Juvenile Susceptibility of Ponderosa Pine to Dwarf Mistletoe

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ABSTRACT

Susceptibility of the new growth of a population of juvenile ponderosa pines to infection by western dwarf mistletoe decreases with increasing tree age; i.e., the rate of infection per infection site declines with age of the host up to about 50 yr. Consequently, other things being equal, mistletoe build-up after a stand is thinned should be slower in older stands than in those less than 50. Two rather common forms of extreme mistletoe susceptibility in older trees are reported: (i) susceptibility to infection, and (ii) susceptibility to damage. In the first form, excessive numbers of mistletoe plants accumulate, lateral endophytic mistletoe growth is limited and host damage results from sheer numbers. Trees of the second category may be indifferently susceptible to infection, but may suffer severely from even a few mistletoe plants because of extensive lateral spread of the endophyte.

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Along the east slope of the Cascade Mountains ponderosa pine (*Pinus ponderosa* Laws.) is severely damaged by western dwarf mistletoe (*Arceuthobium campylopodum* Engelm.) (6). Today, as a result of selective logging, the forest is characterized by sparsely stocked stands of old-growth trees. Scattered, irregular patches of trees attacked by dwarf mistletoe occur on a fifth or more of the forest area (11). During their development these patches have been normally stocked with pines but, since mistletoe distinctively stunts growth rather than kills, the trees are older and have been less productive than their size would indicate.

Before the arrival of fire control, (3) heat from repeated ground fires pruned back mistletoe-infected branches in the lower crowns limiting the mistletoe plants to a sometimes inconspicuous presence high in the forest canopy. With the coming of fire control and timber harvest, the forest floor has become occupied by stands of pine saplings, usually dense, which offer a good start on production of the next forest crop. However, in the mistletoe patches these saplings often become heavily infected and questions arise as to (i) whether they can be carried forward to merchantable size without suffering serious economic loss of growth (1, 2), and (ii) whether they should be treated to control the mistletoe (4, 5, 10, 15) or should be destroyed and a new stand established.

Many physical and biological factors influence the extent to which dwarf mistletoe will damage its host. Two previously unreported factors concerning host susceptibility are presented here.

In an earlier test of the resistance of several grafted pine clones to mistletoe, some of the lot of nursery-run seedlings used as rootstocks were included in the test as controls. The seedlings proved even more susceptible than members of clones selected for high susceptibility (13). All trees were roughly comparable in size (17) and received comparable amounts of mistletoe seed. Consequently the question arose as to whether or not the difference in susceptibility between the seedlings and the susceptible scions resulted from the difference in age, since the scions were derived from trees that were possibly 50 yr old. Among the seedlings, differences also were noted in the amount of damage suffered from infection. The most damaged trees were not always those with the most infections (12) suggesting that ponderosa pine shows differential susceptibility to both infection and damage from infection.

MATERIALS AND METHODS.—In 1965, scions from: (i) 3-yr-old pine seedlings, (ii) trees aged 4, 9, and 15 yr in plantations, and (iii) an "even-aged" natural pine stand around 40 yr old, were side-grafted to potted 3-yr nursery stock. Each age group included scions from five trees. In November of 1966, the grafted trees were outplanted, equally spaced in three randomized blocks of 50 trees each in a recently cleared area on the southwest side of Pringle Butte, Deschutes County, Oregon.

An attempt was made to include 10 trees of each age group (treatment), randomized by source, in each block. This was not entirely possible because of variations in grafting success and, later in the field, mortality resulting from *Armillaria* attack and a misplaced herbicide application. Where mistletoe plants were found on sprayed trees they were included in the data even though the trees had died.

The trees were inoculated immediately after planting, and again the following autumn, with mistletoe seed collected nearby. Mistletoe seeds adhering to paper squares cut from the walls of seed collection bags (14) were transferred to the 1- and 2-yr-old needles of major shoots of the test trees by gently rotating the paper squares against the branch tips. Seven to 15 (usually 10-12) seeds were deposited per tree, in positions comparable to those resulting from natural mistletoe seed dispersal.

RESULTS.—In 1972, 5 years after the last inoculation, mistletoe plants were counted and tabulated (Table 1). The number of mistletoe plants decreased progressively with increasing physiological age of the supporting trees. A multiple-range test (16) based on analysis of variance showed significant differences between means for all ages except for members of chronologically adjacent pairs.

Inspection of Table 1 suggests that susceptibility is a negative exponential function of tree age. To predict the

TABLE 1. Number of mistletoe plants appearing on small pines developed from seedlings grafted with scions from trees of different ages

Age progenitor trees	Replication 1	2	3	Mean[z]
3	28[y]	33	22	28 a
4	10	36	24	23 ab
9	15	22	10	16 bc
15	6	14	9	10 cd
40	0	1	1	1 d

[y]Number of mistletoe plants developing from roughly 440 seeds on 10 trees.

[z]Means followed by different letters are significantly different, $P = 0.05$.

number of infections from these values a curve represented by the equation

$$\hat{I} = a\,e^{b\,A}$$

was fitted to the data, where I is the predicted number of mistletoe plants, A is the physiological age of the host and a and b are parameters estimated by an iterative regression analysis (least squares) (Fig. 1). In this case a and b are 34.844 and −0.88 respectively.

Evidence of susceptibility to damage in contrast to susceptibility to infection (12) is illustrated in Fig. 2. The figure shows two common types of host response to mistletoe infection in 85-yr-old trees. Tree A bears around 100 mistletoe plants, but in spite of this heavy infestation and of strong competition from the surrounding stand, the tree is continuing to grow at nearly the average rate of surrounding healthy trees. Thus, tree A is extremely

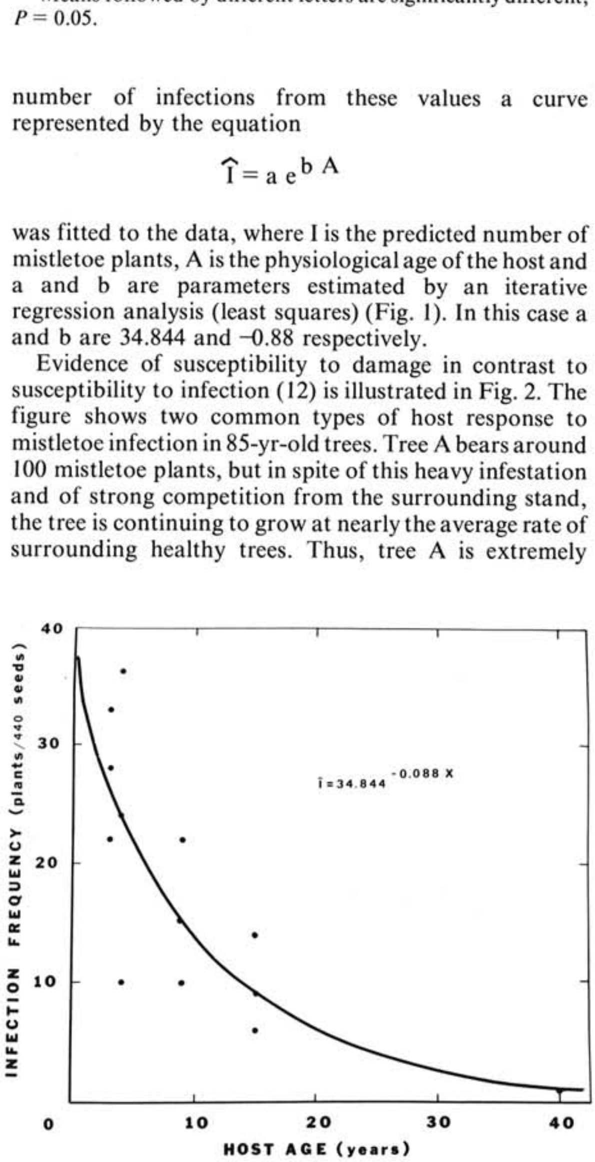

Fig. 1. Regression of infection frequency on host age. Host age is the approximate age of the progenitors of the grafted test trees in each of the five age groups (3, 4, 9, 15, and 40 yr).

susceptible to infection but quite resistant to damage. Tree B by contrast, while supporting only about 27 mistletoe plants, bears greatly shortened, yellow needles and has nearly ceased growth in height. Susceptibility of this tree to infection is uncertain, but it is highly susceptible to damage. In spite of the fact that it has always been relatively open-grown, it may be expected to die fairly soon as occurred in tree C, a somewhat comparable (120-yr-old) tree nearby.

While trees of both types A and B are important to forest operations most trees in a stand are much less susceptible than A and B to both infection and damage.

DISCUSSION.—The data show a marked reduction in susceptibility to dwarf mistletoe as young pines increase in age from 3-40 yr. As long as infection sites are available on pine shoots, the position of the curve in Fig. 1, above the X-axis, will be determined by the amount of mistletoe seed. With more seed, the response of the trees to infection in relation to their age might reasonably be expected to continue beyond the limits of the data at 40 yr. However, since only two infections were obtained on the 40-yr-old trees, the inoculation rate appears to be near the critical minimum for this age at the test location. From the apparent slope of the curve as it approaches age 40, one would not expect great change in infection rate beyond about tree age 50. At the other end of the curve D. M. Knudsen (*personal communication*), working with 1-yr-old ponderosa pine seedlings in growth chambers, found that nearly every healthy mistletoe seedling became established on the host.

It is most unlikely that the response in Fig. 1 should result from susceptibility differences associated with source of the scions. All progenitor sources tested except the 40-yr-old group had the extreme diversity characteristic of trees grown from commercial, uncertified seed. Diversity, in fact, is such a characteristic feature of ponderosa pine that it seems impossible that resistance to mistletoe, a very rare trait, would be common to the 40-yr-old progenitors.

Timber stand improvements in ponderosa pine, including treatment for mistletoe control (4, 5), usually are applied in stands of the upper ages of the range studied here, and older. On the basis of host susceptibility, one would expect the rate of mistletoe increase per unit of exposed stem to be slower after treatment than before.

The rate of mistletoe increase during early years of stand development may not be a good indicator of the increase to be expected in stands 50 or more yr old following treatment for mistletoe control, because it fails to consider increased resistance to infection that develops with increasing tree age. This situation should be borne in mind with others when identifying stands to be treated for mistletoe control. Susceptibility characteristics of older trees also should receive attention when planning timber stand improvement work.

The effect on host function of anatomical and physiological disturbances of tissues invaded by dwarf mistletoe is unsettled (7, 8). Field observations of trees such as those in Fig. 2, indicate that damage is closely related to the proportionate lineal extent of branch invaded by the endophytic system of the mistletoe.

All the mistletoe plants in tree type A cause short, abruptly fusiform swellings. They are often heavily

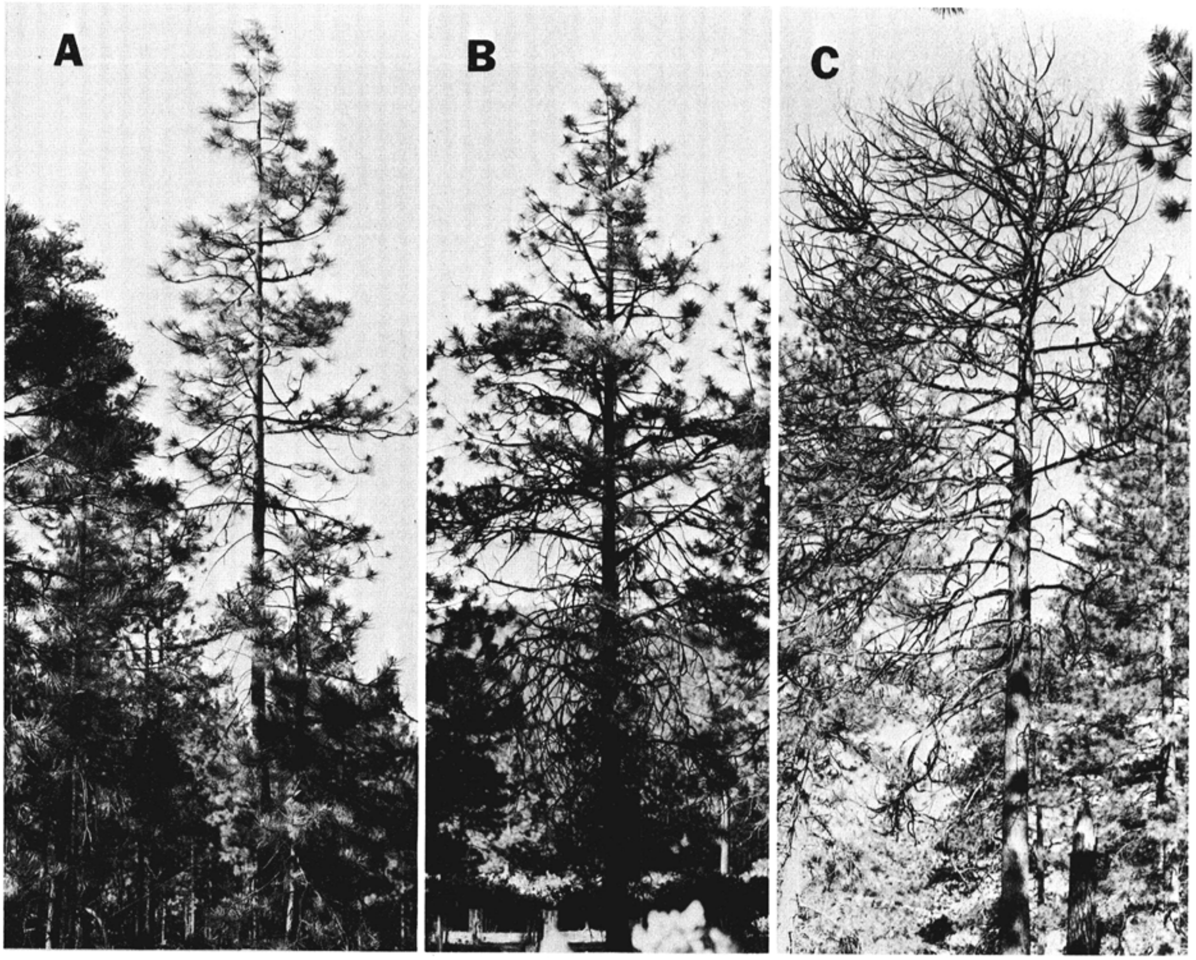

Fig. 2-(A to C). Ponderosa pines showing symptoms of extreme susceptibility to dwarf mistletoe. **A)** An 85-yr-old tree highly susceptible to infection but resistant to damage. In spite of 103 mistletoe plants on this tree, only a small proportion of the total branch length is disturbed. **B)** An 85-yr-old tree in which endophytic development of only 27 mistletoe plants has invaded most of the crown, severely affecting the health and growth of the tree. **C)** A tree of the same general type as B, killed prematurely by dwarf mistletoe.

covered with mistletoe shoots. In even the oldest swellings, internal mistletoe extends only a few centimeters along the branch and only a proportionately small part of the total branch length is invaded. There is almost no tendency to form highly branched mistletoe brooms.

In tree type B, the mistletoe endophytic system apparently spreads so extensively that even a few plants result in invasion of much of the crown framework. Individual branches are strongly swollen, long, and tapering, often from base to tip. Branches thus affected have not been studied histologically, but they appear to have all the gross anatomical features of the anisophasic parasitic habit (9). Mistletoe shoots are infrequent along these branches. Host foliage becomes short and yellow. Little of the crown escapes the direct damaging impact of the parasite on branch tissues. While poorly formed brooms develop to some degree, the trees usually die before reaching the extent of broom development discussed by Kuijt (9).

Most individuals are in an intermediate susceptibility range with regard to infection and possibly also to damage. Trees of type A and B discussed here are usually in the minority, but since both contribute to premature death, they should be recognized and removed during stand treatment. The appearance of these trees should not be allowed to prejudice decisions as to stand value; the importance of conspicuously susceptible trees should be weighed according to their frequency in the total stand.

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