FOREST STAND DYNAMICS AND ECOLOGICAL FACTORS IN RELATION TO DWARF MISTLETOE SPREAD, IMPACT, AND CONTROL

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Abstract: Dwarf mistletoes are markedly host specific, perennial, obligate parasites. The success of mistletoe populations is tied not only to the suitability of the environment, but also to the availability and conditions of the hosts they infect. Thus, the dynamics of forest stand development and change exert major influences on the capacity of dwarf mistletoes to spread, intensify, and cause damage to host trees. Silvicultural control of dwarf mistletoe damage rests mainly with manipulation of stand dynamics to minimize spread and intensification. Thorough understanding of dwarf mistletoe/forest stand interactions is therefore crucial to the development and application of controls.

In North America there are some two dozen species of dwarf mistletoes associated with numerous host species growing in a variety of forest and habitat types distributed over different terrains under widely divergent climatic conditions. Detailed treatment of stand dynamics in each of these associations is beyond the scope of this discussion. Rather, I have attempted to highlight some stand and ecological relationships that appear to be general to dwarf mistletoes, to indicate how these relationships provide bases for dwarf mistletoe control, and to suggest where increased information could improve control application. The literature on dwarf mistletoes is voluminous (Scharpf, et al. 1976). Citations were selected to confirm or to illustrate principles, but no attempt was made to cite all papers dealing with the material discussed here.

DAMAGE, IMPACT, AND DWARF MISTLETOE POPULATIONS

Land managers are concerned about dwarf mistletoes because mistletoes can reduce the number, size, quality, or longevity of trees, and such reductions can affect the productivity and value of trees or stands. Unfortunately, a standard terminology to express disease effects has not evolved. Such terms as effect, damage, loss, and impact are often used interchangeably to designate mistletoe-induced changes in trees or stands. It has been suggested that the term impact be restricted to "...the cumulative net effects of a given pest or pest complex on the productivity, usefulness and value of a tree species or forest type with respect to different resource uses and values (timber production, watershed protection, wildlife cover, recreation, etc.) and the management objectives..." (Waters, 1976). By this definition, various types of damage (growth reduction, quality reduction, mortality, etc.) may or may not have impact, depending upon whether such damage reduces the productivity or value of a stand.

Investigators have seldom dealt with impact. Most available data involve various measures of damage either to individual trees or to stands. The following discussion therefore deals mainly with damage, with the recognition that land managers must ultimately convert damage data to impact data and that this conversion is dependent on the amount of damage to individual trees and the numbers and distribution of damaged trees in a stand. These data in turn are dependent on the rates at which mistletoes spread through stands and


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intensify within trees.

Generally, the amount of damage is related to the numbers of infections and their distribution within tree crowns (Baranyay 1970; Baranyay and Safranyik 1970; Childs and Wilcox 1966; Dooling 1974; Dooling and Brown 1976; Hawksworth 1961a; Hawksworth and Lusher 1956; Korstian and Long 1922; Pierce 1960; Shea 1963; Shea and Orr 1963; Shea and Belluschi 1965; Smith 1969). A number of systems have been devised to rate intensities of dwarf mistletoe infection (Hawksworth 1977; Dooling, this vol.) and to correlate damage with intensities in individual trees or with general conditions of stands.

Damage on a stand basis is usually estimated by comparing volumes, basal areas, or mortality rates in stands without mistletoe to that in stands with various amounts of mistletoe. While absolute volume, basal area or mortality may differ with different host/mistletoe combinations and with a variety of site and stand factors, the association of increasing loss with increasing mistletoe intensity is well established (Andrews and Daniels 1960; Baranyay 1970; Graham 1960a; Graham and Frazier 1962; Haglund and Dooling 1972; Hawksworth 1958a, 1968a; Hawksworth and Hinds 1964; Hawksworth and Lusher 1956; Lightle 1966; Richardson and van der Kamp 1972; Wagener 1961). In general, stand losses below some critical level of mistletoe intensity are negligible (Baranyay 1970; Baranyay and Safranyik 1970; Dooling 1974; Richardson and van der Kamp 1972; Shea and Orr 1963). This level is a function of numbers of infected trees in a stand, the intensities of infection in these trees, and the amount of damage resulting from different intensities.

Whether damage is expressed as decreased radial, height, or volume growth or as increased mortality, significant damage is seldom observed until at least the lower 1/3-1/2 of a tree crown is heavily infected (Baranyay 1970; Baranyay and Safranyik 1970; Dooling 1974; Dooling and Brown 1976; Hawksworth 1961a; Hawksworth and Lusher 1956; Pierce 1960; Shea 1963; Shea and Orr 1963; Shea and Belluschi 1965; Smith 1969). Light infection throughout the crown or heavy infection in the lower crown usually cause little or no damage, except where stem infections may lead to heartrot (Etheridge 1973), where stem infections occur in seedlings and small saplings (Knutson and Toevs 1972; Roth 1971; Wilir 1918), or perhaps where large brooms are produced.

The effects of brooms on host growth has not been investigated thoroughly. Pierce (1960) suggested that the growth of trees with brooms in the lower crown was comparable to trees with healthy crowns of a length equal to the unbroomed portion of infected trees. Hawksworth (1961a), however, showed that growth reduction was greater in broomed trees than in non-broomed trees of the same infection class. Further, Lightle and Hawksworth (1973) illustrate dramatic improvement in host vigor following pruning of brooms from the lower crown. Since the numbers of brooms increase with increasing intensities of infection (Hawksworth 1961a), the amount of damage to trees can be expected to increase with increasing levels of infection.

Rates of increase in dwarf mistletoe population levels undoubtedly are affected by a number of host, stand, and environmental factors. Few data are available on measured rates of increase. Hawksworth (1969) found that the numbers of infections on inoculated digger pines increased from 4 to 240 per tree within 16 years after inoculation, indicating a population doubling rate of about 2.5 years. Doubling rates were estimated to be 1.25 years in lodgepole pine (Nair 1972) and 4 years in hemlock (Richardson and van der Kamp 1972). Scharpf and Parmeter (1976) found that population increases in inoculated red and white firs were highly variable. In two groups of trees, populations doubled within 12-15 years from inoculation; in a third group the population tripled; in a fourth group the population increased 35 times (a doubling rate of about 3 years), and in one group the population scarcely increased. These extreme variations are presently unexplained, but they suggest that the collection of population data in one area may have limited relevance to other areas.

Generalized estimates of population increase rates have been made by rating the mistletoe intensity according to the system of Hawksworth (1977) in stands of different ages or in stands infected for different periods of time. Hawksworth and Hinds (1964) estimated that the average rating (on a 0-6 scale) in lodgepole pine stands increased 0.8-0.9 per decade for the first 4 decades of infection, with increases of 0.6 and 0.3 for the next 2 decades. This indicates an average increase of 1 class each 14 years. Flora (1966) indicated that it takes about 70 years for ponderosa pines to go from a 1.5 to a 5.5 rating, an increase of 1 class each 17.5 years. Wass (1976) suggests that shore pine infection intensities increased by 1 class each 15 years. Myers, et al. (1976) developed an equation for calculating increases in infection intensity for mistletoe in southwestern...
ponderosa pine. By this equation, rates of increase vary according to time of infection, stand density, and site index.

It is obvious that equations or estimates for population or rating increases can apply only to specified time periods, host/mistletoe combinations, and stand/site conditions. With estimated doubling times of 1.25-4 years, dwarf mistletoe populations would reach impossible numbers within normal rotation periods for most host species. On a stand basis, if infection ratings increased by 1 every 15 years (allowing 10 years for establishment), young infected stands would reach damaging 3-4 levels of infection within 55-70 years, and we would be hard pressed to justify rotations beyond this time. However, for each 5-year increase in the number of years it takes for ratings to increase by 1, the rotation is extended by 30 years (Fig. 1). Whether increase rates are straight-line functions or whether they change with stand age and duration of infection (as the data of Hawksworth and Hinds, 1964, suggest), reduction in the rate of increase may be critical to sound management.

Figure 1--Ages at which stand dwarf mistletoe ratings would reach levels of 3 or more with infection ratings increasing by 1 every 10 yr (A), 15 yr (B), 20 yr (C), 25 yr (D), or 30 yr (E), assuming infection is established at about 10 yr.

Fortunately, rates of dwarf mistletoe spread and increase are subject to a variety of limitations that can be manipulated by land managers or that he can take advantage of. These involve the influences of: (1) site quality and host vigor, (2) stand density, (3) host age, (4) stand structure, and (5) stand composition. These various elements of stand dynamics are inextricably interwoven and difficult to discuss in isolation. For convenience, however, they will be discussed individually.

ELEMENTS OF STAND DYNAMICS AFFECTING SPREAD, INTENSIFICATION, AND DAMAGE

Site Quality and Host Vigor

Reports of the relationship of dwarf mistletoe prevalence, intensity or damage to site quality are difficult to interpret. In ponderosa pine, increased mistletoe has been associated with poor site quality (Daubenmire 1961, 1969; Korstian and Long 1922), with intermediate site quality (Larson et al. 1970), or showed no significant relationship to site quality (Hawksworth and Graham 1963), found a higher percentage of infected trees in reproduction on good sites, and Hadfield (1977) found no relationship of site quality to percent of trees infected. Baranyay and Safranyik (1970) found greater growth loss on dry than on wet sites. It has been suggested that because mistletoes affect host growth, heavily infected stands may give the appearance of low site quality (Childs and Edgren 1967; Hawksworth 1961). Since site quality is measured by tree growth, and growth may be affected by a number of factors (soil type and depth, nutrients, available water, drainage, length of growing season, etc.), it is not surprising that data are difficult to interpret. While site quality per se might have some direct effects on dwarf mistletoe activity, it is likely that fundamental host/stand/parasite interactions affected by site factors are more important in determining mistletoe spread and intensification.

Host vigor, which is in part a reflection of site quality, affects mistletoes in several important ways. Vigorous trees are generally larger, have fuller crowns, greater needle complements, and longer needles than do unthriftier or suppressed trees. It has long been recognized (Weir 1916) and repeatedly confirmed (Childs 1963; Childs and Edgren 1967; Gill 1957; Hawksworth 1961a, 1965; Hawksworth and Graham 1963; Roth 1959; Wicker 1967; Wicker and Shaw 1967) that vigorous, full-crowned trees intercept more seeds and are therefore more liable to infection. It
appears well established that for a given level of inoculum, the rate of infection increases with host vigor.

Host vigor also promotes dwarf mistletoe vigor. The endophytic system invades vigorous host tissues more rapidly (Hawskworth 1960a; Scharpf 1962; Parmeter unpubl.), and more robust shoots and larger amounts of seed develop on vigorous hosts (Baranyay and Smith 1972; Childs 1963; Dooling 1974; Hawskworth 1961a; Roth 1953).

It has also been reported that vigorous lodgepole pines are more liable to damage. Statements regarding the effects of host vigor on mistletoe development are not apt to have much significance unless the stand and site characteristics are specified. While a vigorous tree in one stand may be more liable to damage, a similar tree in another stand may be less liable to damage.

Since trees of most species seldom show significant growth losses when mistletoes are confined to the lower crown, factors that affect the rate of vertical spread through tree crowns are important. Alexander (1975) indicated that where the site index exceeded 70, usually only the middle and lower crowns of dominant and codominant lodgepole pines were infected. Below index 70, all crown classes were susceptible to heavy infection throughout the crown. Graham (1967) suggested that vertical spread in ponderosa pine was about 4 inches per year, and Strand (1973) estimated 3 inches per year. Hawskworth (1969) found that vertical spread in digger pines averaged 2 feet per year. Richardson and van der Kamp (1972) estimated vertical spread to be 65 cm (about 2 feet) per year in open grown hemlock and 30 cm (about 1 foot) per year in dense hemlock. Scharpf and Parmeter (1976) found the average vertical spread in red and white firs was about 3 inches per year. Childs (1964), Richardson and van der Kamp (1972), and Scharpf and Parmeter (1976) have suggested that most trees will escape serious damage if the rate of height growth exceeds the rate of vertical spread sufficiently to confine mistletoe to the lower crown and that, in the absence of overstory seed sources, damaging invasion of upper crowns will not occur until host growth slows with age.

The rate of vertical spread is probably governed mainly by crown characteristics. Species with open crowns, such as diggerpine, permit rapid vertical spread, whereas species with dense crowns, such as true firs, greatly impede vertical spread. Among trees within a species, crown characteristics can change with host vigor. Vigorous crowns, because of their fullness, will impede vertical spread, even though the rate of population increase in the lower crown may be high. In contrast, unthrifty or suppressed trees, because of thin crowns, may provide less barrier to vertical spread. For each mistletoe/host combination, it may be possible to construct height-growth/vertical-spread curves that will allow prediction of probable damage for any set of vigor and site conditions (Fig. 2).

Figure 2--Hypothetical relationship of vertical spread rates of 3, 6, 12, or 24 inches per year to position of dwarf mistletoe in crowns of trees at different ages on high and low sites. Infection of young trees is estimated to occur slightly earlier on high sites.
In addition to rates of population build-up within crowns, site and vigor might also affect rate of tree-to-tree spread through a stand. Trees of low vigor on poor sites have thin crowns and might therefore provide less "screening" for lateral spread. Such effects, if any, would likely be small in comparison to the effects of stand density, structure, and composition.

Stand Density

Stand density can affect spread and intensification either directly or through changes in host vigor and growth. In general, mistletoes spread more rapidly in open stands than in dense stands (Hawksworth 1958a, 1961a). Hawksworth (1961a) found that average spread in open stands of ponderosa pine reproduction was 1.5 times as fast (1.7 feet/year) in open stands as in dense stands (1.2 feet/year). Data on spread in lodgepole pine were similar (Hawksworth 1958a) but spread rates were slightly less (average 1.2 feet/year vs. 1.5 feet/year). Density may affect spread in several ways. Beyond some critical distance that varies with tree size and mistletoe species, the chances of seed shooting from one tree to another decrease until trees are so far apart that ballistic spread is very unlikely (Fig. 3). As spacing decreases, the likelihood of seed reaching adjacent trees increases until densities are sufficiently high that trees interfere with spread by "screening" out seeds, thus "protecting" the trees beyond. Where densities are sufficiently high as to reduce host growth and vigor, seed production may be reduced, thus decreasing the opportunities for spread. The generalized relationship of density to spread presented by Hawksworth (1961a) undoubtedly can be applied to most mistletoe/host combinations, but the curve would have to be adjusted according to species and to the sizes of trees involved.

The rate of mistletoe increase and subsequent host damage is also related to stand density, but the relationship is not entirely clear. Some workers have reported an inverse relationship of density to prevalence or damage (Graham 1960b; Richardson and van der Kamp 1972; Williams et al. 1972). Williams et al. (1972) suggested, however, that infection in loblolly pine was directly related to density. Since density relationships are relative and may vary according to a variety of site and stand factors, generalizations are feasible only within specific contexts; e.g., similar densities on high and low sites may not have similar effects on dwarf mistletoes.

Density can affect host vigor, as has already been discussed. Where the relationship of height growth to vertical spread of mistletoe is changed by crowding and suppression, the rate of crown involvement might be expected to change, but the nature of the change may depend on specific densities. Childs (1964) has discussed in some detail the relationship of crown closure to mistletoe population increase and vertical spread. Baranyay and Smith (1972), Childs (1963), Richardson and van der Kamp (1972) and Scharpf and Parmeter (1976) have also suggested that crown closure and subsequent "pruning" of lower branches may stabilize or reduce population increases in tree crowns. If the rate of crown closure and branch pruning is greater than the rate of vertical spread, populations of dwarf mistletoes might virtually disappear from trees not exposed to overstory seed sources (Fig. 2).

The above observations suggest that for each site/host/mistletoe combination there is an optimum density that promotes good height growth and rapid crown closure to minimize population build-up and vertical spread of mistletoe. At densities above optimum, crown thinning and reduced height growth might lead to increased vertical spread, or with densities below optimum, increased branch longevity, increased mistletoe inoculum, and increased opportunities for "stepwise" vertical spread between trees might also lead to increase damage. The relation of site and density to vertical spread and population build-up warrants research emphasis.

Stand Age and Size Structure

Trees of any age or size are susceptible to dwarf mistletoe infections. Seedlings one-year-old or less are readily infected under greenhouse conditions (Knutson and Toews 1972; Knutson 1974), and infection of trees 2.5 inches tall have been observed in nature (Hawksworth and Graham 1963). Infection of very
young or very small trees is, however, relatively rare. Data from many sources indicate that numbers of trees infected, intensity of infection, and degree of damage consistently increase with the age of trees or stands and, in the case of reproduction exposed to overstory seed sources, with size of trees (Baranyay 1970; Childs 1963; Graham 1960a, 1964; Hadfield 1977; Hawksworth 1958a, 1961a; Hawksworth and Graham 1963; Hawksworth and Hinds 1964; Muir 1972; Scharpf 1969a; Stewart 1976). The escape of or reduced infection in young trees involves the relatively small target area, the short duration of exposure to inoculum, and the short period for inoculum production and spread within crowns. Loss of seeds under snow may also reduce infection of small trees (Wicker 1967).

Because young trees tend to escape infection, reproduction following opening of infested stands by logging, fire, insects or other agencies is ordinarily lightly infected until it reaches some critical age or size. Jones (1974), Shea and Stewart (1972), and Scharpf (1969a) have provided guidelines for timing of overstory removal. If overstory sources of mistletoe seed are removed, subsequent buildup and damage in the released stand depend upon the site and density factors already discussed and upon silvicultural manipulation of the young stand, as will be discussed in later sections of this symposium.

At the opposite end of stand development, all trees eventually cease appreciable height growth. In such trees, vertical spread can be expected to involve the entire crown, and the intensity of infection can be expected to increase because of the long duration of exposure to inoculum. Mortality rates are apt to be high in old stands in which heavy infection levels have been reached.

Roth (1953) suggested that less mistletoe seed is produced in old, declining trees than in young trees. Although seed production may be reduced, appreciable numbers of seeds have been trapped under old, heavily infected and broomed trees (Parmeter and Scharpf 1972). It is probably safest to consider all such trees as potential sources of inoculum.

Perhaps the most firmly established of all stand influences on dwarf mistletoes is that of stand structure (Gill and Hawksworth 1954; Graham and Frazier 1962; Graham 1959a; Hawksworth 1961a; Kimey and Graham 1960; Kuyt 1955; Roth 1953; Scharpf and Hawksworth 1968a, Shea 1963; Shea and Stewart 1972; and many others). In stands comprised of susceptible trees of different sizes, the crowns of smaller trees are continually exposed to inoculum from larger trees. Under these circumstances, the upper crowns of understory trees can rarely remain free of increasing mistletoe populations, and reductions in growth with further increase in mistletoe is almost certain. The impact of mistletoe in such stands can render them virtually non-productive.

The rate of spread through two-storied or multistoried stands is more rapid than through single-storied stands. Small trees provide little "screening" of mistletoe seeds, therefore tall seed sources provide for greater unimpeded seed trajectories. Hawksworth (1961a) calculated trajectories for mistletoe seeds discharged at different angles (Fig. 4). From these calculations, it is evident that, in the example shown, a nearby tree less than 40 feet tall would not impede flight from the 50 foot seed source at most discharge angles above the horizontal. A nearby 60 foot tree would, however, intercept seeds and markedly reduce the distance of flight.

![Figure 4](image)

Average distances of maximum spread, based on seed trapping or on infection of reproduction, range from about 40-60 feet in southwestern ponderosa pine (Gill 1954; Gill and Hawksworth 1954; Hawksworth 1961a, 1961b), 25-60 feet in lodgepole pine (Gill and Hawksworth 1964; Hawksworth and Graham 1963; Hawksworth
1973; Muir 1970), and 15-50 feet for western hemlock (Shea and Stewart 1972; Smith 1973). These data correspond well with trajectories calculated by Hawksworth.

Wind may, however, increase the distance of spread. Seed from tall overstory ponderosa or Jeffrey pines can be deposited on smaller trees over distances of 100 feet or more (Roth 1953; Scharpf and Parmeter 1967, 1971; Parmeter and Scharpf 1972) and could infect nearly an acre of reproduction if so dispersed in all directions. Muir found that spread from isolated overstory trees was greater (avg. 45 feet) than from stand margins (avg. 28 feet). The above data indicate that greatest distances of spread are associated with tall, isolated overstory trees exposed to wind. Least distances of spread are associated with relatively even-aged stands.

Stand Composition

The geographic ranges of many species of dwarf mistletoes overlap (Hawksworth and Wiens 1972); however, the occurrence of two species of mistletoe in the same place is not common. While a variety of "crossovers" among host species have been observed (Gill and Hawksworth 1961; Hawksworth 1974; Hawksworth and Wiens 1972; Muir 1973; Smith 1974), in general, one or more species in a mixed stand will be free of mistletoe (Kjuit 1955).

The effects of stand composition on any one host species have not been well documented. In some areas, mistletoe is more frequent in stands where the host species predominates (Graham 1964). In other areas, mistletoe is as abundant or more so in stands where the host species is a lesser component (Acciavatti and Weiss 1974; Graham 1959b, 1960b). In stands undergoing conversion, mistletoe damage is often reduced (Baranyay and Smith 1972; Jones 1974; Hawksworth 1973), and selective pressure on one host may promote stand conversion (Parmeter and Scharpf 1963).

While quantitative data are limited, it can be argued a priori that mistletoe impact will be reduced in mixed stands because a percentage of the trees will not be damaged. Spread through mixed stands may also be reduced if nonsusceptible trees are sufficiently large and sufficiently numerous as to impede flight of mistletoe seeds between susceptible trees. Manipulation of stand composition to reduce damage has been recommended (Baranyay and Smith 1972; Jones 1974; Kimmey 1957; Kimmey and Graham 1960; Parmeter and Scharpf 1963; Scharpf 1964, 1969a; Schwandt 1977).

Stand History

Discussion of dwarf mistletoes and stand dynamics would not be complete without consideration of special events in the history of stand development that affect the characteristics of stands and the incidence of dwarf mistletoes. Chief among these are logging, fire, forest succession, insect activity, and possibly the evolution of resistance mechanisms. These past events probably have had major influences on the mistletoe situations we observe today.

Logging and other stand manipulations will be discussed in following sections of this symposium and will not be dealt with in detail here. Obviously, past cutting practices that have modified vigor, density, age, structure, and composition of stands have influenced mistletoe activity as previously indicated. In a sense we have inherited many of our mistletoe problems from past forest practices. High-grading, selective cutting, and preferential removal of certain species have left many stands open, multitiered, reduced in species complexity, and in a condition to favor rapid buildup and damage by mistletoe. Conversely, extensive clearcutting in some timber types has resulted in large areas of essentially mistletoe-free second growth.

Along with logging, fire has undoubtedly had a major influence on present mistletoe conditions in many areas. The relationship of fire to mistletoe activity has been thoroughly discussed in the excellent reviews of Alexander and Hawksworth (1975) and Wicker and Leaphart (1976) and will be discussed by Muraro in a later section of this symposium. Fires may have positive or negative effects on dwarf mistletoes, depending on the extent and intensity of the burn and on the characteristics of the stand and the terrain. Where large areas of forest have been completely destroyed by intense wildfire, the replacement stand will be mistletoe free except at the margins. Since dwarf mistletoes reinvade such new stands at an average of only 1-2 feet per year following initial infection from the margins (Hawksworth 1958a, 1960b, 1961a; Shea and Stewart 1972; Wagner 1965), large areas of replacement stands remain mistletoe free.

Owing to patchy fuel accumulations, rock outcrops, and other irregularities, even large fires often leave groups or individual live trees within burned areas. When infected, these can serve as sources of inoculum to
reinfest the replacement stand. In some regions, the prevalence of dwarf mistletoes is markedly associated with areas where large, complete burns are rare because of terrain or fuel conditions (Baranyay 1970).

Available evidence suggests that frequent low-intensity ground fires were characteristic of many forest types (Biswell 1967; Neaver 1974). Because heavy dwarf mistletoe infection leads to accumulation of dead trees, witches' brooms, resinous stems and branches, and other fuels, low intensity fires may flare up and consume most of the trees in localized infection centers. In addition, heavy browning provides concentrated fuel for "torchng" and destruction of infected trees, where normal tree crowns are too open to carry fire up the tree. Low intensity fires may also kill infected lower branches, thus reducing mistletoe populations in lower crowns (Roth 1974). These fire effects have probably reduced mistletoes in many areas, but not all fire effects have been beneficial.

In the long view, fires have also served to perpetuate seral fire types in which dwarf mistletoes may be a perpetual problem. In addition, owing to accumulation of fuels in stands with mistletoe levels sufficient to apply selection pressures for resistance, locally intense fires may have greatly reduced opportunities for the evolution of resistance, since any resistant trees within such stands would be consumed along with infected trees (Roth 1966).

Resistance to dwarf mistletoes is infrequently observed and poorly understood. Some trees within stands are essentially free of mistletoe, even when exposed to abundant inoculum (Hawksworth 1961a, Roth 1953, 1971; Wagener 1965). In other cases, stands over large areas may show differing susceptibilities. Hawksworth (1961b) found that inoculation of trees in infested stands produced 10 times the rate of infection obtained from inoculations in uninfested stands, apparently because of differences in the survival of germinated seed. Infection of ponderosa pine by *A. americanum* is uncommon in stands infested by *A. vaginatum* and vice versa (Hawksworth 1960b). Scharpf and Parmeter (1967) provided limited evidence that Jeffrey pines from high elevation seed sources were more susceptible than trees from low elevation sources. Smith and Mass (1976) found that *A. tsugensis* includes forms that preferentially attack shore pine in some areas and hemlock in others. Hawksworth and Wiens (1972) discussed the "exclusion principle", a frequently observed phenomenon in which other species of mistletoes seldom infest trees in stands infested by a principal dwarf mistletoe of the host.

While genetic interactions among hosts and parasites undoubtedly account for some of the above observations and some bases for resistance have been suggested (Roth 1966; Smith 1974), environmental limitations and evolution of ecotypes might also account for different host/parasite interactions in different stands. These phenomena deserve further investigation, since prediction of mistletoe damage in different stands may rest with understanding of the bases for differing host/parasite interactions.

Forest succession has also influenced the present distribution and intensity of dwarf mistletoes. As has been pointed out by Hawksworth (1973), mistletoe damage is often reduced when stands of seral species are replaced by "climax" species. It can be argued that in stands where succession from one species to another is possible, dwarf mistletoes will apply pressure against the susceptible host, thus hastening stand succession (Parmeter and Scharpf 1963). However, if mistletoe species attacking the "climax" species are present in stands, reduction of mistletoe damage by succession may be only temporary.

Mass (1976) indicated that hemlock mistletoe on shore pine is mainly a problem where shore pine tends to be climax. In California, it appears that heavy mistletoe damage is often associated with such timber types as eastside Jeffrey pine, upper elevation red fir, and poor-site lodgepole pine in which the host species are self perpetuating and opportunities for succession to other species or to mixtures are minimal. Perpetuation of "climax" types may eventually lead to heavy mistletoe damage because such types tend, in the absence of catastrophic removal, to develop uneven-aged structures, a condition favoring dwarf mistletoe intensification.

It is difficult to reconstruct past successional changes that have affected present mistletoe conditions. It seems safe to assume, however, that frequent changes in timber type resulting from the interplay of catastrophe and succession have helped to reduce mistletoe incidence. And conversely, perpetuation of the same type, either seral fire types or "climax" types has tended to increase mistletoe damage. Knowledge of such trends can aid land managers in long-range planning.

While logging, fire, and succession are probably the main factors that have shaped the character of stands and the distribution
of mistletoes within stands, other events have likely had significant influence. Epidemic insect activity can change the composition and structure of stands (Schmidt and Hinds 1974). Few data are available to assess possible effects of insect activity on dwarf mistletoe populations, and both plus and minus effects can be postulated. Infected trees are often attacked by bark beetles (Hawksworth 1973), and each killed, infected tree represents a temporary reduction in inoculum. However, random killing of individual trees may lead to open, uneven-aged stands in which mistletoes are ultimately more damaging. Extensive killing, as can result from repeated defoliation of lodgepole pine by needle miners (Koehrer and Struble 1971), might have effects similar to fire in that replacement stands would tend to be even-aged and surviving overstory trees would provide inoculum for infection of reproduction.

Dwarf mistletoes may also influence insect activity. Trees weakened by dwarf mistletoes are often susceptible to bark beetle attack (Hawksworth 1973; Miller and Keen 1960; Struble 1965), although heavily infected trees may provide poor substrate for brood development (Roe and Amman 1970). Details of possible relationships between dwarf mistletoes and population dynamics of destructive forest insects are poorly understood and should provide a fruitful area for further study.

OTHER ECOLOGICAL INFLUENCES

Available evidence suggests that a variety of factors other than stand dynamics per se affect the occurrence and intensity of dwarf mistletoe populations. Many of these factors are not well understood and evidence for their influences is often circumstantial. Mistletoes are higher plants and we can expect that they are subject to many of the same environmental limitations that govern the distribution of other higher plants. Detailed discussion of these ecological factors is beyond the scope of this paper, but mention should be made of their existence and possible implications in land management.

The distribution of dwarf mistletoes is not continuous over the ranges of their host species. These discontinuities have been discussed by a number of workers (Baranay and Smith 1972; Baranay 1970; Hawksworth and Wiens 1972; Smith and Baranay 1970; Wicker 1974b). They include the absence of mistletoes over large geographic areas (Hawksworth and Wiens 1972); the absence from certain habitat types (Acclavatti and Weiss 1974; Hadfield 1977; Hawksworth 1973; Hawksworth and Wiens 1972), and absence or reduced activity in relation to slope, aspect, and other topographic features (Andrews and Daniels 1960; Baranay 1970; Gill 1957; Gill and Hawksworth 1961, 1964; Hawksworth 1958b, 1961a, 1968a; Larson et al. 1970; Roth 1954; Williams et al. 1972).

The absence of dwarf mistletoes on some hosts over major portions of the host range may involve large scale shifts in ranges associated with advance and retreat of ice sheets during glacial epochs (Hawksworth and Wiens 1972). Other large-scale discontinuities may be due to geographical barriers or discontinuities in the distribution of host species (Wicker 1974b). On a smaller scale, absence of mistletoes may involve such catastrophes as volcanic devastation (Hawksworth 1960b).

Environmental limitations may also be responsible for some of the observed patterns of dwarf mistletoe distribution. Seed survival, germination, and radicle development are sensitive to both high and low temperature extremes (Beckman and Roth 1968; Knutson 1971; Scharpf 1969b, Wicker 1974a). Gill (1957) recognized that the upper elevational limit of A. americanum in the Rocky Mountains coincides with the 30 F mean annual isotherm. Baranay and Smith (1974) showed that freezing temperatures before or during seed dispersal permanently damaged fruits and greatly reduced seed discharge of A. americanum and A. tsugense.

In some regions, mistletoes may be restricted by inadequate moisture during the period of germination and infection (Bonga 1969, Hawksworth 1967). Moisture is required for seed germination, and unsuitable moisture conditions may reduce viability, germination, or survival (Bonga 1969; Knutson 1971; Wicker 1974a).

Our present state of knowledge about requirements and limitations is inadequate to permit firm correlation of distribution patterns with environmental limitations in most cases, but it seems reasonably certain that such limitations exist. Future studies may help to distinguish between areas that are mistletoe free because mistletoes haven’t successfully spread into them and areas that are mistletoe free because mistletoes can’t successfully spread into them. In either case, today’s land managers must deal with mistletoes where they are, and prudent land managers will take steps to minimize the possibility of their spread or introduction into areas presently free of mistletoes on important hosts.
CONCLUSIONS

Mistletoe damage and impact in forest stands are mainly functions of the numbers of infected trees and the distribution and numbers of infections within tree crowns. These parameters are in turn functions of the rates at which mistletoes spread through stands, the rates at which they spread vertically within crowns, and the rates at which populations increase. These rates are governed in large part by stand characteristics that can be manipulated by land managers.

Basic principles of tree/stand/mistletoe interactions are well established and provide broad guidelines for stand management. Many refinements of our information base will be necessary to develop precision in the management of the many timber types and host/mistletoe combinations under different geographic, topographic, climatic, and site conditions. Ultimately, predictive models of varying precision, as have been explored by Myers, et al. (1976), Strand and Roth (1976), and Edminster (this vol.), should become available to managers. We need not wait for such models, however. The broad principles already developed can and should be applied to the management of stands in which dwarf mistletoes are an actual or potential problem. Ideally, as these principles are applied, post-treatment research and monitoring on a long-term basis will: (1) provide needed refinement of our data base, (2) confirm or dismiss presently uncertain but suspected relationships, and (3) lead to the development of new concepts and approaches to the control of dwarf mistletoe impact.

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