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Dwarf Mistletoe in Red and White Firs in California—23 to 28 Years after Inoculation

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Spread and buildup of dwarf mistletoe, *Arceuthobium abietinum*, was studied on inoculated white fir, *Abies concolor*, and red fir, *A. magnifica*, in northern California for 23 to 28 years. At the end of these studies (1986), and in the absence of overstory infection, 13 of 23 trees had dwarf mistletoe populations that were the same or smaller than the original populations resulting from inoculation. Mortality of infections was the main factor limiting population increases. Live crown ratio of all trees averaged over 0.8. The average ratio of tree height growth to vertical spread rate of dwarf mistletoe was 11.5 to 1 in white fir and 7 to 1 in red fir in the Sierra Nevada. In the southern Cascades, the average ratio was 1.7 to 1 in red fir. About one fourth of the trees became infected in the bole. Of 14 additional trees infected by lateral spread of the parasite, 13 were within 6 m of the source of infection. Evidence continues to indicate that losses from dwarf mistletoes will be small in well-managed young fir stands free from infected overstory trees and properly spaced to promote good growth.

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

Dwarf mistletoes are widespread in California fir stands. Losses, including reductions in growth and wood quality, predisposition to bark beetles, and damage by secondary decays and cankers, are mainly functions of the numbers of infections and their distribution in tree crowns. We have followed the dynamics of dwarf mistletoe populations in inoculated firs since 1958,[1,2] when we began inoculations with *Arceuthobium abietinum* Engelm. ex Munz on young red firs (*Abies magnifica* A. Murr.) and white firs (*A. concolor* [Gord. & Glendl.] Lindl.) in the Sierra Nevada and southern Cascades.

This note provides an update of population trends in these trees from 1977 to 1986, with data on additional trees, tree-to-tree spread, changes in dwarf mistletoe ratings, and rate of dieback of infected branches.

METHODS

Five red firs at Latour State Forest near Mt. Lassen in the southern Cascades and 13 red firs and 11 white firs on the Stanislaus National Forest in the central Sierra Nevada were studied.[2,3] All trees were less than 10 m tall at the time of inoculation, had branches to within 1 m or less of the ground, and were in areas free from natural infestation by dwarf mistletoe. Thus, these trees were suitable for studying population buildup, rate of change in dwarf mistletoe rating, and distance of vertical and horizontal spread.

The test trees were inoculated by one of three methods with freshly collected, local sources of dwarf mistletoe: (a) in 1960, clumps of fruiting dwarf mistletoes were shaken near trees, approximating natural seed discharge and deposition, (b) in 1958 and 1961, freshly discharged seeds were collected and placed individually on branches,[4] and (c) in 1963-1967, freshly collected seeds were soaked in water and then placed individually on branches.[1]

Initially, the inoculated trees were monitored for mistletoe seed germination, penetration, infection, shoot development, fruit production, and seed dispersal.[3] After these early observations, some trees were examined annually for new infections, shoot and fruit development, and death of infections.[2] For other trees, time and travel constraints precluded annual monitoring of populations and at times data only on tree height, crown length, and highest infection in the crown were taken. Periodically, detailed mistletoe population data were obtained for all trees. Thus, dates of data collection and kinds and amounts of data varied from tree to tree and from year to year and are specified for each factor discussed.

Initially, for most trees, the infections resulting from inoculation and subsequent secondary infections were individually identified with metal tags wired to branches. As numbers of infections increased, this method eventually became too cumbersome and time-consuming. Vandals removed some or all tags from some trees, and other tags were lost for unknown reasons. One red fir was cut, apparently for a

Christmas tree. At different times, tagging was discontinued, and numbers of live infections were recorded for each branch at each branch whorl. Tagging individual dwarf mistletoe infections permitted development of life tables. Counting live infections on branches by whorl provided data on net changes in live populations and their distribution in tree crowns.

As dwarf mistletoe populations increased, the intensity of infection within the tree was determined by the 6-class dwarf mistletoe rating system.[5] For the lower, middle, and upper portions of the living tree crown, the mistletoe in each was rated as absent (0); light—less than half the branches infected (1); or heavy—more than half the branches infected (2). The sum of the numbers is the dwarf mistletoe rating (DMR). Trees with 1 to 3 ratings were considered lightly infected, trees with 4 to 6 ratings, heavily infected.

Tree and branch heights were measured to 7 m with a telescoping, calibrated pole. Beyond 7 m, heights were determined with a clinometer. Dwarf mistletoe infections in upper crowns were detected by climbing trees with a 24-foot (7.3-m) extension ladder or by inspecting carefully with field glasses.

Table 1—*Number of live infections in 1986 in trees inoculated between 1958 and 1967*

Host	Year inoculated	Trees	Initial infections	Live infections 1971	1976	1981	1986
	Stanislaus National Forest						
White fir	1960	2	3	7	1	0	0
	1961	3	13	6	25	22	23
	1963-67	6	111	82	133	129	96
Red fir	1960	3	33	33	43	41	30
	1961	3	22	15	50	83	86
	1963-67[1]	6	119	87	233	499	481
Totals		23	301	230	485	774	716
	Latour State Forest						
Red fir	1958	5	28	596	[2]	905	667

[1]One tree, cut by vandals in 1978, had only a single infection that produced shoots only twice and never fruited.
[2]No data recorded.

Table 2—*Cumulative mortality to 1986 of cohorts of dwarf mistletoe infections detected and tagged at different times*

Host	Interval of observation	Infections	Alive in 1986	Mortality
				Pct
	Stanislaus National Forest			
White fir	1964-67	37	10	73
	1968-71	57	8	86
	1972-76	62	10	84
Red fir	1964-67	40	6	85
	1968-71	51	8	84
	1972-76	109	25	77
	Latour State Forest			
Red fir	1962-65	16	3	81
	1966-68	223	1	99+
	1969-72	731	14	98

RESULTS

Population Buildup and Decline

On the Stanislaus National Forest, population changes were variable and inconsistent among 11 white firs and 12 red firs over the 19 to 26 years since inoculation (*table 1*). Mistletoe fruit and seeds were produced on all but 2 trees, both red firs with single, male infections. By 1986, the number of infections had declined in nine white firs and three red firs, was unchanged in one red fir, and had increased in three white and six red firs. One red fir with a single, male infection was cut by vandals. Among the 13 trees with static or declining populations, all infections had died on three trees, and only one infection was still alive on each of five trees. Population increases on the other nine trees ranged from less than two times to about six times the original population. Total populations on 23 trees increased from 301 to 716 (2.4 times) in 19-26 years.

On Latour State Forest, dwarf mistletoe intensified in all five red firs inoculated, and the rates of population increase were much more dramatic than on the Stanislaus National Forest. From 28 initial infections, the population increased to 905 (about 32 times) in 1981 and then declined to 667 (about 24 times) in 1986.

Population data alone do not indicate the rate of new infections, but rather the balance between new infections and mortality of older ones. For four white firs and four red firs on the Stanislaus, we have yearly data from 1976 to 1986 on the survival of all infections arising from inoculation. By 1986, only 28 (22 percent) of the original infections were alive, but the total numbers of live infections increased to 246, indicating that the change from 1976 to 1986 resulted from 100 deaths and 218 new infections.

Mortality among 1326 infections on all test trees during early population monitoring (1962-1976) ranged from 73 percent to nearly 100 percent within 10 to 26 years from first detection (*table 2*). Surviving infections were generally on the bole or on main branch axes. Since inoculations often involved placing seeds on main branch axes, survival of early cohorts of infection was slightly higher, likely because later cohorts resulted from natural infections occurring mainly on secondary, tertiary, and quaternary branchlets. Among tagged infections recorded from 1964 to 1976 on 10 white and 15 red firs for which data on branch rank were available, mortality for primary, secondary, and tertiary or quaternary branches was, respectively, 48 percent, 66 percent, and 80 percent over the 4 to 16 years (to 1980) in which such data were taken (*table 3*).

Much of the mortality of mistletoe infections was due to death of branches, caused mainly by the parasitic fungus *Cytospora abietis* Sacc. and girdling by rodents.

Table 3—*Mortality by 1980 of dwarf mistletoe infections first recorded on different ranks of branches*

Species	Year recorded	Recorded infections and percent dead by 1980 on branches of different ranks					
		Primary		Secondary		Tertiary/Quat.	
		No.	*Pct*	*No.*	*Pct*	*No.*	*Pct*
Red fir	1964-70	142	49	179	88	123	96
	1971-76	69	33	264	53	172	76
White fir	1964-70	60	62	18	78	2	100
	1971-76	35	49	35	49	29	62
Totals		306	48	496	66	326	80

Table 5—*Infection of trees at various distances from infection loci established by inoculation*[1]

Item	Distance from inoculated trees (m)				
	0 to 2	2+ to 4	4+ to 6	6+ to 8	8+ to 10
Trees	6	14	22	14	13
Mean height (m)	4.8	7.6	7.0	8.1	11.5
Infected	4	5	4	1	0
Infected (pct)	67	38	18	7	0

[1]Spread periods ranged from 23 to 28 years from inoculation.

Table 4—*Cumulative branch mortality to 1986 at various periods after detection of first mistletoe infections*

Species	Years after detection						
	1-7			8-15		16-24	
	Trees	Recorded branches	Dead	Recorded branches	Dead	Recorded branches	Dead
			Pct		*Pct*		*Pct*
White fir	6	41	12	18	56	24	58
Red fir	6	78	15	89	34	23	61
Totals	12	119	14	107	37	47	60

Lower uninfected and infected branches also died as they became shaded and physiologically weaker as the trees grew in height. Many infected branchlets died, thus killing individual infections. In time, entire branches died (*table 4*), killing all infections on the branch. As expected, the longer a branch was infected, the more likely it was to die. Over half of the branches infected for more than 16 to 18 years were dead. Trees at Latour were not monitored regularly enough to provide consistent records on date of initial infection or of branch death, but for three trees, the condition of all branches less than 3 m from the ground was recorded. There were 133 live branches in 1968, 40 in 1978, 7 in 1981, and none in 1986.

Dwarf Mistletoe Rating (DMR)

On the Stanislaus National Forest, records of crown lengths, and location of infected branches permitted determination of live crown ratios (LCR), percent of live crown infected, and DMR for 10 white and 10 red firs (3 trees had cut or broken tops and were not included). Although live crowns were not measured at the time of inoculation, only trees with LCR of 0.8 or more were used. After 23 to 26 years, LCR averaged 0.87 (range 0.75 to 0.93) for white firs and 0.88 (range 0.78 to 0.95) for red firs. Percent of live crown infected averaged 15 (range 0 to 47) for white firs and 27 (range 0 to 65) for red firs. Two red firs with single, male infections were considered to be uninfected, since mistletoe reproduction was precluded. The DMR averaged 1.5 (range 0 to 3) for white firs and 2.0 (range 1 to 3) for red firs. Combined rating for the 20 trees was 1.8. In none of these trees was the upper third of the crown infected, and only seven trees had infections in the middle third.

At Latour after 28 years, LCR of five red firs averaged 0.79 (range 0.61 to 0.92). Percent of live crown infected averaged 43 (range 0 to 70). The "O" value is an artifact owing to the fact that the highest infected branch was also the lowest live branch in one tree. The average dwarf mistletoe rating was 3.0 (range 1 to 5).

Vertical Spread in Relation to Tree Height Growth

On the Stanislaus National Forest, the rate of vertical spread through tree crowns was determined for 11 white firs and 12 red firs. For white firs, the distance from the highest branch infected by inoculation to the highest branch infected by secondary spread indicated an average annual rate of spread of 2.6 cm (range of -35.0 to 7.7 cm). Average annual growth in tree height for the same period (23 to 26 yr) was 30 cm, giving an average ratio of height growth to vertical mistletoe spread of 11.5:1. For the 12 red firs, vertical mistletoe spread averaged 4.5 cm/year (range of -2.2 to 18.0 cm) and tree height growth was 32 cm/year (range 14-59 cm), giving a ratio of tree growth to vertical mistletoe spread of 7:1. For the five red firs at the Latour State Forest, average mistletoe vertical spread over 28 years was 20.0 cm/year (range 13 to 26 cm). Height growth averaged 33 cm (range 25 to 40 cm)/year, giving a ratio of height growth to vertical spread of 1.7:1.

Bole Infections

Two bole infections resulted from inoculations, and 15 resulted from secondary infections within inoculated trees or from spread to surrounding trees. Excluding the two from inoculations, bole infections developed in 10 (24 percent) of 42 trees. Bole infections occurred mainly from branch infections growing into the bole, but some were from direct infection of young needle-bearing main stems.

Tree-to-Tree Spread

Because inoculated trees were in isolated areas free of natural infection, spread of mistletoe to surrounding trees could be monitored. Inoculated trees separated by less than 3 m from one another were considered single loci of infection. Inoculated trees in which mistletoes never fruited were not included. By these criteria, 14 loci of infection were identified. The rate of infection decreased with distance from seed source (*table 5*). Of the 14 trees that became infected, 13 (93 percent) were within 6 m of loci. One of 14 trees between 6 to 8 m and none of 13 trees between 8 to 10 m from loci were infected. Mistletoe spread successfully from 7 (50 percent) of 14 loci of potential spread. Spread occurred at one additional locus, but the new infections died out and spread was therefore considered unsuccessful.

DISCUSSION

Recommendations for managing red or white fir stands infested with dwarf mistletoe include seed-tree establishment of reproduction in infested stands, clearcutting followed by planting or natural regeneration, and release of infested advance regeneration of fir by thinning or overstory removal.[6,7] It is, therefore, important to know how rapidly dwarf mistletoe might increase in young stands with scattered infected trees. Such information ultimately requires long-term monitoring of plots to update and refine data.

Interim results from these studies indicated that rates of buildup and spread through crowns of young firs were slow.[1,7] Furthermore, our results show that after about 2 decades of initial increases, dwarf mistletoe populations have begun to level off or decline in the trees under study. For example, for the Latour red firs, Stanislaus red firs, and Stanislaus white firs, 1986 populations of live infections were 74 percent, 96 percent, and 79 percent, respectively, of the 1976 populations. At least three factors appeared to be important in mistletoe population dynamics: (1) differences in susceptibility among trees in different areas (or different microclimatic conditions in different areas that influence infection), (2) low infectivity of dwarf mistletoe seeds, and (3) rate of death of infected branches.

We have previously reported on differences in population dynamics of dwarf mistletoe at the two Forests.[1] Our infection data in that report indicated that the differences were due in part to the shorter incubation period for dwarf mistletoe plants at Latour.[2] Higher initial rates of infection following inoculation (28 percent) were also noted on red firs at Latour, but not on white firs.[3] The reasons for differences between areas are unknown, but they might involve environmental influences, provenance differences in susceptibility, or variations in virulence among local populations of mistletoes.

Our results indicate that, as previously reported, rates of infection in true firs are low.[2] Among 23 inoculated trees on the Stanislaus National Forest, mistletoe populations have declined to 0 or 1 infection per tree in 8 trees (35 percent). Since seven of these bore fruiting infections, failure to establish viable populations apparently involved low rates of infection, even when seeds were produced for several years.

Death of infections generally involved death of branches or branchlets from one or more causes, especially rodent chewing and branch girdling by secondary fungi and insects.[2] Small secondary and tertiary branchlets apparently were more liable to die from girdling, hence the higher percent of early deaths among infections on these higher branch ranks. Because many of the infections on these branches produce very few seeds and have little effect on the tree, their loss is of little practical importance. In trees on which branches became heavily infected, death of entire branches was frequent and often led to elimination of large numbers of infections and to marked decline in mistletoe populations. On the most heavily infected red firs at Latour, virtually all of the branches less than 3 m from the ground have died.

Vertical spread on the Stanislaus continued to lag well behind height growth in the 29 trees studied. By 1986, ratios of height growth to vertical mistletoe spread for red firs and white firs were 7 to 1 and 11.5 to 1, respectively. These ratios represent a slight increase in the vertical spread rate for red firs and a slight decrease in spread rate for white firs since our earlier report.[1] Thus, nearly all the trees on the Stanislaus National Forest continue to outgrow the upward spread of the parasite by a wide margin.

At Latour, average rates of vertical spread in red firs were greater (20.0 cm/year) by 1986 than they were in 1976 (7.3 cm/year), but the rate of host height growth (avg. 33 cm/year) still exceeded the rate of vertical mistletoe spread by a ratio of 1.7:1. With the diminishing of dwarf mistletoe populations during the last several years, it is likely that tree height growth will continue to outpace vertical spread, and that the amount of uninfected crown will increase.

Damage and growth loss from dwarf mistletoes in firs are related to live crown ratios and to the amount of live crown infected, as has been reported by Scharpf.[7] Scharpf found that trees with good live crown ratios (0.61 to 1.0) and light infection ratings (1 to 3) grew well after release. None of our trees had a live crown ratio below 0.61, and only 5 (20 percent) had ratios below 0.81. Mistletoe ratings were light in 96 percent of the trees and heavy in only 4 percent. Since most trees had good live crown ratios and light infection levels, any damage caused by mistletoe will be small.

Bole infections developed in only 24 percent of the trees. Since such infections do not appear to cause much damage in young, fast-growing firs,[8] significant damage is not expected.

There was some lateral spread of mistletoe to firs adjacent to the test trees, but almost all spread was within about 4 to 6 m after 23 to 28 years. Therefore, the spread among firs in this study was slightly less than the average of about 0.9 ft (0.27 m) lateral spread per year reported for ponderosa pine in the southwest.[9]

These results provide further evidence that losses from dwarf mistletoes should be small in well-managed young stands free of infected overstory. If care is taken to eliminate overstory sources of infection and stands are spaced properly to promote good growth, scattered infections within young fir stands should not affect productivity appreciably.

END NOTES AND REFERENCES

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