1500 Rec'd July 24, 1992

United States
Department of
Agriculture

Forest Service

**Pacific Southwest
Research Station**

Research Paper
PSW–RP-207

One Seed Source of Jeffrey Pine Shows Resistance to Dwarf Mistletoe

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Scharpf, Robert F.; Kinloch, Bohun B.; Jenkinson, James L. 1992. **One seed source of Jeffrey pine shows resistance to dwarf mistletoe.** Res. Paper PSW-RP-207. Berkeley, CA: Pacific Southwest Research Station, Forest Service, U.S. Department of Agriculture; 8 p.

Four seed sources of Jeffrey pine *(Pinus jeffreyi)* were selected for testing through controlled inoculation for resistance to dwarf mistletoe *(Arceuthobium campylopodum)*. The pines were 7 years old and part of a progeny test planting established by the USDA Forest Service's Institute of Forest Genetics, Placerville, California. One of the seed sources (Foresthill) was considered from previous studies to be highly resistant. It was also found to be resistant in this study. Test trees were inoculated in 1980 and 1981 with about 13,500 seeds of dwarf mistletoe. A high proportion of the seeds were lost before germination, but branches covered with bird-proof and insect-proof mesh lost significantly fewer seeds. Mean percentage infection based on remaining seeds was significantly lower on trees from the Foresthill seed source than any of the other sources. Similarly, mean percentage of trees infected was significantly lower for the Foresthill source than for the three others. Development of the endophytic system, as indicated by length of branch swelling, and mistletoe shoot development were not significantly different among the seed sources. However, significantly fewer brooms developed on the Foresthill trees than on trees from two of the other sources.

Retrieval Terms: resistance, *Pinus jeffreyi, Arceuthobium campylopodum,* parasitic plants, conifer diseases

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Acknowledgments:

We thank several current and former Forest Service employees for their assistance in field inoculation and data collection: Gayle Dupper, Anne Delfino Mix, Bill Moyer, Peter Ono, Carline Trummer, Detlev Vogler, and John Wallack. We also thank Dave Azuma and Alice Ratcliff for their help in statistical analyses, and John R. Parmeter, Jr., Frank Hawksworth, and Arthur McCain for technically reviewing the manuscript.

Cover: Young Jeffrey pines were inoculated in fall 1980 with seeds of western dwarf mistletoe to test for resistance (*bottom*). Freshly collected seeds were placed on branches at the base of a needle fascicle or a needle scale. Red paint marks the site of a seed (*top*).

Publisher:

Pacific Southwest Research Station
P.O. Box 245, Berkeley, California 94701
January 1992

☆ U.S. G.P.O.: 1992-687-563

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Branches were inoculated in 1980 and 1981 with freshly collected dwarf mistletoe seeds. In 1980, 9000 seeds were placed on branches at the base of needle fascicles on the test trees, and in 1981, an additional 4500 inoculations were made. In 1980 most of the seeds were lost before infection could occur. In 1981 some of the branches were covered with bird proof mesh bags and some were covered with insect-proof mesh bags to prevent seed depredation. Seed loss from branches, number of trees infected, number of infections per tree, branch swelling, shoot production, and broom development were recorded for 5 years.

A high proportion of the seeds were lost before germination and infection, but branches covered with bird-proof or insect-proof mesh lost significantly fewer seeds than uncovered branches. Percentage of trees infected was significantly lower on the average for the Foresthill source than for any of the other sources. Also, percentage infection based on the remaining seeds on branches was significantly lower for the Foresthill source than for any of the others. Differences in average percentage of trees infected and average number of infections per tree were not found among the other sources.

Development of the endophytic system, as indicated by length of branch swelling, and the production of mistletoe shoots were not significantly different among the seed sources. However, significantly fewer brooms developed on the Foresthill trees than on trees from other sources.

Results of the study show that a source of Jeffrey pine from near Foresthill appears to contain a higher proportion of trees resistant to dwarf mistletoe than do other seed sources tested, and that resistance is not expressed in terms of growth rate or shoot production of the parasite.

Introduction

Dwarf mistletoes (*Arceuthobium* spp.) are parasitic plants damaging to most conifers in California and much of the West. Among the several dwarf mistletoe species in the State, some are host specific, whereas others have a fairly broad host range (Hawksworth and Wiens 1972). One of the species with a fairly broad host range is western dwarf mistletoe (*A. campylopodum* Engelm.). It infects five native pine species in California including Jeffrey pine (*Pinus jeffreyi* Grev. & Balf.). Interest in resistance of Jeffrey pine to dwarf mistletoe has been expressed by land managers, particularly those in southern California, because non-host species of trees are not always suitable or appropriate for planting in their dwarf mistletoe-infested, high value, recreational forests. Dwarf mistletoe-resistant planting stock would be of value to land managers in other areas of the State where dwarf mistletoe is a problem in Jeffrey pine and where all-aged stands and natural regeneration are preferred methods of management.

Differences in resistance to infection by dwarf mistletoes have been observed in several instances, but resistance occurred between host species rather than within a species (Hawksworth and Wiens 1972; Scharpf 1984). For example, many dwarf mistletoes have "principal" hosts on which they occur and "secondary" or "rare" hosts on which they less frequently or rarely occur. Less often has resistance of a given host species to dwarf mistletoe been observed in the field. Hawksworth (1961), Roth (1953), and Wagener (1965) reported that individual trees in heavily infected stands occasionally show some form of resistance to dwarf mistletoe. For example, Roth (1966) reported that the races of ponderosa pine with drooping needles along the coast of Oregon are less frequently infected by dwarf mistletoe than races without drooping needles. Presumably the races with drooping needles are less able to retain the slippery seeds of dwarf mistletoe. Roth (1974a) also showed, for seedlings grafted with scions from "resistant" and "non-resistant" ponderosa pines in central Oregon, that there was strong evidence of inherent resistance to infection in certain ponderosa pines. Roth (1974b) also reported that ponderosa pines exhibit juvenile susceptibility to infection by *A. campylopodum* and that susceptibility decreases with an increase in tree age even on tissues of the same age. For example, the terminal growth of a seedling is apparently more susceptible to infection than the terminal growth of a 50-year-old tree. According to Roth, two kinds of susceptibility are evident in ponderosa pine: 1) "susceptibility to infection," and 2) "susceptibility to damage." In the first case, trees accommodate numerous infections, but individually the infections have little effect on host vigor. In the second case, infection frequency may be low, but individual plants spread extensively and cause much damage. Hawksworth and Edminster (1981) found for ponderosa pines in Colorado that young seedlings grown from parent trees presumed to be resistant to dwarf mistletoe *(A. vaginatum)* and planted in 1932 were as heavily infected in 1979 as seedlings grown from susceptible trees.

Scharpf and Parmeter (1967a) reported that Jeffrey pines grown from seeds from different seed collection sites showed noticeable differences in levels of infection by *A. campylopodum.* When exposed to an overstory of dwarf mistletoe, Jeffrey pines from a high-elevation, east-side Sierra Nevada site were more frequently and heavily infected than pines from a low-elevation west-side stand. Development of the mistletoe in these pines has been followed since 1961, and resistance to dwarf mistletoe in trees from the low-elevation site is still evident (Scharpf 1987).

We undertook a study to determine, under known conditions, the relative differences in resistance among four different seed sources of Jeffrey pine, including the known resistant source (Scharpf 1987), to determine some of the factors influencing infection of the different seed sources, and to follow the progress of development of dwarf mistletoe plants on the sources 5 years after inoculation in 1980 and 1981. This paper reports the results of our study to determine resistance of Jeffrey pine to dwarf mistletoe.

Methods

Tests were conducted in two existing plantations of Jeffrey pine in the northern Sierra Nevada near Camino, California. One was planted near Mt. Danaher at 3400 ft (1935 m) of elevation in 1973 by the USDA Forest Service's Institute of Forest Genetics, as a provenance test of ponderosa and Jeffrey pines. The seed sources of Jeffrey pine in this plantation were the same resistant and susceptible selections as those reported in previous studies of resistance to dwarf mistletoe (Scharpf 1987; Scharpf and Parmeter 1967a). The second planting was established nearby on Fruitridge at 3000 ft (915 m) elevation in the mid-1970's and contains one source of Jeffrey pine. The seed sources planted at the two sites are:

Seed Source	Location	Elevation	Families	Plantation
High Meadows	South Carson Range, east-side Sierra Nevada, Alpine County	8200 ft (2500 m)	10 seed parents	Mt. Danaher
South Lake Tahoe	East-side Sierra Nevada, El Dorado County	6400 ft (1950 m)	10 seed parents	Mt. Danaher
Foresthill[1]	West slope Sierra Nevada, Placer County	3800 ft (1160 m)	10 seed parents	Mt. Danaher
Laguna Mtn	Cleveland National Forest, east of San Diego, California	5500 ft (1675 m)	5 seed parents	Fruitridge

[1]This seed source in an older plantation was one that showed a high level of resistance to dwarf mistletoe (Scharpf 1987).

At Mt. Danaher, the sources were planted in 10-tree plots randomly located throughout the plantation. Within a source plot, seedlings of the 10 families were randomly located in two rows of 5 trees spaced 10 feet (3.0 m) apart. For our tests, five 10-tree plots were selected at random for each source. The trees in each plot were flagged and tagged for inoculation.

At Fruitridge, several sources were randomly located in closely spaced row plots. In 1981, all except the Laguna Mountain source was removed. Twenty-five of the Laguna Mountain trees remained, and were used for inoculation.

For inoculations, fresh seeds of dwarf mistletoe *(A. campylopodum)* were obtained in the fall of 1980 and 1981 from naturally infected Jeffrey pines in the Lake Tahoe Basin, El Dorado County. Seeds were collected and stored for use as described by Scharpf and Parmeter (1962). We inoculated test trees within one month of seed collection by placing moistened seeds on branches at inoculation sites marked by a small dab of red paint. An inoculation site was the portion of a branch at the base of a needle fascicle or at the base of a scale leaf *(fig. 1)*. Only portions of branches with green tissue and undeveloped bark were inoculated.

In general, only a small proportion of the initial number of seeds that land on hosts causes infection. Some seeds are lost before reaching an infection site on a branch, and some are lost before germination and infection can occur. The proportion of dwarf mistletoe seeds that remain on branches after they have reached the site of infection has been recorded as low in most instances (Roth 1959; Scharpf and Parmeter 1967b, 1982; Wicker 1967). Therefore, a large number of inoculations were made to adjust for the low proportion of seeds expected to remain on branches.

In 1980, about 9,000 inoculations were made on 150 trees in the Mt. Danaher plantation. Twenty seeds were placed on each of three tagged branches selected at random on each test tree. An analysis of variance was used to determine significant differences in seed loss among the three sources tested. No inoculations were in the Fruitridge plantation in 1980.

In 1981, the same 150 trees were inoculated again at Mt. Danaher. This time, 10 seeds were used on each of three different branches for a total of 4500 inoculations. One branch on each tree was enclosed in an "insect-proof" mesh bag, one was enclosed in a "bird-proof" mesh bag, and one was left exposed as before *(fig. 2)*. Insect- and bird-proof bags were used in this test because the 1980 inoculations showed that heavy seed loss occurred before seeds could germinate and infect the host. We attributed this loss to either predation by insects or birds or both.

Figure 1—A moist seed of dwarf mistletoe placed on a branch at the base of a needle fascicle.

A

B

Figure 2—An insect-proof mesh bag (a), and a bird-proof mesh bag (b) placed over branches of Jeffrey pine to protect the seeds of dwarf mistletoe from predation.

Trees in the Fruitridge plantation were inoculated and bagged only in 1981, in the same manner described above, for a total of 720 inoculations. The bags on trees in both plantations were removed in late fall of 1981. To determine the fate of dwarf mistletoe seeds placed on branches in November 1980, the odd-numbered trees in each plot were selected and examined for the presence or absence of seeds in April 1981. All trees inoculated in November 1981 were examined in April 1982 for the presence of seeds. Thereafter, infection and development of dwarf mistletoe was recorded each summer from 1982 to 1987. Most data were analyzed using analysis of variance significant at the 5 percent level and including transformations where appropriate. Other data were analyzed using the Tukey t-test, and one data set was analyzed by calculating the binomial proportion with 95 percent confidence intervals.

Results

Seed Retention

Examination of branches inoculated in 1980 showed that retention of seeds placed at infection sites was very low 5 months after inoculation. Seed loss varied markedly even among trees within a plot. For example, out of about 300 seeds per plot, the number remaining ranged from 5 to 93. An analysis of variance using transformed data showed that there were no significant differences in seed loss among the three sources at Mt. Danaher. The reasons why seed loss was heavy and variable were not determined in this study, but observations here and in previous studies (Scharpf and Parmeter 1982, Scharpf and Koerber 1985) suggest that, at least in some instances, the seeds were eaten by either insects or birds. Often, remnants of the seed coat remained on the branch, suggesting that an insect or bird had either eaten the seed or removed it from the branch *(fig. 3)*. On some trees in some plots, nearly all seeds on branches appeared to have been eaten, suggesting that perhaps a seed-eating bird systematically moved along a branch removing seeds. Of the missing seeds from the inoculations made in 1980, 12 percent showed signs of having been partially eaten. It appeared that loss of seeds over a 5-month period was a major factor in limiting the amount of infection.

For the three sources inoculated in 1981 at Mt. Danaher, seed loss after 5 months again appeared heavy on unbagged branches, but an analysis of variance showed no significant differences in mean percentage loss among the sources. On the other hand, average seed loss from uncovered branches on the Laguna Mountain source at the Fruitridge plantation was significantly lower than any of the sources at Mt. Danaher. A

Figure 3—Only a portion of the seed coat of a dwarf mistletoe seed remains on the surface of a pine branch, suggesting the seed had been eaten by a bird or an insect.

Tukey t-test showed that there was a significantly higher percentage of seed loss, on the average, from uncovered branches than from branches covered with a bird-proof or an insect-proof bag *(fig. 4)*. On the other hand, there was no significant difference in the average loss of seeds between branches covered by bird-proof bags and insect-proof bags. Both birds and insects were excluded from the insect-proof bags, but seed predation by insects was not prevented by the bird-proof bags.

Therefore, for uncovered seeds inoculated on branches in both 1980 and 1981, usually fewer than 20 percent remained on branches and were potentially able to germinate and infect the host. For seeds covered by bags, about 30 to 50 percent remained on branches.

Infection

A Tukey t-test showed that the percentage of the trees infected by dwarf mistletoe differed significantly between the Foresthill and other sources *(table 1)*. In 1980, half of the High Meadows trees, 24 percent of the South Lake Tahoe trees, and 8 percent of the Foresthill trees were infected after 5 years. In 1981, nearly half of the High Meadows, South Lake Tahoe, and Laguna Mountain trees were infected in contrast to 20 percent infection of the Foresthill trees. Therefore, in evaluating resistance to dwarf mistletoe based on the proportion of trees in-

Table 1—***Dwarf mistletoe seed retention and infection of Jeffrey pine inoculated in1980 and 1981***

Jeffrey pine seed sources[1]	Trees infected in 1985	Seeds on branches the spring after inoculation[2]	Infections in 1985-1986 from seeds on branches
		pct	
Fall 1980:			
High Meadows	50	12.7	21.8
South Lake Tahoe	24	8.7	14.5
Foresthill	8	6.0	4.4
Fall 1981:			
High Meadows	46	34.6	10.0
South Lake Tahoe	44	28.2	7.8
Foresthill	20	26.2	3.3
Laguna Mt.	48	41.3	9.1

[1]Fifty trees per source were inoculated, except for 25 trees from Laguna Mountain.

[2]Inoculation totaled 3000 seeds per source in 1980, and 1500 seeds per source in 1981, except for 720 for the Laguna Mountain source.

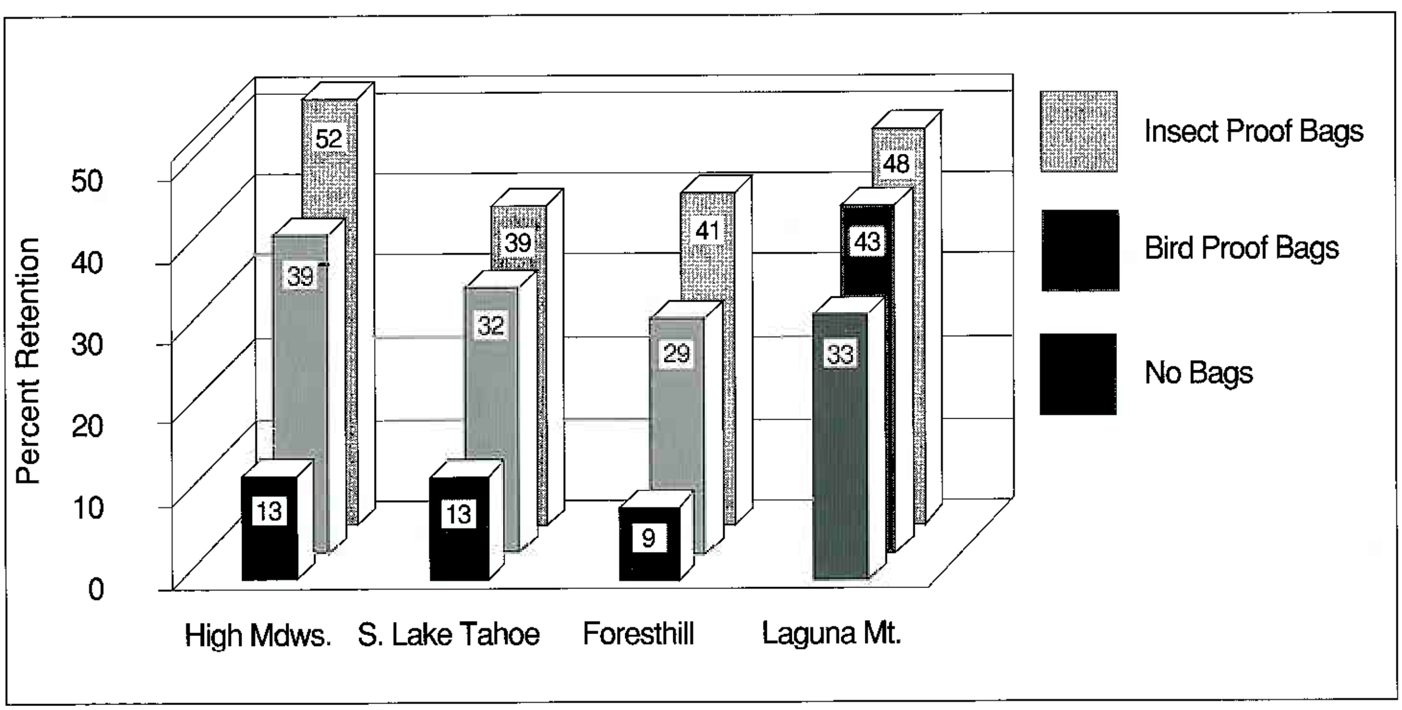

Figure 4—Insect- and bird-proof mesh bags improved retention of seeds on branches of Jeffrey pines for 5 months after inoculation in 1981.

fected, the Foresthill source was significantly more resistant than any of the other three sources of Jeffrey pine.

Percentage of infection from seeds that remained on branches was variable, even for trees within a given source. An analysis of variance of 1980 data based on plot means showed a significantly lower percentage of infection for the Foresthill source than for either of the other two sources *(table 1)*. No significant differences were found between the South Lake Tahoe and High Meadows sources.

A binomial proportion calculated to determine the differences in mean percentage of infection among the 1981 inoculations showed that the Foresthill source had significantly fewer infections on the average than trees from the other three sources *(table 1)*. No significant differences in percentage of infection were found among the other sources.

Branch Swelling and Development of Witches' Broom

Extent of swelling of pine branches infected by dwarf mistletoe is directly related to the development of the root system of the parasite (Scharpf 1962). Growth of the root system in both directions from the infection site usually results in a characteristic, fusiform-shaped branch swelling. In this study we found no significant differences in the average length of branch swelling among the seed sources 6 and 7 years after inoculation *(table 2)*.

Table 2—***Mean length of branch swelling caused by dwarf mistletoe on Jeffrey pine inoculated in 1980 and 1981***

Tree seed source:	Swollen branches	Mean length of swelling in 1987
	no.	*cm ± sd*
High Meadows		
1980	25	16.0 ± 5.6
1981	21	13.1 ± 3.9
South Lake Tahoe		
1980	12	14.4 ± 5.1
1981	23	11.0 ± 3.8
Foresthill		
1980	3	14.3 ± 9.3
1981	14	12.3 ± 3.4
Laguna Mt.		
1981	18	15.8 ± 6.6

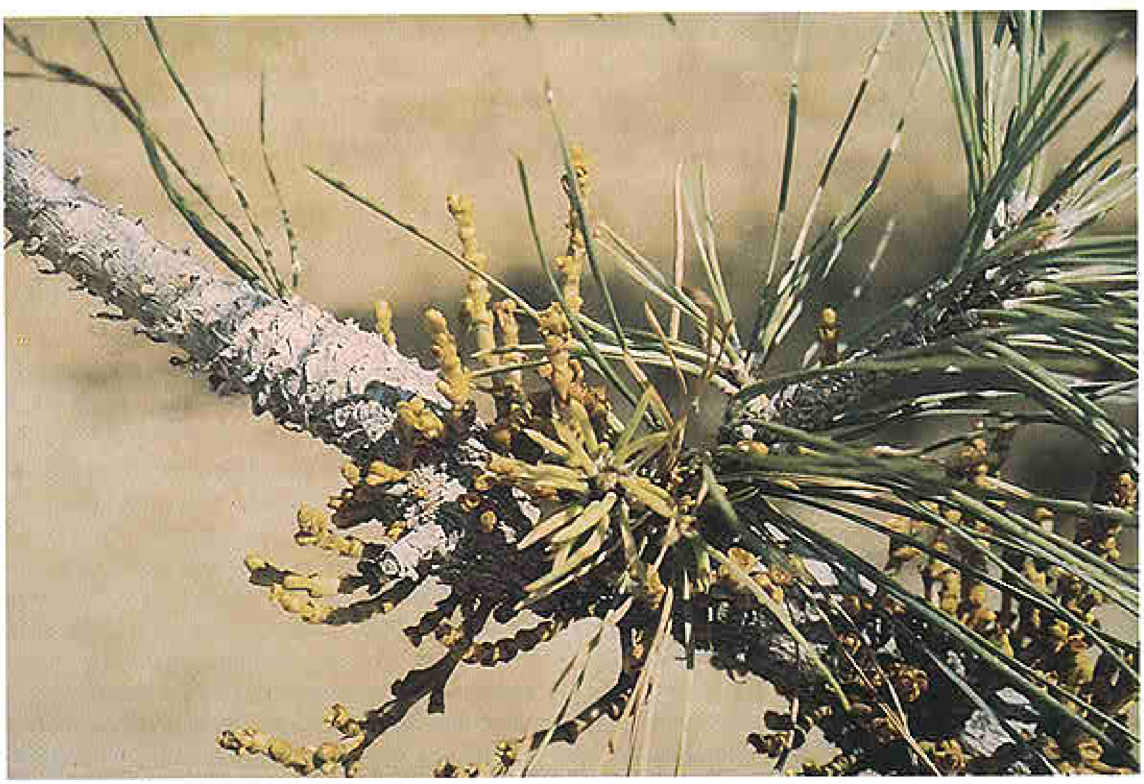

Figure 5—Several dwarf mistletoe infections, like the one shown here, stimulated the production of lateral shoots that result in brooms on Jeffrey pine branches.

However, there was wide variation in length among infections even within sources and among infections on the same tree. It appears that root development of the parasite, as indicated by branch swelling, is probably influenced more by branch vigor or other host conditions not related to resistance.

It is well known that dwarf mistletoe-infected branches that develop into witches' brooms constitute an energy sink that, over time, weakens a tree and reduces growth (Hawksworth 1961). As shown below, a fairly high proportion of the branch infections were stimulating broom development *(fig. 5)*: Using a binomial proportion to determine the mean differences in broom formation, we determined that the Foresthill source was producing significantly fewer brooms than the South Lake Tahoe and Laguna Mountain sources, but not fewer than the High Meadows source.

Seed source	Mistletoe infections in 1985	Infections forming brooms in 1985
	No.	*Pct*
High Meadows	96	26
South Lake Tahoe	42	36
Foresthill	13	23
Laguna Mountain	22	45

Broom development did not appear restricted to certain trees within the sources, but occurred on several trees from different parents and sources. For example, the three brooms that occurred on the resistant, Foresthill source occurred as single brooms on each of three different trees from different parents. Similarly, the 15 brooms on the Lake Tahoe source occurred on trees from eight different parents. Brooms developed on trees from seven parents from the High Meadows source, and 9 of the 18 infected trees from the Laguna Mountain source bore infections that developed into brooms. Because broom development is a function of branch growth, it is possible that additional brooms will develop over time from existing infected branches on trees of all seed sources. It remains to be seen whether brooms increase in number or enlarge at the same or at different rates on trees from the different seed sources.

Figure 6—Localized branch swelling and the presence of small buds of the parasite are the first symptoms and signs of infection by dwarf mistletoe. Note that the dwarf mistletoe seed is often still present when symptoms appear.

Shoot and Fruit Development

No marked differences were noted in the development of dwarf mistletoe shoots among the sources tested. At least some plants on some trees from all sources were showing early signs of shoot development within 2 years after inoculation *(fig. 6)*. By the third year after inoculation, most of the young plants bore either developing shoots or buds pushing through the bark on the swollen portion of branch tissue. Some infections remained latent within branches and did not appear until three or more years after inoculation, however. A major complication arose in attempting to follow the development of shoot and fruit production of the dwarf mistletoe plants. In summer 1984, a plague of grasshoppers ate nearly all the shoots, flowers, and fruit on the test plants, thereby precluding any long-term study on shoot and fruit development (Scharpf and Koerber 1985). However, by 1987, some shoot regrowth had taken place, and a comparison could be made of growth among plants on trees from the different seed sources *(table 3)*. For all seed sources, most plants were observed with 10 or more well-developed shoots. Some plants bore fewer than 10 shoots, and few were observed with no shoots or only buds. As a result, no marked differences in shoot development among seed sources were apparent in the years after shoot removal by grasshoppers. Infections on the resistant, Foresthill source trees appeared to develop as many shoots as did infections on trees from the other sources, and presumably will be able to produce fruit and reproduce equally as effectively.

Table 3—*August 1987 shoot development on dwarf mistletoe infections resulting from inoculation of Jeffrey pine in 1980 and 1981 at Mt. Danaher and Fruitridge*[1]

Tree seed source	Shoot development	1980 Plants		1981 Plants		Total Plants	
		No.	*pct*	*No.*	*pct*	*No.*	*pct*
High Meadows	none	4	16	1	5	5	11
	buds only	0	0	0	0	0	0
	<10 shoots	8	32	3	15	11	24
	>10 shoots	13	52	16	80	29	65
	Total	25		20		45	
South Lake Tahoe	none	2	17	0	0	2	6
	buds only	0	0	1	5	1	3
	<10 shoots	0	0	5	24	5	15
	>10 shoots	10	83	15	71	25	76
	Total	12		21		33	
Foresthill	none	0	0	0	0	0	0
	buds only	0	0	0	0	0	0
	<10 shoots	2	50	4	31	6	35
	>10 shoots	2	50	9	69	11	65
	Total	4		13		17	
Laguna Mt.	none	—	—	0	0	0	0
	buds only	—	—	0	0	0	0
	<10 shoots	—	—	0	0	0	0
	>10 shoots	—	—	18	100	18	100
	Total	—		18		18	

[1]The Mt. Danaher plantation was thinned in 1986, and some branches bearing infections have died. Therefore, the number of infections on which these results are based may be lower than that shown earlier.

Discussion

Results of the study indicate that there probably are valid differences in resistance to dwarf mistletoe among the seed sources tested. The Foresthill source had the lowest percentage of infected trees, and with the exception of a few trees from one parent, this source found to be most resistant in previous studies also appeared to be most resistant in these tests (Scharpf 1984, Scharpf 1987). The High Meadows source found to be most susceptible previously also appeared most susceptible here. However, data were insufficient to show any precise measure of differences in resistance among all the sources tested.

Low percentage of infection within seed sources made it difficult to obtain enough data on infection for a statistical analysis to show clear differences in resistance among all sources tested. Among individual trees and even between plantations only a few miles apart, there were marked differences in dwarf mistletoe seed retention and infection on inoculated trees. These differences appear to be due as much to biotic or unknown factors affecting the inoculum and the infection process as to inherent resistance within the host.

Juvenile susceptibility may be one reason why resistance was not expressed as strongly among sources in this study as in previous studies (Scharpf 1984, Scharpf 1987). In this study, trees less than 10 years old were inoculated, whereas in the earlier studies we were investigating infection on trees of the same seed sources that had been exposed to dwarf mistletoe for about 50 years. If Roth's (1974b) findings on juvenile susceptibility of ponderosa pine to dwarf mistletoe hold true for Jeffrey pine, then one would expect much less expression of resistance among these younger trees than of ones much older. Nonetheless, the studies on the 50-year-old plantation of Jeffrey pines exposed to dwarf mistletoe since planting suggest that juvenile susceptibility may not be an important factor in infection of this pine species. Inoculation studies currently under way in the greenhouse should show whether young pines can be used to determine resistance of Jeffrey pine selections to dwarf mistletoe.

If resistance to dwarf mistletoe was present among the trees, it was not expressed as obvious differences in growth of the endophytic system, parasite shoot production, branch swelling, or broom formation. And, no suggestion of "susceptibility to damage" as reported by Roth (1974b) was observed on the test trees. Therefore, resistance is probably expressed as an inhibition of the infection process rather than as an inherent condition of the host that limits parasite development. However, with time and further study, differences in susceptibility to both infection and damage among the seed sources tested may appear.

Until new methods can be devised, it appears that field testing of pines by artificial inoculation will be a time-consuming and inefficient way of determining resistance to dwarf mistletoes. A method in an earlier study that was tried in an attempt to speed up the testing of Jeffrey pine for resistance to dwarf mistletoe was the inoculation of pine callus tissue in culture. By this method we hoped to find some reaction of the tissue to infection that would indicate resistance. We were unable to grow Jeffrey pine callus tissue in culture for a sufficiently long period of time for infection to occur after the callus was inoculated with germinated dwarf mistletoe seeds. However, improvements in the ability to grow pine callus tissue in culture, or to develop plantlets from Jeffrey pine callus could be valuable for testing dwarf mistletoe resistance among trees and seed sources. Until new techniques are developed, it appears that the best approach to field testing is to outplant large numbers of candidate trees in natural forest stands where heavy infection occurs. With this method, many trees can be tested, even though 5 years or more are required before results can be obtained.

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- Participation with other agencies in human resource and community assistance programs to improve living conditions in rural areas
- Research on all aspects of forestry, rangeland management, and forest resources utilization.

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Research Paper
PSW–RP-207

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