Resistance of Libocedrus decurrens to Phoradendron bolleanum subspecies pauciflorum

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ABSTRACT

The true mistletoe *Phoradendron bolleanum* subsp. *pauciflorum* found on white fir *Abies concolor* of the Sierra Nevada has not been reported on incense-cedar *Libocedrus decurrens*, even though both conifers are found in the same stands. Possible explanations for this apparent resistance of incense-cedar were determined by inoculation studies. Resistance mechanisms included wash-off, bark exfoliation, and the formation of a cork barrier in response to penetration. Phytopathology 61:875-876.

Additional key words: phanaerogamic parasite, obligate parasite, periderm, host specificity.

Incense-cedar (*Libocedrus decurrens* Torr.) occurs in the mixed conifer forests of the Sierra Nevada along with white fir (*Abies concolor* [Gord. & Glend.] Lindl.). The true mistletoe, *Phoradendron juniperinum* subsp. *libocedri* (Engelm.) Wiens, occurs on incense-cedar. The true mistletoe, *P. bolleanum* subsp. *pauciflorum* (Torr.) Wiens, occurs on white fir. Bluebirds and robins, two important vectors of both mistletoes, have been observed flying indiscriminately between the fruiting mistletoes on each host (1). Their droppings were observed to contain both types of mistletoe seeds. Thus, the seeds of both mistletoes are undoubtedly deposited on both hosts. Incense-cedar true mistletoe occasionally occurs on white fir, but white-fir true mistletoe has never been reported on incense-cedar.

Possible explanations for the absence of white-fir true mistletoe on incense-cedar were investigated. On 18 October 1968, 260 seeds of the white-fir true mistletoe were squeezed out of their fruit coats onto branches of incense-cedar saplings. One hundred and five incense-cedar true-mistletoe seeds were similarly placed on incense-cedar. After 48 days, 4% of the white fir mistletoe seeds and 31% of the incense-cedar mistletoe seeds remained on the branches. Many white fir mistletoe seeds were recovered from the duff, and both types of mistletoe seeds were assumed to have been washed off. After 1 year, four white fir mistletoe seeds (1.5%) remained. All had germinated, but one had died. Of the three live seeds, one was on exfoliating bark and two had formed holdfasts on tight bark. Seventeen incense-cedar mistletoe seeds (16%) remained.

Since the loss of white fir mistletoe seeds was heavy, 98 seeds of white fir mistletoe that had been deposited by birds and that had germinated in the field on white fir stems or branches were removed and glued with Elmer's glue to the branches of four incense-cedar saplings and the main stem of another on 22 May 1969. The exfoliating bark was removed from the sites prior to inoculation. The glue was placed only on the bottoms of seeds, and did not touch the radicles. Strips of glue were placed on several branches to determine toxic effects, if any, of the glue. In addition, 26 germinated seeds were similarly glued onto white fir to determine if the seeds could become established on their natural host. Finally, strips of glue were placed on white fir branches.

Of the 98 seeds on incense-cedar, 64 (65%) formed "holdfasts", and were presumed to have attempted penetration. Twenty-two seeds (23%) died without forming holdfasts, and 12 seeds (12%) were eaten by predators or were otherwise missing. Some of the 23% mortality may have been due to the fact that a few seeds had begun to form holdfasts on their white fir host when they were harvested for inoculation. They may have been irreparably injured when removed. Of the 26 seeds on white fir, all but three were eaten by predators. All three formed holdfasts.

Of the 64 seeds that formed holdfasts on incense-cedar, 42 (66%) were alive 1 year after inoculation (26 May 1970). Four months later (22 September 1970), after a period of host growth and summer drought, only nine seeds (15%) were still alive. One of the three seeds on white fir was alive on 22 September 1970.

The 33 of 42 seeds that suddenly failed on incense-cedar were examined. Small-to-large amounts of host tissue around the primary haustoria of the seeds were corked out and killed, leaving a sunken area of bark around most holdfasts (Fig. 1-A).

Microscopic examination of eight of these sunken areas showed a thin enclosing periderm at the interface

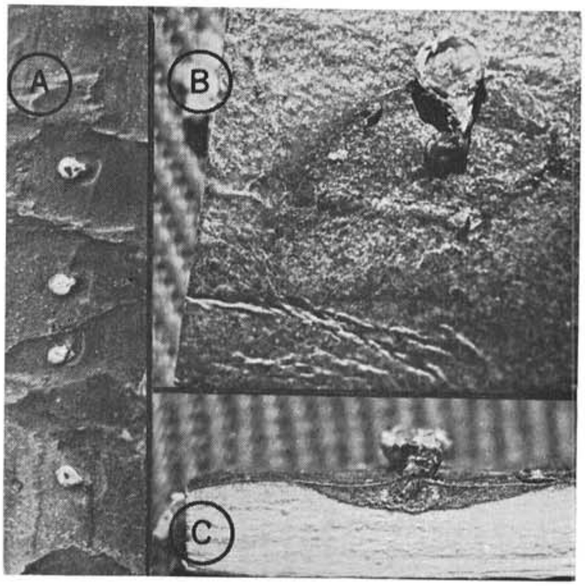

Fig. 1. A) Failing seeds of white-fir true mistletoe glued to incense-cedar and showing sunken bark beneath holdfasts. **B)** Close-up of failing seed. **C)** Section through primary haustorium of seed in Fig. 1-B showing depth of wound periderm.

of the live and corked-out host tissues. A dark red stain with Sudan IV (0.5 g in 100 cc of 80% EtOH) verified this observation. Figure 1-B shows a sunken area around a holdfast on the bark of incense-cedar. Figure 1-C shows the depth of the periderm.

One of the nine seedlings of white fir mistletoe that remained alive on incense-cedar was examined. Its primary haustorium had breached a relatively shallow cork barrier. The other eight seedlings have been left undisturbed to follow further developments. The glue caused no apparent injury to either incense-cedar or white fir.

The resistance of incense-cedar to white-fir true mistletoe apparently involved three aspects: wash-off, bark exfoliation, and the formation of a cork barrier in response to penetration.

The much higher retention of incense-cedar true-mistletoe seeds than white-fir true mistletoe seeds may be explained in part by the fact that the seeds of incense-cedar mistletoe were noticeably stickier and drier than those of white fir mistletoe when both were first squeezed from their fruit coats. This may be related to the relative wettability of the viscin of each type of seed. In addition, the larger size of white-fir true-mistletoe seeds, which perhaps makes them more suited to capture between needles on fir, probably made them less suited to slipping under exfoliating bark of incense-cedar during a rain. The effects of passage through birds on this relative retention is not known. Germination of the retained white-fir true-mistletoe seeds was not inhibited, but bark exfoliation further reduced penetration.

Wash-off and bark exfoliation may be important to other mistletoes and their hosts. Tainter (3) stated that rain probably easily washes seeds of *Arceuthobium pusillum* off the smooth bark of twigs, but not the short shoots of *Larix laricina*. The exfoliation of bark of *Eucalyptus*, *Platanus*, *Arbutus*, and *Arctostaphylos* may also impart some resistance to mistletoes to these genera (2).

The large mortality, from 26 May 1970 to 22 September 1970, of fir mistletoe seeds that were glued to incense-cedar was probably due to the formation of wound periderm during the period of host growth with subsequent desiccation of seeds which had not breached the cork barriers. The possible production of toxins by the penetrating seeds could not be discounted.

Tainter (3) reviewed the phenomenon of wound periderm in association with mistletoes. It apparently has not been reported for *Phoradendron*. Tainter (3) found that *Arceuthobium pusillum* is often found on *Picea mariana* but rarely on *Larix laricina*, even though the two trees are intermingled in heavily infested areas. This may be due to the formation of cork around established infections on *Larix*.

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