

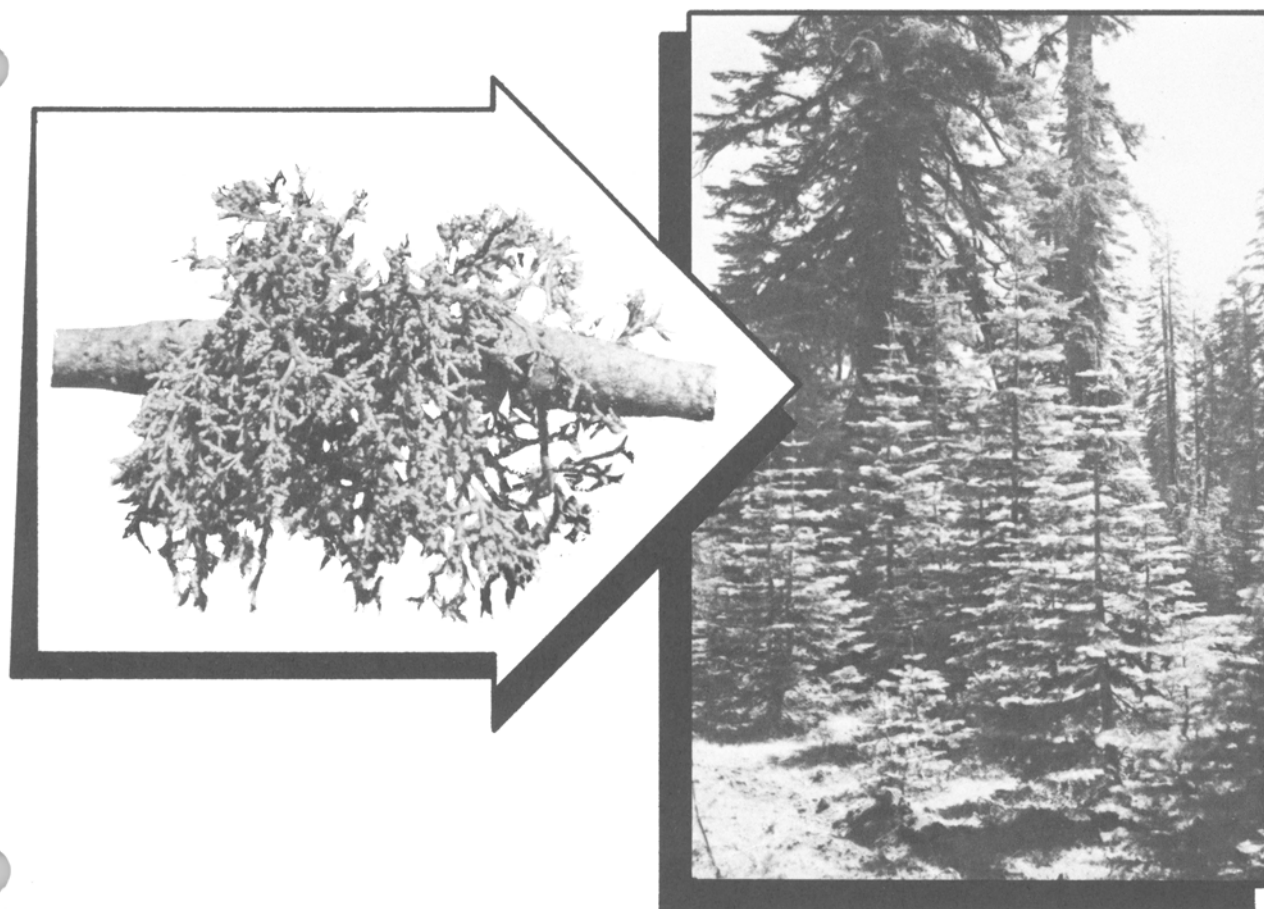
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PACIFIC SOUTHWEST Forest and Range Experiment Station

Population Buildup and Vertical Spread of Dwarf Mistletoe on Young Red and White Firs in California

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SUMMARY

Scharpf, Robert F., and John R. Parmeter, Jr.

1976. **Population buildup and vertical spread of dwarf mistletoe on young red and white firs in California.** USDA Forest Serv. Res. Paper PSW-122, 9 p., illus. Pacific Southwest Forest and Range Exp. Stn., Berkeley, Calif.

Oxford: 176.1 *Arceuthobium abietinum*: 181.51 :174.7 *Abies* spp.

Retrieval Terms: dwarf mistletoe; population dynamics; epidemiology; vertical spread; red fir; white fir; *Abies concolor*; *Abies magnifica*; *Arceuthobium abietinum*; *Viscaceae*.

Population buildup and vertical spread of dwarf mistletoe (*Arceuthobium abietinum* Engelm. ex Munz.) in young red firs (*Abies magnifica* A. Murr.) and white firs (*Abies concolor* [Cord. and Glend.] Lindl.) were studied in the southern Cascades and central Sierra Nevada. Sixteen red firs and ten white firs, free from an overstory source of infection, were inoculated; all became infected following inoculation. The number of infections per tree resulting from inoculation varied widely, however. After 12 to 15 years, secondary infections developed on only 44 percent of the red firs and on only 40 percent of the white firs. With few exceptions, population buildup of the parasite was greater in red firs than in white firs, but again, the number of infections per tree varied greatly. In general, where population buildup did occur, the infections were clustered within the lower portion of the tree crowns.

Greatest distance of vertical spread, after 12 to 15 years, between the lowest female primary infection and the highest secondary infection was 16 feet (4.8 m). Over the same period of time, however, the mean annual distance of spread of the parasite in test trees was 3 inches (7 cm) or less. No vertical spread occurred in some trees. Rate of vertical spread in red fir was not noticeably different from that in white fir.

Tree height growth was not affected by the para-

site after 12 to 15 years, even in trees with the greatest population buildup. Test trees were growing in height several times faster than the parasite was able to spread vertically. When the ratio of tree height growth to vertical spread is 4 to 1, the proportion of a tree's height infected over time is about 25 percent. With greater ratios of growth to spread, similar to those found in the study, even less of a tree's height becomes infected, assuming tree height growth remains relatively constant.

Several factors account for the slow rate of vertical spread of the parasite. The generation time from seed, production, infection, and development of a mature fruiting plant is 5 years or longer. Also, the dense, persistent foliage of true firs limits the upward dispersal of dwarf mistletoe seeds.

Knowledge of the rate of vertical spread of infection in young firs is important for control of the parasite in managed stands. Our findings suggest that dwarf mistletoe spreads vertically much more slowly than young, vigorous firs grow in height. These parasites will have little impact if firs on good sites are managed for optimum growth consistent with other management considerations. Firs on poor sites, or firs that are not growing well in height for other reasons, will suffer infection buildup, with possible severe impact on the trees.

The dwarf mistletoes are widespread and damaging parasites of true firs in the coniferous forests of California (Scharpf 1964; Scharpf 1969). Two species (*Arceuthobium abietinum* Engelm. ex Munz. f. sp. *magnificae* Hawksw. and Wiens and f. sp. *concoloris* Hawksw. and Wiens) affect red fir (*Abies magnifica* A. Murr.) and white fir (*A. concolor* [Gord. and Glend.] Lindl.), respectively. The mechanism of spread of these parasites from mature stands to adjacent young trees, and the distance covered, are well understood. In brief, ripe seeds of dwarf mistletoe are forcibly discharged from fruits on female plants in large trees and spread about 100 feet (30 m) or less to surrounding smaller trees (Scharpf 1969). Thus, small trees near larger infected ones are constantly exposed to an overhead source of dwarf mistletoe seeds and are often severely infected.

Little is known about population buildup and spread of dwarf mistletoe in small firs when an infected overstory is absent or has been removed. Some information on other conifer species in the West is available, however. Graham (1967) assumed *A. campylopodum* Engelm. in ponderosa pines (*Pinus ponderosa* Laws.) in the Pacific Northwest was able to spread upward an average of about 4 inches (10 cm) a year. Unpublished studies by Strand (1973) for the same host-parasite combination suggest that vertical spread was about 1.5 feet (46 cm) in 6 years or about 3 inches (8 cm) per year. Hawksworth (1969), on the other hand, found that *A. occidentale* Engelm. growing on Digger pine (*P. sabiniana* Dougl.) in California, spread vertically an average of about 2 feet (61 cm) per year over a 16-year period, or at a rate about equal to the height growth of the trees. After 16 years, 1250 infections on test trees had resulted from 20 infections caused by initial inoculation.

Studies of *A. tsugense* (Rosend.) G. N. Jones on western hemlock (*Tsuga heterophylla* [Raf.] Sarg.) in British Columbia (Richardson and Van Der Kamp 1972) suggest a vertical rate of spread approaching that found by Hawksworth (1969). Spread was 12 inches (30 cm) and 23 inches (58 cm) per year in dense and open-growing stands respectively; this was about the same rate as the height growth of the infected trees. The number of new infections increased exponentially with time, doubling about every 4 years over a 20-year period.

For predictions of future impact of dwarf mistletoe in true fir stands, it is important to know both the vertical rate of spread and the rate of population buildup of the parasite in relation to tree height growth. If a tree is able to grow in height and put on healthy crown more rapidly than the crown is being invaded from below by dwarf mistletoe, growth reduction or vigor loss should diminish over time, at least until tree height growth slows.

The objectives of this study of dwarf mistletoe were to determine:

1. Rate of population buildup over several years from an initial number of seed-producing plants.
2. Vertical distance and rate of spread in crowns of young red and white firs.
3. Rate of vertical spread in relation to tree height growth.

METHODS

Studies were conducted at two different areas in California: the Stanislaus National Forest near Pinecrest in the central Sierra Nevada, and the Latour State Forest south of Burney in the southern Cascades. Test trees were located in either pure red fir stands or in mixed conifer stands containing either red or white firs. These areas are described in detail in a previous publication (Scharpf and Parmeter 1967).

On the Stanislaus, a total of 21 trees were selected for study. In 1960, two red firs were inoculated with several hundred seeds; in 1961, three red firs and four white firs were inoculated with several hundred seeds; and in 1963-67, six red firs and six white firs were inoculated for 5 successive years with about 100 to 200 seeds per tree each year.

On the Latour State Forest, five red firs growing within 6 feet (1.8 m) of each other were used as test trees. Trees 1 to 4 were inoculated with a total of 100 dwarf mistletoe seeds in 1958. The remaining tree was not inoculated but was included in the data gathering because of its close proximity to inoculated trees and because some secondary infection did occur in its crown.

All test trees were in areas where dwarf mistletoe was present but out of range of infection from overstory trees. All trees were inoculated with freshly collected seeds each year of inoculation—white firs with

seeds from dwarf mistletoe on white firs, and red firs with seeds from dwarf mistletoe on red firs. Inoculations were made by placing ripe seeds on branches 2 to 6 feet (0.6 to 1.8 m) above ground line. Except for the five red firs on the Latour, all test trees were out of range of infection from adjacent inoculated trees. The trees on both areas ranged in height from 5 to 32 feet (1.5 to 9.8 m) at the beginning of the study.

The test trees were examined periodically, usually once a year, for population buildup and vertical spread of the parasite. Total height of the trees was measured at the beginning and end of the study. Tree height growth was measured for the last 5 years of the study period.

The terms used in reporting results are defined as follows:

Primary infections—Those mistletoe plants resulting from initial inoculation of the test trees with dwarf mistletoe seed.

Secondary infections—All subsequent mistletoe

plants on the inoculated trees, arising from seeds produced by primary infections or other secondary infections.

Maximum distance of vertical spread—The distance measured between the lowest female primary infection in the crown and the highest secondary infection. Because it was not possible to determine the specific origin of the seeds which caused secondary infections, we assumed the greatest possible distance of vertical spread as the maximum. We recognized, however, that it was unlikely that the highest secondary infections actually represented spread from seeds produced by the lowest primary female infection.

Mean distance of vertical spread—The distance computed between the mean height of female primary infections and the mean height of secondary infections. Mean distance was divided by the number of years since inoculation to obtain the *mean annual rate of spread*.

RESULTS

Population Buildup

All trees inoculated on both the Stanislaus National Forest and Latour State Forest became infected with dwarf mistletoe. The number of primary and secondary infections differed greatly among the test trees, however.

On red firs, the number of primary infections ranged from 1 to 72, 12 to 15 years after inoculation. Secondary infections developed on only 7 of the 16 test trees. Striking differences between the Stanislaus and Latour areas (*table 1*) were noted in the occur-

Table 1—*Primary and secondary infections on inoculated red firs and white firs, Stanislaus National Forest and Latour State Forest, California*

Host, area, and study period	Test trees	Primary infections			Secondary infections
		Male or unknown	Female	Total	
RED FIR					
Stanislaus N.F.					
1960-75	2	20	10	30	29
1961-76	3	8	14	22	42
1963-75	6	71	48	119	123
Total	11	99	72	171	194
Latour S.F.					
1958-73	5	12	16	28	955
WHITE FIR					
Stanislaus N.F.					
1961-76	4	3	10	13	17
1963-75	6	71	40	111	18

Table 2—Number of new secondary infections observed at intervals following inoculation of red firs and white firs

Host and area	New infections observed after—				Total number of infections
	5 yr	10 yr	12 yr	15 yr	
Red fir:					
Stanislaus N.F.	0	13	147	34	194
Latour S.F.	0	231	267	457	955
White fir:					
Stanislaus N.F.	0	2	25	8	35

rence of primary infections and the buildup of secondary infections. On the Stanislaus, 194 secondary infections occurred over a 12-to-15 year period from an initial 72 primary female infections; on Latour State Forest, 955 secondary infections developed from only 16 primary female infections. This constitutes a buildup at Latour of five times as many secondary infections from only about one-fifth as many primary infections. Thus, the proportion of secondary infections to primary female infections is about 25 times greater on the Latour than on the Stanislaus.

On white firs, the number of primary infections per tree ranged from 2 to 36 and only 4 out of 10 test trees developed secondary infections. A very slow rate of population buildup was noted for dwarf mistletoe on white fir. Only 35 secondary infections resulted after 12 to 15 years from an initial 50 primary female infections.

The reasons why the number of primary infections and population buildup differed greatly among trees and test areas is not known. Possible explanations are discussed later in this report.

Minimum generation time of dwarf mistletoe on firs is 5 to 6 years; in other words, 5 to 6 years are required for a fruit-bearing mistletoe plant to develop from a seed (Scharpf and Parmeter 1967). Therefore we would not expect to see any secondary infections in the present study within 5 to 6 years after initial inoculation of test trees. Except in the red firs at Latour State Forest, very few secondary infections were observed before 12 years after inoculation (table 2).

Distance of Vertical Spread

The maximum distance of vertical spread of dwarf mistletoe was nearly the same on both the Stanislaus and Latour areas. After 15 years, at Latour the maximum spread in any one tree was 14 feet (4.2 m). On the Stanislaus, the spread within a tree was 11 feet (3.4 m) in 12 years. For nearly all trees on both areas,

the spread after 12 to 15 years was considerably less than the maximum reported above.

The mean distance of vertical spread is another way to consider vertical spread. For this value, we compared the mean height of the secondary infections with the mean height of the female primary infections. It may be assumed that not all secondary infections will occur above the primary infections in the crown, although Hawksworth (1961) has shown that seeds of dwarf mistletoe are discharged primarily above the horizontal. Nonetheless, some are discharged downwards and some are likely to be washed onto lower branches by rains following dispersal.

From the combined data for the trees it is clear that at each location, a greater proportion of secondary infection occurred above mean height of primary female infections. For both red fir and white fir on the Stanislaus, about 60 percent of the secondary infections were above the mean height. Certainly the trees at Latour, which bore the greatest number of secondary infections, indicate that spread is predominantly upwards. The height distribution of the secondary infections¹ on the Latour trees was not uniform, however. Ninety percent of all secondary infections at Latour occurred above the mean height (4.1 feet, 1.2 m) of primary infections, but less than 4 percent of all secondary infections were more than 8 feet (2.4 m) above the mean. No secondary infections occurred more than 12 feet (3.7 m) above mean height of the primary infections. Thus, nearly all the secondary infections were tightly clustered within the crowns of the test trees.

¹ Heights of secondary infections at Latour were not measured until 10 to 12 years after the study was begun. As a result, some infections were not recorded because they were missing or tags were lost. We feel, however, that these missing data will not significantly alter the overall results obtained.

Rate of Vertical Spread Compared with Tree Height Growth

The rate at which dwarf mistletoe spreads upward in tree crowns over time in relation to tree height growth is important in predicting future levels of infection and subsequent impact on tree vigor (*table 3*).

Mean distance and rate of vertical spread were very slow over the duration of the study. Greatest rate of vertical spread occurred after 15 years at Latour but was slightly less than 3 inches (8 cm) a year. In white firs, at the 10-year interval, mean annual spread of dwarf mistletoe was principally downwards or below the mean height of the primary infections.

How does the mean annual rate of vertical spread of mistletoe compare with the rate of height growth of the test trees after 15 years?

In all instances, mean annual height growth of test trees was several times greater than mean annual rate of vertical spread of the parasite (*table 3*). On the Stanislaus, the ratio of height growth to vertical spread varied markedly among the red firs and white firs with secondary infections. For red firs, the smallest ratio found was 4 to 1 and the largest 18 to 1; whereas for white firs, the range in ratios was 8 to 1 and 35 to 1. The reasons for the wide variation in ratios are not known and cannot be explained on the basis of differences in tree height growth or differences in levels of dwarf mistletoe populations among individual trees.

At Latour State Forest, the height growth/spread ratio was less variable among trees than on the Stanislaus. The rate of height growth ranged between five and seven times that of vertical rate of spread.

The proportion of a tree's height that is infected by dwarf mistletoe depends on the ratio between tree height growth and vertical rate of spread of the parasite. Regardless of what percentage of a tree's height is initially infected, over time the proportion of the

height infected approaches a constant, assuming the ratio of height growth to vertical spread remains the same.

This principle might be best illustrated by a hypothetical model (*figure 1*). Using data based on the results obtained in this study, we will assume that two 30-year old trees, 20 feet (6.1 m) tall, with full

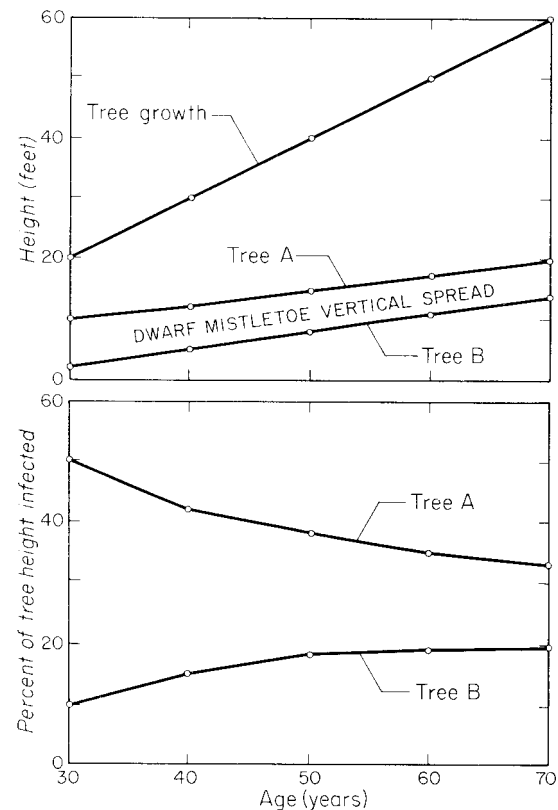


Figure 1—Young, vigorous firs outgrow the vertical spread of dwarf mistletoe. Above, in two hypothetical trees, growth-to-spread ratio is 4 to 1. Below, percent of trees infected increases or decreases, depending on proportion of tree infected at age 30.

Table 3—Tree height growth rate and annual rate of vertical spread of dwarf mistletoe in red and white fir test trees at intervals following inoculation

Host and area	Mean annual tree height growth rate	Mean annual rates of vertical spread of mistletoe—			Ratio of height growth rate to vertical spread at 15 years
		10 yr	12 yr	15 yr	
Red Fir:		Feet			
Stanislaus N.F.	0.7	0.08	0.13	0.06	12/1
Latour S.F.	1.5	0.17	0.12	0.24	6/1
White fir:					
Stanislaus N.F.	0.7	–0.23	0.06	0.08	9/1

crowns, are growing in height a foot (30 cm) a year. In tree A the lower half of the crown is infected—in tree B only the lower 10 percent. Dwarf mistletoe spreads upwards at the rate of 3 inches (8 cm) a year: thus we have a growth-to-spread ratio of 4 to 1. When we plot tree height infected against tree age for tree A, we find the percentage of crown infected diminishes. Conversely, when we plot tree height infected against tree age for tree B, we find the percentage of crown infected increases. In both trees, however, the level of infection over time is approaching 25 percent. The relationship holds true for trees of all sizes and ages as long as a growth-to-spread ratio of 4 to 1

remains constant. In practice, this ratio is not likely to remain constant over the years. We feel, however, that the model demonstrates the relationship between tree height growth and vertical spread of dwarf mistletoe and the proportion of tree crown infected over time.

If we have growth-to-spread ratios more like those found in the study (6 to 1 or 12 to 1), then over time a much smaller proportion of tree's height will be infected. Also, as trees grow older, less of their total height is composed of living crown. Therefore, the percentage of living crown infected will be even less than the percentage of total tree height infected.

DISCUSSION AND CONCLUSIONS

Results of the present study suggest that vertical spread of dwarf mistletoe in red and white firs in California averages less than about 3 inches (8 cm) a year. Our results also indicate that *A. abietinum* spreads vertically at a slower rate than any of the other dwarf mistletoe species and host combinations investigated to date (Graham 1967, Hawksworth 1969, Richardson and Van Der Kamp 1972, Strand 1973).

Several factors may account for the slow rate of spread. First, *A. abietinum* has a rather long generation time between seed dispersal, infection, and subsequent development of infections to the mature, fruiting stage. This period has been shown to be at least 5 to 6 years and may be even longer (Scharpf and Parmeter 1967; Parmeter and Scharpf 1972). Second, the characteristic growth of the branches and foliage of true firs limits distance of spread. The branches of young firs characteristically arise in quite regular tight annual whorls from the main trunk. Also, the foliage on true firs is retained for many years rather than a few years, as in the pines, for example. The physical barrier created by the dense foliage and branches in a whorl is very effective in intercepting seeds dispersed by female infections on lower branches. Thus, most vertical dispersal of seeds of dwarf mistletoe on young firs is restricted to one or two whorls above the fruit-bearing plants. As a result, even high populations of dwarf mistletoe tend to be localized within the crowns of firs rather than distributed throughout much of the crown as they are in the more sparsely foliated, irregularly branched Digger pine (Hawksworth 1969). A third factor in the slow spread evident in our study may be that not every year is favorable for fruit production, seed germination, and infection by dwarf mistletoe. At least

one fungus parasite periodically destroys the shoots and fruits of dwarf mistletoe on firs when climate conditions are favorable for the disease (Parmeter and others 1959). Also, certain climatic conditions in themselves, we feel, often limit fruiting, germination, and infection. As a result, population buildup and to some degree vertical spread vary considerably from one year to the next.

The variation in numbers of secondary infections within individual trees does not appear to be necessarily related to the number of primary seed-producing dwarf mistletoe plants in a given tree. At Latour, the test trees may have been inherently more susceptible to infection than those on the Stanislaus, or climatic conditions may be more favorable for infection at Latour. Even on the Stanislaus, unexplainable wide differences in numbers of primary and secondary infections were recorded. Further studies are needed.

Because this study extended over a period of 12 to 15 years, we can assume that secondary infections in the crowns of the test trees were produced by seeds from both primary and first-generation secondary infections. What the rate of buildup will be in the future is not known and needs to be further investigated. We can anticipate, however, that perhaps the rate of population buildup will increase as more seed-bearing plants among succeeding generations of plants also begin to bear fruit. On the other hand, mortality of dwarf mistletoe plants as a result of natural pruning of the lower branches as trees grow in height will lower the population levels of the parasite and reduce the proportion of the live crown infested. Additional mortality of dwarf mistletoe from squirrel feeding, the fungus *Cytospora abietis* (Scharpf and Bynum

1975), and other causes will also aid in keeping populations in check.

Rate of vertical spread should not increase markedly over time, however, unless distance between annual branch whorls increases markedly. Vertical spread appears to be regulated more by the physical barrier imposed by the branches and foliage of the annual whorls than by population levels of the parasite. Even if mean annual rate of spread increases as a result of the greater distance between annual whorls, the ratio between tree height growth and vertical spread of dwarf mistletoe should remain more or less constant.

Measurements of tree height growth at Latour for 1971-73 suggest that the buildup of the parasite in the lower crown is having no noticeable impact on

growth. All test trees were growing in height over these later years at a mean annual rate comparable to that measured for the years 1958-70. This is in agreement with studies by Hawksworth (1961) that have shown that little growth reduction or impact occurs in pines if dwarf mistletoe is restricted to the lower third to one-half of the tree crown. We have found from studies in progress that the same phenomenon applies to true firs.

We envision that the vertical spread rate will approach that of height growth in (1) older fir trees that have reached maturity and are growing very slowly in height, and (2) low vigor trees growing slowly in height and with very thin foliage or irregularly branched crowns, for example, suppressed trees or trees on poor sites.

MANAGEMENT IMPLICATIONS

Results of the study have important implications for management and control of dwarf mistletoe in young-growth red fir and white fir stands. The principle behind the management approach is that *dwarf mistletoe populations will not spread and build up over time beyond a certain proportion of the tree height in young trees with good height growth and in the absence of overstory infection*. Several important points should be considered in dwarf mistletoe management or control decisions:

1. Dwarf mistletoe spreads vertically in crowns of young red and white firs an average of 3 inches (8 cm) or less per year.
2. Young, vigorous red and white firs will suffer little growth impact if dwarf mistletoe can be restricted to the lower half of the tree's height (or crown).
3. A tree growing an average of 1 foot (30 cm) a year will have a ratio of height growth to vertical spread of about 4 to 1 or more. This ratio is adequate to ensure that no more than about a quarter of a

tree's height and even less of its living crown will be infected with age until the tree reaches maturity and slows in height growth.

4. Even trees infected throughout a substantial portion of the crown will become proportionately much less severely infected if a growth-to-spread ratio of 4 to 1 or greater can be achieved.

The key to dwarf mistletoe control in young fir stands is the same as good silvicultural management of healthy, young fir stands. Use whatever means necessary to insure good height growth of young stands consistent with proper stocking levels and other management considerations.

Young trees on poor sites, or trees that for other reasons are not growing in height, are likely to experience buildup and impact from these parasites. Also, once height growth slows in vigorous, older trees, an increase in the proportion of crown infected, and in the impact of the dwarf mistletoe on tree growth, can be expected.

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Rate of population buildup of dwarf mistletoe, *Arceuthobium abietinum* Engelm. ex Munz., was slow in most small red firs and white firs 12 to 15 years after inoculation with the parasite. Where population buildup did occur, it remained clustered in the lower portions of tree crowns near inoculation sites. Maximum distance of vertical spread was 16 feet (4.8 m), after 15 years. The mean annual rate of vertical spread of the parasite in 12 to 15 years was 3 inches (7 cm) or less in test trees. No vertical spread occurred in some trees. Rate of vertical spread was much slower in all trees than the mean annual height growth of vigorous young red or white firs. Therefore, the test trees were outgrowing the spread of dwarf mistletoe within tree crowns. Vertical spread rate and rate of tree height growth together determine the proportion of tree crown that will be infested at a given time after inoculation.

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Rate of population buildup of dwarf mistletoe, *Arceuthobium abietinum* Engelm. ex Munz., was slow in most small red firs and white firs 12 to 15 years after inoculation with the parasite. Where population buildup did occur, it remained clustered in the lower portions of tree crowns near inoculation sites. Maximum distance of vertical spread was 16 feet (4.8 m), after 15 years. The mean annual rate of vertical spread of the parasite in 12 to 15 years was 3 inches (7 cm) or less in test trees. No vertical spread occurred in some trees. Rate of vertical spread was much slower in all trees than the mean annual height growth of vigorous young red or white firs. Therefore, the test trees were outgrowing the spread of dwarf mistletoe within tree crowns. Vertical spread rate and rate of tree height growth together determine the proportion of tree crown that will be infested at a given time after inoculation.

Oxford: 176.1 *Arceuthobium abietinum*: 181.51:174.7 *Abies* spp.

Retrieval Terms: dwarf mistletoe; population dynamics; epidemiology; vertical spread; red fir; white fir; *Abies concolor*; *Abies magnifica*; *Arceuthobium abietinum*; *Viscaceae*.

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