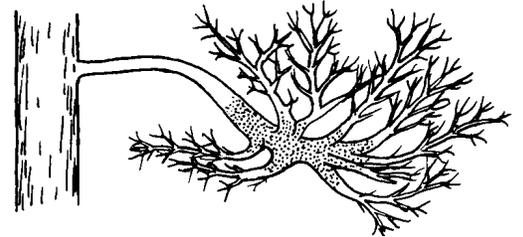


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# Chapter

# 5

## Damage, Effects, and Importance of Dwarf Mistletoes



All dwarf mistletoes are parasites that extract water, nutrients, and carbohydrates from the infected host; they are also pathogens that alter host physiology and morphology (Gill and Hawksworth 1961, Hawksworth and Wiens 1996). Disease or direct effects are reductions in diameter and height increment, survival, reproduction, and quality; witches' brooms are formed in many pathosystems (Knutson and Tinnin 1980). Where dwarf mistletoe populations develop significant, long-term infestations, cumulative tree damages have various ecological and evolutionary effects. Depending on management objectives and priorities, these effects are interpreted as positive, negative, or usually of mixed consequences. In chapter 4, we discuss in general how the mistletoe's environment affects its growth and development and relate how mistletoe abundance is described by a relative severity index, DMR. In following chapters, the authors present information for quantifying host and mistletoe populations;

they also indicate numerous ways in which managers can influence mistletoe through manipulation of biotic agents, host genetics, and forest stands. In this chapter, we review the physiology of mistletoe parasitism, describe disease effects on infected host trees, identify some of the complex ecological and evolutionary interactions of which mistletoes play a role, and relate these effects and interactions to their consequences for resource management.

## Physiology of Dwarf Mistletoe Parasitism

Dwarf mistletoes cause tree disease by affecting host water relations and growth (Knutson 1983, Kolb 2002). The shoot and leaf surface of dwarf mistletoes is small compared to other mistletoes, but they have significant effects on host water relations (Fisher 1983, Sala and others 2001, Wilson and Calvin 1996). Although dwarf mistletoe shoots do transpire, significant transpiration loss is by host foliage, especially those with large witches' brooms. Dwarf mistletoes affect host growth through the interaction of the host with the mistletoe endophytic system (Alosi and Calvin 1985, Calvin and Wilson 1996). The physiological processes involved include: (1) production of growth regulating compounds and (2) expropriation and reallocation of water, minerals, and carbohydrates (Livingston and others 1984, Rey and others 1991, 1992, Snyder and others 1996). The pathological symptoms are retention of infected branches, abnormal growth of infected branches (witches' brooms), crown dieback, and death (Anderson and Kaufert 1959, Broshot and Tinnin 1986, Hawksworth 1961).

Dwarf mistletoe infection affects host foliage, phenology, and respiration. Numerous authors report that needles of severely infected trees are smaller, fewer, and yellowish (Andrade and Cibrián 1981, Hawksworth 1961, Hawksworth and Johnson 1989a, Korstian and Long 1922, Weir 1916b). *Pseudotsuga menziesii* with *Arceuthobium douglasii* initiate bud break earlier and form longer shoots on brooms (Briede and others 1991). Dwarf mistletoe infected trees have lower respiration rates (Ryan 1990, Wanner and Tinnin 1986), perhaps the result of carbohydrate deficiency. Tree vigor as a single "health" index is evaluated in numerous ways; Schaffer and others (1983a) relate mistletoe infection with vigor and electrical resistance of bark tissues. Srivastava and Esau (1961) and Cibrián and others (1980) examine the effects of infection for distorting the host wood anatomy. One difficulty in researching dwarf mistletoe–host physiology is detecting and quantifying the endophytic system especially during incubation and latency. Marler and others (1999) demonstrate a polymerase chain reaction

(PCR) method for identifying infected branches based on presence of mistletoe DNA.

## Direct Effects to Host Trees

The pathological results of dwarf mistletoe infection are seen as reductions in reproduction, growth, longevity, and quality. The nature and magnitude of these effects are determined by the mistletoe and host species involved, infestation severity (usually measured as DMR, see chapter 4), and vigor of the host. These factors are in turn affected by age, history, and the influences of insects, other disease agents, competition, site quality, and climate (Hawksworth and Scharpf 1978, Hawksworth and Shaw 1984, Hawksworth and others 1992a). From a management perspective of mitigating these effects, the important considerations are time and opportunity. Both mistletoe intensification and damage are progressive and cumulative; they begin at a slow rate, with little effect, but increase exponentially, accumulating to a large effect. Damage first becomes evident when the crown of the host tree is about half infected (moderately infected, DMR class 3) and becomes increasingly severe as the infection intensifies to its culmination when the entire crown is infected and the tree dies. Mistletoe intensification and damage are also interactive with each other and responsive to numerous external factors. Models such as documented by Hawksworth and others (1995) integrate these numerous interactions and factors and portray the development of an infestation with useful management indicators such as numbers of trees, basal area, volume, and ingrowth.

## Reproduction

Dwarf mistletoe affects host reproduction through cone production, seed quantity and quality, and seedling survival. Mature trees are large and usually have numerous reserves; a severe mistletoe infection, however, can reduce cone and seed production. Seedlings are especially vulnerable; a single mistletoe infection on the seedling is either lethal or so damaging the host sapling appears more like a bush than a tree.

**Cones and seeds**—Few studies are available on cone and seed production of dwarf mistletoe-infected trees. Cone production on witches' brooms as measured by numbers and size is usually reduced, but some viable seed may still be produced (Bonga 1964, Kuijt 1960b, Sproule 1996b, Weir 1916b). The reproductive output of infected trees appears to vary by species and severity of infection. Seed germination from parent *Pinus ponderosa* trees infected by mistletoe is reduced (Pearson 1912); germination is only 60 percent for seeds from moderately infected trees and

75 percent for severely infected trees (Korstian and Long 1922). Seed from infected *P. jeffreyi* are smaller, germinate less (80 percent), and produce poor seedlings (Munns 1919). For *P. contorta*, Schaffer and others (1983b) report cone size, seed size, and seed germination are negatively correlated with infection severity. Although Wanner (1986) has similar results for cones and seeds, he observes an initial increase in seedling stocking (at age 1 year) for some in heavily infested stands and attributes this increase to better seedbed conditions, which in these cases offset reduced numbers of seeds produced. Infected *Picea mariana* produce fewer cones, fewer seeds, lighter seeds, and lower germination rates than uninfected trees (Singh 1981, Singh and Carew 1989). In contrast to these reports, Reid and others (1987) did not observe an effect on cone production for infected *Pinus rudis*.

**Seedlings**—Disease incidence in young stands can be high (see for example Roth 1971, Scharpf and Vogler 1986, Weir 1916b). This is especially serious because seedlings and saplings are severely damaged by infection with even a few mistletoe plants. Reduced height of infected seedlings compared to uninfected seedlings is reported by Knutson and Toevs (1972) and Roth (1971). Seedlings are usually infected on the main stem and quickly killed by the mistletoe. Because of high turnover rates and rapid deterioration after death, mortality rates among seedlings are difficult to determine. Studies such as Roth (1971) in which he observed 50 percent loss of infected seedlings after 12 years, however, support the claim that early mistletoe infection is usually lethal. Those that survive for a few years at least, often develop into little more than a single broom and resemble a bush or bonsai.

## Growth

An obvious and important fact about conifer trees is that they grow; they accumulate stem wood on a bole that increases in width, length, and volume. The annual increment for accretion in width varies along the bole and is measured for convenience at a given reference height. The variation in width along the bole is described as form; measures of width, length, and form are used to compute volume. By diverting the tree's resources to other outputs, a mistletoe infestation in a tree affects diameter growth and height growth, and so consequently affects form and volume. Fundamental to forest management is the ability to project expected tree growth under various treatment options. These projections are now often made with simulation models such as the Forest Vegetation Simulator (FVS, Forest Management Service Center 2001) and PrognosisBC (British Columbia Ministry

of Forests 2000). Numerous intrinsic and extrinsic factors determine tree growth; these can be categorized as species, site, history, competition, and for infected trees, mistletoe severity. Site covers those long-term, generally fixed factors related to the potential productivity of the area such as soil fertility, water holding capacity, and climatic suitability. History reflects past events (droughts) and conditions (stagnation) that affect a tree's crown, its photosynthetic engine. Competition encompasses factors measured by stand density as basal area. Mistletoe severity is usually quantified as DMR (Hawksworth 1977, chapter 4). Quantitative studies reveal that these factors are usually confounded; that is, they interact so the effect of one factor varies as the level of another factor is changed.

Several techniques exist for study of tree growth. Stem analysis (for example, Baranyay and Safranyik 1970) is the most intensive but provides detailed information on diameter and height increment as well as form and volume. Individual trees can be identified and reexamined after a period of time to obtain information on each tree's change in diameter and height (for example, Hawksworth 1961). Alternatively, trees can be examined once and past diameter growth determined from an increment core (for example, Tinnin and others 1999). Some studies compare the diameters (or heights) for trees of different mistletoe classes; but unless all the trees were the same size and infected at the same time, this method introduces several complications and does not really measure growth response to infection.

Although numerous studies relate mistletoe severity to tree growth, few generalities can be made (Hawksworth and Wiens 1996). Some recent studies use a stem analysis technique (Andrade and Cibrián 1980, Baranyay and Safranyik 1970, Pousette 1991, and Smith 1969). Other studies that examined trees and increment cores include those by Barrett and Roth (1985), Filip and others (1993), Knutson and Tinnin (1986), Mathiasen and others (1990), Tinnin (2001), Tinnin and others (1999), and Vera (1984). Reduction in diameter increment is related to infection severity in nonlinear fashion: with little or no significant reduction for the DMR classes 1 to 3, some reduction for DMR class 4, more for DMR class 5, and much for DMR class 6. The magnitude of these reductions depends on numerous factors (Hawksworth and others 1995, Hawksworth and Shaw 1984, Thomson and others 1997, Wicker and Hawksworth 1988). Reduction in height increment is also related to infection severity; height effects usually appear at a lower severity and are proportionally greater with increase by DMR class. The combined effects of diameter reduction and height reduction on form and volume can vary by species and age (Pousette 1991, Tinnin 2001). Volume reductions,

either accounting for stem form or not, are proportionately greater than reductions for diameter or height alone. Because mistletoe infection often occurs earliest on some of the larger trees of a stand, size comparisons of trees in different severity classes do not well reflect effects on growth increment.

## Longevity

Mistletoe not only kills small trees but in time, a severe infection can even kill a mature, large tree (Roth 2001). A severe infestation (for example, Wood and others 1979) with many seriously infected trees can generate a high mortality rate. Mortality rates (see Hawksworth and Wiens 1996) are determined from either reexamining a plot after a known period of time (dependable) or estimating which trees had died within the reference period (undependable). The effect of mistletoe on tree survival can also be expressed in terms of tree longevity, the period of time over which a fraction (usually 50 percent) of trees are expected die. Because tree mortality is infrequent and then occasionally synchronous with events such as droughts (Childs 1960, Page 1981, Smith 1983), longevity studies over a long period with frequent observations (Hawksworth and Geils 1990) are especially useful. Like growth effects, mortality is related to a number of interacting factors; the most important are species, size, infection severity, and other mortality agents.

Hawksworth and Wiens (1996) identify 17 mistletoe species that are especially lethal for certain hosts and locations (table 5-1). These hosts include many important forest species such as *Abies magnifica* (Parmeter and Scharpf 1982), *Larix occidentalis* (Weir 1916a), *Picea mariana* (Baker and French 1991), *Pinus contorta*

(Baranyay and Safranyik 1970, Hawksworth and Johnson 1989a), *P. ponderosa* (Hawksworth 1961, Roth 2001), and *Pseudotsuga menziesii* (Filip and others 1993, Mathiasen and others 1990). A study reported by Hawksworth and Geils (1990) and Geils and others (1991) demonstrates the interacting (and nonlinear) effects of tree size (diameter) and infection severity (DMR) on the longevity of mistletoe-infected pine. The expected longevity for 50 percent of trees with a severe infection (DMR 6) is less than 10 years for smaller trees (less than 9 inches diameter) and more than 10 years for larger trees. Over 40 years, however, many of the larger, severely infected trees died. During this time, some of the originally moderately infected trees became severely infected and died at a rate greater than that for uninfected trees. Elevated mortality rates due to mistletoe infection are built into the Dwarf Mistletoe Model Impact Model (Forest Health Technology Enterprise Team 2002).

Extremes in temperature and moisture can affect mortality rates of dwarf mistletoe-infected trees. Mortality rates are often highest following periods of drought, but there are few quantitative data. The most comprehensive studies of the interaction of drought and mistletoe are by Page (1981) and Smith (1983) for the California drought of 1975 through 1977. Drought may increase mortality of mistletoe-infected trees more than four times that of uninfected trees. Smith and McMahan (2002) describe an eco-physiology extension for the Forest Vegetation Simulator (Forest Management Service Center 2001). The method they present could be modified and developed for adjusting mistletoe-caused mortality rates to account for climatic variation.

**Table 5-1**—Combinations of North American taxa of *Arceuthobium* and their hosts in which host mortality rates are particularly high.

<i>Arceuthobium</i>	Host	Location
<i>A. abietinum</i> f. sp. <i>magnificae</i>	<i>Abies magnifica</i>	CA
<i>A. americanum</i>	<i>Pinus contorta</i> ; <i>Pinus banksiana</i>	Western US and Canada; MB, SK, and AB, Canada
<i>A. blumeri</i>	<i>Pinus</i> spp.	Chihuahua and Durango, Mexico
<i>A. campylopodum</i>	<i>Pinus ponderosa</i>	Southern CA
<i>A. cyanocarpum</i>	<i>Pinus flexilis</i> ; <i>Pinus albicaulis</i>	ID, UT, WY, CO; northern CA
<i>A. douglasii</i>	<i>Pseudotsuga menziesii</i>	Western North America
<i>A. durangense</i>	<i>Pinus</i> spp.	Jalisco, Mexico
<i>A. gillii</i>	<i>Pinus</i> spp.	Chihuahua and Durango, Mexico
<i>A. guatemalense</i>	<i>Pinus ayacahuite</i>	Southern Mexico and Guatemala
<i>A. laricis</i>	<i>Larix occidentalis</i>	Northwestern US and BC, Canada
<i>A. microcarpum</i>	<i>Picea pungens</i>	AZ, NM
<i>A. nigrum</i>	<i>Pinus</i> spp.	Durango and Puebla, Mexico
<i>A. occidentale</i>	<i>Pinus sabiniana</i>	CA
<i>A. pusillum</i>	<i>Picea mariana</i> ; <i>Picea glauca</i>	Eastern North America
<i>A. strictum</i>	<i>Pinus leiophylla</i>	Durango, Mexico

## Wood Quality, Decay, and Breakage

Although mistletoe infections usually occur on branches, the endophytic system can invade the bole and potentially affect wood quality. Infections and broken branches caused by heavy witches' brooms provide an entry court for decay fungi. Infected branches and brooms are resinous and dense with other flammable materials. These effects of mistletoe infection are important in some situations.

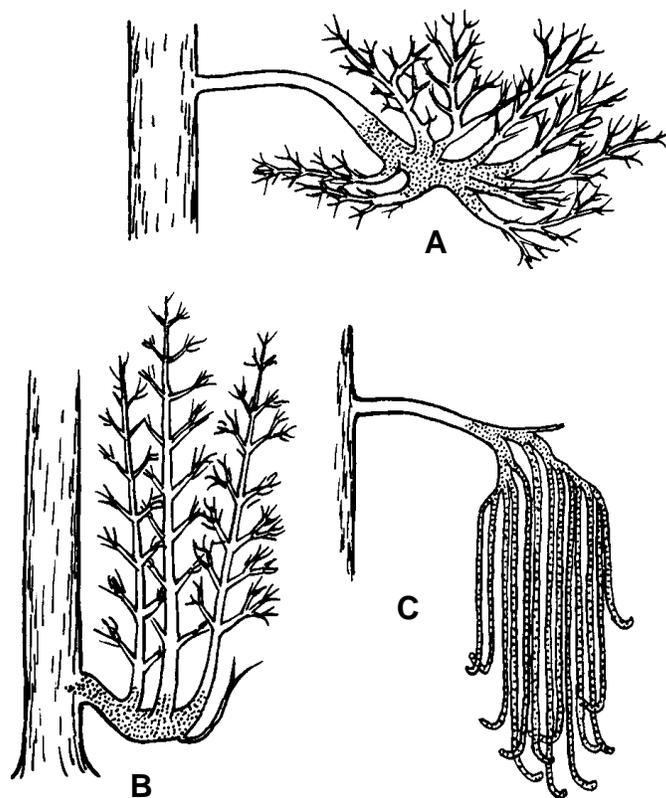
Wood quality of mistletoe-infected trees is affected by production of larger knots, development of abnormal grain, reduced strength, and other altered physical and chemical properties. Infected wood such as found in mistletoe-burls is characterized by shorter, distorted tracheids, increased ray volume, included pitch, frass, and decay (Cibrián and others 1980, Piirto and others 1974, Weir 1916a). The effects on sapwood moisture content and specific gravity are variable: higher, lower, or not different from uninfected wood (Hawksworth 1961, Knutson 1970, Wellwood 1956). Piirto and others (1974) report, however, that infected wood and wood from other parts of infected trees is weaker in strength for modulus of elasticity, modulus of rupture, and work to proportional limit. The effects on pulp quality, however, are negligible (Dobie and Britneff 1975, Hunt 1971, Wilcox and others 1973).

The association of decay and mistletoe varies by species and tree age. In fir, larch, or hemlock trees, mistletoe infections often provide an infection court for decay fungi, especially if the wood is exposed (Aho 1982). Englerth (1942) reports that nearly a third of the decay in hemlock entered through dwarf mistletoe stem infections and adjacent swollen limbs. Several decay fungi are associated; the most frequent is the common brown cubical slash decay fungus *Fomitopsis pinicola* (Etheridge 1973). Decay is usually limited to the area of the swollen bole canker (Aho 1982). Decay is rarely associated with mistletoe infection in the more resinous pines, spruce, and Douglas-fir. Well-managed, young-growth stands of true fir in California should also have little loss from mistletoe-associated decay (Parmeter and Scharpf 1982).

## Witches' Brooms

Most dwarf mistletoes and several other disease agents induce abnormal development of host branches into witches' brooms. Mistletoe brooms are infected host branches with excessive branching and shortened (or lengthened) internodes that develop in response to elevated levels of plant growth compounds (Schaffer and others 1983c). Broom form is determined by the mistletoe and may even be a useful taxonomic character. There are a variety of broom forms and classification schemes based on the distribution of the endophytic system, on the host branching

pattern, and on the boom position relative to the bole. Systemic or isophasic brooms are those in which the endophytic system of the mistletoe grows with the apical and cambial tissues of the host and produces mistletoe shoots either along the branch or at branch girdles (Hawksworth 1961, Kuijt 1960b). Nonsystemic or anisophasic brooms are those in which the endophytic system remains localized near the original site of infection and only grows with the host cambium (fig. 5-1). *Arceuthobium globosum* subsp. *globosum* and *A. occidentale* do not induce typical broom formation. Most North American mistletoes usually develop nonsystemic brooms and rarely systemic brooms. *Arceuthobium americanum*, *A. douglasii*, *A. guatemalense*, and *A. pusillum* consistently produce systemic brooms (Hawksworth and Wiens 1996). Hawksworth (1961) classifies brooms of *Arceuthobium vaginatum* as typical for nonsystemic brooms where the localized infection is far from the bole, and although branching is prolific, segments are short (fig. 5-1A). He describes the uncommon, volunteer leader



**Figure 5-1**—Witches' brooms on *Pinus ponderosa* induced by *Arceuthobium vaginatum*; stipple areas indicate region invaded by the mistletoe. **A**, typical broom; **B**, volunteer leader broom; **C**, weeping broom. Adapted from Hawksworth (1961), figure 45.

brooms (fig. 5-1B) as localized infections, near the base of the bole in which one or several leaders develop as long, erect, normally branched forks. Weeping brooms are very rare systemic brooms of numerous, long, pendulous infected branches (fig 5-1C). Tinnin and Knutson (1985) classify the systemic brooms of *A. douglasii* by position. Type I brooms originate away from the bole on long branches and thereby form large brooms on drooping branches. Type II brooms form on branches but near the bole and with a sturdy, upright supporting branch; the supporting branch makes a horizontal platform between the bole and mass of the broom. Type III brooms form at or close to the bole and lack the dominant, platform branch. Witches' brooms can also be produced by rust fungi (broom rusts and gall rusts), other fungi (*Elytroderma deformans*), chromosomal condition (trisomatic cells), and physiological reaction to canopy opening or age (stimulation brooms). Mistletoe brooms can be distinguished by the presence of aerial shoots or their remnant basal cups.

Witches' broom formation by dwarf mistletoes can have a major impact on host growth and crown form. Brooms become quite large on Douglas-fir or numerous on pine and larch. Brooms are a preferred growth-sink; host resources that would have gone to the bole and roots are diverted into broom growth. The importance of this effect is evident from the improved vigor, growth, and survival of broom pruned trees (Lightle and Hawksworth 1973, Scharpf and others 1988). Large brooms, especially on trees with brittle wood, may break off (Hadfield 1999). Brooms differ from normal crown branches for numerous features: needles, twigs, and accumulated detritus (Bonga 1964, Broshot and others 1986, Tinnin and Knutson 1980). These differences are important for their consequences on canopy structure, wildlife habitat, and fuel loading.

## Ecological and Evolutionary Effects

The effects of mistletoe infection on trees have numerous consequences for associated species and various natural processes. Mistletoes, especially in significant infestations, act as both keystone species (Watson 2001) and controlling disturbance agents (Holling 1992). From this perspective, we view how dwarf mistletoes affect community dynamics by their interactions with fungi, insects, and fire, effects on vegetation, and use by wildlife. Hawksworth and Wiens (1996) also discuss these topics and providing examples of pathogenic and biotic associates.

## Interactions

The forest communities to which dwarf mistletoes belong include large numbers of species of various

taxonomic groups and ecological roles. For consideration of the most obvious ecological effects, we focus here on the interactions of mistletoes with other disease, injury, or disturbance agents.

**Fungi**—Forest fungi are important in nutrient recycling (decay and mycorrhiza) and as pathogens of mistletoes and their hosts. The relation of mistletoes and decay fungi is discussed above, and the pathogens of mistletoes are described in chapter 7 as biological control agents. In many forests, mistletoes are only one of many tree pathogens; the most important are canker fungi (Filip 1984), root disease fungi (Marsden and others 1993), and stem rusts (Hawksworth and others 1983).

**Insects and Spiders**—Insects and spiders that react to mistletoe infestations can be categorized as those associated with shoots, with brooms and infected branches, and with infested trees (Stevens and Hawksworth 1970, 1984). Insects associated with shoots include pollinators, herbivores, and their predators, parasites, and associates. Some of the important shoot insects are potential biocontrol agents (see chapter 7), others include lepidopterians such as *Mitoura spinetorum* (Grimble and Beckworth 1993) and aphids with their attending ants. Numerous insects and spiders use mistletoe brooms with their accumulation of needles and other detritus as a special habitat for foraging and hunting. The significant insects associated with infected trees are tree defoliators and bark beetles. Defoliators may feed upon mistletoe-infected trees and contribute to tree damage and mortality (Filip and others 1993, Wagner and Mathiasen 1985). Mistletoe may affect tree phenology and shoot development, which has a consequence to defoliator development (Briede and others 1991). The attraction of bark beetles to mistletoe-infected trees depends on the species combination (mistletoe-tree-insect) and severity of infection. Hawksworth and Wiens (1996) review the combinations for which mistletoe infection appears to increase, decrease, or be unrelated to bark beetle attack. For example, Johnson and others (1976), McCambridge and others (1982), and McGregor (1978) discuss mistletoe as a predisposing factor for mountain pine beetle; Wilson and Tkacz (1992) for an outbreak of *Ips* in pinyon. Nebeker and others (1995) and Linhart and others (1994) consider the possible chemical bases for insect attraction to infected trees. An intermediate hypothesis to explain aggressive bark beetle (for example, mountain pine beetle) attraction to infected trees suggests that there would be no difference in beetle attack between similar sized trees that are uninfected or lightly infected (DMR 1 or 2), greater attack for moderately infected trees (DMR 3 or 4), and reduced attack for severely infected trees (DMR5 or 6). This hypothesis requires testing in various situations.

**Fire and Fuels**—The fire ecology of dwarf mistletoes is reviewed by Alexander and Hawksworth (1975) and updated by Zimmerman and Laven (1984). Several features of mistletoe infection increase the tree's flammability. Infection induces excess resin deposition and increases litter accumulation (including detached brooms). Retained brooms and infected branches form a fuel ladder from the ground into the canopy. Mistletoe severity (DMR) is related to scorching, mortality, and sanitation (Conklin and Armstrong 2001). Although an extreme, stand-replacing fire kills most trees, a few isolated mistletoe-infected trees can escape to not only reseed the stand but also reinfest it. Disturbance regimes and stand structure resulting from mistletoe and fire interactions are discussed by Bradley and others (1992) and Kipfmüller and Baker (1998).

### Forest Structure and Composition

Forest insects and pathogens are increasingly being recognized as important agents in shaping the structure and composition of forests (Hessburg and others 1994, Holling 1992, Monning and Byler 1992). Besides their interaction with fire described above, mistletoes affect the forest canopy, landscape pattern, and tree species mix (Baker and French 1991, Mathiasen 1996, Parker and Parker 1994, Reich and others 1991, Wanner and Tinnin 1989). The ecological importance of witches' brooms on community dynamics is examined by Tinnin and others (1982); and the role of mistletoes in forest canopies is reviewed by Mathiasen (1996). The paper on canopy light and mistletoe distribution by Shaw and Weiss (2000) is an example of detailed, canopy ecology studies at the Wind River Canopy Crane. Mistletoe and forest vegetation studies include examinations of plant association (Marshall and Filip 1999) and biotic diversity (Mathiasen and Marshall 1999). Two additional topics that have received special attention are effects and dynamics of mistletoe in old-growth stands and on wildlife habitat.

**Old-Growth Forests**—Numerous studies have examined mistletoe effects on immature and mature trees in managed stands, but there are few studies for old trees (over 200 years) and old-growth stands. Hawksworth and others (1992a) described a 300-year-old *Pinus contorta* stand infested with *Arceuthobium americanum*. Although infected trees occurred on over half the area, there were no isolated infection centers as were found in nearby 70-year-old stands. Tree mortality was higher among infected trees, but diameter growth was significantly reduced only among the most severely infected trees (DMR 6). These older trees grew slower, and on a percentage basis mistletoe had less effect than seen in younger, faster growing trees. Parker and Parker (1994) examined the spatial

pattern of tree density in seven *P. contorta* stands about 120 to 140 years old. They observed dense, closed-canopy stands that appeared to have developed and closed rapidly after initiation (fire) and low density, open-canopy stands with recruitment that is more continuous. They speculated that the open stand might have resulted from low initial stocking and high mortality from mistletoe. Kipfmüller and Baker (1998) describe another set of 43 *P. contorta* stands also in the Central Rocky Mountains and also representative of unmanaged, older stands (some to 500 years). They found that half of the stands were infested, and the average disease severity (DMR) increased with time since stand establishment. At the landscape scale, mistletoe often occurred as severe infestation patches but was absent from other areas of similar age. They concluded that a healthy forest would include a mosaic of infection centers and uninfested stands with periodic stand-replacing fires that vary in intensity.

**Wildlife Habitat**—Although dwarf mistletoes do not provide large incentives for birds or mammals to visit for pollination or seed dispersal as do other mistletoes, dwarf mistletoes provide forage, foraging sites, protected and special sites, and desirable stand structures for numerous wildlife species. (Bird dispersal is important for *Arceuthobium verticilliflorum* and possibly *A. occidentale*.) Hawksworth and Geils (1996) review the use of mistletoe by birds and mammals for food, nesting, and cover. Numerous studies have since been reported. Allred and Gaud (1994) describe tree selection and bark grazing by Abert squirrels and their high use of mistletoe-infected trees. Brooms in Douglas-fir are frequently used for cover and nesting (Hedwall 2000, Parks and others 1999a, Parks and Bull 1997, Tinnin and Forbes 1999). Brooms in ponderosa pine are also used (Garnett 2002). Brooms and associated mistletoe-infested sites are important for nesting by the northern spotted owl (Everett and others 1997, Marshall and others 2000). Steeger and Hitchcock (1998) describe the effects of several tree diseases, including mistletoe, on stand structure preference for nuthatches. Reich and others (2000) examine the relationship of canopy opening in a mistletoe-infested stand on bird usage. Although Bennetts and others (1996) found a positive association between the stand severity of mistletoe and bird usage in Colorado, Parker (2001) for a similar study in Arizona found a mixture of responses depending on bird species. Mistletoe presence, incidence, and severity may not be good indicators themselves of wildlife habitat value. Wildlife species are probably responding in a complex way to special features such as brooms and snags, to vertical crown structure, to canopy gap pattern, and other factors affected by mistletoes (Reynolds and others 1992).

## Consequences to Resources and Other Values

Dwarf mistletoes are important because they are serious pathogens of valuable conifers in many forests of North America. These conifers are valuable economically, primarily for their timber yields and ecologically for their role in forest ecosystems (Hawksworth and Shaw 1984). Importance and worth, however, are only meaningful and relevant within a given value system that is selected by the forest manager, owner, policymaker, stakeholder, or society.

### Importance

**Species Affected**—Conifers that are hosts to dwarf mistletoes can be divided between major species that occur in great numbers over large areas, and rare species with few, sparse populations. In Canada, the major host species are *Larix occidentalis*, *Picea mariana*, *Pinus contorta*, *P. banksiana*, and *Tsuga heterophylla*. In the Eastern United States, the major species are *Picea mariana*, *P. glauca*, and *P. rubens*; and in the Western United States, they are *Abies magnifica*, *A. concolor*, *Larix occidentalis*, *Pinus ponderosa*, *P. contorta*, *Pseudotsuga menziesii*, and *Tsuga heterophylla*. Mexico has a great abundance and diversity of conifers (over 30 taxa) that are mistletoe hosts (Hawksworth 1980, Hawksworth and Cibrián 1985). *Abies religiosa* and *Pseudotsuga menziesii* are infested; but the most common hosts are pines, including yellow pines, white pines, and pinyon pines. One of the more rare conifers that are hosts for *Arceuthobium abietinum* is *Picea breweriana* in Oregon; it is severely infested (Hawksworth and Wiens 1996).

**Area Affected**—In Canada, Magasi (1984) reports *Arceuthobium pusillum* is common in the Maritime Provinces. Overall, 20 percent of sites are infested and 6 percent of trees infested, but nearly all of the infested sites, infested trees, and mistletoe-caused mortality are in wet areas. Brandt and others (1998) map and summarize the distribution of severe mistletoe infestation (by *A. americanum*) in Manitoba, Saskatchewan, and Alberta. About 5 percent of the forest area or 500,000 ha are specifically identified as severely infested sites, where mistletoe-caused mortality and brooming are visually obvious (also see Baker and others 1992). Moody and Amirault (1992) estimate mistletoe incidence in individual, severely infested stands ranges from 73 to 100 percent. In British Columbia, *A. americanum* and *A. tsugense* are widespread, common, and damaging at many sites (Moody 1992, Thomson and others 1997). Hodge and others (1994) report only 2 percent of managed stands infested and only 3 percent of trees infested (except in a few stands, however, infection reaches 34 percent).

In the United States, *Arceuthobium pusillum* ranges widely across the Northeastern and Lake States; but its occurrence varies from locally common to rare in some States (Hawksworth and Wiens 1996). Drummond (1982) estimates 14 percent of the spruce area in the Lake States is infested. Numbers for dwarf mistletoe-infested area for each of the Western United States, however, are available (Forest Health Protection 2002). Westwide, about 25 percent (Drummond 1982, Bolsinger 1978) or 28.7 million acres of Western forests are infested (Forest Health Protection 2002). In contrast to the report (and accompanying compact disk) by Brandt and others, the United States' summaries (Drummond 1982, Forest Health Protection 2002) and the data on which they are based provide only statistical estimates of area infested and cannot map the specific, infested sites. A number of regional summaries are available. Andrews and Daniels (1960) report on the distribution of dwarf mistletoe in Arizona and Mexico in terms of administrative area (forest), harvest status, and various ecological factors. The most important forest types are ponderosa pine and Douglas-fir; Andrews and Daniels classify 36 percent of the ponderosa pine type as infested and 47 percent of the Douglas-fir type as infested. Maffei and Beatty (1988) report on a resurvey of the ponderosa pine area examined 30 years previously by Andrews and Daniels (1960). Maffei and Beatty (1988) attribute the apparent increase of infested area (8 percent more of the type) to ineffective mistletoe control. Other regional summaries are prepared by Bolsinger (1978) for the Pacific Northwest, Byler (1978) for California, DeNitto (2002) and Stipe and others (1992) for the Northern Region (Montana), and Johnson and others (1981) for the Rocky Mountain Region (Colorado and Wyoming).

Dwarf mistletoe occurs throughout the conifer forests of Mexico. Vázquez (1994a) states that an estimated 1.8 million ha in Mexico are infested. Most the information related to mistletoe damage in Mexico occurs as reports of infested area and infection incidence at various localities (see Hawksworth 1980). Caballero (1968, 1970) indicates the percentage of inventoried forest sites infested for several States: Zacatecas 24 percent, Durango 15 percent, Jalisco 12 percent, Nayarit 10 percent, Sinaloa 10 percent, Sonora 9 percent, Chihuahua 8.5 percent, and Baja California 7 percent. Within stands, the extent of the area infested and the percent of infected trees can be as high as 85 percent (Acosta and Rodriguez 1989, Gutierrez and Salinas 1989).

**Growth Loss**—Information on reduction of volume increment, mortality, and area infested can be used to estimate mistletoe impact to stand yield on an area basis. The difference between realized volume in an infested stand (reduced by loss of increment and

mortality) and potential yield for the site (if mistletoe were not present) is described as *growth loss*. The growth loss concept can be applied nationally, regionally, forestwide, and to individual stands (Baker and Durham 1997 describe a method for computing growth loss). Drummond (1982) estimates a total annual growth loss from mistletoe in the United States at 418 million cubic feet per year; Vázquez (1994a) for Mexico reports a loss of 2 million cubic m per year. Estimates for Canada are available for Newfoundland at 1 cubic m per year per ha (Singh and Carew (1989); for Manitoba, Saskatchewan, and Alberta at 2.4 cubic m per year (Brandt and others 1998); and for British Columbia at 1.8 million cubic m per year (Forest Insect and Disease Survey 1994). DeNitto (2002) provides a growth loss estimate of 33 million cubic feet per for Montana (broken down by host species). Johnson and others (1981) describe growth loss for forests of Colorado and Wyoming. Marsden and others (1993) illustrate use of a forest growth and yield program to compare expected yield for a mistletoe-infested stand to what might be had were the stand not infested. Growth loss can be so significant in severely infested stands (especially immature and infected at an early age) that commercial yield cannot be obtained (Hawksworth and Hinds 1964).

## Amenity Values

Dwarf mistletoes are sufficiently unusual and influential that they are important to a number of resource and amenity values besides commercial timber yield. Other forest products have traditionally included watershed protection, recreation opportunity, and wildlife habitat. Over a half century ago, concern over the effects of dwarf mistletoe to old-growth ponderosa pine at the Grand Canyon National Park lead managers to an intensive control project (Lightle and Hawksworth 1973). The effects of dwarf mistletoe on fuel loading and fire behavior are still a serious interest to managers (Zimmerman and Leven 1984). We have already discussed how witches' brooms and forest structure affect wildlife abundance and diversity (Bennetts and others 1996, Parker 2001, Reich and others 2000). Mistletoes are also valuable as mistletoes themselves and as members of a biotic community.

Mistletoes possess aesthetic, scientific, and intrinsic values. Although the mistletoe plant and diseased trees are not usually considered attractive (exceptive by some forest pathologists), a distinctively broomed,

dead tree against the backdrop of the Grand Canyon does make a strong and interesting picture. Mistletoes can provide chemical analogs that may be developed into useful drugs. They serve as models for understanding the evolution of parasitism (Atsatt 1983a) and phylogeny of their hosts (Hawksworth 1991). Rolston (1994) describes the value of living entities beyond their worth to humans as achievement and part of the system of life.

Forests are not only managed for the resources they produce but also to sustain and protect forest health (Monning and Byler 1992) and ecosystem values (Taylor 1995). Dwarf mistletoes are important disturbance agents (Holling 1992) with distinct ecological functions (Hessburg and others 1994). They contribute to natural diversity structurally (Mathiasen 1996) and biologically (Mathiasen and Marshall 1999). Some mistletoes are considered species of special concern (Hildebrand 1995), and truly rare species such as *Arceuthobium hondurense* probably deserve protection. A balanced view of mistletoes as the cause of losses of valuable resources, but also as natural agents that shape forests, is emerging (Wittwer 2002).

## Coevolution

Information from biogeography, paleobotany, host relations, and molecular systematics indicates the dwarf mistletoes have a long evolutionary history of parasitism with their conifer hosts (Hawksworth and Wiens 1996). Mistletoes are physiologically dependent on their hosts but cause symptoms that eventually result in death for both. What really matters, however, from an evolutionary perspective is their success at leaving descendents. To the present, host and parasite have lived, reproduced, and died in natural ecosystems. These natural ecosystems, even wildlands, are increasingly controlled and affected by managers and human society. We have a fair understanding of the physiology of mistletoe–host parasitism and a good ability to predict the effects of infection on tree growth and survival. We are beginning to appreciate the complex ecological interactions in which mistletoes participate. By management with biological agents, chemicals, genetic manipulation, and silviculture, we attempt to influence how mistletoe affects resources and our environment. For that management to have a beneficial outcome, which is sustaining to the biotic system on which we depend, it is advisable to consider not only immediate results but also ecological and eventually evolutionary consequences.