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Population Dynamics of Dwarf Mistletoe on Young True Firs in the Central Sierra Nevada, California

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CONTENTS

Introduction	1
Methods	2
Study Area	2
Inoculation of Hosts	2
Results and Discussion	3
Germination of Seeds	3
Incubation Period	3
Fruiting of Plants	4
Second-Generation Infections	6
Mortality of Infections	6
Conclusions	8
References	8

IN BRIEF . . .

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The true firs—red fir (*Abies magnifica* A. Murr.) and white fir (*A. concolor* [Gord. & Glend.] Lindl. ex Hildebr.)—are infected in large proportion by a potentially damaging parasite, dwarf mistletoe (*Arceuthobium abietinum*). The parasite can build up to large numbers in trees and stands where it reduces tree growth and vigor, deforms trunks, and predisposes trees to mortality from other agents, such as drought and bark beetles.

The rate at which young trees and stands become infected to damaging levels by dwarf mistletoe is information needed by the land manager to determine how best to manage infested stands to keep losses to a minimum. To provide this information, this study on population dynamics of dwarf mistletoe—the rate of buildup and decline of infection and the variables involved—was begun in fall 1963, on the Stanislaus National Forest, in the central Sierra Nevada, California. Several sapling red and white firs were inoculated with dwarf mistletoe seeds over a 5-year period, 1963 to 1969, and examined annually for an additional 12 years for infection and buildup of dwarf mistletoe populations.

Although based on a small sample of trees, results of the study point out several aspects about infection and buildup of the parasite. Relatively few—3 to 4 percent—of the almost 7000 seeds placed on branches resulted in infection. Many seeds were either missing from branches or failed to germinate. Of the seeds that germinated, annual infection for the 5-year inoculation period ranged from 10 to 50 percent. For dwarf mistletoe on each host species, however, percent infection was similar during the 5 years. Greater variation in infection was observed among individual trees than among years. This observation suggests that possible differences in resistance to dwarf mistletoe or unfavorable climatic influences may regulate infection of trees on different sites.

Buildup of parasite populations varied more among individual trees than between fir species. On some trees, no second-generation infections developed; on others, dwarf mistletoe populations doubled after 17 years. Variables other than possible genetic or climatic influences that appeared to regulate rate of population buildup included a long time period (8- to 9-year average) between inoculation and production of fruit bearing plants, low rate of fruit production on young female plants, low proportion of female plants producing abundant fruit (100 or more/year), and the irregular production of fruit by plants over the years. Population buildup was limited also by death of a high proportion of the infected branches. This dying-off of infected branches suggests that dwarf mistletoe plants may have a short average life span and that the death rate of plants helps slow the rate of population buildup.

Because of the slow rate of population buildup of dwarf mistletoe, it may be possible to manage infested, even-aged, young-growth stands in the central Sierra Nevada without appreciable damage from this parasite. Although the results of this study may apply to young firs in other locations, the rate of buildup of the parasite has been found to be more rapid on young red firs in the southern Cascades.

Among the most valuable timber-producing species in California, the true firs—red fir (*Abies magnifica* A. Murr.) and white fir (*A. concolor* [Gord. & Glend.] Lindl. ex Hildebr.)—grow mainly in the mid- and upper-elevations of the Sierra Nevada and southern Cascades. Here they help to maintain and to regulate the snowpack, thereby conserving the water resources of the State. Fir forests are also prized for their recreational and scenic values.

Unfortunately, red firs and white firs are infected by damaging dwarf mistletoes. *Arceuthobium abietinum* Engelm. ex Munz f. sp. *magnificae* Hawksw. & Wiens infects red fir, and *A. abietinum* Engelm. ex Munz f. sp. *concoloris* Hawksw. & Wiens infects white fir. Surveys done by the Forest Service, U.S. Department of Agriculture, show that about 40 percent of the red fir stands and about 30 percent of the white fir stands in the State are infested with these parasites (Calif. Forest Pest Control Action Council 1961). This means that thousands of acres of true fir stands are infested to some degree by these parasitic plants.

The dwarf mistletoe problem in true fir stands is not expressed by catastrophic mortality or rapid decline of trees, as is true for some disease—host species combinations. Rather, losses stem primarily from a continued drain on a tree's vigor and energy resources by the parasites. Eventually, reduced growth, tree deformation, or premature death from other agents such as bark beetles or drought results.

Because of the relatively slow rate at which dwarf mistletoe spreads and damages trees, managers have time to evaluate the situation and to plan control strategies. Effective evaluation and control require knowledge of present infection levels and damage as well as projected levels of mistletoe buildup and damage. How rapidly dwarf mistletoe builds up and spreads within trees and stands and the type and extent of damage that can be expected over time in infested stands is information needed by the forest manager.

Within the past several years research has answered some of the questions asked by forest managers concerning the biology and control of dwarf mistletoes in true firs. As a

result, the general biology and infection processes of fir mistletoe are now fairly well understood (Scharpf and Parmeter 1967). We know that two host-specific forms of fir mistletoe occur in California, one that infects only red fir and one that infects only white fir (Parmeter and Scharpf 1963). Small firs are nearly disease free, even in heavily infested stands (Scharpf 1969b). In the absence of overstory infection, vigorous young firs can outgrow the vertical spread of mistletoe within infected crowns (Scharpf and Parmeter 1976). Dwarf mistletoe in true firs does not affect trunk taper (Scharpf 1977) but can reduce both height and radial growth of released red firs (Scharpf 1979).

Population dynamics—the rate at which mistletoe populations build up or subside within trees or stands—is one aspect of the biology of these parasites that is not well known, mainly because a decade or more is needed to obtain meaningful information on population dynamics.

This paper reports results of studies over a period of 16 years, from 1963 to 1979, that were designed to help clarify the population dynamics of these parasites during the early stages of their life on young true firs.

Specifically, this paper reports answers to these questions:

- Do a high proportion of dwarf mistletoe seeds placed on branches of firs germinate and cause infection?
- Do red fir and white fir differ in susceptibility to infection by dwarf mistletoe?
- Are there "wave years" of infection or is the infection level in trees fairly constant over successive years?
- What is the rate of population buildup of dwarf mistletoe on young trees? Are the incubation periods, generation times, and rates of population buildup different for dwarf mistletoe on red fir and white fir or among individual trees of a species?
- What are some of the variables that regulate population buildup of dwarf mistletoe? What proportion of the mistletoe plants produce seeds and does seed production vary among different plants over time? What is the average life expectancy of dwarf mistletoe plants and what variables are involved in mortality?

METHODS

Study Area

The general study area, described earlier (Scharpf and Parmeter 1967), was in the Summit District, Stanislaus National Forest, in the central Sierra Nevada of California. Twelve vigorous saplings—six red firs and six white firs—were inoculated and studied. Two trees of each species were selected at each of three different elevational zones within the natural range of the species (*table 1*). None of the trees selected was located within seed dispersal range of dwarf mistletoe in overstory trees, although dwarf mistletoes were present throughout the general study area.

Inoculation of Hosts

Beginning in fall 1963, the six sapling red fir and six sapling white fir trees were inoculated for 5 successive years with freshly collected dwarf mistletoe seeds. Each fall, ripe seeds were collected in paper bags (Scharpf and Parmeter 1962) from infected red and white firs within the study area. Each test tree was inoculated with a sample of the

combined collection of seeds of either red fir dwarf mistletoe (RFDM) or white fir dwarf mistletoe (WFDM).

To inoculate trees, dwarf mistletoe seeds were placed in water in petri dishes until the outer viscin coating swelled. The seeds were picked up carefully with forceps and placed on a branch at the base of a living needle. The site of each inoculation was marked with red paint and each branch identified with a numbered tag. Five different main branches were inoculated each year on each test tree. From 600 to 700 inoculations were made on each species yearly for the 5-year period (*table 2*).

Germination of seeds was recorded in the summer of each year after inoculation, and subsequent infections were recorded yearly from 1963 to 1979. Data recorded on infection by dwarf mistletoe included sex of the plant, dwarf mistletoe shoot and fruit production, development of second-generation infections, and damage and mortality of inoculated branches and mistletoe plants.

Shoot and fruit production were rated each year as absent, sparse, moderate, or abundant. Five or fewer shoots per plant was considered sparse, 6 to 10 moderate, and more than 10 shoots, abundant. Ten or fewer fruits per plant was judged sparse, 11 to 100 moderate, and more than 100 fruits abundant, by visual estimate.

Table 1—*Sites on which red and white firs were selected for study*

Host	Plot	Elevation (feet)	Description
Red fir	1	6200	Mixed-conifer stand at the lower elevational limit for red fir; moderately shaded, gently sloping, northern exposure.
	2	6500	Open-grown trees on a gently sloping western exposure in the mid-elevational range of red firs; surrounding stands mainly mixed red and white firs.
	3	7000	Trees selected were on a level exposed site, within stands of pure red fir interspersed with a few scattered western white pines and Jeffrey pines.
White fir	1	5300	Open-grown trees on a gently sloping southern exposure, in a mixed-conifer stand.
	2	6100	Open-grown trees on a moderately sloping western exposure and within a mixed-conifer stand of mainly white fir.
	3	6900	Open-grown trees on a flat exposure and within a nearly pure red fir stand.

Table 2—*Total number, germination, and infection of seeds of dwarf mistletoe placed on red and white firs, 1963 to 1967*

Year of inoculation	Seeds used	Germination	Infection		
			By all seeds	By germinated seeds	
Percent					
Red fir dwarf mistletoe					
1963	602	6	1	0.4	50
1964	662	103	16	4	26
1965	709	196	28	7	24
1966	790	52	7	2	23
1967	648	181	28	4	15
Total	3411	538	16	3	22
White fir dwarf mistletoe					
1963	799	284	36	3	10
1964	623	183	29	3	11
1965	753	244	32	3	11
1966	756 ¹	109	21	2	12
1967	654	340	51	5	9
Total	3337	1160	35	4	10

¹The total number of seeds used in 1966 was 756, but only 508 seeds on four white firs were examined for germination.

RESULTS AND DISCUSSION

Germination of Seeds

Germination of seeds placed on red and white fir branches during the 5-year period varied considerably, particularly for the seeds of RFDM (*table 2*). Germination of RFDM seeds was as low as 1 percent in 1963 and as high as 28 percent in 1965 and 1967. Germination of WFDM seeds ranged from 21 to 50 percent. Total number of seeds germinating for 5 years on red fir was 538 (16 percent), and on white fir was 1160 (35 percent). From 1963 to 1967, therefore, about twice as many seeds of WFDM on branches germinated as did seeds of RFDM. Most seeds recorded as not germinating were missing from branches. Causes of seed loss were not determined. However, many of the seeds probably did not become firmly attached to branches and fell off or were dislodged before germinating in the spring. In some instances, it appeared that seeds had been eaten by birds or other animals because portions of the seed coats were found still adhering to the branch. For the ungerminated seeds on branches, some were probably nonviable at the time of placement, some probably molded during the winter, and some appeared to have been hollowed out by insects. Seed loss, damage to seeds by birds, animals, insects or molds and some nonviable seeds can account for much of the variation in germination between species during the 5 years.

Percentage of infection that resulted from seeds placed on branches was fairly consistent on both host species for the 5-year inoculation period (*table 2*). In general, from 3 to 4 percent of the placed seeds resulted in infection. Only for RFDM in 1963 was the infection rate lower. Of the seeds that germinated, about twice as many resulted in infection on red firs than on white firs. On red firs, 15 to 50 percent of all germinated seeds resulted in infection, but on white firs only 12 percent or fewer of the germinated seeds resulted in infection.

Percent infection resulting from germinated seeds differed among the individual test trees. For RFDM, it ranged from 1 to 47 percent and for WFDM from 3 to 38 percent. Why infection rates from germinated seeds were low on some trees and high on others is not known. Natural resistance to infection among certain populations of trees in an area is a possibility. Another explanation may be that some trees were on sites or in microclimates that were less favorable for survival and infection by the germinated seed. Infection of trees on two of the plots indicated that this may be true. Infection percentages were low for red fir on one plot and low for white fir on another. These plots were located at the extreme upper elevational limit for white fir and in the upper elevational range for pure red fir stands in the area. No white fir trees were naturally infected by dwarf mistletoe at these elevations, but some red fir stands in the area were infected. On lodgepole pine, the

upper limits of elevation for dwarf mistletoe are 200 to 600 feet below the upper limits of the host in the Rocky Mountains (Hawksworth 1956). Also, the frequency of *A. vaginatum* was highest at the medial elevations of the ponderosa pine type in the Southwest (Hawksworth 1959). It is possible, therefore, that dwarf mistletoe may be more successful in infecting true firs within the median elevational range than at the upper elevational limits of the host. Why fewer infections occurred at the upper elevational limits of firs in this test is not known, but the short growing season, harsh climatic conditions, or both, may be involved.

Incubation Period

The incubation period—the time between placement of seeds on branches and first symptoms of infection—was similar for RFDM and WFDM (*fig. 1*). Branch swelling was almost always the first symptom of infection. Few infections appeared within 2 years after inoculation, most appeared in the third and fourth years, and then the number tapered off until none occurred after 10 years for RFDM, and 12 years for WFDM. It is possible that these later infections were second-generation ones resulting from naturally dispersed seeds of first generation plants infecting branches at an inoculation site. We believe, however, that the chance of this occurring is remote. Dwarf mistletoe seeds on firs do not remain viable for more than 1 year, and newly dispersed seeds must germinate and penetrate branches by the end of summer if they are to infect the host (Scharpf and Parmeter 1967). Why some dwarf mistletoe infections fail to develop and remain hidden in the host branch for as long as 10 or more years after penetration has not been explained. Our results correspond closely to those found by Wagener (1962) for *A. campylopodum* on

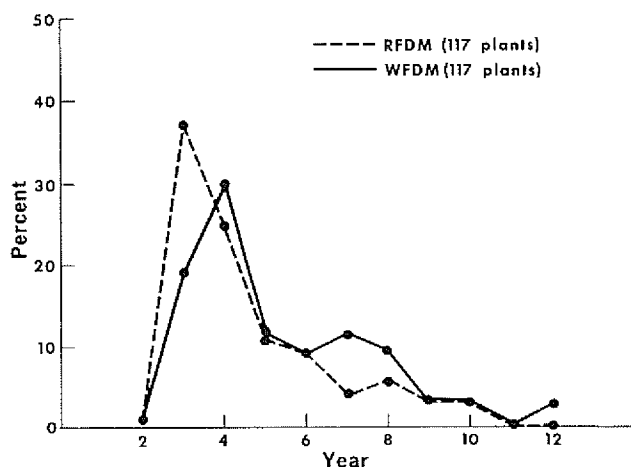


Figure 1—The incubation period of red fir dwarf mistletoe (RFDM) and white fir dwarf mistletoe (WFDM), expressed as a percentage of the plants developing from inoculation in 1963 to 1967, varied widely.

ponderosa and Jeffrey pines and by Scharpf and Parmeter (1967) for *A. abietinum* on both red and white firs. Although Wagener (1962) did not follow the incubation periods for more than 6 years and Scharpf and Parmeter (1967) for more than 5, they observed that most infections appeared in the third and fourth years on ponderosa pine, Jeffrey pine, and white fir, and in the third and fifth years on red fir.

Seventy-two percent (for RFDM) and 83 percent (for WFDM) of the newly developed infections initially were recognized by branch swelling only or by the presence of swelling and small shoot buds. Dwarf mistletoe plants at this stage of development are not readily seen and to recognize them requires careful searching of branches. The remainder of the infections were recognized by the presence of well-developed dwarf mistletoe shoots.

Differences in the average length of the incubation period of the parasite among individual test trees were not significant. Because the average incubation period ranged from 4 to 6 years for both RFDM and WFDM, inherent characteristics that might regulate the length of the incubation period were not apparent in this study.

Fruiting of Plants

Sex Ratio

The ratio between male and female plants that develops from seeds has never been determined for dwarf mistletoes on true firs. Studies on *A. vaginatum* in the Southwest (Hawksworth 1961) and on *A. campylopodum* in the Pacific Northwest (Wicker 1967) showed that the ratio of male to female plants was 1:1. Of the 117 RFDM plants that resulted from a random selection of seeds, 62 (53 percent) were female, and of 117 WFDM plants, 51 (44 percent) were female. The remaining plants were identified as males, or in a few instances the sex was unknown. Results of a chi-square test applied to each mistletoe indicated that a 1:1 sex ratio is probable. Chi-square for red fir dwarf mistletoe = 0.42; for white fir dwarf mistletoe, 1.9.

Frequency of Fruiting

The number of years between inoculation of branches with dwarf mistletoe seeds and the development of infections bearing mature fruit varied markedly among female dwarf mistletoe plants. For 62 female RFDM plants, the period ranged from 4 to 12 years for fruit production, and for 51 female WFDM plants, from 5 to 16 years. The average number of years before fruit was produced on both RFDM and WFDM was about 8. Several years often elapse after infection, therefore, before shoots bear mature fruit. The long incubation period of most plants was a major factor in the long interval between infection and fruit production. The interval was further extended by the normal period of fruit maturation, which is about 1 year after the pollination of female flowers. Other reasons, however, were noted for the lack of fruit production on plants in some years. On some plants, shoots did not

mature and produce flowers for several years after the first shoot buds appeared. On other plants, mature shoots were broken off, damaged, or killed by various agents including tree squirrels, insects, and two parasitic fungi (*Colletotrichum gloeosporioides* Penz., and *Cylindrocarpon gillii* [Ellis] J. A. Muir). In 1978, many fruits aborted during maturation before the seed dispersal period. Hudler and French (1976) attributed fruit abortion to freezing temperatures before seeds had ripened and could be dispersed. Other variables affecting fruit production may have been involved, but were not determined in this study.

Some plants produced fruit nearly every year. One RFDM plant, for example, produced fruit 9 out of 12 years after the first year of shoot production and another 8 out of 11 years. Two WFDM plants produced fruit 10 out of 13 years after first shoot production. At least some female plants, therefore, were able to produce fruit nearly every year for more than 10 years.

The average number of fruiting years for female plants during three 5-year intervals after inoculation were analyzed (table 3). On the average, during the first 5-year interval, a small proportion of the female plants produced fruit; during the second 5-year interval about one-third of female plants of both dwarf mistletoes produced fruit each year; during the third 5-year interval RFDM fruit production was about the same as the previous interval, but WFDM fruit production was about double. Yearly fruit production varied widely among individual plants, however.

Quantity of Fruit Produced

The amount of fruit produced by female plants varied among different plants and also among the same plants in different years. One of the major variables in fruit produc-

Table 3—Fruit production by female plants of red fir and white fir dwarf mistletoe during 5-year intervals after inoculation

Years after inoculation	Plants ¹	Fruit-producing years ²	Mean annual fruiting of plants
<i>Percent</i>			
Red fir dwarf mistletoe			
1 to 5	62	12	4
6 to 10	53	96	36
11 to 15	15	30	40
White fir dwarf mistletoe			
1 to 5	51	3	1
6 to 10	51	95	37
11 to 15	10	36	72

¹Mortality accounts for some reduction in number of plants over time.

²The cumulative number of years the female population of first-generation dwarf mistletoe plants produced fruit over a given 5-year interval after inoculation.

tion was the plant's ability to produce shoots. In general, dwarf mistletoe plants growing on larger, more vigorous branches produced more shoots and fruit than did plants on smaller branches (*fig. 2*). On branches of the same size, however, shoot and fruit production often varied markedly.

The quantity of fruit produced by female plants was calculated from the cumulative number of years in which all female plants of dwarf mistletoe bore fruit (*fig. 3*). On

the average for both mistletoes, 50 to 60 percent of the fruit production on plants during the study period was rated sparse, about 30 percent was rated moderate, and only about 10 to 15 percent was rated abundant. These proportions were similar when fruiting was broken down into 5-year intervals after infection (*fig. 3*). Except for the early years before shoots are produced, therefore, age of female dwarf mistletoe plants did not seem to be related to the

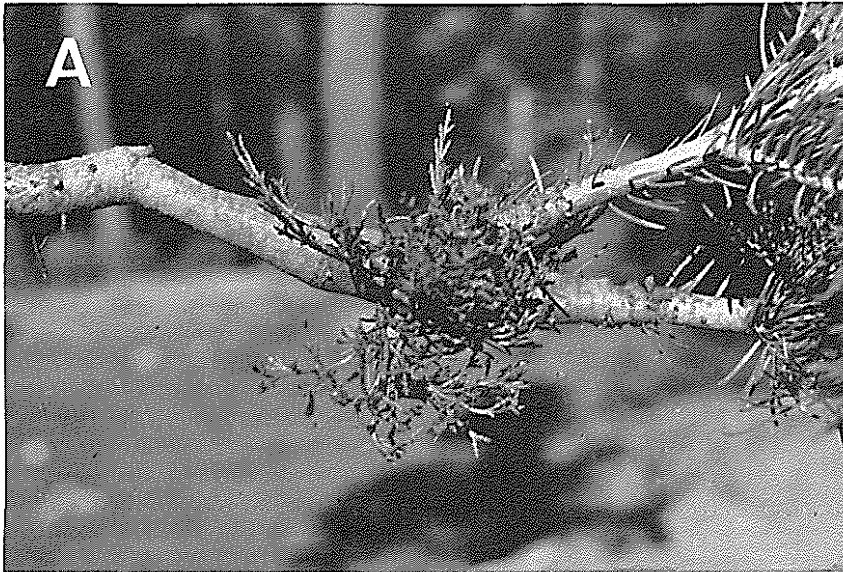
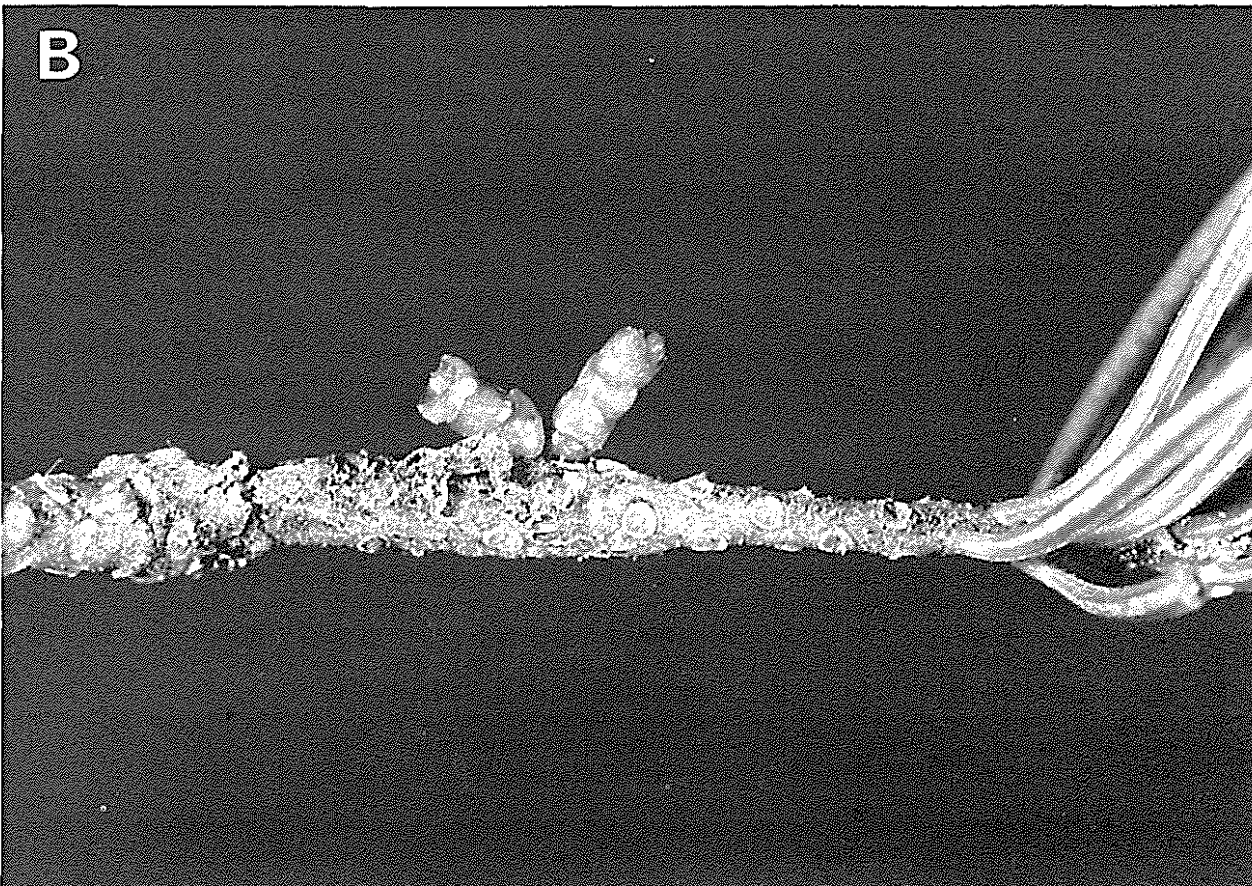


Figure 2—A dwarf mistletoe plant growing on a large main branch is able to produce more shoots (A) than a plant growing on a small lateral branch (B).



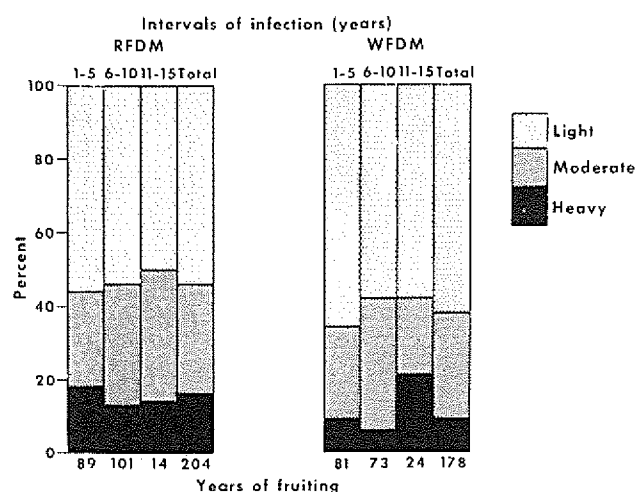


Figure 3—Fruit production by fruiting plants of red fir dwarf mistletoe (RFDM) and white fir dwarf mistletoe (WFDM) at 5-year intervals and 15 years after inoculation expressed as a percentage of the total number of years of fruiting.

amount of fruit produced. Results from these tests indicate that, in most years, most dwarf mistletoe plants are poor or moderate producers of fruit. Preliminary results from unpublished studies suggest that many dwarf mistletoe plants show a fairly regular, fluctuating pattern of fruit production over the years. A fluctuating pattern, however, was not determined in this study. On the average, abundant fruit is produced on only about 20 percent or less of the female plants of RFDM and WFDM in any 1 year. Much of the seed produced for spread and buildup of dwarf mistletoe, therefore, is produced by a relatively small proportion of the dwarf mistletoe population.

Second-Generation Infections

Second-generation infections refer to all dwarf mistletoe plants on test trees except those that resulted from the initial inoculations. Because the average time period between inoculation and development of new fruit-bearing plants was about 8 years, we believe that most of the new plants appearing during the 16-year study were second generation plants (*table 4*). Some third-generation plants may have been part of the total dwarf mistletoe population, but we could not distinguish between second- and third-generation plants.

Second-generation infections were not produced on every test tree; rather, they failed to develop on four red firs and three white firs. On two of the red firs, secondary infections were precluded because only male plants developed. Lack of secondary infections on the two other red firs cannot be explained. On these trees, female plants produced fruit for several years, some as early as 1969 and 1973. On one white fir, infection was precluded because only male plants were produced, but on the other two,

Table 4—Years of fruit production by first-generation female plants and the development of second-generation plants of dwarf mistletoe on test trees from 1963 to 1979¹

Species	First-generation plants	Fruit-producing years ²	Second-generation plants
Red fir dwarf mistletoe	62	207	149
White fir dwarf mistletoe	50	175	105

¹Based on two red firs and three white firs.

²The total number of years the female population of first-generation dwarf mistletoe plants produced fruit over 16 years.

female plants produced fruit for several years beginning as early as 1971.

For more than one-half of the test trees infected with dwarf mistletoe, therefore, no secondary infections developed during the 16-year period. For both red and white firs with secondary infections, populations after 16 years were about double the population level that resulted from inoculation. These levels do not represent the total number of living dwarf mistletoe plants on test trees after 16 years, but only the total numbers that developed during the test period. As will be discussed later, dwarf mistletoe plants are killed off by certain agents, and the total number of living plants on trees is reduced thereby.

Mortality of Infections

Although dwarf mistletoe plants can live for many years on their hosts, many are killed. The mortality rate in relation to the rate at which plants regenerate and increase in number is information pertinent to understanding the population dynamics of these parasites. We investigated the mortality of dwarf mistletoe infections at yearly intervals and noted some of the variables that were involved either directly or indirectly in their mortality.

Causes of Mortality

We have not found evidence to indicate that dwarf mistletoe plants die out, leaving the infected portions of branches free of disease. As mentioned earlier, portions of the shoot or root system of dwarf mistletoe plants may be killed by various animals, insects, diseases, or climatic agents, but no dwarf mistletoe plants we observed have ever died out in a living branch. Instead, a plant dies only when either the infected branch or the tree dies. We could determine in the field only a few of the variables that were responsible for death of branches or portions of branches bearing dwarf mistletoe. From observations of 122 dead mistletoe plants on firs, broken branches and rodent chewing accounted for about 3 percent of the mortality. Chewing of dwarf mistletoe-infected portions of branches by rodents (presumably for starches and sugars stored in

the infected tissue) was not uncommon on the test trees, but of 25 branches chewed, only 3 died.

Cause of death of 97 percent of the infected branches was not determined. We suggest, however, that a large portion of the undetermined mortality of dwarf mistletoe was probably caused by the canker fungus *Cytospora abietis* Sacc. killing dwarf mistletoe-infected branches. The fungus is common in true fir forests in California, frequently causes severe branch flagging, and often infects fir branches at the site of a dwarf mistletoe infection (Scharpf and Bynum 1975). In one study, about one-fifth of all red fir and white fir dwarf mistletoe-infected branches sampled in the field were infected with *C. abietis* (Scharpf 1969a). We think it is likely, therefore, that *Cytospora* canker was involved in some and, probably, in a considerable portion of the undetermined mortality.

We observed periodically that some infections on secondary and tertiary branches died when a main branch bearing an infection died. This type of mortality was more frequent on trees with second-generation infections and on branches with multiple infections. Over time, as multiple branch infections increased with an increase of dwarf mistletoe populations, we would expect to find more of this type of mortality.

Another cause of some of the undetermined mortality, we believe, was the result of natural pruning or dying of older, lower branches as the test trees grew in height and age. Part of the developmental stage in the growth of many trees, including firs, is the natural death of the weaker, physiologically less active branches, particularly those that become shaded out in the lower crown. Some of the dwarf mistletoe-infected branches in this study probably died for this reason.

In addition to dead infected branches, a number were recorded as missing. In this study it was impossible to

determine if an infected branch was missing from the tree or if only the tag marking it was missing. A number of tags were removed from one tree in 1976, probably by hunters. Although we could record the total number of infections, we could not tell, in most instances, which were new ones, which ones had recently died, or which were missing.

Mortality Rate of Dwarf Mistletoe Plants

Annual mortality was recorded for all plants that resulted from inoculation between 1963 and 1967. In red firs, no plants died before 1970 (fig. 4) and in white firs, none died before 1971 (fig. 5). Thereafter, some died almost every year for 10 years. The percentage that died each year was consistent (less than 10 percent) for both dwarf mistletoe species, except that for WFDM the death rate was 13 percent for 1975 to 1976 and 23 percent for 1977 to 1978.

Although annual mortality was low, cumulative mortality after 10 years among all plants was high. About 30 percent of the original population of RFDM and about 48 percent of the original WFDM plants were dead. We might say that the half-life—the number of years after which half of the original population is still alive—for a given population of RFDM is 15 to 20 years if the present rate of mortality continues, and that the half-life of a population of WFDM in young trees is about 10 years.

Dwarf Mistletoe Buildup as Influenced by Branch Mortality

As stated earlier, a substantial portion of the original population of dwarf mistletoe died within 10 years. During this same period, however, new infections were produced. To understand whether dwarf mistletoe populations are increasing, decreasing, or remaining more or less static, it is necessary to determine the rate at which new infections develop in relation to the rate at which established infections die.

If we consider the total number of infections on all trees for the 16-year test period, the population of dwarf

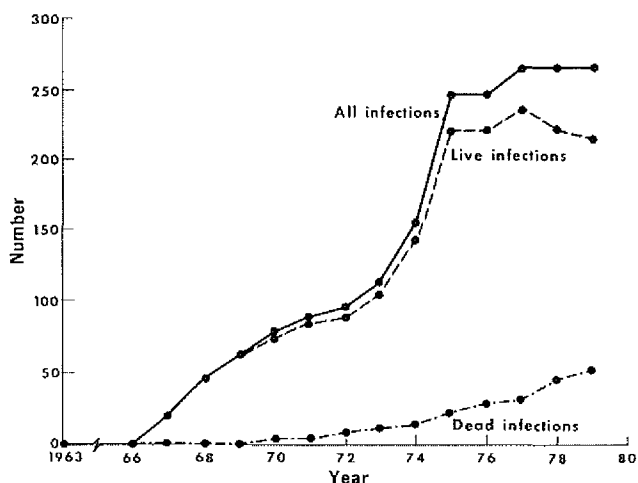


Figure 4—Total number of dwarf mistletoe plants developing on test red firs from 1963 to 1979.

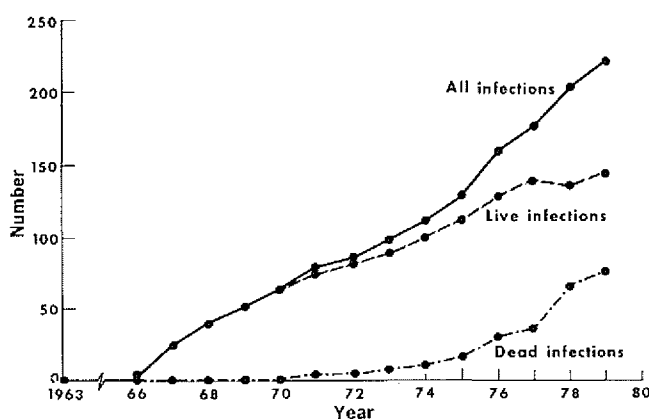


Figure 5—Total number of dwarf mistletoe plants developing on test white firs from 1963 to 1979.

mistletoe increased considerably over time (*figs. 4 and 5*). During most of this period, infections were increasing in number faster than they were dying. From 1975 for RFDM and from 1977 for WFDM, however, the total number of live infections remained more or less constant. For RFDM, this appears to be the result of both a slowing down in the reproductive rate and an increase in infection mortality. But for WFDM, the leveling-off of the population appears to be primarily the result of an increase in infection mortality. The apparent leveling-off of the population of live dwarf mistletoes, particularly if it continues, may markedly reduce future damage to infected firs by this parasite. Vigorously growing firs can outgrow the vertical spread of dwarf mistletoe (Scharpf and Parmeter 1976). If, in addition, dwarf mistletoe populations reach a plateau and fail to intensify, then firs will grow and add healthy crown faster than the parasite can either spread or build up. In such situations, it is difficult to imagine firs suffering much damage from dwarf mistletoe until their growth and vigor subside at maturity. One unanswered question, to date, is: does dying-off of the dwarf mistletoe-infected branches seriously affect growth rate of the firs by reducing a tree's live crown ratio? Live crown ratio has been shown to be a significant variable in height and radial growth of both dwarf mistletoe-infected and uninfected true firs (Scharpf 1979). The extent to which dwarf mistletoes reduce live crown ratios of fir over time, however, needs further investigation.

CONCLUSIONS

From 3 to 4 percent of all seeds placed on branches resulted in infection. The low percentage of infection was the combined result of seed loss from branches, a fairly low average percentage germination of remaining seeds, and the failure of many germinated seeds to infect branches.

From the percentage of seeds resulting in infection, it is possible that red firs are more susceptible to infection, on the average, than white firs. The wide variation in percent infection among individual trees, however, suggests that greater variation in susceptibility occurs among individual trees of a species than between the two species. Further research is needed to demonstrate inherent resistance of true firs to dwarf mistletoes.

In general, we found no evidence of wide fluctuation or wave years in the amount of infection: percentage of seeds germinating, and infecting hosts during the 5-year inoculation period varied more among trees than among years of inoculation. It is possible, however, that wave years of infection may result from conditions that influence fruit production, but this information was not obtained in our study.

The rate of population buildup on red and white firs varied markedly among individual trees. On more than one-half of the test trees, mistletoe population did not increase from the original levels that resulted from inoculation. In fact, because of mistletoe mortality, populations actually decreased on some of these test trees. On the remaining trees, average populations were about double or less after 16 years. On some trees, therefore, either no buildup occurred or mistletoe population increased slowly. Some of the test trees grew dramatically (20 feet or more in height and several inches in diameter) over the 16-year test period. If the slow rate of dwarf mistletoe buildup continues, it is unlikely that any of the infected firs will suffer any measurable damage or growth loss.

Several variables were involved in the rather slow rate of dwarf mistletoe buildup. The long interval (8- to 9-year average) between inoculation and production of fruit, the low rate of fruit production of female plants, particularly at an early fruit-bearing age, the low proportion of female plants producing abundant fruit, and the irregular production of fruit over the years were some of the recorded phenomena that limited population buildup. In addition, the relatively short life span of many plants helped limit the rate of population buildup during the test period. Continued mortality of plants could even result in decreased population levels in the infected trees in the future.

We emphasize that these data were obtained from relatively few trees within one localized area of the true fir belt in the central Sierra Nevada in California, and may not apply to other areas within the range of red and white firs. Previous studies (Scharpf and Parmeter 1967) have shown that the incubation period of dwarf mistletoe on red firs in one location in the southern Cascades was on the average a year shorter than that which occurred in the area of the study reported here. Unpublished results of studies suggest that in the southern Cascade firs, rate of dwarf mistletoe population buildup may be more rapid than that reported in this paper. Caution should be used, therefore, in applying the results of this study to fir stands in other areas.

REFERENCES

- California Forest Pest Control Action Council. *Forest pest conditions in California*, official report. Sacramento, CA; 1961. 21 p.
- Hawksworth, Frank G. *Upper altitudinal limits of dwarfmistletoe on lodgepole pine*. *Phytopathology* 46:561-562; 1956 October.
- Hawksworth, Frank G. *Distribution of dwarfmistletoes in relation to topography on the mescalero Apache Reservation, New Mexico*. *J. For.* 57(12):919-922; 1959 December.
- Hawksworth, Frank G. *Dwarfmistletoe of ponderosa pine in the southwest*. *Tech. Bull.* 1246. Washington, DC: U.S. Department of Agriculture; 1961. 112 p.
- Hudler, G.; French, D. W. *Dispersal and survival of seeds of eastern dwarf mistletoe*. *Can. J. Forest Res.* 6:335-340; 1976 September.

- Parmeter, J. R., Jr.; Scharpf, R. F. Dwarfmistletoe on red fir and white fir in California. J. For. 61(5):371-374; 1963 May.
- Scharpf, Robert F. *Cytospora abietis* associated with dwarf mistletoe on true firs in California. Phytopathology 59(11): 1657-1658; 1969a November.
- Scharpf, Robert F. Dwarf mistletoe infected red fir . . . infection and control in understory stands. Res. Paper PSW-50, Berkeley, CA: Pacific Southwest Forest and Range Experiment Station, Forest Service, U.S. Department of Agriculture; 1969b. 8 p.
- Scharpf, Robert F. Dwarf mistletoe does not increase trunk taper in released red firs in California. Res. Note PSW-326. Berkeley, CA: Pacific Southwest Forest and Range Experiment Station, Forest Service, U.S. Department of Agriculture; 1977. 3 p.
- Scharpf, Robert F. Dwarf mistletoe infected red fir: growth after release. Res. Paper PSW-143. Berkeley, CA: Pacific Southwest Forest and Range Experiment Station, Forest Service, U.S. Department of Agriculture; 1979. 9 p.
- Scharpf, Robert F.; Bynum, H. H. Cytospora canker of true firs. Forest Pest Leaflet 146. Washington, DC: U.S. Department of Agriculture, Forest Service; 1975. 5 p.
- Scharpf, R. F.; Parmeter, J. R., Jr. The biology and pathology of dwarf mistletoe, *Arceuthobium campylopodum* f. *abietinum* parasitizing true firs (*Abies* spp.) in California. Tech. Bull. 1362. Washington, DC: U.S. Department of Agriculture; 1967. 42 p.
- Scharpf, Robert F.; Parmeter, J. R., Jr. The collection, storage and germination of seeds of a dwarf mistletoe. J. For. 60(8):551-552; 1962 August.
- Scharpf, Robert F.; Parmeter, John R., Jr. Population buildup and vertical spread of dwarf mistletoe on young red and white firs in California. Res. Paper PSW-122. Berkeley, CA: Pacific Southwest Forest and Range Experiment Station, Forest Service, U.S. Department of Agriculture; 1976. 9 p.
- Wagner, Willis W. Dwarfmistletoe incubation period on ponderosa and Jeffrey pines in California. Forest Sci. 8(1):16-20; 1962 March.
- Wicker, E. F. Appraisal of biological control of *Arceuthobium campylopodum* f. *campylopodum* by *Colletotrichum gloeosporioides*. Plant Dis. Rep. 51:311-313; 1967 April.



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Scharpf, Robert F., Parmeter, J. R., Jr. **Population dynamics of dwarf mistletoe on young true firs in the central Sierra Nevada, California.** Res. Paper PSW-161. Berkeley, CA: Pacific Southwest Forest and Range Experiment Station, Forest Service, U.S. Department of Agriculture; 1982. 9 p.

Young red firs (*Abies magnifica* A. Murr.) and white firs (*A. concolor* [Gord. & Glend.] Lindl. ex Hildebr.) on the Stanislaus National Forest, California, were inoculated with seeds of dwarf mistletoe (*Arceuthobium abietinum*) for 5 successive years. Only 3 to 4 percent of about 7000 seeds placed on branches resulted in infections. Second-generation infections developed and populations of the parasite built up on some trees but not on others after 17 years. Variables that appeared to regulate population increases included an 8- to 9-year average between inoculation and fruiting of plants, low rate of fruit production among female plants, low proportion of plants producing abundant fruit (100 or more/year), and irregular production of fruit on plants over the years. Death of infected branches also helped keep populations of the parasite in check. In vigorous, well-managed stands of young firs, dwarf mistletoe populations may not build up rapidly enough to result in serious losses.

Retrieval Terms: *Arceuthobium abietinum*, *Abies magnifica*, *Abies concolor*, parasitic plants—population(s), mistletoes—effect on increment