

Dwarf Mistletoes in Forest Canopies

Abstract

Dwarf mistletoes (*Arceuthobium* spp.) are parasitic flowering plants found throughout much of western North America on members of the Pinaceae. Heavy infection by these parasites affects biomass distribution on individual trees, and hence within forest canopies. Most dwarf mistletoes induce the formation of witches' brooms on infected hosts, and these brooms can significantly alter the structure of forest canopies as well. Conversely, forest canopy structure greatly affects horizontal and vertical spread of dwarf mistletoes. Dwarf mistletoes interact with other organisms that also inhabit forest canopies, such as birds, mammals, insects, and fungi. The principal interaction is the mistletoes serving as a food source for these organisms, but birds and mammals also use witches' brooms as nesting and foraging sites. Another interaction is long-range dissemination of dwarf mistletoe seeds by animal vectors, primarily birds and squirrels.

Introduction

Dwarf mistletoes (*Arceuthobium* spp., Viscaceae) are parasitic flowering plants that parasitize members of the Pinaceae in North America, Central America, Asia, and Africa. Because dwarf mistletoes are widespread in the western United States and Canada and most of the commercially important conifers of this region are severely parasitized by one or more dwarf mistletoes, foresters consider the dwarf mistletoes to be serious forest pests (Hawksworth and Wiens 1972, 1995). Heavily infected trees die prematurely, have reduced growth in height and diameter, and are often predisposed to attack by other diseases and insects (Hawksworth and Wiens 1972, 1995). Therefore, resource managers in many private, state and federal land management agencies have implemented strategies specifically designed to reduce the damage caused by dwarf mistletoes. Despite these efforts, dwarf mistletoes are common inhabitants of canopies in western forests.

My discussion of the dwarf mistletoes as components of forest canopies will concentrate on dwarf mistletoe population dynamics, witches' broom formation, effects of dwarf mistletoes on forest canopy structure and what we know about the ecological interactions between dwarf mistletoes and other forest canopy inhabitants.

Population Dynamics

To understand how dwarf mistletoes function in and affect forest canopies, how these parasites spread and intensify within forests (population dynamics) must first be examined. This exami-

nation will include a short discussion of the life cycle and seed dispersal mechanism. Hawksworth and Wiens (1995) provide a more detailed discussion of these processes.

The dwarf mistletoes are dioecious seed plants that have an unusual method of seed dissemination. Fruits produced on female plants mature in the late summer to early winter, contain one seed per fruit, and discharge the seed explosively (Hinds et al. 1963). Seeds are expelled at an initial velocity of about 27 m/sec and can fly as far as 15 m, depending on several factors (Hinds and Hawksworth 1965, Hawksworth and Wiens 1972, 1995). Seeds are coated with a substance called viscin that acts like a glue and allows dispersed seeds to adhere to objects they strike.

Seeds that land on susceptible trees can initiate new infections. Thousands of seeds are dispersed from heavily infected trees, but only about 5 percent of the dispersed seeds are estimated to land on a potential host and only 1-2 percent of those seeds establish successful infections (Hawksworth and Wiens 1972, 1995).

About two years after infection occurs, mistletoe shoots appear on the outside of the branch. In another two years, shoots produce flowers, and pollination occurs. In another 5-19 months, mature fruits disperse their seeds. On the average, the entire life cycle takes about 4-7 years to complete, depending on the species of dwarf mistletoe.

Because dwarf mistletoes are primarily disseminated by the explosive seed dispersal mechanism, forest canopy structure and density greatly influence spread of these parasites. Rates of ver-

tical spread in individual trees is largely governed by crown characteristics. Species with open crowns, such as pines (*Pinus* spp.), permit more rapid vertical spread. Species with dense crowns, such as true firs (*Abies* spp.), have less rapid vertical spread because their dense crowns influence seed flight more than trees with open crowns (Hawksworth 1965, 1969, Scharpf and Parmeter 1976, 1982). In addition, crown structure influences horizontal spread from tree to tree. Canopies composed of tree species with open crowns may allow more seeds to escape from within crowns and thereby provide less screening to prevent infection of nearby crowns. This factor probably has less influence on horizontal spread than on spread of dwarf mistletoes within individual trees, however (Parmeter 1978).

Tree density, which directly influences the canopy structure of a forest, also influences dwarf mistletoe population dynamics. Generally, dwarf mistletoes spread more rapidly in open canopy structures (lower densities of trees) than in dense canopy structures (Parmeter 1978). In areas with few trees, canopies may be so far apart that mistletoe seeds cannot reach neighboring canopies. Beyond some critical distance that varies with canopy height, topography, and the species of dwarf mistletoe, the probability of seed dispersal from one tree to another is unlikely. As distance between tree crowns decreases between infected and healthy trees, the probability of seeds reaching other trees increases. When canopies close, they screen seeds from reaching beyond the trees immediately surrounding infected trees. In addition, spread is influenced by the number of unsuppressible trees with crowns intermixed between those of susceptible trees (Parmeter 1978, Geils and Mathiasen 1990).

Probably the most clearly understood concept in dwarf mistletoe population dynamics is the effect of canopy height structure. In dwarf mistletoe-infested forests with different crown heights, the crowns of small trees are constantly exposed to dwarf mistletoe seeds from above. In these forests, the crowns of susceptible smaller trees can rarely remain free of increasing dwarf mistletoe populations. That the horizontal and vertical spread of dwarf mistletoes is more rapid in forests with multistoried canopies than in forests with single-storied canopies is well documented (Gill and Hawksworth 1954, Kuijt 1955, Kimmey and Graham 1960, Hawksworth 1961, Scharpf and

Hawksworth 1968, Scharpf and Parmeter 1976, 1982, Parmeter and Scharpf 1989, Geils and Mathiasen 1990).

Dwarf mistletoe population dynamics is greatly influenced by management activities because they obviously influence stand density, species composition and forest canopy structure. In some forests, dwarf mistletoe infection is undoubtedly greater because past forestry practices, such as high grading or partial cutting, have left forests more open, created multistoried canopies, or removed healthy or unsuppressible trees and left infected trees. These practices have often greatly favored population increases of dwarf mistletoes in forest canopies (Parmeter 1978, Maffei and Beatty 1988).

Along with past logging practices, the avid suppression of wildfire for the past 80 years has affected dwarf mistletoe populations. Fire is the primary natural disturbance that has influenced dwarf mistletoe population distribution in large forested areas (Alexander and Hawksworth 1975, Wicker and Leaphart 1976). Where large areas have been destroyed by intense wildfire, the replacement forests are free of dwarf mistletoes except at their margins. Because dwarf mistletoes slowly reinvade these forests at an average rate of only 30-60 cm/year (Hawksworth 1958, 1960, 1961, Shea and Stewart 1972, Wagener 1965, Crane and Fischer 1986), these replacement forests can remain free of dwarf mistletoes for many years. Because of patchy fuel accumulations and topographic features such as rock outcrops, even large, intense fires frequently leave individual or groups of infected trees within fire boundaries. These trees serve as sources of new infection as new regeneration becomes established after the fire. Frequently, dwarf mistletoe populations are centered around old, infected residuals that have survived fires and serve to reinfect the replacement trees in their immediate vicinity (Shea and Stewart 1972). This reinfection is certainly common in the dwarf mistletoe-infested stands of western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) and western larch (*Larix occidentalis* Nutt.) stands throughout much of the Pacific Northwest (Alexander and Hawksworth 1975, Wicker and Leaphart 1976, Crane and Fischer 1986).

Heinselman (1970) contends that because of the fire exclusion policy of public and private forestry protection agencies and organizations,

dwarf mistletoe populations in forested areas have greatly increased. Fire exclusion has helped create multistoried canopies which are conducive to increasing dwarf mistletoe populations and have essentially eliminated this natural control mechanism for dwarf mistletoes in unmanaged forests.

Witches' Brooms

One of the principal effects dwarf mistletoes have on their hosts, and hence on the canopies of infested forests, is that they induce the formation of witches' brooms (Figure 1). Witches' brooms exhibit several characteristics atypical of healthy host tissue, such as increased longevity (Weir 1916), elimination or reduction of cone and seed production by broomed branches (Bonga 1964, Kuijt 1969), increased branch elongation on some host species (Hawksworth 1961, Tinnin and Knutson 1980), increased biomass relative to healthy branches of the same age (Tinnin and



Figure 1. Witches' brooms caused by dwarf mistletoe infection on Douglas-fir in east-central Washington.

Knutson 1980), or decreased number, length, and mass of needles (Broshot et al. 1986.). A given species of dwarf mistletoe tends to stimulate brooms of a similar type on each infected principal host and on closely related alternate hosts (Hawksworth and Wiens 1972, Tinnin et al. 1982).

Witches' brooms have been characterized based on the pattern of infection, within the infected branches of the brooms, by their general shape, or their growth habit (Kuijt 1955, 1960, Hawksworth 1961, Hawksworth and Wiens 1972, 1995, Tinnin and Knutson 1980, Tinnin et al. 1982).

Formation of witches' brooms as a response to infection by dwarf mistletoes is thought to be related to an imbalance in one or more plant growth regulators in infected host tissue. Paquet (1979) and Schaffer et al. (1983) detected increased concentrations of cytokinins in infected branches compared to healthy branches of the same age. Livingston et al. (1984) reported increases in cytokinin and indole acetic acid concentrations and decreases in abscisic acid, in dwarf mistletoe-infected host tissue of black spruce (*Picea mariana* (Mill.) B.S.P.). The exact mechanisms through which these substances are related to witches' brooms remain unclear. Whether increased concentrations of cytokinins, indole acetic acid, or both disrupt the dominance exerted by the apical meristem of infected branches, thereby allowing the rapid growth of lateral twigs, or whether decreased concentrations of abscisic acid cause this phenomenon, is uncertain. How dwarf mistletoes cause changes in plant growth regulator concentrations is also not understood. Does the parasite produce and then release these substances into the host tissue to cause concentration increases? Or does it stimulate the host to produce additional amounts (or, for abscisic acid, reduced amounts) of the substances? Some evidence suggests that the first mechanism may be responsible for the increases in plant growth regulator concentrations (Paquet 1979, Schaffer et al. 1983), but more research is needed on this topic. A few dwarf mistletoes do not induce witches' brooms (Hawksworth and Wiens 1972, 1995), but again it is unclear why.

Dwarf mistletoe parasitism greatly alters the host's carbon allocation. Obviously, because the parasite is absorbing nutrients from its host, these nutrients are no longer available to the host. Eventually, the host begins to suffer as the dwarf mistletoe population it is supporting reaches a level where

the host cannot provide enough nutrients to supply the parasite's needs as well as its own. Gradually, host growth in height and diameter begins to decrease. Trees weakened extensively by dwarf mistletoe parasitism may be attacked by other diseases and insects that contribute to eventual death. As heavily infected trees die, their crowns thin and needles become chlorotic. Uninfected branches and witches' brooms in the upper crown often die first. Frequently, dead tops develop on these trees (Knutson 1983). The last branches to fade and die are typically the largest brooms near the bottom of the crown. This process usually takes several years, depending on the age of the tree and a variety of environmental factors. Witches' brooms are believed to act as nutrient sinks and command a large share of the metabolites produced by the host (Hull and Leonard 1964a, 1964b, Leonard and Hull 1965, Clark and Bonga 1970, Miller and Tocher 1975, Knutson 1983). Little information is available on the actual energy demands of infected branches compared to healthy branches, however. Careful measurements of the energy budget of infected trees and the effects of dwarf mistletoe parasitism on carbon allocation within infected branches are needed (Wanner and Tinnin 1986).

Changes in Canopy Structure Related to Dwarf Mistletoe Infection

Forests infested with dwarf mistletoes have very different canopy structures than do similar non-infested forests, for several reasons. As infection spreads and intensifies, the crown structure of trees changes dramatically. As more branches become infected, more brooms form, until a tree may become one large mass of dwarf mistletoe brooms (Figure 2). As dwarf mistletoe infection spreads through a forest, the whole canopy structure becomes dominated by trees with large witches' brooms, trees with spike tops, and dead trees with old brooms that may remain on trees for several years (Figure 3). These changes in canopy structure take many years.

Often, dwarf mistletoe infection is patchy within a stand, with discrete infection centers. Over time, many of these centers may coalesce to form infestations that cover many hectares. These forests consist of a mixture of dead trees, heavily broomed older trees, lightly infected younger trees, and some trees that have escaped infection for various reasons. As trees die, directly or indirectly

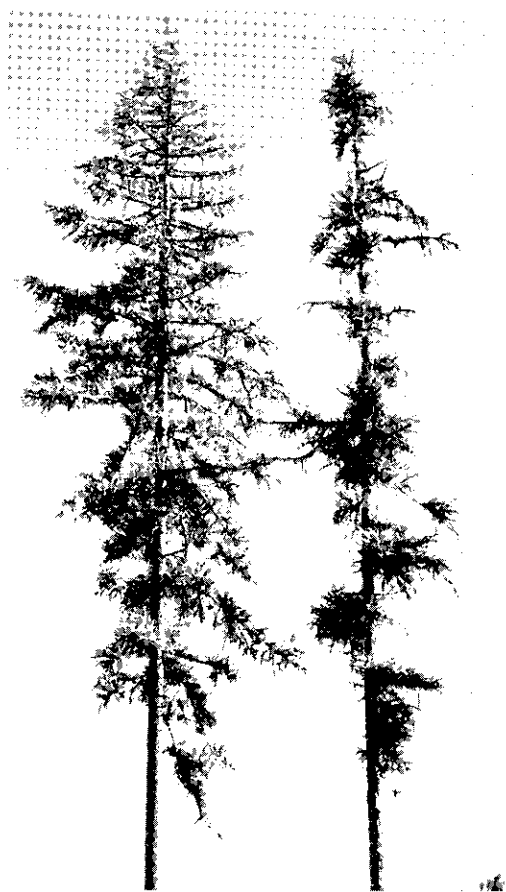


Figure 2. Western larch infected with dwarf mistletoe in northern Idaho. Tree on right is heavily infected and tree on the left is moderately infected. Note the difference in crown structure between the two trees.

as a result of parasitism by dwarf mistletoe, many snags are created within infested stands. Eventually, gaps develop in the forest canopy. These processes alter the canopy structure of the infested stand to the point where it no longer resembles the canopy structure of a similar, but uninfested stand. In mixed species forests, where one or more less susceptible or immune species are intermixed among highly susceptible species, the effect of dwarf mistletoe infection on canopy structure will be less pronounced.

Given that many other organisms directly benefit by using dwarf mistletoes for food or witches' brooms for shelter, or indirectly by using dead trees for nesting sites as do many cavity-nesting animals, the benefits to wildlife habitat derived from this gradual canopy structure conversion



Figure 3. Lodgepole pine stand heavily infested with dwarf mistletoe in northern Colorado. Canopy is composed of broomed and dead trees. Most of the understory trees are infected but are not yet heavily broomed.

could be substantial (Tinnin et al. 1982, Tinnin 1984). The infested stand is as highly complex ecologically (if not more so) as an uninfested stand and is ecologically distinct in its function and canopy structure. However, there are few studies comparing species diversity of dwarf mistletoe-free forests with similar, infested forests. Only in recent years have investigators examined these relations (Tinnin et al. 1982, Tinnin 1984, Bennetts et al. 1991, Sever et al. 1991).

Dwarf Mistletoes and Other Forest Canopy Inhabitants

Complex interrelations exist between dwarf mistletoes and a wide variety of other organisms that inhabit forest canopies in western North America (Hawksworth and Wiens 1995). Insects pollinate dwarf mistletoes and mistletoe shoots, pollen and nectar serve as food for various fungi, arthropods, birds, and rodents and other mammals. Animals forage among mistletoe shoots and witches' brooms. Witches' brooms serve as nesting sites for several species, and animals can serve as seed

vectors for dwarf mistletoes. These various interactions will be discussed separately below.

Arthropods and Dwarf Mistletoes

Dwarf mistletoes harbor numerous arthropods, but we know little about the ecological relations among them. Insects are thought to play an important role in pollinating dwarf mistletoes (Hawksworth 1961, Stevens and Hawksworth 1970, 1984, Gregor et al. 1974, Penfield et al. 1976, Player 1979, Hawksworth and Wiens 1995). The principal pollinators identified thus far are thrips (Thysanoptera), ants (Hymenoptera), and a wide variety of flies (Diptera).

Several species of arthropods, especially Lepidoptera larvae, feed on dwarf mistletoe shoots, and some are thought to be specific to dwarf mistletoes (Stevens and Hawksworth 1970, 1984, Hawksworth and Wiens 1995). Feeding by insects is sometimes highly destructive to the shoots (Scharpf and Koerber 1986), but little is known about the effects of insect feeding on dwarf mistletoe populations over long periods. Only a few

insects that feed on dwarf mistletoes have been commonly collected or have had their life histories studied (Stevens and Hawksworth 1970, 1984, Hawksworth and Wiens 1995). These include the following Lepidoptera: *Filatima natalis* (Heinrich), *Dasypygia alternosquamella* Raganot, and *Mitoura spinetorum* (Hewitson). Each of these insects is specific to dwarf mistletoes and has been destructive to shoots in some locations (Heinrich 1921, Hawksworth 1961, Shields 1965, Stevens and Hawksworth 1970, 1984). Another species, *Mitoura johnsonii* Skinner, occurs on hemlock dwarf mistletoe from Oregon to British Columbia (McCorkle 1962).

Another group of arthropods commonly found associated with dwarf mistletoe shoots is plant bugs in the genus *Neoborella*, particularly *N. tumida* Knight. This species is a widespread associate of several dwarf mistletoes throughout the western United States (Stevens and Hawksworth 1970, 1984, Hawksworth and Wiens 1995). Although plant bugs are commonly associated with dwarf mistletoe shoots, they seem to cause little if any observable damage to the shoots.

One of the most interesting and easily observed arthropods found frequently associated with dwarf mistletoes, particularly in the Southwest, is a spittlebug, currently classified as *Clastoptera distincta* Doering (Stevens and Hawksworth 1984, Hawksworth and Wiens 1995). Spittlebugs are sucking insects, some of which are important plant pests. Their common name describes their nymphs, which live and feed in masses of a secreted material that resembles spittle. High populations of this insect have destroyed large numbers of dwarf mistletoe shoots (Hawksworth 1961), but spittlebug populations are seldom large enough to seriously affect dwarf mistletoe populations over large areas.

Several species of mites have been found associated with dwarf mistletoes. The life histories, habits, and ecological relations of dwarf mistletoe-inhabiting mites have received little study, however (Stevens and Hawksworth 1970, 1984, Hawksworth and Wiens 1995).

Spiders have been found associated with dwarf mistletoes in Colorado (Jennings et al. 1989). More than 20 spider species were found to be associated with three different species of dwarf mistletoe. The ecological relationships of these spiders with dwarf mistletoes have not been investigated in any detail. Possible relations include spiders

as pollen vectors or deterrents to pollen dispersal (webs catch pollen), as predators of insects that are directly associated with dwarf mistletoes (pollinators or herbivores), and as predators of casual insect visitors to dwarf mistletoes (Jennings et al. 1989).

Because tree mortality greatly affects the stand and canopy structure of western forests, insects that kill trees and their relations with dwarf mistletoes must be mentioned. Much of this information is based on observations, but some quantitative data are available. Most of the completed work has dealt with the relations between dwarf mistletoes and bark beetles in the genus *Dendroctonus*. Dwarf mistletoes evidently do increase the susceptibility of infected trees to attack by certain bark beetles. The best documented examples are for western pine beetle (*Dendroctonus brevicornis* Lec.) and mountain pine beetle (*D. ponderosae* Hopkins) in ponderosa pine (*Pinus ponderosa* Laws.) (Stevens and Hawksworth 1984). In addition, "secondary" insects (*Ips* spp. and *Melanophila* spp.) have often been reported to attack and kill dwarf mistletoe-infected trees. Stevens and Hawksworth (1984) and Hawksworth and Wiens (1995) present excellent summaries of the reported relations between tree mortality, insects, and dwarf mistletoes.

Fungi and Dwarf Mistletoes

Several species of fungi have been identified as hyperparasites of dwarf mistletoe shoots (Kuijt 1963, Wicker and Shaw 1968, Hawksworth et al. 1977, Scharpf 1986, Hawksworth and Wiens 1995). Table 1 lists these fungi and their known geographic distribution in western North America.

Several species of fungi infect branch tissue that is already infected by dwarf mistletoes. These fungi are referred to as "canker fungi" because they kill the cambium of the host branch as well as the dwarf mistletoe. Most of these fungi have been described in association with the western hemlock dwarf mistletoe (*Arceuthobium tsugense* (Rosendahl) G.N. Jones subsp. *tsugense*) in British Columbia (Baranyay 1966, Funk and Baranyay 1973, Funk 1981, Funk and Smith 1981). Little is known about how these fungi affect dwarf mistletoe populations. One of these fungi, *Nectria macrospora* (Wr.) Ouellette, has been reported to reduce dwarf mistletoe reproduction in some areas (Funk et al. 1973, Smith and Funk 1980).

TABLE 1. Fungi known to be hyperparasites of dwarf mistletoe shoots in western North America and their known geographical distribution based on parasitism of dwarf mistletoes.¹

Fungus	Reported Distribution
<i>Wallrothiella arceuthobii</i> (Peck) Sacc.	United States, Canada, and Mexico
<i>Colletotrichum gloeosporioides</i> Penz.	Western United States, Canada, and Mexico
<i>Cylindrocarpon gillii</i> (Ellis) J. A. Muir	Western United States, Canada, and Mexico
<i>Cylindrocarpon</i> sp.	Southern Mexico
<i>Alternaria alternata</i> (Fr.) Keissler	Manitoba, Canada
<i>Metasphaeria wheeleri</i> Linder	California
<i>Herpotrichia juniperi</i> (Duby) Petrak	California
<i>Pestalotia maculiformans</i> Guba & Zeller	Washington
<i>Pestalotia heterocornis</i> Guba	Dominican Republic

¹ Based on information in: Kuijt 1963; Hawksworth et al. 1977; Scharpf 1986; Hawksworth and Wiens 1995.

Scharpf (1969, 1983) demonstrated that *Cytospora abietis* Fr. is consistently associated with dwarf mistletoe infections of red fir (*Abies magnifica* A. Murr.) and white fir (*A. concolor* (Gord. & Glend.) Lindl.) in California. About 20 percent of the dwarf mistletoe-infected branches he examined were also infected by *C. abietis*. Scharpf concluded that infection by this fungus is responsible for a reducing the total dwarf mistletoe population on dwarf mistletoe-infected true firs in California. Filip et al. (1979) reported that *C. abietis* also infected dwarf mistletoe-infected branches on noble fir (*A. procera* Rehd.) and Pacific silver fir (*A. amabilis* (Dougl.) Forbes) in Oregon. They also reported two additional fungi associated with dwarf mistletoe infections on these two true firs: *Cryptosporium pinicola* Linder and *Cylindrocarpon cylindroides* Wollen (the imperfect stage of *Nectria fuckeliana* Booth). Byler and Cobb (1972) reported *N. fuckeliana* infections associated with dwarf mistletoes on bishop pine (*Pinus muricata* D. Don) and white fir in California. Diplodia tip blight (*Sphaeropsis sapinea* (Fr.) Dyko & Sutton) has been associated with dwarf mistletoe infections on both digger pine (*Pinus sabiniana* Dougl.) and bishop pine (Hunt 1969).

A rust fungus, *Peridermium bethelii* Hedgcock and Long, is consistently associated with infections of lodgepole pine dwarf mistletoe (*Arceuthobium americanum* Nutt. ex Engelm.) on lodgepole pine (*Pinus contorta* Dougl. ex Loud.) in the Rocky Mountains and California (Hawksworth et al. 1983). The role of the dwarf mistletoe in

the life cycle of the rust is not well understood, however. More work is needed on the relation of the rust and the mistletoe as well as the taxonomic status of the rust (Hawksworth et al. 1983).

Animals and Dwarf Mistletoes

The majority of the investigations on the relations between animals and dwarf mistletoes have been related to animals acting as vectors for long-range dissemination of dwarf mistletoe seeds (Hawksworth and Wiens 1995). This relation has now been well documented by several investigators (Nicholls et al. 1984, 1989, Punter and Gilbert 1989, Hawksworth and Wiens 1995). Although the importance of animal dissemination of dwarf mistletoe seeds remains uncertain, it is undoubtedly responsible for establishing new infection centers at much greater distances than could be attained by the explosive seed dispersal mechanism (Hawksworth and Wiens 1995). Several animals, primarily birds and squirrels, have been identified as vectors of dwarf mistletoe seeds (Table 2).

Another relation that has been well documented between animals and dwarf mistletoes is the use of witches' brooms as nest sites (Table 3) (Hawksworth and Wiens 1995). Whether animals rely on or preferentially select dwarf mistletoe-induced witches' brooms as nest sites is still under study. Recent studies of the northern spotted owl (*Strix occidentalis caurina*) in the eastern Cascade Range of Washington indicate that these owls frequently nest in dwarf mistletoe brooms (Irwin et al. 1989, Richards 1989, Forsman et al. 1990, Martin et al. 1992). Recent observations in

TABLE 2. Animals identified as vectors of dwarf mistletoe seed.¹

Birds	Mammals
Steller's jay	Red squirrel
Gray jay	Flying squirrel
Three-toed woodpecker	Golden-mantled squirrel
Williamson's sapsucker	American marten
Robin	Least chipmunk
Dark-eyed junco	
Gray-head junco	
Hermit thrush	
Northern saw-whet owl	
Audubon's warbler	
Yellow warbler	
Palm warbler	
Yellow-rumped warbler	
Mountain chickadee	
Cassin's finch	
Pygmy nuthatch	
Chipping sparrow	
Townsend's solitaire	
Red crossbill	
Brown creeper	
Swainson's thrush	
Red-breasted nuthatch	

¹Based on information in: Nicholls et al. 1984, 1987, 1989; Punter and Gilbert 1989; Hawksworth and Wiens 1995.

western Oregon have confirmed that marbled murrelets (*Brachyramphus marmoratus*) use witches' brooms caused by western hemlock dwarf mistletoe in western hemlock as nest sites (Clint Smith, Oregon Department of Forestry, Salem, pers. comm.). Red, Abert, and flying squirrels also use dwarf mistletoe brooms for nest sites (Farentinos 1972, Hawksworth and Wiens 1995).

Several animals feed on dwarf mistletoe shoots or indirectly on the endophytic system, by chewing and eating dwarf mistletoe-infected bark (Hawksworth and Wiens 1995). Table 4 lists the animals reported to use dwarf mistletoes as a food source. Although the use of dwarf mistletoes as food by various animals is well documented, the importance of dwarf mistletoes in the diet of these animals is uncertain. Much of the use of dwarf mistletoes appears to be during the winter when other food sources are less common or completely unavailable. Dependence by birds, rodents or

TABLE 3. Animals that use dwarf mistletoe-caused witches' brooms for nesting.

Birds	Mammals
Pine siskin	Red squirrel
Gray jay	Abert squirrel
Red crossbill	American marten
Robin	
Raven	
House wren	
Mourning dove	
Western tanager	
Chipping sparrow	
Hermit thrush	
Cassin's finch	
Marbled murrelet	
Northern spotted owl	
Mexican spotted owl	
Great gray owl	
Great horned owl	
Long-eared owl	
Cooper's hawk	
Goshawk	
Sharp-shinned hawk	

¹Based on information in: Farentinos 1972; Tinnin et al. 1982; Smith, pers. comm. 1994; Hawksworth and Wiens 1995.

TABLE 4. Animals that use dwarf mistletoes as food.¹

Birds	Mammals
Black-headed grosbeak	Chipmunks
Evening grosbeak	Porcupine
Blue grouse	Elk
Spruce grouse	Mule deer
Richardson grouse	White-tail deer
Ruffed grouse	Red squirrel
Black-capped chickadee	Abert squirrel
House sparrow	
Thrush	
Western bluebird	
Mountain bluebird	
Phainopepla	
Mourning dove	
Robin	
Band-tailed pigeon	

¹Based on information in: Pinkowski 1981; Tinnin et al. 1982; Crawford et al. 1986; Pederson et al. 1987; Allred 1989; Hawksworth and Wiens 1995.

mammals on dwarf mistletoes has not been reported. Investigators have demonstrated that dwarf mistletoe shoots are highly digestible; they are high in carbohydrates but low in mineral and protein content (Urness 1969, Craighead et al. 1973).

Little information is available on the use of dwarf mistletoe brooms by animals for hiding cover, resting sites, or foraging sites. Martinka (1972) reported the use of brooms for hiding cover by blue grouse (*Dendragapus obscurus*) in Montana. Martens (*Martes americana*) have been observed using dwarf mistletoe-caused witches' brooms for resting sites (Campbell 1979, Hauptman 1979, Burnett 1981, Spencer 1987, Buskirk et al. 1987). Other animals probably use dwarf mistletoe brooms for cover, resting sites, and foraging sites but these relations are poorly documented.

In general, the relations between dwarf mistletoes and the myriad of organisms that inhabit forest canopies are not well understood. Because dwarf

mistletoes are common parasites in western forests, investigators working on forest canopy research should consider the effects of dwarf mistletoes on canopy structure and possible interactions between dwarf mistletoes and other species. We may find that species diversity is much greater within dwarf mistletoe-infested canopies than in the canopies of mistletoe-free forests in the Pacific Northwest, if we examined these canopies more thoroughly. For example, studies in the Front Range of Colorado have demonstrated that the abundance and number of species of passerine birds and the abundance of cavity-nesting birds is higher in dwarf mistletoe-infested ponderosa pine stands than in non-infested stands (Bennetts et al. 1991, Sever et al. 1991). Bennetts et al. (1991) also reported that elk and deer activity were higher in dwarf mistletoe-infested stands. Further studies of this nature may demonstrate that similar relations exist between many other organisms and dwarf mistletoes.

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