edge of the Great Basin, the canyon country of the Colorado River, and the mountains south of the Colorado Plateau. Populations containing the 1-needled trees of the mountains south of the Colorado Plateau, recently described as P. edulis Engelm. var. fallax Little, are shown to exhibit the same pattern of variation as populations in more northerly areas where hybridization has occurred. It is therefore suggested that these trees be retained under the name P. *monophylla*.

Key words: Natural hybridization, introgression, geobotany, paleobotany, evolution.

Zusammenfassung

Natürliche Bastardierung zwischen Pinus edulis und P. monophylla wurde früher schon vermutet. In der vorliegenden Publikation benutzte man die Häufigkeit einnadliger Kurztriebe als Hauptmerkmal, um ein Vorhandensein von Hybridisation nachzuweisen. Es ließ sich der Schluß ziehen, daß sich diese Hybridisation großräumig in 3 Zonen ereignet hat: Ostteil des Great Basin, im Canyon-Gebiet des Colorado-Flusses und in den Gebirgen südlich des Colorado-Plateaus. Die einnadelige Bäume enthaltenden Populationen der letztgenannten Zone, die kürzlich als P. edulis var. fallax beschrieben worden waren, hatten dasselbe Variationsmuster wie diejenigen in nördlicheren Gebieten, wo Hybridisierung aufgetreten ist. Es wird deshalb vorgeschlagen, daß auch diese Bäume den Namen Pinus monophylla behalten sollten.

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Resistance of Ponderosa Pine to Dwarf Mistletoe

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Improvement of genetic resistance is receiving increasing attention as a means of controlling forest diseases (Gerhold et al. 1966, U. S. Forest Serv. 1972, Bingham, Hoff, and McDonald 1971). The procedures are applicable especially to introduced diseases where tree hosts lack the resistance that naturally evolves from long association of host and parasite and to native diseases where intensified silviculture has greatly aggravated damage from organisms that are relatively innocuous in the natural forest. A less common situation in which improvement of resistance is appropriate is the native disease in its natural environment where, for one reason or another, a high level of resistance has failed to develop. The dwarf mistletoes (Arceuthobium spp.) are good examples of this condition.

Since dwarf mistletoes are currently the most destructive pathogens in the coniferous forests of western North America (Childs and Shea 1967) it may appear surprising that no effort is being made to improve resistance to these parasites. This situation results from the rather common conviction that damage can be effectively controlled by silvicultural methods. This belief disregards the facts that: 1) the availability of resistant stock could greatly improve the silvicultural control program and, 2) investments that would bear much of the cost of improving disease resistance are already being made in improving other characteristics of some of the major susceptible species. Indifference to the possibilities of genetic control in forest practice has greatly limited acquisition of knowledge of the basic biological resources available for genetic control. Every fragment of information to be had would therefore seem potentially useful. This report concerns the availability of genetic resistance in ponderosa pine (Pinus ponderosa Laws.) to western dwarf mistletoe (Arceuthobium *campylopodum* Engel.).

Problems in identifying resistant trees

The first step to improve disease resistance usually involves a search for sources of genes for resistance. Only part of the pine forest is available for this purpose because

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dwarf mistletoe occurs locally as patches of various sizes scattered through the otherwise mistletoe free stands. The significance of these patches will be considered later in the paper. Within many of the patches damage is severe enough to be convincing that selection pressure is real. Initial observation of trees small enough to be effectively examined (10 M or less) may give the impression that resistance is common, because trees with all degrees of infection — from no plants to 100 or more — are found, usually in roughly equal numbers. These trees appear to represent, and in fact may represent, varying degrees of heritable resistance or susceptibility. However, analytical examination usually discloses that the number of plants on a given tree is more likely to be a function of: 1) size and density of the crown of the target tree (Wicker and Shaw 1967), 2) abundance of mistletoe seed, 3) location of the seed source relative to the target tree, 4) screening effects among the trees (Hawksworth 1961) and, 5) needle and branch characteristics, than of genetic resistance. These are all features that change with time and may be modified by influences of site, topography and weather. In order to display resistance and thus be recognizable, a tree must have been hit by mistletoe seeds often enough to have become abundantly infected had it been a susceptible individual. This high level of seed interception does not always occur even in heavily infected patches. Detection of trees sufficiently resistant to appear useful in a breeding program therefore presents a challenge (Hawksworth 1961, Roth 1966). Very infrequently, trees are found with few mistletoe plants, or none, under circumstances where only genetic resistance seems adequately to explain their health.

In the writers many years of work on the mistletoe problem trees that are promising for resistance have never been discovered as the result of deliberate search. Most often they have been chanced upon in the course of critical examination of young stands for other purposes. The following test shows the resistance performance of seven such trees.

Establishment of the test

Scions of "candidate" trees were side-grafted (Bingham, Squillace and Duffield 1953, Roth 1954) to 3 year old pine nursery stock ("Deschutes" seed source) in number 10 food cans. Scions of several trees selected because of their high susceptibility also were grafted to serve as controls. The grafts from resistant candidates, the grafted controls, ungrafted seedlings from the same lot as the graft stocks, and a number of seedlings of the *scopulorum* variety of ponderosa pine from Colorado were outplanted at two locations to allow natural inoculation from the mistletoe infected overstory.

The first planting, located on the southwest side of Pringle Butte, Deschutes County, Oregon was laid out as four concentric elipses around the base of a heavily mistletoe-infected old-growth pine. The elipses conformed with the pattern of mistletoe seed dispersal as previously measured. The inner elipse being in the area of heaviest seed fall and the outer in the lightest. Representatives of each of the seven candidate trees and the controls were randomly planted along each elipse. Spacing between trees and between elipses was 1.5 meters.

Location of the candidate trees in the forest is as follows: trees 1 through 6 are on the west side of Pringle Butte and number 7 is on Lookout Mountain 10 kilometers distant. Its exact location is no longer known. Numbers 1—4 are marked as "mistletoe resistant" with embossed aluminium labels. These trees, growing in heavy infestations were selected on the single criterion of freedom from mistletoe at the time of scion collection. Numbers 5 and 6 combined relative freedom from mistletoe with a drooping habit of the small branches and needles, features thought to contribute to reduced infcetion by mistletoe (Roth 1966). However, this growth habit was not retained by the grafted trees when out-planted on the exposed test site. All candidates but number 7 are 3 to 8 meters tall and grow in the suppressed understory. They range from 50 to 80 years old. Number 7, while slightly suppressed by a nearby old-growth stand is a 25 meter co-dominant member of an even-aged stand approximately 100 years old.

The number of trees tested varied among the candidates as a consequence of differing numbers of scions available and variations in success of grafting. Data concerning some clones are very limited because of loss through logging damage to trees in a replicate randomized block planting at another location on the forest.

Inoculations

Mistletoe plants in the overstory pine, intended to serve as a source of seed for inoculation, cast as many as 200 seeds per square meter on part of the planting area the year before the test. However, few seeds have been produced since and in order to insure adequate inoculation of the test trees it became necessary to hand inoculate with seed freshly collected in the vicinity.

As long as the test trees were fairly small, they were inoculated annually by distributing 7—15 seeds as naturally as possible over the new and 1 year-old needles of each shoot. This was accomplished by gently wiping and rotating the face of a paper square bearing 10—20 sticky seeds against needles of the shoot tip. Seeds transferred in this random manner were later moved by fall rains into positions more suitable for infection, or were washed off. This is the natural process (Roth 1959). Annual inoculation was discontinued after 5 years. However, existing mistletoe plants in the plantation, resulting from earlier inoculations, together with the few active plants in the overstory tree failed to provide adequate inoculum to sustain a high rate of infection and subsequent inoculations were required at about four year intervals. In all, inoculation of these trees has been heavy. The procedures placed more seeds on each branch and each tree than would normally have occurred in the most heavily infected natural stands.

Development of infections

While a few mistletoe plants were noted as early as the second year following inoculation the rate of plant establishment relative to seed deposit seemed very low. This effect later proved to be much more apparent than real because of under appreciation of the high attrition rate from natural causes that regularly occurs to mistletoe prior to seedling establishment. The rate of plant accumulation ultimately proved to be quite high and enough plants developed to show not only clear differences in resistance to infection among the test trees but also in susceptibility to damage (Roth, 1971).

Frequency of infection varied somewhat among the test trees independently of parentage. Most of this was traceable to differences in tree size during the third to fifth years of inoculation. Larger trees presented more branches for inoculation and consequently received more seed. Because of these differences and the small and unequal number of trees the data are poorly suited to statistical analysis. Significant resistance should be inferred for a candidate only where infections are minimal or absent.

Table 1. — Number of mistletoe plants developing on grafted pines and on seedlings interplanted as controls. Progenitors of the grafts ("candidates") were selected for mistletoe resistance.

Test Clones	Number of Trees	Mean Tree Height	Total plants on all trees	Range among individual trees	Average plants per tree
		cm		*number*	
Resistant clone 1	13	62	0	0—0	0.0
Resistant clone 2	8	66	11	0—4	1.4
Resistant clone 3	5	66	1	0—1	0.2
Resistant clone 4	4	70	0	0—0	0.0
Resistant clone 5	5	88	18	0—10	3.6
Resistant clone 6	4	80	20	4—8	5.0
Resistant clone 7	3	51	1	0—1	0.3
Susceptible grafts	9	63	55	0—16	6.1
Deschutes nursery stock	27	84	433	6—43	16.0
Colorado nursery stock	10	77	134	2—32	13.4

As seen in *Table 1,* each of the resistant clones averaged fewer plants per tree than either the seedling or grafted controls. However, resistant clone 6 with an average of 5 plants per tree was not significantly better than the susceptible grafts with 6.1 plants. The same is true of clone 5 and also of the small difference between clones 5 and 6. Clone 2, on the basis of 8 trees, with only 1.4 plants per tree and none heavily infected, certainly is resistant, but probably is not good enough to include in a breeding program unless its resistance should be particularly heritable.

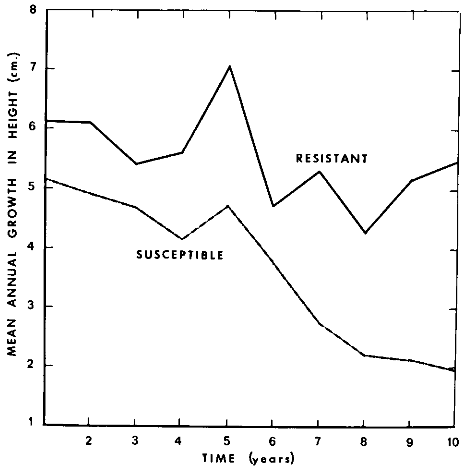

Figure 1. — Mean annual growth in height of clonal members from candidates 1, 3, 4 and 7, compared with susceptible controls and with nursery stock of "Deschutes" and "Colorado" seed sources.

In *Figure 1* mean annual growth in height of resistant selections 1, 3, 4 and 7 is compared with annual means for the susceptible controls and the poor performing clones 5 and 6 combined. Growth is conspicuously superior in the resistant trees.

After fourteen years of testing, members of each of three clones bore a total of only one or a few mistletoe plants and members of two clones bore none. However candidate trees represented by test grafts of the latter two are not immune. One and two mistletoe plants respectively have developed on them over the last two decades. Candidate one, now more than seven m. tall, grows with its branches intermixed with surrounding trees so severely damaged by mitletoe that all are declining and many have been killed. Clearly, this is a superior tree. Subsequent to starting this test an apparently immune tree has been found.2)

Comparison of the grafted trees as a group with the seedlings is of interest. Whether of Deschutes or Colorado origin, these seedlings could reasonably be expected to show the complete range of reaction since they were grown from commercial lots of open pollinated seed. Notably, they became even more heavily infected than the grafted, susceptible controls which had been selected for extreme field susceptibility. Since all of the scion material came from trees at least 50 years old, the differential response between the two age groups suggests the existence of juvenile susceptibility in the seedlings (Roth, 1974). However, in spite of their generally high susceptibility differential resistance appears among the seedlings as well as among the older trees. The Deschutes seedlings, which were very uniformly inoculated, ranged in infection frequency from six to 43 mistletoe plants per tree. Most of the 27 seedlings (with 11—21 mistletoe plants) clustered close to the mean of 16 however, three seedlings had 30 or more plants and one had 6. The latter probably has considerable resistance, possibly as much as the better of the grafted trees, if the juvenile susceptibility is considered.

Discussion

The above results show that resistance to western dwarf mistletoe occurs in ponderosa pine and that occasionally this may be of high order.

Little is known of the nature of resistance to mistletoe. Roth (1966) has discussed foliar characteristics enabling trees to escape infection.

In this study among the grafted trees, with their more mature shoots as contrasted with the seedlings, only tissues of the current year's growth appear to be regularly infected indicating that anatomical features accompanying shoot differentiation are involved. The differential behavior between the two age groups could reflect either anatomical or physiological influences. Recent examination of

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2) This 12 meter tree, first brought to the author's attention by Mr. Tom Greathouse, stands on the Ochoco National Forest an estimated 15 meters north of the Newsome Creek Road, 402 meters southwest of the road fork to Gibson Spring. Sec. 34, T 17S, R 18E.

numerous mistletoe plants in the early stages of infection has disclosed necrotic host tissues beneath the holdfast in a small number of cases. Since mistletoe is an obligate parasite this necrosis reflects an incompatibility between host and parasite and strengthens the notion that physiological factors also are operating.

Unfortunately the experiment reported here contains no trees among the seedling controls in which seedling scions were grafted to seedling stocks. Such trees would have accounted for the unlikely possibility of an effect of grafting on the probability of becoming infected. This paper suggests that sufficient resistant material exists in wild populations to provide the basis for a breeding program for mistletoe resistance in ponderosa pine. The quality of the trees and the ease with which they may be located will be improved if the searcher remains sensitive to the developmental history of mistletoe in the pine forest.

Over much of its range ponderosa pine develops a climax forest which, except for mistletoe is exceptionally healthy. Most stands originated long ago following catastrophes, probably most often fire, and were essentially even-aged. Today most stands are mature or over-mature, or are remnants of such stands. In great age stand structure becomes variable as groups of young trees fill scattered openings caused by intermittent death of large and ancient trees. Scars on old trees show that ground fires burned through the study area at about 15 year intervals and kept the forest floor free of pine saplings and brush. Unter these conditions turnover of generations has been very slow and, since this mistletoe species primarily reduces growth rather than kills, the generations, in patches of mistletoe infestation have been little shortened by disease.

With the coming of fire control and of continuous timber harvest, even the relatively young forest has become more heterogeneous in age and structure and today an understory of pine saplings grows almost everywhere.

Mistletoe was common in the mature stands but even in the very old was not universal. It occurred in the younger stands only as it slowly invaded where stand edges met infected old-growth, or as spots of infection arose around occasional old infected trees surviving the catastrophe that gave rise to a new stand, or possibly as new introductions by birds or other vectors.

Mistletoe, conspicuous in the understory, occurs in irregular patches varying from a few meters to several kilometers across. Factors other than fire that have controlled the size and shaped the distribution of these patches are poorly known. Certainly limitations on distance of mistletoe seed dispersal have been paramount. At maturity in early autumn the adhesive mistletoe seeds are ejected from explosive single seeded fruits for distances up to 10 meters. During storms they may be blown an additional 20 meters from the most exposed trees but in stands with close canopies they appear to fall almost straight down. The rate of lateral spread is therefore very slow. Birds or some other agent are thought to account for infrequent long distance spread. Selection pressure for resistance to mistletoe is necessarily limited to these patches. As a result of stunting, broom production, branch and tree mortality, the mistletoe patches become trashy, flammable places, highly liable to severe fires that destroy both understory progeny, with whatever mistletoe resistance they may have gained, and the parent trees with their resistance as well (Roth 1966). Areas that burned to the point of stand destruction probably always have reseeded primarily with seed from surrounding, generally susceptible, trees not previously subjected to mistletoe selection pressure.

Tree generations lengthened by many factors, limited spread of the pathogen which restricts selection pressure to small areas, and fire that destroys selected progeny places very stringent limitations on development of resistance. It is not surprising therefore that, even though mistletoes have been present since tertiary times (Hawksworth and Wiens 1972), general mistletoe resistance has not developed.

With removal of fire, which in the past has been the agent controlling mistletoe, from the ponderosa pine forest, control of dwarf mistletoe must rest heavily on silvicultural and management practices. Special opportunities occur to enhance this work by planting stock resistant to dwarf mistletoe.

In spite of the previously stated natural limitations, location of good resistant material is not impossible. It is noteworthy that the five trees that performed either well or very well in the preceeding test included all of the candidates that had been selected on the single criterion of near freedom from mistletoe when growing in a destructive infestation. On this same basis 15 additional trees (marked with metal tags and numbers between 13—20 and 40—50) have been located in study block 7 on the west side of Pringle Butte. All of these have average or better silvicultural quality and in another experiment have been brougth under test for resistance.

Whatever its cause and however great, any degree of resistance in a stand is a useful positive value. As noted earlier, greater damage from mistletoe results from loss of growth than from loss of life. Since growth loss is directly related to frequency of infection (Roth 1971) any reduction in the number of infections as the result of improved resistance will enhance the stand.

Summary

Ponderosa pine is generally susceptible to *A. campylopodum,* apparently departing from the principle that natural forests are not normally liable to serious damage by native pathogens. Limits to the distance of mistletoe seed dispersal which restrict selection to a fractional forest area, loss by fire of progeny with improved resistance, and stand re-establishment with seed from mistletoe free stands possibly account for this anomalous susceptibility. Occasionally, however, trees with useful resistance are found. Their detection is hindered because of unequal exposure to seed sources and by infection variables. Susceptibility to infection and growth responses of clonal progeny of seven such trees are reported. Three clones carried very little mistletoe and two had none. Control clones selected for susceptibility were less heavily infected, than ungrafted nursery stock suggesting a high level of juvenile susceptibility. Extremes of resistance were seen among the 27 equally inoculated seedling controls; 1 tree had six infections while three had more than 30. Others clustered about the mean of 16. Both morphological and physiological factors appear to be involved in resistance.

Key words: Forest disease, *Pinus ponderosa, Arceuthobium.*

Zusammenfassung

Pinus ponderosa ist im allgemeinen für *Arceuthobium campylopodum* (Zwergmistel) anfällig. Die Ausbreitungsmöglichkeiten sind jedoch für Mistelsamen nur begrenzt und beschränken sich auf einzelne Waldgebiete. Fallweise werden auch Bäume mit gewisser Resistenz gefunden. Über die Infektionsanfälligkeit und das Wachstum von 7 Klonen

von solchen Bäumen wird hier berichtet. Auf 3 Klonen fand man nur sehr kleine Misteln und auf 2 Klonen überhaupt keine. Kontroll-Klone, die man auf Anfälligkeit ausgelesen hatte, waren weniger stark infiziert, als ungepfropftes Baumschulmaterial, das eine hohe Jugendanfälligkeit vermuten ließ. Eine extreme Resistenz zeigten 27 in gleicher Weise geimpfte Sämlingskontrollen; ferner hatte 1 Individuum 6 Infektionen und 3 weitere Individuen mehr als 30 Infektionen. Andere bewegten sich im Mittel um 16. Morphologische und physiologische Faktoren spielen bei diesen Resistenzerscheinungen eine Rolle.

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Some unusual seedlings of Eucalyptus; their genetic significance and value in breeding

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Introduction

Seedling characters have been widely used in applied genetics and plant breeding (HASKELL, 1961) to permit early screening and selection from large populations within a limited space. These are particularly important advantages in forest tree species which take a long time to become adult, and occupy much space in experimental fields. The atypical seedling variants reported here were first noticed when germinating in petri dishes in the laboratory seeds collected from individual trees of *Eucalyptus camaldulensis* DEHN. and *E. tereticornis* SM. selected for use in a breeding programme. Similar seedlings were also detected later in duplicate sowings in the nursery of the same seed sources in clay pots containing soil. However, their detection in the latter situation was not as easy as against the white background of the moist filter paper in the petri dish. Therefore, had they been raised only in the nursery, such seedlings could readily have escaped notice. The different unusual seedlings recovered from the various seed sources can be broadly classified into the following four kinds — 1) twins, 2) abnormal seedlings, 3) pleiocotylous seedlings and 4) albino or chlorophyll-deficient seedlings. These are described and their genetic significance and value in breeding are then discussed.

Twin Seedlings

The twin seedlings were of two kinds viz. independent twins and conjointed twins. *Figure 1 A, B* illustrates a pair of independent twins arising from a single seed. One of this pair *(fig. 1, B)* is less robust than its mate *(fig. 1, A)*. The two are however free from and unattached to each other. Conjointed twins on the other hand are organically one from the hypocotyl downwards. They have only one primary root but two stems, each with its cotyledons *(fig. 1, C, D)*. Of two twins recovered of this kind, one had a swollen carrotlike hypocotyl tapering down into the primary root below but branching above into two stems, of which one had two cotyledons whereas the other had three *(fig. 1, C)*. When a batch of 25 seeds were softened by soaking in water and then dissected, one seed was seen to consist of two embryos, one smaller than the other *(fig. 1, E)*. It is from such twin embryos that the independent twin seedlings described above must have arisen and so they are the result of polyembryony which has so far not been recorded in the genus *Eucalyptus*. However, in *Eugenia* and *Syzigium*, two other genera of the same family Myrtaceae, nucellar polyembryony is well known (TIWARY, 1926; JOHNSON, 1936; NARAYANASWAMI & ROY, 1960; and ROY & SAHAI, 1962). The exact origin of the twin embryos in *Eucalyptus* reported here can be ascertained only from detailed embryological studies. However, the fact that they have so far always been found in pairs and not in larger numbers is significant as will be discussed later.

Abnormal seedlings

These were of different kinds characterized by poor formation, malformation or total atrophy of one or more of the three primary organs of the normal seedlings viz. root, hypocotyl and cotyledons. The rootless type illustrated in *fig. 2, A* lacked a primary root and had one of its two coty-

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