within the range of densities usually found in forests, mistletoes spread more rapidly in open than in dense stands, i.e., most stands are to the left of the apex in Fig. 9 (Hawksworth & Johnson 1989, Parmeter 1978).

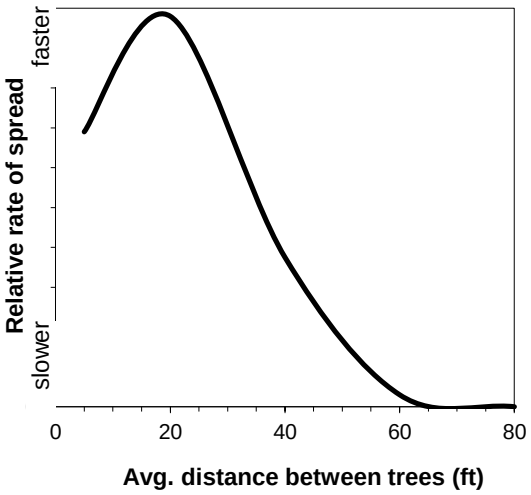


Figure 13. Hypothetical rate of dwarf mistletoe spread in relation to stand density for ponderosa pine 30-40 years old in the Southwest (from Hawksworth 1961b). The curve would be shifted to left for younger stands and to the right for older stands.

Spatial arrangement of trees can affect dwarf mistletoe spread as does density. Particularly

important is the consideration that host-free areas greater than 27 m wide provide an effective barrier to spread of the disease. This can include meadows or other forest openings, streams, roads, etc.

Composition. Composition of stands also affects dwarf mistletoes. In a mixed stand containing hosts and nonhosts, with the nonhosts large and abundant enough to intercept flying seeds, the spread rate of dwarf mistletoe between host trees is likely slower than in pure stands of hosts (Parmeter 1978). Also, it seems safe to predict that the frequency of infection should be less in mixed stands because a portion of the trees cannot be infected. However, these relationships have not been quantified.

6.3 Historic practices

In presettlement forests, it is generally considered that dwarf mistletoes tended to be patchily distributed (Kipfmueller & Baker 1998). Some early management practices tended to increase the abundance and distribution of dwarf mistletoes. Thinning commonly practiced in ponderosa pine of the Southwest ("improvement selection") may have prevented mortality due to mistletoe, but also contributed to its spread and intensification (Conklin 2000, Hawksworth 1961b, Heidmann 1968, Heidmann 1983). Selectively harvesting the most valuable trees (high-grading) concentrated the mistletoe in the overstory while creating opportunities for reproduction, establishing ideal conditions for dwarf mistletoe spread and intensification. Similarly, incomplete clearcuts left unmerchantable, infected trees that led to heavy infection of the regeneration. Excessive grazing, road building, and direct fire suppression have decreased fire frequency, enhancing multi-story, dense stands that are more susceptible to dwarf mistletoes in some forest types, while at the same time removing the single most important natural control of dwarf mistletoes.

These factors contributed to an increase in the distribution and abundance of dwarf mistletoes in many forests of the western United States (Shaw *et al.* 2004, see also section 4.2, Forest dynamics). In ponderosa pine forests of the Southwest, for instance, it is widely acknowledged that past overgrazing, fire suppression and logging practices have resulted in increased distribution and severity of southwestern dwarf mistletoe (Pollock & Suckling 1995). Surveys conducted in the 1950s and 1980s indicate an increase in the distribution of southwestern dwarf mistletoe on National Forests of Arizona and New Mexico from 30% to 38% of the ponderosa pine type, a 27% increase (Maffei & Beatty 1988). Similar surveys conducted with consistent methods over a 41-year period on the Bighorn National Forest indicate continuing increase in incidence of lodgepole pine dwarf mistletoe from 31% in 1958 to 36% in 1978 and a conservative estimate of 44% in 1999 (Harris 2003), an increase of 42% in only 41 years. Forest changes since European settlement east of the Cascades in Washington and Oregon are associated with increased distribution and severity of dwarf mistletoes in Douglas-fir and true fir forests (Hessburg *et al.* 1994). Because of changes in fire frequency, a similar increase in western dwarf mistletoe is inferred for ponderosa pine forests in that region. Douglas-fir dwarf mistletoe has increased in the Inland West where historic practices have made the host more widespread and continuous (Hadfield *et al.* 2000).

Veblen *et al.* (2000) hypothesized that logging and changes in fire regime have increased mistletoe infection over large areas in lodgepole pine of the Pike and San Isabel National Forests, Colorado. Dwarf mistletoe infection in lodgepole pine increased with time since the last fire in several studies, and a general increase in dwarf mistletoe intensity and distribution over time was anticipated due to changes in fire return interval (Kipfmueller & Baker 1998, Zimmerman & Laven 1984). In lodgepole pine forests of eastern Oregon and Washington, although dwarf mistletoe was undoubtedly severe in some presettlement forests, it is now more widely distributed and carrying over between stands now partially replaced by mountain pine beetle rather than more completely replaced by fire (Hessburg *et al.* 1994). In lodgepole pine of western Montana and northern Idaho,

the increase in dwarf mistletoe, together with fire exclusion and increasing mountain pine beetle vulnerability, have created a huge potential for fires, likened by Monnig & Byler (1992) to "holding water behind a leaky dam. We can either draw the water down gradually or we can wait for the dam to break." An exception is the Targhee National Forest in Idaho, where incidence of dwarf mistletoes declined in both lodgepole pine and Douglas-fir between 1978 and 1996 (Smith & Hoffman 1998). In that case, widespread bark beetle outbreaks and threat of wildfire led to a huge effort at salvage, regeneration and seedling protection that shifted forest structure from mostly mature, heavily infested stands to younger, lightly infested stands.

6.4 Host vigor and site

The chief attributes of host vigor that influence dwarf mistletoes are crown density and rate of height growth. Vigorous trees tend to have larger, denser crowns with more foliage and longer needles. All else being equal, these trees should intercept more seeds and therefore be more liable to infection than trees growing poorly (Parmeter 1978). The rate of infection would therefore increase with host vigor, assuming constant inoculum.

Dwarf mistletoe plants on vigorous trees also grow better. It is a common misconception that all parasites grow better on weak hosts than on vigorous hosts. Cortical strands invade vigorous tissue more quickly, shoots are larger and more fruit is produced on vigorous hosts (Parmeter 1978). This is a common, if unwanted, side effect of thinning.

The rate of height growth may have an opposite effect, giving vigorous trees an advantage over the mistletoe. Infection of only the lower crown usually has little effect on tree growth or survival (unless a large broom develops). Severe damage is usually associated with infections in the middle and upper crown. In the absence of seed sources from above, a tree infected in the lower crown is in a race with the dwarf mistletoe. If the tree can grow in height faster than the mistletoe can climb, the tree will be in little danger from that infection and may even outgrow it as lower branches die (Parmeter 1978, Scharpf 1978, Scharpf & Parmeter 1976). However, if the mistletoe climbs the crown faster than the crown grows, infection becomes severe.

Vigorous trees, with faster height growth, may thus prevent the infection from becoming severe by staying ahead of it. The denser crown of a vigorous tree provides an added advantage because it slows the vertical spread of the mistletoe. Whether these advantages of vigor outweigh the disadvantages discussed above probably depends on other factors, such as stand structure, location of infected trees, etc. Rates of vertical spread have been estimated or measured for various mistletoe-host combinations, and range from 3 inches to several feet per year (Parmeter 1978). Estimates for our area have apparently not been made.

Perhaps because of slow height growth, southwestern dwarf mistletoe in Colorado was most severe on the driest ponderosa pine sites, typically the *Pinus ponderosa*/ *Muhlenbergia montana* habitat type (Merrill *et al.* 1987). The wetter *P. ponderosa*/*Quercus gambelii* habitat type had the lowest severity.

Dwarf mistletoes are often more abundant on ridgetops than on slopes and least common on bottom sites. This pattern is often observed with southwestern and lodgepole pine dwarf mistletoes, but Douglas-fir dwarf mistletoe had only a weak relationship to topographic position (Hawksworth & Wiens 1996, Merrill *et al.* 1987). Steep slopes often have lower incidence of dwarf mistletoe than gentle slopes. These relationships may be due to differences in fuel accumulation and fire behavior, but they may also be due to differences in host vigor in different topographic positions.

6.5 Diseases and herbivores of dwarf mistletoes

A number of fungi parasitize and kill dwarf mistletoe shoots, or kill host tissues colonized by the endophytic system, indirectly killing the mistletoe. It is not known how much these diseases impact dwarf mistletoe populations, nor do we have systems for effectively encouraging the activity of these organisms as biological control agents. Tests of inundative biological control of lodgepole pine dwarf mistletoe using *Colletotrichum gloeosporioides* were unsuccessful (Ramsfield *et al.* 2005). Similar tests of *Neonectria neomacrospora* (anamorph *Cylindrocarpon cylindroides*) against hemlock dwarf mistletoe on Vancouver Island had partial success, particularly when swellings were wounded prior to inoculation (Rietman *et al.* 2005). Two diseases are described here.

One of the most specialized diseases of dwarf mistletoes is caused by *Caliciopsis arceuthobii* synonym *Wallrothiella arceuthobii*). The spores of this fungus germinate on and grow into the stigma of the female flowers in the spring, like a pollen grain. However, the fungus takes control of fruit development, replacing most of the fruit with its own black reproductive structure and preventing viable seed from being produced. The following spring, spores are released to initiate a new cycle of infection. This pathogen infects *A. americanum* and *A. douglasii* in our area (Hawksworth & Wiens 1996). Cases have been observed where the fungus killed up to 90% of the fruits of *A. douglasii*. In a four-year study, fruit production in *A. americanum* was reduced an average of 58% by natural infection (Ramsfield *et al.* 2009).

A rust fungus, *Peridermium bethelii*, infects lodgepole pine branches where they are already infected by *A. americanum* (Hawksworth & Wiens 1996). It occurs in Colorado and Wyoming in forests where *A. americanum* occurs, especially in forests where comandra blister rust also occurs (B. Geils, personal communication). The rust fungus apparently infects both the tree bark and the mistletoe's cortical strands. Infected branches die, killing the mistletoe as well. Generally the rust is not abundant enough to have a substantial impact on mistletoe populations.

Herbivory may also potentially reduce populations of dwarf mistletoes, but no impact by herbivory has been demonstrated or suggested. Herbivory of dwarf mistletoes by by vertebrates is discussed in section 5.1.1, Dwarf mistletoes as a food source for vertebrates, and that by insects is discussed in section 5.3, Effects of dwarf mistletoes on insects.

7. DETECTION AND EVALUATION

7.1 Symptoms and signs

Although dwarf mistletoes are easier to detect and diagnose than many other types of tree diseases, there are substantial limitations to detection. Latent infections (too young to have shoots or to cause witches' brooms are a major factor, but older infections in a large tree can also be difficult to detect.

Swellings. Swelling, the first symptom of infection, is due to an increase in the size and number of cells (hypertrophy and hyperplasia). It is more common and persistent with local infections than with systemic infections (see section 2, Life cycle). Swelling at the site of infection usually precedes shoot production and is fusiform (tapered gradually at the ends). On pines, swellings may also be caused by rusts. However, rust swellings are either distinctly spherical (western gall rust) or the rust causes cankers soon after swelling.

Witches' brooms. Infection by dwarf mistletoes typically leads to profuse, dense branching, forming a mass called a witches' broom. Branches are often distorted. Witches' brooms may be a

side effect of the elevated cytokinin levels in the mistletoe plant, which serve to direct allocation of nutrients to infected branches.

It is important to distinguish witches' brooms caused by dwarf mistletoe from other abnormal branching. Old ponderosa pine in the Southwest may develop a broom-like branching habit that is not due to dwarf mistletoe (B. Geils, pers. comm.). Elytroderma needlecast, caused by *Elytroderma deformans*, also causes witches' brooms in ponderosa pine, but it is generally restricted to wet sites; one-year-old needles turn red in spring; black, elongate fungal fruiting bodies occur on diseased needles; and brooms are generally small. Lodgepole pine may develop "stimulation brooms" as a physiological response to canopy opening or age (Hawksworth 1961a). Several features can help in distinguishing them from mistletoe brooms (Table 7).

Table 7. Features distinguishing dwarf mistletoe brooms from stimulation brooms in lodgepole pine (Hawksworth 1961a).

	Dwarf mistletoe brooms	Stimulation brooms
Dwarf mistletoe shoots and basal cups	Yes	No
Location	Any height or distance from bole	Usually < 30 ft high, at or near bole
Crown class of tree	Any	Suppressed or intermediate trees, or whose tops are dead or broken
Branches	Many branches, tips usually point upward	Fewer branches, tips may point upward or sidways
Dead brooms	Can usually be found on other trees in vicinity, sometimes on trees with living brooms	None

Other crown effects. The upper crown eventually begins to thin in trees with many infections or with one or more large brooms in the lower crown. This symptom may progress to branch die-back and then death of the top of the tree. Because resources are preferentially allocated to infected branches, they are often the last part of the crown to die.

Cankers. Cankers (death of cambium and bark due to disease) are usually seen on main stems, but may also be common on branches in limber pine. Although infection of young shoots often causes swelling, older tissues often die when infected for a long period.

Mistletoe shoots. Shoots were described in section 2, Life cycle, and in the description of each species. In systemic infections (Douglas-fir and lodgepole pine dwarf mistletoes) shoots may be aggregated at the points where the annual bud scars occur. Although shoots are often useful for detecting infection, several factors must be considered:

a) There is a latent period, typically 2–5 years, between infection and shoot production.

b) Shoots of some species (e.g., Douglas-fir dwarf mistletoe) are very small and difficult to see in a mature tree, even with binoculars.

c) Shoots are relatively short-lived, 5–7 years. Although new shoots are typically produced, it is not unusual for established infections to have no shoots because of drought or other factors. Although this hinders detection, the mistletoe plant survives well without shoots.

It has been estimated that we may detect only 2/3 of infections in a stand visually (Hawksworth *et al.* 1977, Knutson & Tinnin 1980, Merrill *et al.* 1988). Put another way, there may be 50% more infections than we can see in a stand. A major reason for this is latent infections. The "half-again" rule, developed from studies in lodgepole pine, states that the proportion of trees infected about 5 years after sanitation will be about half the amount removed in the first operation (Hawksworth 1978, probably does not apply at very high infection levels).

Basal cups. When a shoot dies and falls off, it leaves behind on the bark surface a small basal cup. Suspected infections without shoots can often be confirmed by seeing these cups.

7.2 Dwarf Mistletoe Rating (DMR)

Although many systems have been used to rate levels of infection of dwarf mistletoe, one system is now used almost universally: Hawksworth's 6-class system (Hawksworth 1977). Since this system has been used for many years, many disease parameters and management recommendations are provided in terms of DMR. Actually a 7-class system since it ranges from 0 (uninfected) to 6, it is based on rating each third of the crown on a scale from 0–2, then summing for the tree rating (Figure 14). Binoculars should be used to enhance detection. A common mistake is to stand too close to the tree, which can obscure symptoms and signs as well as cause perspective errors in dividing the crown into thirds.

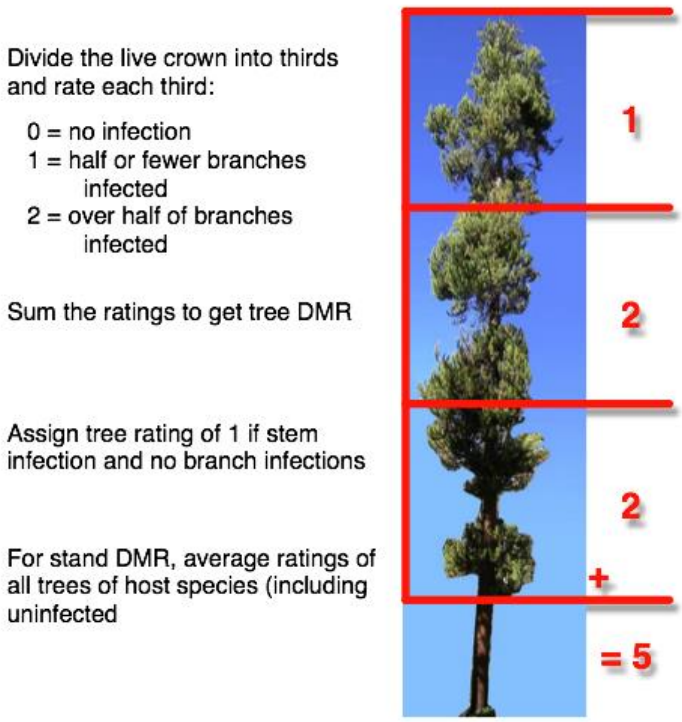


Figure 14. The system for rating dwarf mistletoe infection. For this purpose, a branch is considered a primary branch with all subsidiary branches.

In a comparison of ratings of standing Douglas-fir trees with those after felling, ratings were accurate about 75% of the time (Geils & Mathiasen 1990). Rating was very reliable for trees up to 6 m tall but less so for taller trees. Heavily infected trees tended to be underrated because of failure to detect infected branches in the upper crown. Lightly infected trees tended to be overrated because of a tendency to lower the boundary between the lower and middle third. These rating errors tended to cancel each other out, although overall there was a slight underestimate.

Although initially a "1" was assigned to any third that has no branch infections but does have stem infection (Hawksworth 1977), in more recent applications stem infections are only considered if there are no branch infections at all, in which case the tree is scored "1" (Hawksworth & Wiens 1996).

Several stand parameters can be estimated from rating a sample of trees (Hawksworth *et al.* 2002). (When variable-radius plots are used for sampling, they must be expanded to an area basis

(Arvanitis 2002) before calculating stand parameters.) The basic data are incidence (percentage of host trees infected) and severity or DMI (average DMR among infected trees only). The overall stand DMR integrates incidence and severity. Stand DMR is the average rating of all trees in the population (usually of the principal host species), including the uninfected trees. These parameters are related as follows:

$$\text{DMR} = \text{DMI} \times (\text{incidence expressed as a proportion})$$

7.3 Surveys

Surveys for dwarf mistletoe vary in their intent and extent. Here we will focus on surveys designed to provide information for planning specific projects. The objective is primarily to get information on the severity and distribution of the disease, but also to relate it to stand attributes including density, basal area, size structure, etc. A suitable extent for surveys of this kind ranges from a single stand up to perhaps several thousand acres.

Survey design. The considerations in designing a sampling scheme are the same as those in cruise design. Numerous sampling procedures have been recommended and used successfully (Brown 1975, Hawksworth & Johnson 1989, Johnson & Hawksworth 1978, Muir & Moody 2002, Walters 1978, Walters & Brown 1973), and it is not essential that a particular one be used. The following considerations are important in designing a survey:

a) Sampling must be either random or systematic, i.e., no bias may influence the selection of sample points.

b) The sample must be large enough to reasonably represent the total project area under consideration, given the variability within the area.

c) Sample intensity should be consistent. If certain stands or groups of stands are sampled more heavily than others, the data must be summarized only by stand or group, as overall summaries will be invalid.

A sampling scheme modeled after the common stand examinations (Anonymous 2005c) is an efficient one and uses standard mensuration techniques. In it, a variable-radius (prism) plot is used to sample large trees (e.g., ≥5″ DBH) and a fixed-radius plot centered at the same point is used for smaller trees. A prism with an appropriate basal area factor (BAF) should be chosen that gives about 4–8 sample trees at each point. The fixed plot size can be adjusted similarly to give a suitable sample. In the fixed plots, trees can be recorded by DBH class, as is done in stand exams, or by height class.

Sampling intensity should be at least one point per 10 acres. With a systematic sample (the easiest and probably the most useful), this equates to a sample grid of 660 x 660 ft, or 10 x 10 chains. In small, variable, or high-value areas, such as developed recreation sites, a smaller sample grid should be considered (Table 8), although of course the decision is subject to time and funds available. It is not important that the points be located precisely, only that they be located without bias (this may not be true if the same survey is to be used for cruising). To make navigation easy, we typically preload the sample points in a pocket GPS unit. When we get close enough that the point starts to wander, we stop and put the plot there. A proximity alarm setting in the GPS could also be used to place the points without bias.

Table 8. Minimum sampling intensity suggested for various survey sizes by Walters (1978).

Area to survey	Grid of sample points	Pts. per 10 acres
< 200 acres	4 x 4 chains (264 ft)	6.25
200-800 acres	8 x 8 chains (528 ft)	1.56
> 800 acres	10 x 10 chains (660 ft)	1.00

In traveling between sample points, it is important that the crew look for and sketch-map the location and approximate intensity

of dwarf mistletoe. This information, together with the sample data, allows preparation of an accurate map of mistletoe location and severity that can be useful in planning treatments, tailoring them to specific locations, and conducting environmental analysis.

A mistletoe survey can be integrated with surveys for other purposes, and modified accordingly. Types of surveys that a mistletoe survey can be combined with include:

a) Stand examination

b) Timber sale reconnaissance

c) K-V planning survey

d) Cruise (timber sale volume estimation)

Data analysis. If using mistletoe data from a stand exam, or putting special survey data through the computer program for analyzing stand exams, the data should be interpreted with caution. We have found that some mistletoe data are calculated incorrectly in the printouts, and the user's guide does not make clear how the calculations are done. We suggest calculating the mistletoe data manually in Excel to be sure of the results.

Calculations based on fixed-size plots are straightforward. For variable-radius plots, DMR cannot be calculated by simply averaging the sample trees. Each sample tree must be expanded to trees per acre (TPA) that it represents (TPA = BAF/(0.005454*DBH^2)/number of plots), and the DMR multiplied by that number before averaging (Arvanitis 2002).

8. MANAGEMENT

The information on the effects of dwarf mistletoes in the preceding sections can be used to determine what levels of dwarf mistletoe are compatible with the multiple objectives that drive decisions in managing a stand. This section assumes that such a determination has been made, and that one of the objectives is reducing the impact of dwarf mistletoe by reducing its distribution and/or severity. This could be the case under a variety of management emphases, including timber production, range, wildlife, recreation, etc.

Several features of dwarf mistletoes should make them particularly amenable to management:

1. **Dwarf mistletoes are obligate parasites**. They cannot survive without a living host. Once the branch or tree dies or is cut, the parasite dies.
2. **Dispersal distance is limited and spread is slow**. Explosive seed dispersal is only up to about 60 ft from a tall, isolated tree. In single-storied stands, spread is usually about 2 ft per year. This creates possibilities for protecting trees by distance from infected trees.
3. **The life cycle is long**. From dispersal to production of a new generation of mature fruit typically takes 6–8 years. Disease intensification (multiplication of infections and increase in severity within trees) and spread (horizontal movement of infection front) are therefore fairly slow.
4. **Dwarf mistletoes tend to be host specific**. Mixed stands and changes in composition therefore can create a disadvantage for the mistletoes.
5. **They are relatively easy to detect**. Unlike most pathogens, dwarf mistletoes are entirely above ground, partly exposed on the surface of the host, visible without a microscope, and usually cause distinctive symptoms.
6. **Impact low until infection severe**. Hosts are minimally affected by dwarf mistletoe during the first 30-40 years of infection.

If control of dwarf mistletoe were the only, or even the primary, consideration in forest management, it would be a relatively simple matter. The biology of this group of diseases is understood better than any other. In fact, development of effective management approaches was one of the first success stories of forest pathology in North America (Meinecke 1914, Weir 1916b). Today, however, despite the huge increase of knowledge in the interim (Hawksworth & Wiens 1996), management of dwarf mistletoes is more complex and challenging than it seemed back then. The challenges making mistletoe management more difficult include:

1. **Historical practices**. Fire suppression and other past practices have tended to increase the abundance and distribution of dwarf mistletoes (see sections 4.2, Forest dynamics and 6.3, Historic practices).
2. **Integrating disease management with modern silviculture**. Because of advances in silvicultural understanding, tailored to management of particular forest types and conditions, approaches that might be ideal for disease control are sometimes unacceptable silviculturally. Management approaches must also be consistent with management of other potential diseases and insect pests.
3. **Social issues**. Opposition to approaches that may be silviculturally and ecologically appropriate in some cases, such as even-aged management systems, have made disease management more difficult. In addition, the value of dwarf mistletoes to wildlife is often cited in opposition to disease management projects.
4. **Severity over time**. Because dwarf mistletoe spreads and intensifies slowly by human standards, it can be difficult to appreciate its effects on stand growth and development within the time scale of a forest. Attention is often given to issues that cause more abrubt change, even though they may involve less damage over the long term.
5. **Management over time**. It may not be feasible to accomplish dwarf mistletoe management goals in one project. In some cases, multiple entries may be required to achieve success consistent with other goals.

8.1 Management options

Management decisions can be complex, and this guide cannot anticipate all circumstances. Managers are strongly encouraged to consult with forest health specialists while assessing stands to be managed, well before prescriptions are developed. The information here should be regarded as guidelines only, and should not be translated into management plans without thorough evaluation.

8.1.1 Models

In cases where management decisions are unclear, stand growth models that incorporate dwarf mistletoe may be of use. Although they may not predict outcomes with perfect accuracy, they incorporate more considerations into their predictions, and with more quantification, than can be accomplished with the usual process of assessment and expert judgment.

The Forest Vegetation Simulator (FVS, Anonymous 2005b), which incorporates the Dwarf Mistletoe Impact Model (DMIM, Anonymous 2005a) is the system generally used and supported in USDA Forest Service. The bases of DMIM and its use are well documented (Hawksworth *et al.* 1995). An example of its use with animated stand imagery is available online (Worrall & Geils 2006).

8.1.2 Widely applicable management strategies

Management approaches that have broad applicability for many species and at various stages of development:

1. **Find borders without inoculum**. Regardless of stage of stand development or the management approach, treated areas should be bordered as much as possible by areas that will not be sources of inoculum. This includes nonsusceptible or uninfested stands, roads, forest openings, etc.
2. **Size matters**. To avoid reinfestation of treated areas that have infested stands on the border, treated areas must be large enough that spread into them from the borders is insignificant, or at least acceptable, during the life of the stand. The proportion of a treated area exposed to inoculum from an infested border or infested after 50 years decreases as the treated area becomes larger (Figure 15). In this situation, 20 acres is considered a minimum and 40 acres is recommended. At 40 acres (assuming a circular area with infested border), 13% of the area is exposed to direct inoculum at the maximum distance, and roughly 31% is infected after 50 years. As patches increase in size beyond this point, the advantage of increasing size becomes less. Irregularly shaped or long, narrow patches must be larger to have a similar area protected.

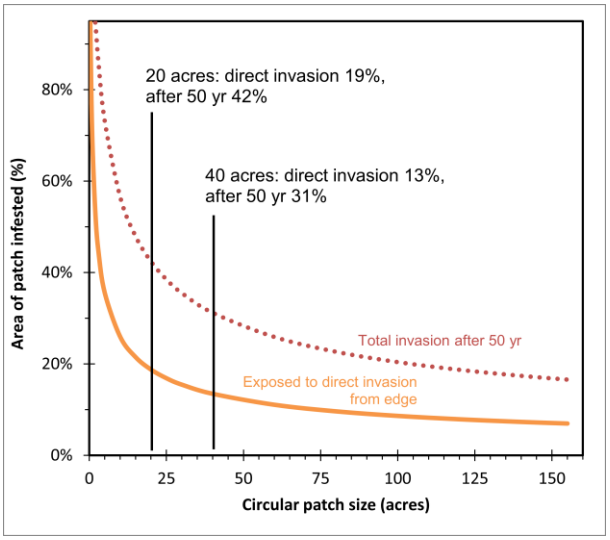


Figure 15. Proportion of a circular, treated area exposed to direct inoculum of dwarf mistletoe from the edge at the at the maximum dispersal distance (16 m or 52 ft), used because plants in tall trees are showering seed on regeneration. Also shown is the additional effect of lateral spread for 50 years, assuming lateral spread rate for a single-storied stand of 0.5 m (1.5 ft) per year. This spread rate is the average estimated for lodgepole pine dwarf mistletoe (Hawksworth & Dooling 1984) and is a conservative estimate for our other species (Beatty & Mathiasen 2003, Hadfield *et al.* 2000, Mathiasen *et al.* 2002, Taylor & Mathiasen 1999). Note that any shape other than a circle would lead to more rapid invasion.

3. **Favor nonhosts**. Whether planting, spacing, thinning, selecting seed trees, etc., encourage and favor tree species that are not hosts of the mistletoe in the stand.
4. **A grace period for seedlings**. Because of their small size as targets and their short exposure to inoculum, seedlings generally can be considered safe from infection until they are 10 years old or 3 feet tall, whichever comes first (Wicker 1967, Wicker & Shaw 1967). This gives some time before infected overstories must be treated. Infection of smaller or younger trees does occur, but it is generally rare.
5. **Sanitation**. Sanitation, removal or killing of infected trees to protect other trees, is important in many kinds of stands at various developmental stages. "Sanitation cutting" (or simply sanitation) has been distinguished from "sanitation thinning" (Hawksworth 1978). Sanitation cutting is the attempted removal of all visibly infected trees, though it usually is combined with thinning goals also. In sanitation thinning, the emphasis is on spacing, and only the most severely diseased trees may be removed, which may have little impact on reducing dwarf mistletoe.
6. **Prescribed stand-replacing fire**. As discussed earlier (section 4.2, Forest dynamics), wildfire has been a major determinant of dwarf mistletoe distribution and severity. Both even-aged and uneven-aged, infested stands can be treated with prescribed, stand-replacing fire to establish a

new stand in the absence of inoculum. Because lodgepole pine generally regenerates well after fire, consistent with its natural disturbance regime, this can be an effective, economical and ecologically beneficial means of stand replacement (Zimmerman *et al.* 1990). Fire can be used in heavily infested stands that have little economic value, or after merchantable trees are harvested. Muraro (1978) provides operational details for its use in interior British Columbia. In merchantable, infested stands, limbing is done prior to forwarding to ensure a fuel bed for the sanitizing fire. After about four weeks, the slash provides good fire coverage with a minimum of ignition effort. In any case, stands must be inspected following the fire and any infected residuals felled.

7. **Prescribed fire – low or mixed severity**. Prescribed fire may decrease severity and distribution of dwarf mistletoe without replacing the stand. Infected trees may be selectively killed because of brooms and fuel accumulation around infected trees. Also, fire may be directed at them by manipulating the location of ground fuels or selecting ignition points (Muir & Geils 2002). Lower branches of surviving trees are often killed by scorching, reducing mistletoe severity (Conklin & Armstrong 2001). In some stands of lodgepole pine, where ponderosa or Douglas-fir seed sources exist, a series of low-severity fires may encourage replacement of infested lodgepole pine by the more fire-resistant species (Muir & Geils 2002).
8. **Pruning**. Pruning may have two objectives. Pruning of large brooms, which are generally in the lower crown, can allow trees to recover vigor and substantially prolong their life. It is not likely to affect spread and intensification of the disease in the stand. Broom pruning can be used when it is important to maintain large tree cover, more aggressive silvicultural techniques are less acceptable, and the tree value justifies the cost. It is most often used in developed recreation sites, which often meet these criteria. Another objective of pruning is sanitation (i.e., sanitation pruning). Again, this is only feasible in high-value sites, but male infections can be ignored for this purpose if they can be identified as such. In lodgepole pine, candidate trees should have the following features (Hawksworth & Johnson 1989):
   a) Infected only in the lower half of the crown
   b) DMR ≤ 3
   c) No infections on parts of the bole < 5″ diameter.
   d) Infections on branches from bole < 5″ diameter are > 4″ from the bole.

   Pruning branches with infections near the main stem may not be successful because the endophytic system may already have entered the stem. The following rules of thumb can be used. For lodgepole pine dwarf mistletoe, stem infection is likely if shoots are < 4″ from the main stem. For southwestern dwarf mistletoe on ponderosa pine, stem infection is likely if shoots are < 6″ from the main stem on branches up to 1″, and the distance should be increased 2″ for every additional 1″ in diameter. Pruned stands should be retreated in 3-5 years to remove latent infections and those that were missed.

8.1.3 Recently regenerated stands (≤ 15 yrs old)

Stands that have been recently regenerated, whether by wildfire, prescribed fire, harvest, or other disturbance, provide the best opportunities to reduce dwarf mistletoe impacts through the life of the new stand. It is the only situation in which a mistletoe-free result (only over the area treated, and until it can spread in again from the edges) is highly likely. Options to consider at this point include:

1. **Kill infected residuals**. If regeneration will include susceptible species, remove or kill any residual overstory trees (at *least* those with any evidence of infection) within 10 yr after establishment of regeneration or before regeneration is 3 ft tall, whichever comes first. *This is*

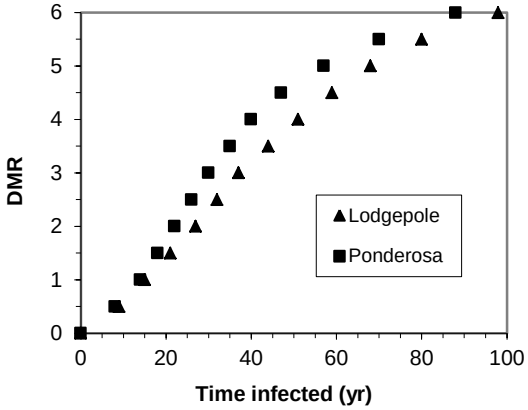


Figure 16. Approximate relationship between time since initial infection by dwarf mistletoe and stand DMR for some even-aged stands of lodgepole pine and ponderosa pine in the southern Rocky Mountains. Data from Hawksworth & Myers (1973).

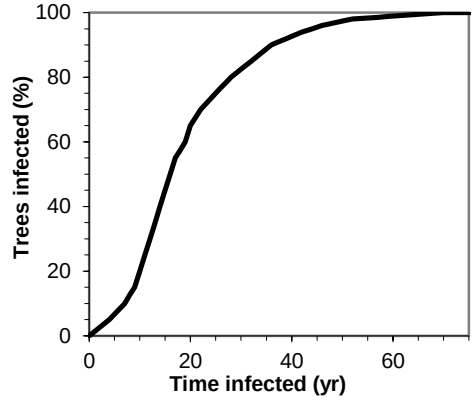


Figure 17. Approximate relationship between time since initial infection by dwarf mistletoe and incidence of infection for some even-aged stands of lodgepole pine and ponderosa pine in the southern Rocky Mountains. Data from Hawksworth & Myers (1973).

extremely important, as failure to do so can make the difference between the ideal mistletoe treatment and a worst-case scenario. It is better to do nothing than to start a shelterwood or seed-tree system and then fail to remove infected residuals on time. Because infections can be difficult to detect, and may be stimulated by the recent opening, it is best to fell or otherwise kill all trees from the previous stand, whether they appear infected or not, if consistent with other management goals. If not, the stand should be revisited within 5–10 years to remove infected residuals and sanitize the regeneration as needed. Snags can be created and/or left if desired, and of course any nonsusceptible tree species can be left. If a decision is made to retain infected trees over a developing understory, consideration should be given to pruning, occasional understory sanitation, and removing the overstory trees at a later time.

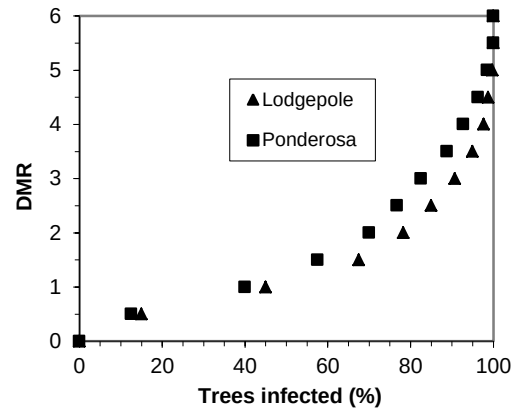


Figure 18. Approximate relationship between incidence of dwarf mistletoe and stand DMR for some even-aged stands of lodgepole pine and ponderosa pine in the southern Rocky Mountains. Data from Hawksworth & Myers (1973).

2. **Sanitize regeneration**. If there has been any opportunity for spread from residuals or from the edge, regeneration must be carefully inspected and infected trees killed. Again, because of latent infections, this should be repeated in 5–10 years.
3. **Make a "donut"**. The "donut" is created by felling all infected trees in the bordering stands 20 m (1 chain) back from the edge of the regenerated patch. With lodgepole pine, it is best to fell all trees in the 20-m zone because it regenerates well and may have infections that are difficult to detect. This prevents direct infection of the original regenerated patch from the edge. Even after dwarf mistletoe spreads through the border zone, it is less likely to spread into the original patch because the trees in the donut hole will be taller. This approach is essential if the regenerated patch is both: a) less than 20 acres or larger but irregularly shaped, and b) bordered by residual infested stands. It is optional with larger patches and completely unnecessary if there are no infected trees near the border.

8.1.4 Sapling stands

The relationships between time since infection, percent of trees infected, and stand DMR have been quantified for even-aged stands (Figure 16, Figure 17 and Figure 18). These relationships are useful in assessing stand condition and estimating parameters when one of them is known. They may have some general predictive value also. However, the basis of these data is not precisely documented, and some stands may not follow the pattern portrayed in the data.

Many stands of saplings can be sanitized like recently regenerated stands. However, because the incidence of infection can be higher and density lower, occasionally the ratio between the two will be so high that insufficient trees would be left after all infected trees are removed. This can be represented as curves for each target density, showing increasing permissible incidence of infection as initial density increases (Figure 19). Stands to the right of the curve may be successfully sanitized without falling below the minimum density.

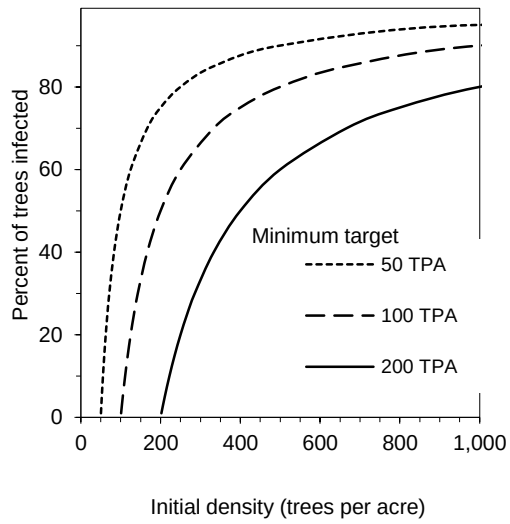


Figure 19. Guide for sanitation of young stands based on initial density, minimum target density, and percent infection. If initial density and percent infection coincide to the right of the curve representing minimum target density, strict sanitation should be feasible while leaving adequate stocking. Patchiness may alter this relationship.

Highest priority for sanitation should be given to younger stands with relatively low infection levels. Also, the better the site, the more worthwhile and effective thinning is likely to be. Action in these situations will have the greatest impact with the least cost. In general, guidelines for sapling stands can be characterized as follows:

1. **Sanitation**. Remove all trees with symptoms or signs of dwarf mistletoe if feasible, and schedule a followup treatment in about 5–7 years (some suggest 3-5 years). Strict sanitation cutting in lodgepole pine and ponderosa pine is traditionally attempted only in stands younger than 30 or 40 years (Hawksworth 1978). This is because incidence of infection in older stands is often so high that removal of all infected trees would create unacceptably large openings or low density and depress yields (Hawksworth 1978). Stands infested for 30 years can have 80% infection (Figure 17). However, the incidence of infection and minimum acceptable density is a better guide for decision-making than stand age. In lodgepole pine, strict sanitation may not be feasible with infection greater than about 40%, approximately equivalent to DMR about 0.5 (Hawksworth & Johnson 1989) or 1.0 (Figure 18). Heavily infected trees that must be left may not respond to release, and residual dwarf mistletoe will produce more seed and spread faster through the more open stand. The acceptability of such openings and possible benefits of heterogeneous stand structure to wildlife must be considered. Growth models with mistletoe modules, such as FVS, may be helpful in making such a decision. If further management is warranted, incorporate sanitation into regular thinnings. Recommendations in the literature vary slightly (Hawksworth & Johnson 1989, Muir & Geils 2002), but a good general guide for prioritizing leave trees in stands greater than 2″ (5 cm) DBH is (see also Table 9):
   a) Dominants and codominants uninfected.
   b) Dominants and codominants with infections confined to lower third of the crown (DMR ≤2)
   c) Intermediates apparently uninfected.

d) Dominants and codominants with infection in less than half the branches in the lower two-thirds of the crown (DMR ≤3)

2. **Regeneration**. In heavily infested sapling stands on good sites in timber emphasis areas, consideration should be given to regeneration of the stand.
3. **No action**. When sapling stands are heavily infested and regeneration is not feasible, it may be best to devote the stand to wildlife and invest management efforts elsewhere, where they will provide more benefit in reducing mistletoe severity.

Table 9. Guidelines for leave trees in sanitation thinning of ponderosa pine in the Southwest (Conklin 2000). These guidelines are recommended here for single-story stands only. DMR in this table refers to that of individual trees, not stands.

DBH class	Maximum allowable DMR
0-4″	0
4-6″	1
6-9″	1 or 2
> 9″	2 or 3

8.1.5 Mature stands (even-aged)

In stands of larger trees (more than about 7 or 8″ DBH), average stand DMR may be a more important measure than percent of trees infected. There is less opportunity to select trees for future development of the stand, less concern for protecting uninfected trees, little chance of strict sanitation, and more concern for overall condition. On the other hand, there may be timber sale opportunities that can make management and stand improvement more feasible.

One consideration that becomes more important in mature stands is mortality and growth loss of moderately to heavily infected trees. Because of their shortened expected lifespan (Table 3, Table 5), as well as their limited growth, trees with DMR of 3 or more should be considered for harvest if intermediate cuts are feasible.

1. **Sanitation thinning**. Where regeneration is not anticipated in the near future, and stand DMR is less than 3, sanitation thinning may improve the condition, growth and longevity of the stand (Hawksworth & Johnson 1989). In more heavily infested stands, if a regeneration cut is not an option, selective harvesting of the most heavily infected trees can salvage them before they die. However, if this is likely to stimulate abundant regeneration, doing nothing may be the best option in that situation. Little growth response can be anticipated in heavily infected trees, and stimulating regeneration under those circumstances may lead to a worse infestation in the future. In ponderosa pine in the southwest, guidelines have been suggested for maximum allowable DMR in leave trees (Table 9).
2. **Regeneration by even-aged reproduction method or fire**. Where silviculturally appropriate, even-aged management, especially at the stage of regeneration, offers the best opportunity to establish a mistletoe-free stand. This can be accomplished by clearcut, seed-tree, or shelterwood methods. If using shelterwood or seed-tree reproduction methods, select residual trees that are mistletoe free or only lightly infected (tree DMR ≤ 2). This will contribute to higher seed production, better survival, and reduced infection of any pre-existing regeneration. For ponderosa pine in the Southwest, 20–40 ft^2/acre (5–9 m^2/ha) of uninfected seed trees are recommended; this should be doubled for infected seed trees (Heidmann 1983). See other important considerations (patch size, border guidelines, favoring nonhosts, removing residuals, etc.) in sections 8.1.2, Widely applicable management strategies and 8.1.3, Recently regenerated stands. Most important is that, *if infected residuals are used as seed/shelter trees, they* must *be removed before regeneration is 10 yr old or 3 ft tall, whichever comes first.*

8.1.6 Uneven-aged stands

As noted previously, uneven-aged stands with infected overstory trees are ideal for maximizing spread and intensification of dwarf mistletoes. Management of such stands in an uneven-aged sys-

tem is problematic. Infected understory trees have the problem of the mistletoe, but its effects are compounded by their slower growth from being in the understory. Worse, inoculum continues to rain down on them from above during their most vulnerable years. Such trees have little chance of outgrowing the mistletoe and within-tree intensification is virtually assured. Because they are infected when young, the impacts are great.

The possibility of uneven-aged management has been considered primarily for ponderosa pine, and that is the focus of this section. If severity is low to moderate (stand DMR ≤ 2) there may be a chance of maintaining some uneven-aged conditions while reducing severity and, most importantly, preventing severe infection of the understory. However, it would most likely require aggressive treatment, frequent entries and, in some patches, more or less complete removal of the overstory. When overstory trees are infected, strict adherence to uneven-aged systems is probably not compatible with reducing impact from dwarf mistletoe. Options include:

1. **Convert to single-story stand**. Overall conversion to even-aged management is the surest way to reduce severity and improve long-term productivity.
2. **Adapt management to mistletoe conditions**. If overall conversion to even-aged management is not desired, the next best approach is to be flexible. Where mistletoe is present, the overstory can be removed (moderate to high severity) or sanitized (low to moderate severity) and the understory sanitized. In mistletoe-free patches, uneven-aged conditions could be maintained. Marking rules must be oriented toward aggressive removal of infected trees, or the mistletoe will bounce back quickly and may even be stimulated to faster spread and intensification by the opening of the stand. Because some infected overstory trees and latent infections in the understory will be missed, monitoring and retreatment on a frequent basis may be required. Nonsusceptible tree species can be favored in any size class.

THE FORT VALLEY STUDY

A study of dwarf mistletoe management was initiated in a previously unmanaged area at Fort Valley Experimental Forest, near Flagstaff, Arizona, in 1951 and followed for 27 years (Heidmann 1968, Heidmann 1983, Herman 1961). The forest was not explicitly described as uneven-aged, but the description shows this (Heidmann 1968). DMR and incidence of infection were not reported. The primary measure used was percentage of the area stocked by infected and uninfected trees, and some data were given in terms of infected volume. The three treatments and their results were:

Light Improvement Selection (LIS): This treatment was the standard silvicultural practice in previously unmanaged stands in 1951. Generally, sanitation was limited to measures that did not reduce stocking below that recommended for uninfected areas. The first cut harvested merchantable trees that were dying or expected to die within 20 years. This removed 30-40% of the total board-foot volume. Subsequent stand improvement was limited to that possible from K-V funds, and including release and pruning of trees in lightly or uninfected groups, favoring uninfected trees. Severely infected groups were left alone.

LIS was a complete failure. The initial treatment actually increased the proportion of area stocked by infected trees. After 13 years, the infected volume was 44% of total volume, compared to 40% before treatment began.

Limited Control (LC): This treatment was intended to reduce infection to a level that did not impact timber production, to the extent it could be financed and accomplished by contemporary allotments and regulations. Unlike LIS, sustained yield was relegated to secondary importance until reasonable control of dwarf mistletoe could be obtained. See Heidmann (1968) for detailed marking guidelines.

LC was also deemed a failure. Although it reduced infected volume from 44% at the beginning to 23% after 13 years, infection was increasing rapidly and had tripled since the initial treatment.

Complete Control (CC): This treatment reduced infection as near to 0 as possible. All uninfected trees were retained and all infected trees were cut, except that nonmerchantable, infected trees were retained in most cases if needed for stocking.

A final evaluation of the experiment concluded that complete control is the only effective approach in heavily infested, mature ponderosa pine (Heidmann 1983). After 27 years, infected stocking in the CC treatment was still well below what it was at the start. The CC treatment had the lowest proportion infected of the area stocked in 1977, and it already had higher overall stocking than the LC treatment.

3. **Push it back**. Focus on edges of infection centers, cutting most heavily there to push the edges back, decreasing the area infested.
4. **Individual tree selection**. This may be appropriate in ponderosa pine when at most 15% of trees are infected (Muir & Geils 2002). It may also be appropriate in mixed stands where nonsusceptible or resistant species can be favored (Mathiasen 1989). For individual-tree selection, recommendations are:
   a) Cut severely infected trees (DMR ≥ 5) at each entry.
   b) Retain lightly infected and healthy trees (DMR ≤ 2).
   c) Retain moderately infected trees (DMR 3 and 4) only where height growth is expected to exceed 12 in (30 cm) per year or where the next entry is scheduled within 20 years.
   d) Consider pruning infected branches or large brooms.
5. **Group selection**. Opinions differ on the potential for group selection in managing dwarf mistletoe in ponderosa pine. It may allow removal of infection centers and regeneration of disease-free patches under certain circumstances (Conklin 2000), or it may be unlikely to meet management objectives in infested stands (Edminster & Olsen 1996). In the Southwest, it may be considered when 15–25% of stems are infected (roughly corresponding to maximum stand DMR ≤0.7, Figure 18) (Muir & Geils 2002). Group size is up to 1 ha (2.5 acres). It will only be effective, and should only be considered, when the infestation is strongly aggregated in discrete patches. Individual-tree selection may be applied between the groups when light infection occurs throughout (Mathiasen 1989). A major problem is the presence of infected edges, often from latent infections, at the group boundary. Ensuring that boundaries go 30–40 ft beyond visibly infected trees should reduce the likelihood of infected edges (Conklin 2000).
6. **Do nothing**. When infection levels are high (stand DMR > 2) and there is little flexibility in diverging from strict uneven-aged management, the best alternative may be no action. Interceding under such constraints is not likely to improve matters over the long term and may make things worse.

8.2 Integrating mistletoe management with other objectives

Dwarf mistletoes are native elements of many western forests and, because of their intrinsic value in biodiversity, role in ecosystem function, and the influence they may have on other species, a balance should be sought in their management. Management objectives often include reducing the distribution and/or severity of dwarf mistletoe on part of a landscape, but eradication of *Arceuthobium* species has never been a goal.

8.2.1 Dwarf mistletoe conservation

Dwarf mistletoes are in no danger of extirpation; far from it. Indeed, in many areas it is thought that dwarf mistletoes are more widely distributed and abundant than they were before European settlement (see section 6.3, Historic practices). Still, a concern is sometimes raised that dwarf mistletoes provide valuable diversity to the forest. Although this is often justified on the basis that dwarf mistletoes enhance wildlife habitat (see section 5, Impacts of dwarf mistletoes on animals), a stronger justification may be the diversity provided by and value of the dwarf mistletoe as a species in its own right.

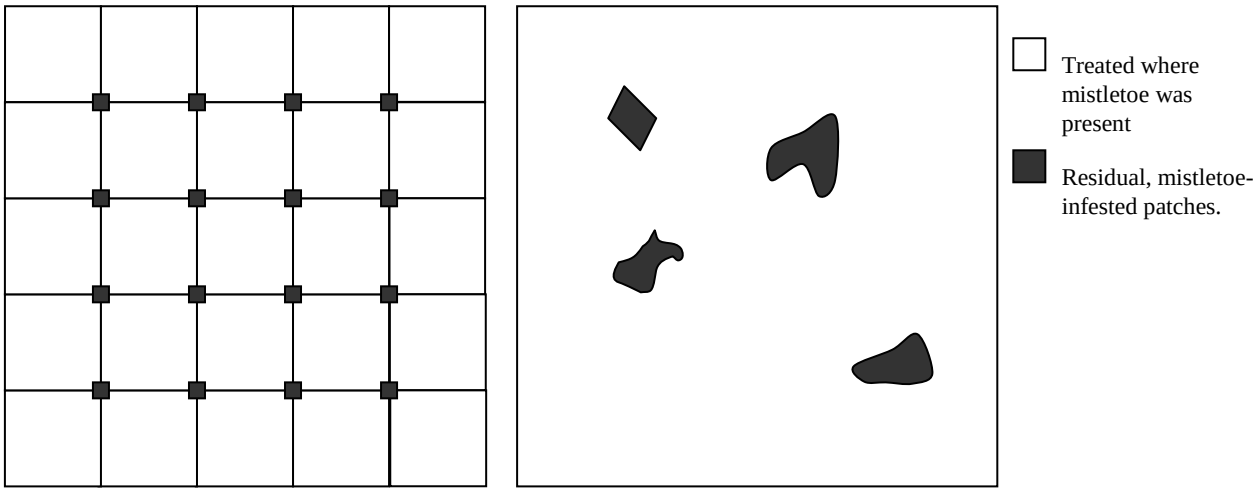
In many projects, the area proposed for treatment is surrounded by additional mistletoe-infested forest, and there is little need to be concerned about retaining dwarf mistletoe in treated units. In fact, rendering portions of the landscape more or less free of mistletoe often *increases* diversity in ways that may have important wildlife benefits.

In other projects, the area to be treated may encompass a majority of the infested forest in the immediate area. Depending on management emphases and objectives in this situation, there may be a desire to explicitly retain some mistletoe in treated units.

In this situation, what may happen is a compromise: reducing mistletoe somewhat, but leaving enough to nominally satisfy the diversity objective. However, partial treatment of mistletoe over a whole unit in this way can be a lose-lose proposition. The best-developed brooms and clusters of trees that may have the best wildlife value are removed, but enough mistletoe is left behind that the goal of improving productivity may not be met over the long term.

Rather than partially treating dwarf mistletoe uniformly over the unit, spatial segregation of dwarf mistletoe may be much more effective at achieving both objectives. Islands of heavy infestation can be left to achieve whatever diversity benefits are ascribed to them, and the remainder treated to allow trees to grow larger and live longer. An additional advantage of this approach is that it creates a patchy distribution of infection, in keeping with the natural distribution of the disease in a landscape. The only cost is the lowered productivity within the residual islands, and some expansion of the mistletoe from them over time.

Because of considerations on the size of treated areas in relation to subsequent spread from untreated areas (Figure 15), this strategy is most effective with larger treatment units. To avoid reinfestation of treated portions of the stand within a reasonable time, treated portions should be a minimum of 40 acres. Small, infested, residual patches could be left between them. In a thousand-acre treatment area, for instance, there could be a maximum of 25, 40-acre treated patches, with small (≤ 1 acre) infested patches between them (Figure 20A). However, treatment and residual patches would have to be on a perfect grid to be effective with that number. If fewer infested patches were left, they could be larger (perhaps up to 5–10 acres), and their placement and shape would be less critical and could be designed to take advantage of high mistletoe severity, patches with the biggest brooms, the most snags and other features that may be preferred by wildlife (Figure 20B).



A. 1000 acres with 25, roughly 40-acre treated areas. Small (≤ 1 ac.), mistletoe-infested patches could be left between them if desired.

B. The same area with fewer residual mistletoe-infested patches. In this approach the position, shape and size of the residual patches is more flexible. This approach would lead to less mistletoe spread, would be easier to lay out, and may be preferable for wildlife.

Figure 20. Two alternatives for leaving residual, mistletoe-infested patches in a hypothetical treated area of 1000 acres if this is desired while managing to reduce dwarf mistletoe impacts on tree growth and survival

8.2.2 Fuel reduction

In recent years, there has been an increasing need to reduce the risk of severe fire, particularly near communities and where the fire regime is substantially altered from the historic range of variability. In planning and accomplishing fuel reduction projects, it is important that dwarf mistletoe be incorporated into decision-making. Fuel reduction treatments in infested stands, if done without considering the effect on dwarf mistletoe, may increase the spread and intensification of the mistletoe. In the long run, this could lead to more heavily infested stands that actually increase the risk of severe fire.

A rapid evaluation of the mistletoe situation by a forest health specialist and a silvicultural prescription, based on forest health and fuel specialists' recommendations and information in this guide, take little additional time and are highly recommended. In addition to short-term fuel reduction, these fuel reduction projects should be an opportunity to improve forest conditions in a broader and longer sense.

8.2.3 Bark beetle prevention

Management of dwarf mistletoes and reduction of bark beetle risk are generally compatible and should be viewed as an integrated objective. Although risk factors vary slightly among the bark beetle species, stands of older, larger diameter, less vigorous trees are generally most susceptible. Dwarf mistletoe sanitation is compatible with reduction of basal area or average DBH to reduce stand susceptibility to bark beetles. Regeneration to establish new stands free of dwarf mistletoe is compatible with enhancing age diversity across the landscape to reduce landscape vulnerability to bark beetles.

In most cases, dwarf mistletoe increases susceptibility of trees to bark beetle attack (see section 4.1, Tree growth and longevity), suggesting that dwarf mistletoe management should be part of any objective to reduce stand susceptibility to bark beetles. Although lodgepole pine may be an exception to this generality, management objectives would often include low levels of both dwarf mistletoe and bark beetle mortality.

For lodgepole pine, stand susceptibility to mountain pine beetle is based on elevation, age and average stand DBH (Amman *et al.* 1977, McGregor & Cole 1985). Treatments recommended to reduce susceptibility include: a) patch cuts to regenerate stands with high susceptibility or with tree sizes conducive to beetle outbreaks, creating landscapes with low overall risk; b) partial cuts to remove individual trees in the high-risk category (>8″ DBH), and; c) favoring nonhosts. These approaches are all consistent with dwarf mistletoe management. Patch cuts would need to meet size and border guidelines for mistletoe management. Thinning may enhance resistance to bark beetle attack by increasing tree vigor (McGregor & Cole 1985), although it can also lead to thicker phloem development that can render trees more susceptible and increase brood development in attacked trees (Amman *et al.* 1977). Partial cuts, when appropriate from both mistletoe and beetle perspectives, could accomplish sanitation while reducing beetle susceptibility.

For ponderosa pine, risk of mountain pine beetle is rated based on basal area, average DBH and stand structure (Schmid & Mata 1992, Stevens *et al.* 1980). For most of Region 2, stands are rated high-risk if they are single-storied, average DBH is > 10″, and basal area is > 150 ft^2/acre, or if 2 of the 3 factors meet those criteria and the third meets the medium (2-storied, avg. DBH 6–10″, basal area 80–150). In the Black Hills, Nebraska and Samuel McKelvie National Forests, the basal area factor has a lower threshold for high risk (120 ft^2/acre). Treatments to reduce average DBH or basal area are almost always compatible with sanitation. The only potentially incompatible approach would be shifting from single-story to 2-story stands to reduce bark beetle risk; this would tend to increase the spread of dwarf mistletoe in most cases.

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