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Resistance of Ponderosa Pine to Western Dwarf Mistletoe in Central Oregon

Robert F. Scharpf **Lewis F. Roth**

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Ponderosa pines with little or no dwarf mistletoe in infested stands on the Deschutes, Ochoco, and Rogue River National Forests in Oregon were tested for resistance to dwarf mistletoe *(Arceuthobium campylopodum)*. Small trees produced by grafting scions from the resistant and susceptible candidates onto seedling rootstock were planted in 1967-69 beneath a heavily infested stand of ponderosa pine in central Oregon. Between 12 and 15 grafted trees from each of 30 resistant parent selections and about the same number from each of eight susceptible parents were included in a replicated, randomized planting. Also included as controls were about 125 ungrafted seedlings. In 1989, fewer than half of the resistant grafts from selections from the Deschutes and Ochoco National Forests were infected, and the average level of infection per tree was very low. Mortality among the resistant selections was also low over the test period. About 85 percent of all Rogue River grafts, the susceptible grafts, and the seedlings were infected during the test period. Few Rogue River grafts died, but 52 percent of the susceptible grafts and seedlings died in comparison to 24 percent of the resistant trees. Size of the test trees, foliar habit, and crown characteristics were not found to be correlated with resistance. High levels of resistance to dwarf mistletoe are present in some native ponderosa pines in central Oregon.

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

The Authors:

ROBERT F. SCHARPF is supervisory research plant pathologist in charge of the Station's Forest Disease Research Unit at the Station headquarters in Berkeley, Calif. **LEWIS F. ROTH** is professor emeritus of forest pathology at Oregon State University, Corvallis.

Cover: The tallest ponderosa pine in the center is only lightly infected with dwarf mistletoe, even though adjacent pines were heavily infected. Grafts made from this tall pine and exposed to heavily infected overstory also showed low levels of infection after 20 years in stands in northern California.

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(Mailing address: P.O. Box 245, Berkeley, California 94701-0245
Telephone: 510-559-6300)

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In Brief . . .

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Several ponderosa pines *(Pinus ponderosa)* on the Deschutes, Ochoco, and Rogue River National Forests in Oregon were thought to be resistant to western dwarf mistletoe, *Arceuthobium campylopodum.* The pines on the Deschutes and Ochoco National Forests were considered to be resistant to infection, whereas the pines from the Rogue River National Forest were believed to escape infection because dwarf mistletoe seeds slide off their long, drooping needles. Scions taken from candidate trees on the three forests were grafted to seedlings for testing for resistance. Seedlings grafted with scions from susceptible trees were used as controls. Ungrafted seedlings were also included in the tests.

All test trees were planted from 1967 to 1969 on the Pringle Butte Experimental Forest in central Oregon in a stand of ponderosa pines heavily infested with dwarf mistletoe. About 12-15 grafts from each of 30 resistant parent selections, and the same number of grafts from eight susceptible selections were outplanted in the infested stand in a replicated, randomized plot design. About 125 ungrafted seedlings grown from seed from the Deschutes National Forest seed bank were also planted as susceptible controls. Infected overstory was maintained to provide abundant inoculum, with only a moderate level of suppression.

The objectives of the study were 1) to determine the resistance of clonally propagated ponderosa pines from apparently resistant and susceptible trees, 2) to determine the survival of resistant and susceptible trees with different levels of infection, and 3) to determine whether resistance was correlated with tree size, foliar habit, or crown characteristics. It was also possible to compare the resistant and susceptible trees produced from scions to those grown from seeds.

Tree survival, growth, crown size, and dwarf mistletoe infections were recorded in 1989. Of all the resistant grafts from selections on the Deschutes National Forest, only 29 percent became infected with dwarf mistletoe. Grafts from four of the resistant selections were disease free. In addition, the mean number of infections per tree was one or fewer in grafts from 20 of the 25 selections. Fifty percent or fewer of the grafts from three of the five selections from the Ochoco National Forest were infected, and of these selections fewer than one infection per tree on the average was recorded.

Grafts produced from the Rogue River source and the susceptible selections were much more frequently infected than trees produced from resistant selections. On the average, 85 percent of all the susceptible grafts were infected, and the average number of infections per tree per source ranged from 1.9 to 9.0. Similarly, 87 percent of the susceptible seedlings were infected, and the average number of infections per tree was 5.7.

Seventy-six percent of the resistant and Rogue River grafts survived since outplanting, but only 48 percent of the susceptible grafts and seedlings were still alive in 1989. Seventy-eight percent of the dead resistant trees died from causes other than dwarf mistletoe, whereas dwarf mistletoe was involved in the death of about 73 percent of the susceptible trees.

Dwarf mistletoe populations built up very slowly in resistant trees but more rapidly in susceptible ones from 1968 to 1980. In 1981 an exceptionally large population increase occurred. In 1982 and 1983 the rate of increase returned to the previously established norm. Thereafter, the trend is not known because there was insufficient time between 1983 and 1986 for incipient infections to become visible.

Tree growth and form varied markedly among the selections. Grafts from some selections grew straight and tall; some had few branches, whereas others branched profusely. However, neither tree size nor growth habit appeared to be correlated with disease intensity in most cases. In addition, the "drooping needle" pines from the Rogue River National Forest failed to develop the drooping habit when grown in central Oregon, and showed no resistance to dwarf mistletoe. On the other hand, most susceptible grafts showed lower levels of infection than the ungrafted seedling stock, demonstrating the presence of juvenile susceptibility among young seedlings compared to grafts from older susceptible trees.

High levels of resistance were found in grafts produced from resistant selections of ponderosa pines on the Deschutes and Ochoco National Forests in Oregon. Dwarf mistletoe resistant ponderosa pines should be considered an important component of the native forest biodiversity, and should be identified, preserved, and used in future tree improvement and pest management programs.

Introduction

Dwarf mistletoes *(Arceuthobium)* are important pathogens of coniferous forests in western North America. In spite of attempts to limit the impacts of these parasites through silvicultural methods, severe damage continues to occur. Planting resistant trees is another method that could be used to reduce losses from these pests.

Many dwarf mistletoe species are host specific; therefore manipulation of tree species composition in a forest can often reduce the levels of infection, particularly in stands where only one dwarf mistletoe species occurs. In pure stands where dwarf mistletoe occurs, planting other species that are resistant to the pathogen or clearcutting to remove the infested stand may not be possible or desirable. In these stands, use of resistant members of the host species would be a sound method of reducing the losses from dwarf mistletoe.

Relatively few cases of resistance to dwarf mistletoe have been reported (Scharpf 1984). The earliest test for resistance to dwarf mistletoe was conducted in Colorado in 1932 (Hawksworth and Edminster 1981). About 1500 seedlings of "resistant, non-resistant and doubtful" ponderosa pines *(Pinus ponderosa* var. *scopulorum* Engelm.) were planted among overstory trees infected with *A. vaginatum* subsp. *cryptopodum* (Engelm.) Hawks. & Wiens. When the surviving trees were examined 47 years later in 1979, no difference was found in susceptibility between what was believed to have been "resistant" and "non-resistant" trees.

Most research on resistance to dwarf mistletoe has been done on resistance of ponderosa pines *(P. ponderosa* Laws.) to western dwarf mistletoe *(A. campylopodum* Engelm.) (Wagener 1965; Roth 1966, 1971, 1974a,b). Wagener (1965) noted on an experimental plot in Lassen County, Northern California, that Jeffrey pine *(P. jeffreyi* Grev. & Balf.) was more heavily infected than ponderosa pine, but that a few trees of both species appeared to show noticeable resistance to infection. Roth (1966) found that some ponderosa pines on the Rogue River and the Deschutes National Forests in Oregon exhibited a morphological characteristic (drooping needles) that appeared to impart some measure of resistance (escape) to infection by dwarf mistletoe. On these pines, seeds of the parasite slid off the needles rather than sliding onto branches where infection takes place. In a subsequent study, Roth (1974a) used grafted material from "drooping" needle pines from the Deschutes National Forest as well as grafts from scions from several resistant selections of ponderosa pines in central Oregon. Grafts from resistant and susceptible selections, and seedlings from susceptible parent trees in central Oregon were artificially inoculated for several years after outplanting under infected overstory. After 14 years, the resistant selections showed little or no infection, whereas the susceptible grafts and seedlings had numerous infections. The drooping needle selections did not express the drooping needle characteristic when grown on an exposed test site, nor did they show any evidence of resistance. Ponderosa pine seedlings infected with dwarf mistletoe showed a much higher level of mortality and slower rate of growth than uninfected seedlings (Roth 1971). Roth (1974b) also found that susceptibility of the new growth of ponderosa pine decreases with increasing tree age up to about 50 years. In addition, he reported that while some trees are susceptible to infection, they are little damaged, whereas other trees less susceptible to infection suffer severe damage.

In California, at least one seed source of Jeffrey pine has been shown to be highly resistant to dwarf mistletoe (Scharpf 1987, Scharpf 1991). This source is undergoing further laboratory and field testing.

This paper reports the results of a study that determined the relative resistance of clonally propagated ponderosa pines based on a field selection of scions from apparently resistant and susceptible trees, determined the survival rate and damage to resistant and susceptible trees over time with different levels of dwarf mistletoe infection, and determined whether resistance was related to tree size, foliar habit, or crown characteristics.

Methods

Between 1955 and 1967, several ponderosa pines on the Deschutes, Ochoco, and Rogue River National Forests in Oregon were identified as resistant or susceptible to dwarf mistletoe *(table 1)*. Selections for resistance were made on the basis of field observations of trees that had remained uninfected or slightly infected over many years in the presence of heavy infection pressure by dwarf mistletoe. Some trees were selected for resistance on the basis of their "drooping needle" growth characteristic.

As Roth (1974a) points out, "resistant trees have not been found as a result of a deliberate search. Rather, they

Table 1—***Resistant and susceptible ponderosa pine candidates selected for grafting and testing for resistance to western dwarf mistletoe***

Resistant trees	
R1-R4, R8-R20, R41-R47, R49	Deschutes National Forest (NF)
R22-R26	Ochoco NF
R31-R32, R38-R39 (Drooping needle pines)	Rogue River NF
Susceptible trees	
S3, S5-S6, DS1-DS2	Deschutes NF
PSS[1] (potted trees)	
BRT[1] (bare root trees)	
S1-S2, S11	Ochoco NF

[1]These trees were not grafted but were propagated from seeds from parent trees considered to be susceptible. Several years were needed to accumulate a useable population allowing in some cases for root binding. Bare root and potted, ungrafted seedlings were included as a check on root binding effects.

have been found by chance during the course of examining young stands for other purposes."

Successful grafts were made with scions from resistant and susceptible selections grafted onto potted seedlings in the greenhouse. From twelve to fifteen grafts were made from each parent. Both resistant and susceptible grafts were made from the previous year's growth of parent trees that were of about the same age. Several years were required to develop a population of grafts.

Another treatment was used in determining the "normal" level of susceptibility of ponderosa pines to dwarf mistletoe on the Deschutes and Ochoco National Forests. Ungrafted seedlings considered to have a normal background level of resistance were used. These were obtained from the USDA Forest Service nursery in Bend, Oregon, from seed of parent trees in which dwarf mistletoe was not considered in seed collection. These were of two groups: one group that was used to check the effect of root binding on resistance was held in containers large enough for the seedlings to develop root characteristics like those of the potted grafts. The other group was planted as bare root seedlings without the influence of root binding.

The planting site was on the southwest side of Pringle Butte, Pringle Falls Experimental Forest in Central Oregon, and consisted of a heavily infected ponderosa pine stand that had been cleared of brush in 1965. Overstory trees were thinned enough to accommodate planting and exert only moderate suppression, but dense enough to provide sufficient inoculum from dwarf mistletoe in the residual pines. Some overstory trees died from mistletoe late in the study, and a few were periodically removed to maintain a proper balance between overstory with dwarf mistletoe and growing space for the planted seedlings. Seventy-eight live overstory trees were on the plot in 1989, the basal area was about 50 square feet per acre (11.4 sq. meters per hectare), and the average dwarf mistletoe rating in the overstory trees was heavy (5.5) (Hawksworth 1977).

A replicated, random plot design was used which consisted of three plots, each of which contained 12 square subplots large enough to contain 16 trees each. Trees in each subplot were planted at 4-feet (1.2-m) intervals in four rows spaced 4 feet (1.2 m) apart. At least 8 feet (2.4 m) separated subplots from one another. A third of all the resistant grafts, susceptible grafts, and seedlings were planted at random in each of the three large plots. On some subplots, fewer than 16 trees were planted. In all, about 180 trees were planted in each plot for a total of 542 trees.

The plots were visited periodically from 1967 to 1989, and brush and other unwanted vegetation removed as needed to reduce competition on the young trees. In September 1989, all trees were examined for survival, growth, and infection. Height growth and crown size (the cumulative length of all living and dead branches) were measured to the nearest inch (2.54 cm). Each dwarf mistletoe infection, dead or alive, was recorded, and the year in which each infection occurred was estimated by counting the number of annual growth segments on a stem beginning with the current segment and counting back to the one nearest the midpoint of the dwarf mistletoe infection. This method assumes that most infection occurs on current year's growth. Branch infections and main stem infections were recorded separately. For dead trees, the cause and year of death were determined from growth segments, from external signs and symptoms, and from the stage of tree deterioration during the examination in 1989. Some trees disappeared for unknown reasons during the course of the study.

Data were analyzed statistically to determine: 1) differences in levels of infection and proportion of resistant and susceptible trees infected, 2) the relationships between tree survival and infection level; and 3) relationships between level of dwarf mistletoe infection and tree height and total branch length.

Results

Number of Trees Infected and Intensity of Infection

Resistant Tree Selections

Only 29 percent of all the grafts from the 25 resistant selections from the Deschutes National Forest became infected with dwarf mistletoe over the 20- to 22-year test period *(table 2)*. Grafts from four of the selections were uninfected. Of another 14 selections, half or fewer of the grafts became infected. Only in seven selections did more than half of the grafts become infected.

Mean number of infections per tree was low for all resistant selections. In only one of the 14 selections of which half or fewer of the grafts were infected was the mean number of infections per tree greater than one. On the other hand, for the selections with more than half the grafts infected, the number of infections ranged from a mean of 0.8 to 3.7 per tree. Therefore, a measure of resistance appears to be expressed both in the percentage of trees infected and in the number of infections per tree, and it is possible that some selections are immune.

On the Ochoco National Forest, a trend similar to that on the Deschutes National Forest followed in the percentage of grafts infected and the mean number of infections per tree *(table 3)*. No sources were uninfected, but three showed 50 percent or fewer of the grafts uninfected, and on these trees the mean infection level was fewer than one per tree. The other two sources had more than 75 percent of the trees infected, and means of 2.2 and 3.3 infections per tree.

Therefore, for nearly all sources selected for resistance on both the Deschutes and Ochoco National Forests, the percentage of grafts infected, and the mean infection level per tree were very low during the 20-22 years of the test. A Tukey test for mean separation showed that only five selections (R12, R20, and R47 from the Deschutes National Forest, and R25 and R26 from the Ochoco National Forest) had trees with significantly higher mean numbers of infections per tree than the others, but even these levels of infection were regarded as low considering the duration of exposure to heavy overstory infection.

Table 2—*Percent of grafted ponderosa pines infected and the mean number of infections per tree by resistant parent source on the Deschutes National Forest, Oregon, 20-22 years after exposure to dwarf mistletoe*

Parent tree source	Number live trees	Percent trees infected	Mean number (± one standard deviation) of infections per tree
R1	11	0	0 ± 0
R2	12	50	0.7 ± 0.8
R3	13	8	0.1 ± 0.3
R4	11	9	0.2 ± 0.6
R8	13	62	1.0 ± 1.1
R9	12	8	0.1 ± 0.3
R10	12	0	0 ± 0
R11	12	25	0.3 ± 0.5
R12	12	58	2.4 ± 3.8
R13	12	8	0.1 ± 0.3
R14	11	55	1.2 ± 1.5
R15	16	13	0.1 ± 0.3
R16	7	57	1.0 ± 1.4
R17	13	69	0.8 ± 0.7
R18	13	38	0.9 ± 1.3
R19	13	46	1.2 ± 1.5
R20	15	80	2.9 ± 2.7
R41	8	25	0.3 ± 0.5
R42	12	8	0.1 ± 0.3
R43	7	0	0 ± 0
R44	10	10	0.3 ± 0.9
R45	10	0	0 ± 0
R46	10	10	0.1 ± 0.3
R47	3	100	3.7 ± 3.1
R49	12	8	0.4 + 1.4
Total	280	29	

Table 3—*Percent of grafted ponderosa pines infected and the mean number of infections per tree by resistant parent source on the Ochoco National Forest 20-22 years after exposure to dwarf mistletoe*

Parent tree source	Number live trees	Percent trees infected	Mean number (± one standard deviation) of infections per tree
R22	11	18	0.2 ± 0.4
R23	7	14	0.2 ± 0.4
R24	12	50	0.8 ± 1.2
R25	13	77	2.2 ± 2.6
R26	6	83	3.3 + 2.8
Total	49	49	

Susceptible Tree Selections

1) Grafts

Grafts produced from eight susceptible tree selections on the Deschutes and Ochoco National Forests, and grafts from four selections from the Rogue River National Forest were analyzed for percentage of trees infected and mean number of infections per tree *(table 4)*. In only one selection from the Ochoco National Forest did a high proportion of the grafts survive during the test period. And, of all grafts from susceptible parents 85 percent were infected with dwarf mistletoe. In none of the selections was the mean infection level per tree lower than 1.9, and in two cases on the Ochoco National Forest, the average number of infections per tree was 8.5 and 9.0. With the exception of the Ochoco National Forest trees, an analysis of variance showed no significant differences in the mean number of infections per tree among all the susceptible selections.

There was a significant difference in proportion of trees infected and the level of infection between the resistant and the susceptible grafts, however. A t-test of the proportion of trees infected from each source showed that only 33 percent of all the resistant grafts were infected in contrast to 85 percent of the susceptible grafts *(tables 2, 3, 4)*. A greater variation in percentage of trees infected was found among the resistant graft selections than among the susceptible ones. This suggests that inheritance of resistance from open-pollinated trees selected for susceptibility was very low or at least not expressed, whereas in resistant selections, varying levels of resistance were observed. The mechanism of resistance or levels of inheritance are not known, however.

2) Ungrafted grown seedlings

Ponderosa pine seedlings grown from seed at the Forest Service nursery in Bend, Oregon, and used as "field run" controls for resistance ranked among the highest in susceptibility to dwarf mistletoe of any of the selections in the test. Regardless of whether the trees were planted as bare root stock or outplanted as potted seedlings, the mean infection levels were 90 and 85 percent, respectively. And, except for two grafted susceptible selections from the Ochoco National Forest, nursery-grown trees also had the highest mean number of infections per tree *(table 4)*.

Table 4—*Ungrafted seedlings, and grafted ponderosa pines from susceptible parent selections are infected with dwarf mistletoe in Oregon after 20 to 22 years*

Parent tree source	Number live trees	Percent trees infected	Mean no. (± one standard deviation) of infections per tree
		Grafted trees	
Deschutes National Forest			
DS1	14	79	3.4 ± 3.2
DS2	20	70	2.8 ± 3.2
S3	12	83	3.3 ± 3.1
S5	10	100	2.9 ± 1.3
S6	11	73	1.9 ± 1.9
Ochoco National Forest			
S-1	2	100	9.0 ± 5.7
S2	4	75	8.5 ± 8.2
S11	9	89	2.4 ± 1.5
Rogue River National Forest[1]			
R31	10	70	3.9 ± 4.0
R32	10	90	4.1 ± 3.1
R38	12	100	4.5 ± 2.6
R39	11	91	2.2 + 1.3
Total	125	85	
		Seedlings	
USDA Forest Service Nursery, Bend, Oregon			
BRT	21	90	6.8 ± 5.9
PSS	41	85	5.1 + 4.3
Total	62	87	

[1]The foliage on these selections failed to show the drooping growth habit when grown in central Oregon. Therefore, they were not considered genetically resistant and so were grouped with the susceptible selections.

These results appear more dramatic, as discussed later in this paper, in that many of these seedlings were infected early in life and died over the duration of the test.

Tree Survival

Paired t-tests showed that the percentage of resistant trees that died from dwarf mistletoe on each of the three plots was not significantly different *(table 5)*. Similarly, no significant differences were found in the percentage of susceptible trees killed by dwarf mistletoe among the three plots. Therefore, for further analysis of mortality, the data from resistant trees were pooled, and the data for all susceptible trees pooled.

A paired t-test showed there was a statistically significant difference in the percentage of tree mortality from 1967 to 1989 between the resistant and susceptible trees *(table 5)*. Overall, 76 percent of the resistant trees were still alive after 20-22 years, whereas only 48 percent of the susceptible trees were alive. Of the resistant trees that died, only 22 percent apparently died from dwarf mistletoe infection. The remaining 78 percent died mostly from cutting by rodents, poor survival after planting, or from unknown causes.

Of the susceptible trees that died, we believe that 73 percent were killed by dwarf mistletoe mostly from one or a few infections occurring on the main stem, especially those that occurred early in the life of the tree. The remaining 27 percent of the death among the susceptible trees was caused by other factors as mentioned above. There were no significant differences in the proportion of trees that died from other causes between the resistant and susceptible trees.

The percentage of resistant and susceptible trees that died each year since the time of planting was determined for the years 1977-1988 *(fig. 1)*. The trees that died before 1977 were either missing or too badly decomposed for us to determine in 1989 their year of death. However, field observations over these early years suggest that most trees died mainly from factors mentioned earlier rather than from dwarf mistletoe. We estimated that about 13 percent of all the resistant and about 14 percent of all the susceptible trees died between 1967-69 and 1976.

Mortality among the resistant trees was low and relatively constant from 1977 to 1988 *(fig. 1)*. Only in 1984 was the percentage of dead trees greater than 2 percent. On the other hand, mortality of the susceptible trees increased dramatically from 1981 to 1984, decreased somewhat, but remained relatively high, thereafter. We attribute this increased mortality in the susceptible trees, and somewhat increased mortality in the resistant ones to the buildup of dwarf mistletoe beginning in 1981.

We also noted that among the susceptible trees that died, 64 percent of the seedlings planted as controls died from dwarf mistletoe in comparison to 30 percent of the grafts produced from older susceptible trees. These results support earlier studies by Roth (1974b) that showed that seedlings of ponderosa pine exhibit greater susceptibility to infection and damage from dwarf mistletoe than trees produced by grafting scions onto seedling rootstock.

In summary, the resistant trees died mostly from causes other than dwarf mistletoe, whereas dwarf mistletoe appeared to be the primary cause of death of most of the susceptible trees.

Table 5—***Survival of resistant and susceptible ponderosa pines from 1967 to 1989, and the percentage of death caused by dwarf mistletoe***

Plot	Total trees	Total dead trees	Percentage of deaths caused by dwarf mistletoe
	no.	*pct*	*pct*
		Resistant trees[1]	
1	109	28	23
2	107	15	19
3	116	29	24
total	332	24	22
		Susceptible trees	
1	68	49	70
2	68	51	69
3	74	55	80
total	210	52	73

[1]Based on all trees selected as resistant excluding those with droopy needles from the Rogue River National Forest. They were not considered genetically resistant.

Population Dynamics of Dwarf Mistletoe

The number of dwarf mistletoe infections and year in which each infection became established were determined for all infected resistant and susceptible trees *(fig. 2)*. The numbers of infections occurring each year on the resistant selections were low and quite consistent from 1968 through 1980. In none of these years did more than 19 infections become established, and only in 1981 were more than 26 infections recorded. For the susceptible trees, the number of infections per year rose to 20 or more by 1972 and continued to increase steadily each year until 1980 when 50 infections were noted. A marked increase in the number of infections occurred in 1981 among both the resistant and susceptible trees. More than 50 infections were recorded on resistant trees, and nearly 150 recorded on susceptible trees in that year. Thereafter, infection levels dropped to about what they were in 1980, and continued to decrease to nearly none in 1986. We attribute the apparent decrease in infection from about 1984 to 1989 to our inability to detect recent latent infections. Symptoms or the presence of dwarf mistletoe plants may not appear for several years after infection, particularly on slow growing trees.

The differences between the levels of infection on resistant and susceptible trees are even greater when one considers that about twice as many resistant as susceptible trees were used in the study. In addition, about half of the susceptible trees died between 1968 and 1989, reducing opportuni-

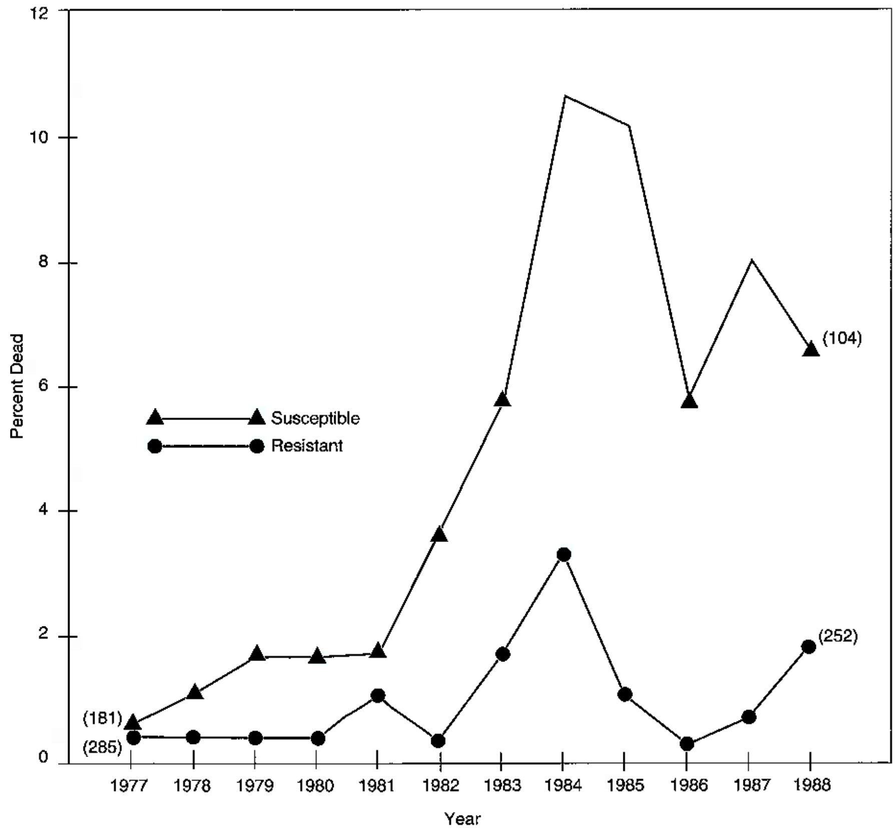

Figure 1—Percentage of the remaining resistant and susceptible ponderosa pines that died each year from 1977-1988.

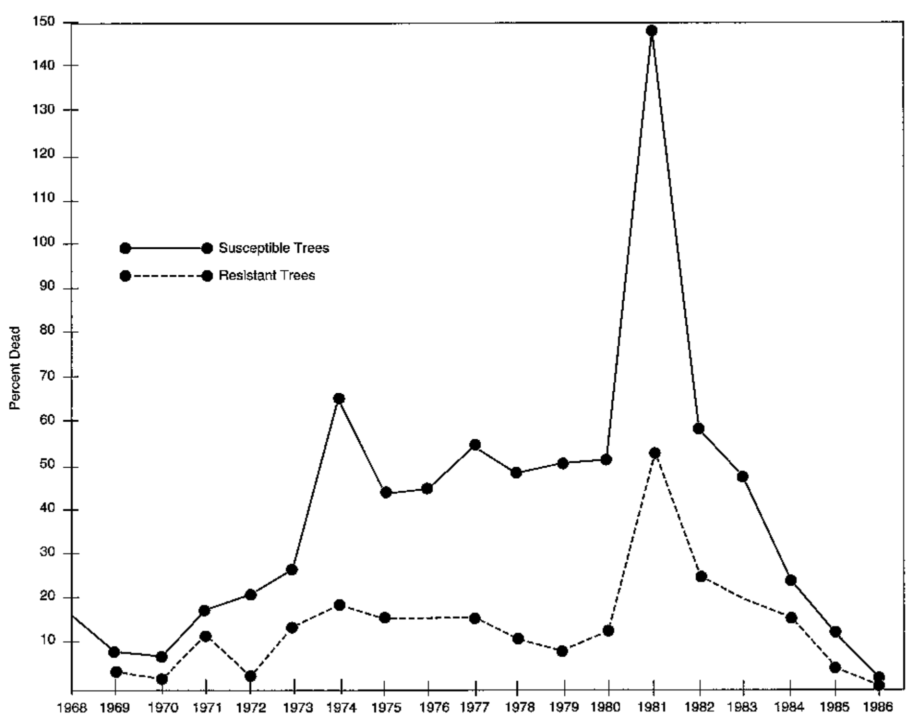

Figure 2—Number of infections by year of infection for resistant (332 trees) and susceptible (210 trees) selections of ponderosa pines in Oregon.

Figure 3—Most trees propagated from scions from one resistant parent selection (R22) on the Ochoco National Forest grew straight and tall, had short lateral branches, and were mostly uninfected with dwarf mistletoe.

Figure 4—Trees produced from scions from one resistant parent (R1) on the Deschutes National Forest grew nearly as tall as those from the Ochoco National Forest *(fig. 3)*, branched profusely, and were completely free of dwarf mistletoe.

ties for infection, whereas only about one quarter of the resistant trees died during this period.

Tree Growth and Infection

Before evaluating the effect of dwarf mistletoe on tree growth, it was necessary to understand the variability and characteristics of growth of both the infected and uninfected trees. Tree height and growth varied widely within and among the selections of trees. For example, some grafts grew straight, tall, and had relatively few short branches *(fig. 3)*. Others grew equally as tall and branched profusely *(fig. 4)*. Some trees hardly grew at all, and others lost apical dominance and developed into "coniferous brush" *(fig. 5)*. In some cases, the growth characteristics of the tree were affected by dwarf mistletoe infection as in the loss of apical dominance, multiple tops, or brooming. Therefore, a wide range of tree growth characteristics were expressed among both the infected and the uninfected trees.

The average tree heights from 1967-1989 for the resistant and susceptible selections were grouped as follows:

Mean tree height		No. tree selections	
inches	*(cm)*	resistant	susceptible
20-40	(51-103)	8	6
41-60	(104-153)	18	7
61-77	(154-196)	4	1

These results show that, on the average, trees from all selections were more than a half meter tall after 22 years, but none averaged 2 meters in height. A few trees were about 3 meters tall. These tree sizes represent poor growth rates for ponderosa pine with or without the influence of dwarf mistletoe, and were caused in large part by competition from the overstory. The area on Pringle Butte on which these trees are growing is a poor site (low site IV) for growth of ponderosa pine.

One assumption we made during the course of the study was that the number of mistletoe infections on a tree would be directly related to tree size (tree height) or to crown size (total length of living and dead branches). The larger the tree, the greater its probability over time to trap dwarf mistletoe seeds and become infected. However, results of the study showed no relationship between tree height and number of infections for nearly

Figure 5—All trees produced from a parent tree from the Rogue River National Forest (R38) became infected with dwarf mistletoe, lost apical dominance, and were severely reduced in growth and vigor.

all the selections tested. R^2 and regression analyses showed that among 13 resistant selections in which at least five or more trees were infected, only two cases showed what could be interpreted as a significant relationship between tree height and amount of infection. Of the same 13 selections, only three showed what was considered a significant relationship between crown size and amount of infection.

Of 11 selections of susceptible trees in which at least five trees were infected, only three showed a significant relationship between tree height and amount of infection. In four out of the 11 susceptible selections crown size possibly was related to amount of infection. These results agree with a study of dwarf mistletoe infection in seedlings of Jeffrey pines in southern California, in which neither seedling age nor height seemed related to amount of infection (Scharpf and Vogler 1986).

Branch Versus Main Stem Infections

The disease impact that an individual infection has on a small pine for the most part is related to where the infection occurs. An infection located on the main stem exerts more disease stress on the tree than one located on a branch. Main stem infections affect the normal flow of nutrients within the tree and often bring about the loss of apical dominance, resulting in trees with forked or multiple tops. Also, loss of vigor and the inability of these trees to compete with others in the stand often result in premature death.

Of 225 infections recorded on trees selected as resistant, 55 percent were on branches, 45 percent on main stems. For susceptible trees, half (377) of 749 infections were on branches, and half (372) were on the main stem. Scharpf and Vogler (1986) also found a high proportion of the infections on young Jeffrey pines in the main stem. Therefore, both the resistant and susceptible trees had about the same proportion of branch and main stem infections. Survival of resistant and susceptible trees with main stem infection was quite different, however. Of 76 resistant trees with main stem infections, only 18 percent had died by 1989, whereas 47 percent of 164 susceptible trees with main stem infections had died by 1989. More frequent death of susceptible trees infected on the main stem can probably be attributed to a higher proportion of these trees having more than one main stem infection earlier in the life of the tree, and to a greater number of branch infections.

Two resistant selections grafted to susceptible rootstock particularly illustrate the differences in resistance between resistant and susceptible pine material. In these two cases, intertwined forks developed, one from a bud on the susceptible rootstock, and the other from the resistant scion *(fig. 6)*. In both these cases, the fork developing from the resistant scion was uninfected, whereas the fork arising from the rootstock bore several branch and main stem infections, even though both forks were approximately of equal size. It seems very unlikely that the uninfected forks could have been exposed to different amounts of inoculum or different growing conditions that would have prevented infection. This condition was even more striking in a few resistant trees that became infected very early on the rootstock just below the graft union; yet in nearly two decades the parasite has failed to cross the union and become visible on tissues of the resistant selection *(fig. 7)*.

Figure 6—A forked tree developed from a bud of a susceptible rootstock (left) and from a scion from a resistant parent selection (right). Note several dwarf mistletoe plants growing on the susceptible fork and the absence of infection on the resistant fork. The two forks were artificially held apart for photographing.

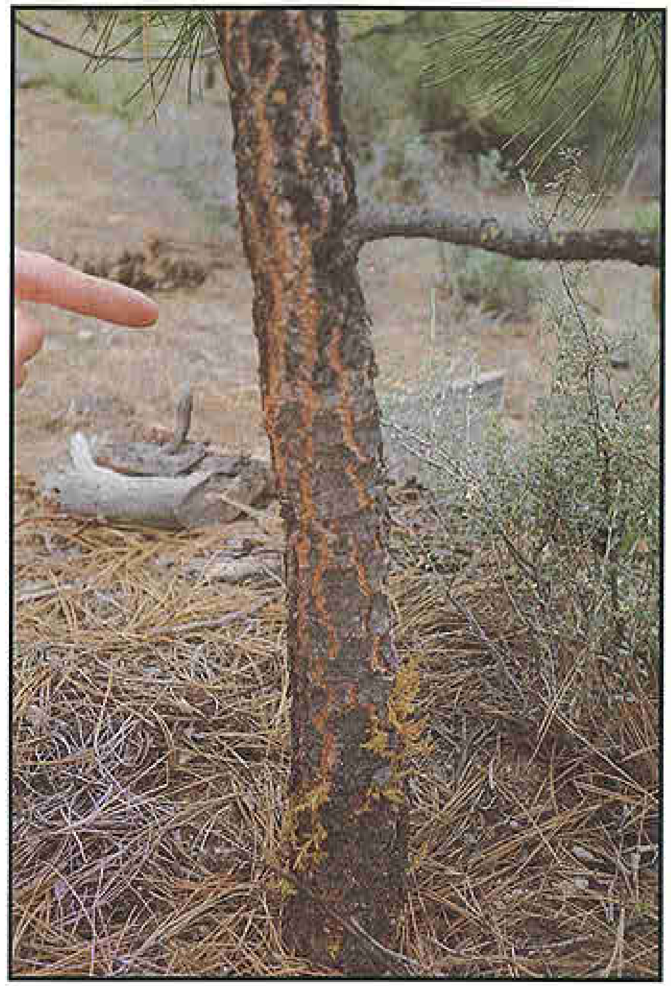

Figure 7—Note the dwarf mistletoe shoots growing from the susceptible rootstock of the tree. The graft union is slightly below where the finger is pointing. No dwarf mistletoe was observed in the trunk or in any other portion of the tree above the graft.

Discussion and Conclusions

One of the problems in determining resistance of a given selection of trees is in finding out what variables influence infection, and whether these variables operate the same or differently on both the resistant and susceptible selections. In this study we attempted to eliminate some of the complicating factors of genetic variability and experimental testing through the use of seedlings, clonally propagated material, and replicated, random plot design on a heavily diseased natural site. Other variables we believe could have been related to resistance to dwarf mistletoe in this study included foliar habit, tree size, and crown characteristics.

In contrast to reports of resistance by Roth (1966), grafts propagated from parent trees with drooping needles from the Rogue River National Forest were found not to be resistant to dwarf mistletoe in our tests. A possible reason for the lack of resistance in these sources may be similar to that reported by Roth (1974a) for the lack of resistance in the drooping needle pines from the Deschutes National Forest. The needles of the coastal, Rogue River sources did not droop when the grafts were grown in central Oregon. As a consequence, these selections were as susceptible to infection as the local sources.

Tree size and crown characteristics also were not related to number of trees infected or to infection intensity for most of the resistant selections, and for more than half the susceptible selections. These results agree with those of Scharpf and Vogler (1986) for young Jeffrey pines in California. Possibly there was not enough of a range in tree size to show a significant difference in intensity of infection based on height or total branch length.

Another reason might be that the test trees were infected mainly by overstory inoculum distributed at random, with little intensification of the parasite within the tree. However, as the trees grow, those with larger crowns may become more heavily infected from the developing infections within the crown.

Another variable we tested was the reputed juvenile susceptibility of seedlings as compared to that of less susceptible trees produced from scions from susceptible, mature trees (Roth 1974b). Unpublished studies in California indicate that juvenile susceptibility is expressed in Jeffrey pine for only about the first 10 years (Scharpf, Kinloch, and Jenkinson 1991). Although the ungrafted seedlings (PSS, BRT) did not show a significantly higher average number of infections per tree in most cases, they were among the groups with the highest mean numbers of infected trees. The lower mean number of infections per tree probably resulted from early tree death before infection could intensify. This is an important consideration, in that about half of the seedlings in these groups became infected and were killed at a fairly early age. Therefore, young seedlings do appear to be more susceptible to infection by dwarf mistletoe, and as a result die at a younger age than trees produced by grafting with scions from older trees. Our conclusion is that the resistance of ponderosa pines reported in this paper is not based on simple inheritance, but involves juvenile susceptibility and a range in resistance among the parent trees selected.

High levels of resistance to dwarf mistletoe exist within populations of ponderosa pines in central Oregon. And, the probability of identifying resistant pines from field observations is good. It is also likely that dwarf mistletoe resistance is present in ponderosa pines and other species of conifers elsewhere in the western United States (Wagener 1965). Further efforts should be made to identify and preserve resistant selections, propagate resistant material in seed orchards, and study the mechanism and inheritance of resistance. Dwarf mistletoe resistance is a component of the native forest ecosystem and is an important mechanism by which trees resist disease. These trees, as well as others identified as resistant to other pests, can become important tools in the forest manager's battle to maintain healthy forests.

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