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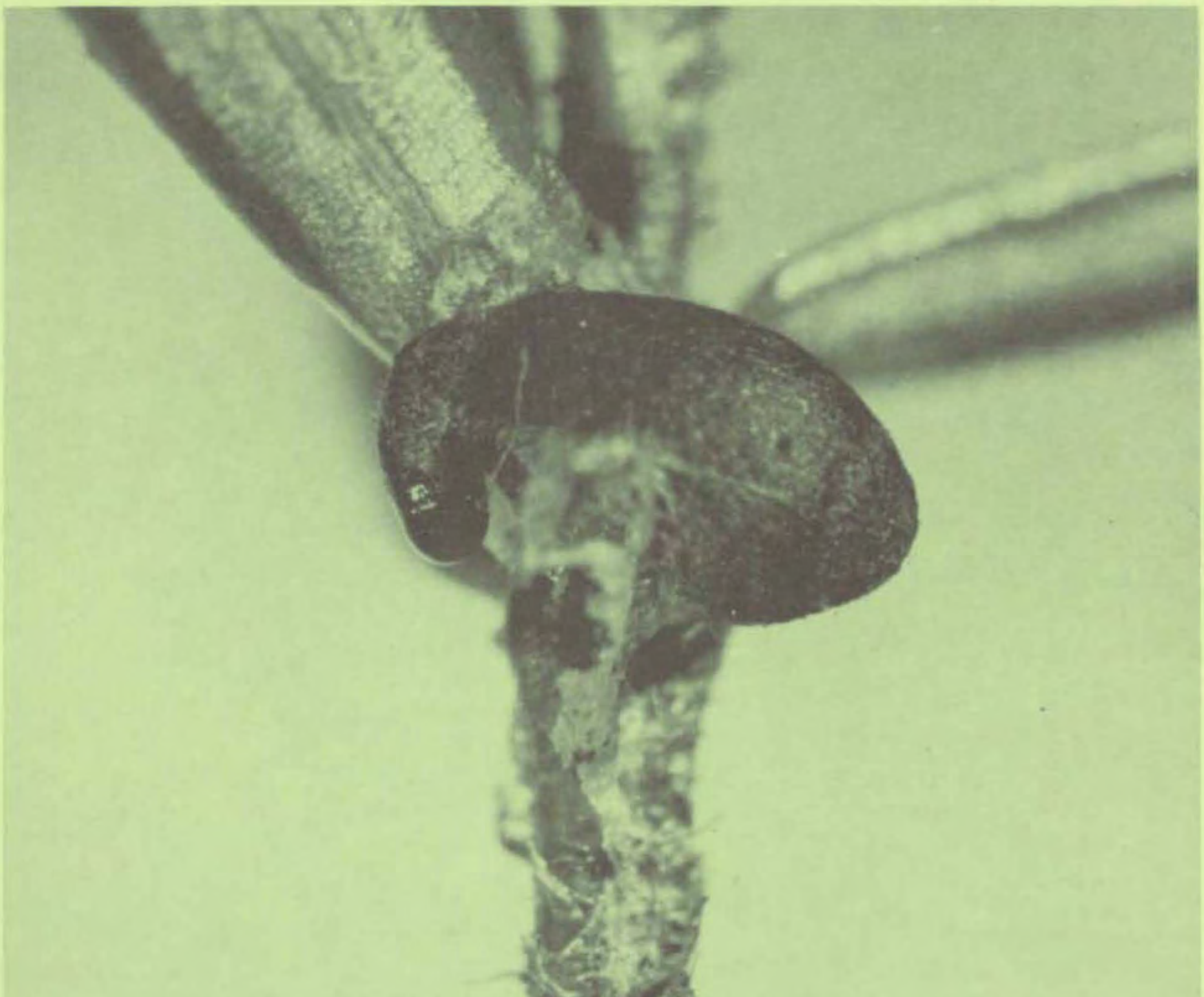
R.B. Smith



Dwarf mistletoe seed germinating on western hemlock branch

INFECTION AND DEVELOPMENT OF DWARF MISTLETOES ON PLANTATION-GROWN TREES IN BRITISH COLUMBIA

by

R. B. Smith

CANADIAN FORESTRY SERVICE

PACIFIC FOREST RESEARCH CENTRE

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ABSTRACT

Artificial inoculations were made on 11 species of conifers in a plantation at Victoria, using four dwarf mistletoe species native to British Columbia, and on two species of conifers, using one dwarf mistletoe species native to Washington. An assessment of the degree of compatibility between host and parasite was made by comparing dwarf mistletoe seed retention and germination, infection percentages, endophytic growth rates and aerial shoot production on the same host species. Resistance mechanisms were shown to operate at various stages and levels in the life cycle of the parasite, ranging from a reduction of seed germination of some dwarf mistletoes on certain hosts to apparent immunity. *Arceuthobium douglasii* was the most host specific, followed in order by *A. americanum*, *A. laricis* and *A. tsugense*. The latter was able to infect species of six genera of conifers. The results pointed to two physiologically differing populations of *A. tsugense*, one on western hemlock (*Tsuga heterophylla*) and the other on shore pine (*Pinus contorta* var. *contorta*).

RÉSUMÉ

Les auteurs inoculèrent artificiellement quatre espèces de Faux-gui indigènes en Colombie-britannique sur 11 espèces de résineux dans une plantation à Victoria; et une espèce de Faux-gui indigène dans l'état de Washington dans deux espèces de résineux. Ils évaluèrent le degré de compatibilité entre l'hôte et le parasite en comparant la rétention des graines de Faux-gui, leur germination, les pourcentages d'infection, les taux de croissance endophytique, et la production de pousses aériennes sur la mêmeespèce-hôte. Il s'avéra que les mécanismes de résistance opéraient à différents stades de développement du parasite, variant d'une réduction de la germination des graines concernant certains Faux-gui à une immunité apparente. *Arceuthobium douglasii* se révéla le plus spécifique quant au choix de l'hôte, suivi en cela par *A. americanum*, *A. laricis* et *A. tsugense*. Ce dernier pouvait infecter des espèces appartenant à six genres de résineux. Selon les résultats obtenus, il existe deux populations physiologiquement différentes d'*A. tsugense*, l'une sur la Pruche de l'Ouest (*Tsuga heterophylla*), l'autre sur le Pin de Murray, variété côtière (*Pinus contorta* var. *contorta*).

INTRODUCTION

Dwarf mistletoes (*Arceuthobium* sp.) are serious pathogens of conifers throughout the Northern Hemisphere, particularly in western North America. The four species occurring in British Columbia cause an estimated loss of more than 150 million cu ft of wood each year, due to increased mortality and decreased growth of infected trees (1).

Field observations and early experimental inoculations (10) showed that individual dwarf mistletoe species were not strictly specific as to host. However, most have a principal host species on which they are particularly infectious. For this reason, it has been often assumed that dwarf mistletoes are host specific. The common names of dwarf mistletoes, e.g., hemlock dwarf mistletoe, larch dwarf mistletoe and lodgepole pine dwarf mistletoe, reflect this view. To assume host-specificity might be dangerous where forest management includes manipulation of stand composition or where non-native species are used. For these reasons, we initiated host-specificity studies involving all dwarf mistletoe species native to British Columbia and many commercially important conifers, excluding the cedars, established in a plantation at Victoria. Seed of one of the dwarf mistletoe species, *Arceuthobium tsugense*, was collected from both western hemlock and shore pine[1/] to determine if there were differences in infection and subsequent development. A limited test was carried out with *A. campylopodum*, a non-native species which parasitizes ponderosa pine in the United States, including stands in Washington, 20 miles from the British Columbia border.

Inoculations were initiated in 1963 in the plantation, and observations and measurements of successful infections continued until 1973. New host records were published as they emerged (5, 6, 7, 8, 9). These and one unpublished record are summarized herein.

This report provides data on dwarf mistletoe seed retention, germination, frequency of infection, branch swelling enlargement, broom formation and aerial shoot, flower and fruit development for different dwarf mistletoes on a number of conifers. The significance of differences in dwarf mistletoe development among the various combinations of host and parasite is discussed

MATERIALS AND METHODS

Eleven species of trees, grown from seed originating from 13 geographic locations, were raised in pots until 3 to 4 years of age. In October 1962, 50 trees of each of the 11 species and two provenances were transplanted to the plantation at an initial spacing of 3 x 3 ft (Table 1).

[1/] Shore pine = coastal lodgepole pine

TABLE 1. Species and geographic origin of trees inoculated

Tree species	Origin
Ponderosa pine (*Pinus ponderosa* Laws.)	British Columbia (south interior)
Lodgepole pine (*Pinus contorta* Dougl. var. *latifolia* Engelm.)	Montana
White pine (*Pinus monticola* Dougl.)	Montana
Engelmann spruce (*Picea engelmannii* Parry)	Montana
Engelmann spruce (*Picea engelmannii* Parry)	British Columbia (south interior)
White spruce (*Picea glauca* (Moench) Voss)	British Columbia (central interior)
Sitka spruce (*Picea sitchensis* (Bong.) Carr.)	British Columbia (coast)
Western larch (*Larix occidentalis* Nutt.)	British Columbia (southeast interior)
Western hemlock (*Tsuga heterophylla* (Raf.) Sarg.)	British Columbia (coast)
Douglas-fir (*Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco)	British Columbia (interior)
Douglas-fir (*Pseudotsuga menziesii* var. *menziesii* (Mirb.) Franco)	British Columbia (coast)
Grand fir (*Abies grandis* (Dougl.) Lindl.)	British Columbia (coast)
Amabilis fir (*Abies amabilis* (Dougl.) Forbes)	British Columbia (coast)

Occasional thinning of noninfected trees was carried out throughout the term of the study.

Dwarf mistletoe seeds to be used in inoculations were collected in September and early October as fruit neared maturation. The exact time varied among the dwarf mistletoe species. Aerial shoots with berries were clipped off and the seeds were discharged into paper bags. Expelled seeds were transferred to petri dishes and stored at 5°C until inoculation time in late October and early November. Moistened seeds were placed on 1- and 2-year-old branches and main-stem segments in 1963, and on 1-year-old branch sections in 1964, 1965 and 1966. The seeds were adjusted so that the radicular end was adjacent to the base of a needle, needle bundle or bud. The natural viscin of the seeds fixed them to the bark surface. The seeds were then left undisturbed over the winter. Except for *A. campylopodum*, equal numbers of seeds of each dwarf mistletoe species or, in the case of *A. tsugense*, each dwarf mistletoe / host category were inoculated on each of the 11 tree species and two provenances for four consecutive years (Table 2). For *A. campylopodum*, only ponderosa pine and western hemlock were inoculated. Generally, 10 seeds were inoculated on each of four trees for every combination of host and dwarf mistletoe each year. The same trees were used in 1963 and 1965 and a separate group in 1964 and 1966. The lower total amount of *A. americanum* seeds was occasioned by a shortage of collected seeds in 1963 and 1965 (Table 2).

TABLE 2. Species and origins of dwarf mistletoe seeds

Dwarf mistletoe (*Arceuthobium*)	Total no. of seeds	Tree species and location[a]
A. americanum Nutt. ex Engelm. (lodgepole pine dwarf mistletoe)	1664	Lodgepole pine, southern interior (Lac le Jeune)
A. campylopodum Engelm. (western dwarf mistletoe)	200[b]	Ponderosa pine, Bend, Oregon
A. douglasii Engelm. (Douglas-fir dwarf mistletoe)	2080	Douglas-fir, southern interior (several locations)
A. laricis (Piper) St. John (larch dwarf mistletoe)	1872	Western larch, southeastern interior (several locations)
	390[c]	Lodgepole pine, southeastern interior (several locations)
	39[d]	White pine, southeastern interior (Castlegar)
A. tsugense (Rosend.) G.N. Jones (hemlock dwarf mistletoe)	2080	Western hemlock, southern coast (Cowichan Lake, Vancouver Island)
	2080	Shore pine, southern coast (Horne Lake, Vancouver Island)

a/All from British Columbia except *A. campylopodum*.
b/Inoculations in 1966 only (50 seeds on each of two ponderosa pine and 50 on each of two western hemlock).
c/Inoculations in 1963 and 1964 only.
d/Inoculations in 1963 only.

Seeds were checked the spring following inoculation for retention over the winter and for germination. Thereafter, observations were made twice each year (spring and fall) for swellings or other indications of infection. Successful infections were examined and their progress was recorded at 2-month intervals. Measurements were made of swelling length and diameter, number of aerial shoots and length of the tallest shoot.

RESULTS

Retention and Germination of Dwarf Mistletoe Seeds

Ninety-one per cent of the seeds of all dwarf mistletoe species remained on the branches after the first winter. Retention varied among dwarf mistletoe species (Table 3) and, more widely, among tree species (Table 4). The greatest retention occurred on the spruces (Engelmann, Sitka and white) and the lowest on ponderosa pine and western larch.

TABLE 3. Retention and germination of dwarf mistletoe seeds

	Dwarf mistletoe species				
	A. americanum	*A. douglasii*	*A. laricis*	*A. tsugense* (from hemlock)	*A. tsugense* (from shore pine)
Retention - %[a]	82	89	91	96	95
Germination - %[b]	32	19	31	45	55

[a]Percentage of seeds retained on the host during the first winter.
[b]Percentage germination of seeds retained over the first winter.

Seed viability differed among dwarf mistletoe species (Table 3), *A. tsugense* obtaining a consistently high percentage of germination. There was also a marked and consistent difference in the percentage of germinants on different tree species (Table 4). The poorest germination occurred on the spruces; the best was on western hemlock, coastal Douglas-fir, ponderosa pine and grand fir. The differences were greatest with the interior mistletoes (*A. americanum*, *A. douglasii* and *A. laricis*) (Fig. 1), and least with the coastal *A. tsugense* from both shore pine and western hemlock (Fig. 2). White pine and lodgepole pine had different effects on germination of the interior and coastal dwarf mistletoes. Germination of interior mistletoes on white pine was 55% of the average for the interior mistletoes, while germination of *A. tsugense* on the same host was 112% of the average for *A. tsugense*. In contrast, on lodgepole pine, the germination of interior dwarf mistletoe seeds was 141% and that of *A. tsugense* was 88% of the average.

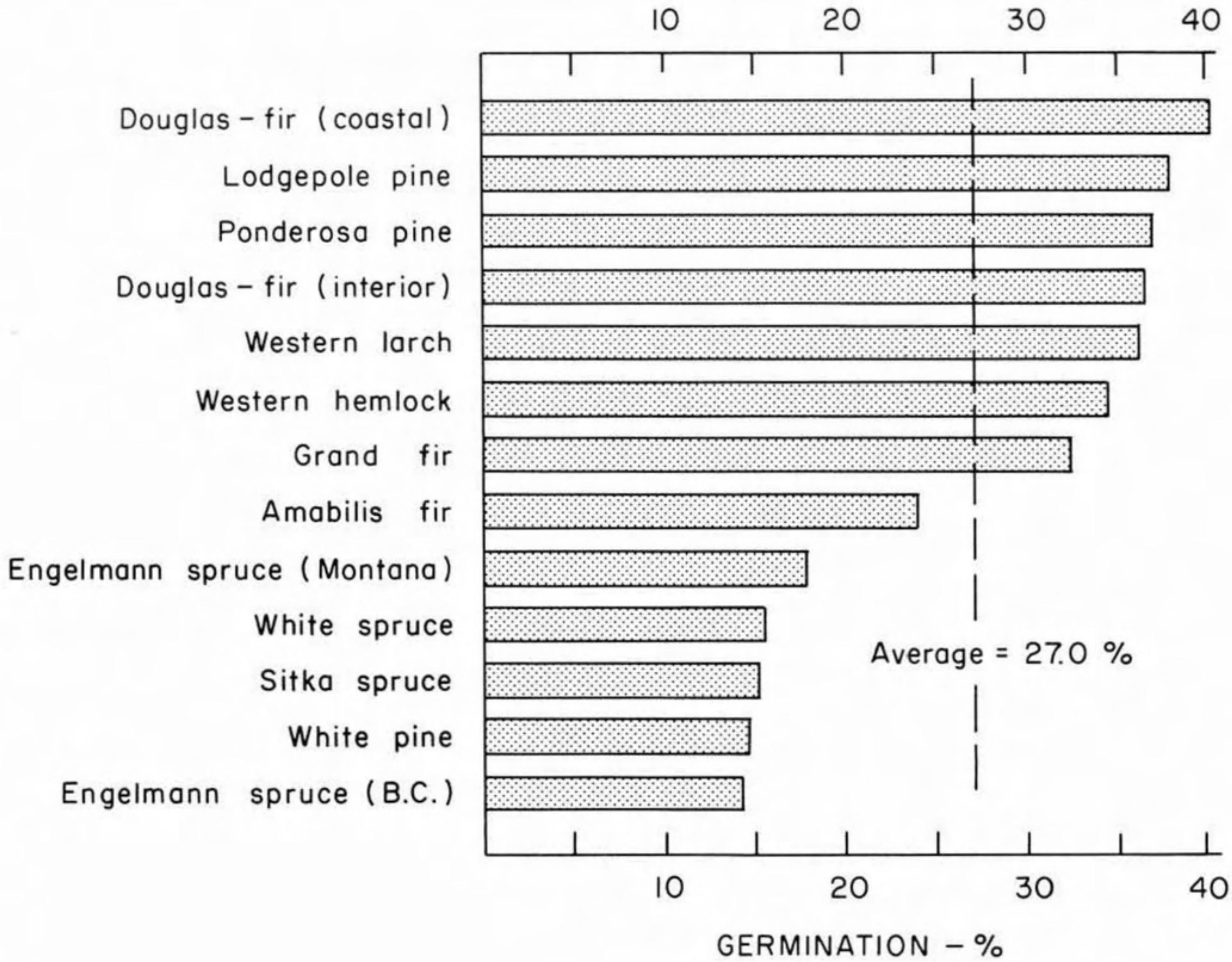


Fig. 1. Average germination for *A. americanum*, *A. douglasii* and *A. laricis* combined on each of the inoculated tree species.

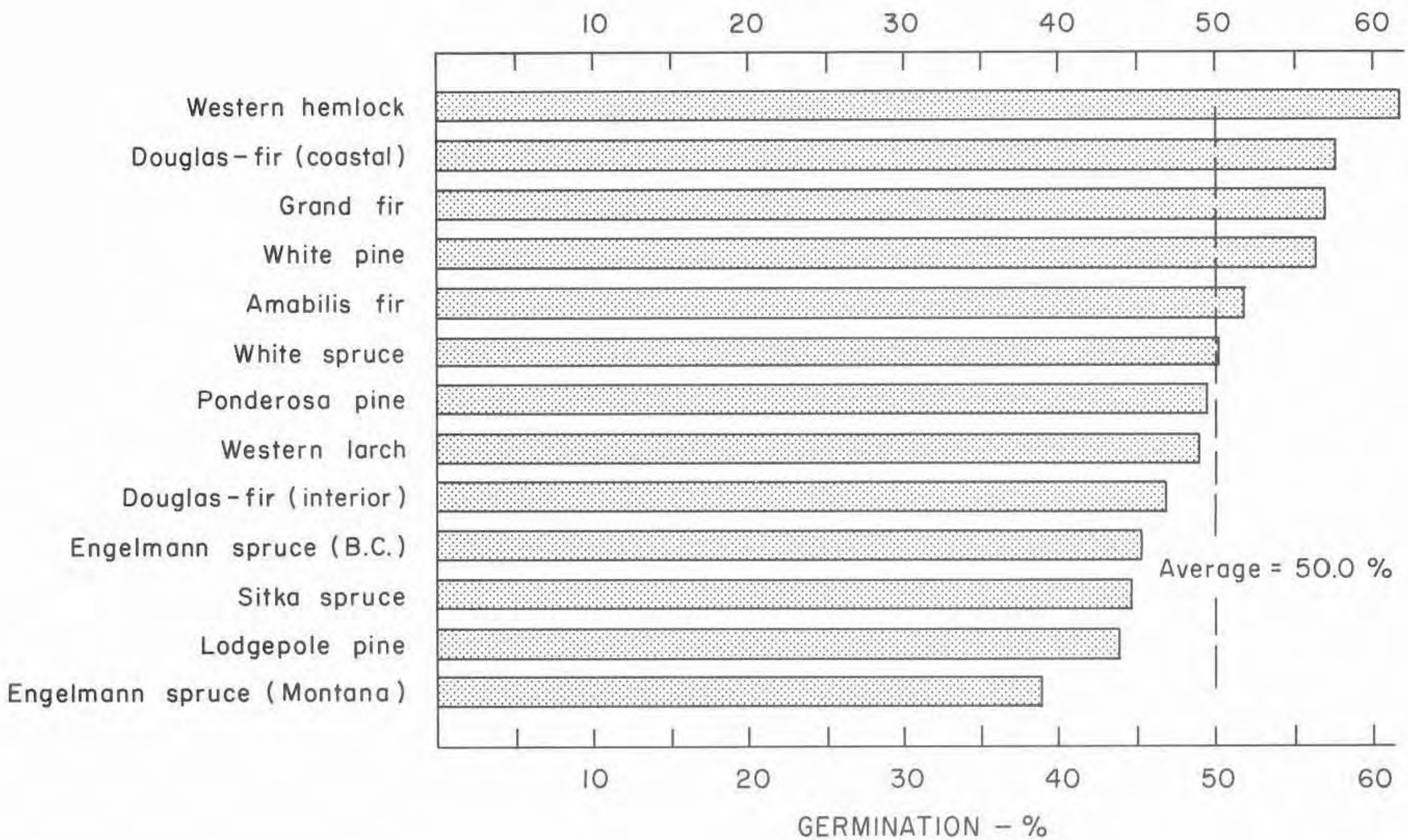


Fig. 2. Average germination for *A. tsugense* from western hemlock and shore pine combined on each of the inoculated tree species.

TABLE 4. Retention and germination of seeds of all dwarf mistletoes on each tree species

	Tree species												
	Ponderosa pine	Lodgepole pine	Western larch	Douglas-fir (interior)	White pine	Engelmann spruce (B.C.)	Engelmann spruce (Montana)	White spruce	Sitka spruce	Grand fir	Douglas-fir (coastal)	Western hemlock	Amabilis fir
Retention - %[a]	77	88	82	91	84	98	98	97	96	93	87	96	92
Germination - %[b]	43	41	42	41	34	28	27	30	28	43	48	46	36

[a] Percentage of seeds retained on the host during the first winter.

[b] Percentage germination of seeds retained over the first winter.

Fig. 3. *A. laricis* on white spruce. Swelling and aerial shoots (X 1).

Fig. 4. *A. tsugense* (from shore pine) on interior Douglas-fir. Swelling and aerial shoots (X 1)

Fig. 5. *A. tsugense* (from western hemlock) on western larch. Swelling and aerial shoots (X 0.7).

Fig. 6. *A. tsugense* (from shore pine) on western hemlock. Note bark cracking on swelling (a) and absence of aerial shoots (X 1).

Fig. 7A. Cross-section of the infected branch illustrated in Fig. 6. Note disruption of cells in third annual ring (a) from the cambium (b) and thickened host ray (c) (X 25).

B. Close-up of thickened host ray (a) and its disintegration in third annual ring (X 125).

Figs. 8-10. *A. tsugense* (from shore pine) on ponderosa pine.

Fig. 8. Twenty months after inoculation. Note stimulation of two intrafascicular buds denoting two separate infections (arrows) (X 1).

Fig. 9. Thirty-two months after inoculation. Note aerial shoots of dwarf mistletoe (a) and stimulated branches (b) (X 0.7).

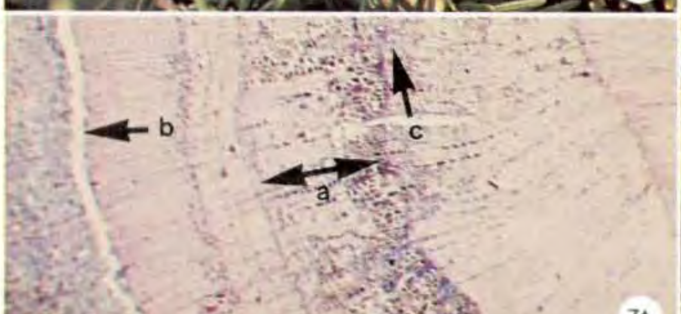
Fig. 10. Fifty-six months after inoculation. Note large non-systemic witches' broom (X 0.2).


3


4


5

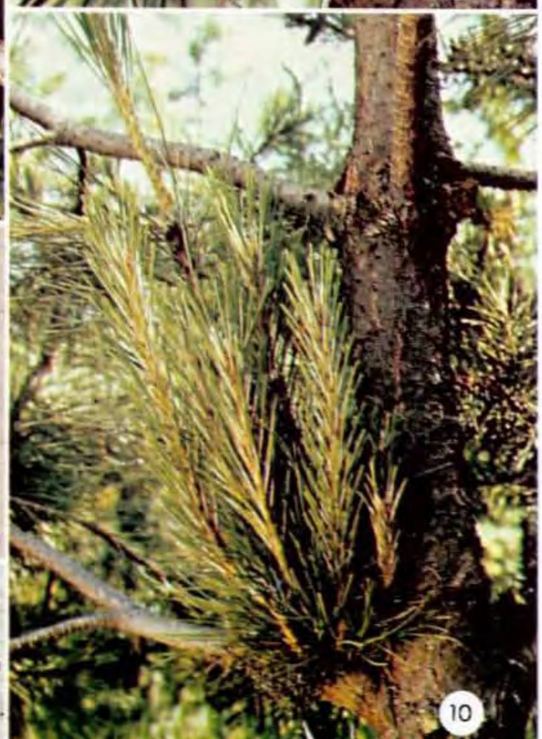

a
6


b
c
a
7A


a
7B


8


b
b
a
a
9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Infections and Aerial Shoots

A. americanum infected lodgepole pine, the principal natural host, and ponderosa pine, an occasional natural host (Table 5)(2). Aerial shoots were produced on all infections (Table 5). Rare natural hosts (2) tested in this study, but not infected, were white and Engelmann spruce and Douglas-fir.

A. campylopodum inoculated on western hemlock and ponderosa pine only infected the latter, a principal host in the United States (2) (Table 5). All infections produced vigorous aerial shoots.

A. douglasii infected interior Douglas-fir, a principal natural host in Canada and the United States, and coastal Douglas-fir, a principal natural host in California and southern Oregon. Other hosts occasionally or rarely infected in nature, but not in this study, were grand fir and Engelmann spruce.

A. laricis successfully established on western larch, lodgepole pine, Engelmann spruce (both origins), white spruce, ponderosa pine and amabilis fir. Western larch is a principal natural host, while lodgepole pine, Engelmann spruce and ponderosa pine are secondary or occasional hosts (2). Infection of amabilis fir was previously reported as a new record (Table 6). Aerial shoots were produced on all but three infections on Engelmann spruce from Montana (Table 5).

White spruce has hitherto not been recorded as a host for *A. laricis*; consequently the infection requires further description. Five infections were obtained from 144 seeds. All five infections produced aerial shoots (Fig. 3) and both of the female infections bore mature fruit. Swellings averaged 82 mm in length 6 years after inoculation. Grand fir and white pine, rare natural hosts (2), were not infected by *A. laricis* in this study.

A. tsugense became established on the greatest number of tree species. These were western hemlock, a principal natural host, amabilis fir and white pine, secondary natural hosts, and grand fir, a rare natural host. In addition, Engelmann spruce, western larch, interior lodgepole pine, white spruce, interior Douglas-fir (Fig. 4) and ponderosa pine (Fig. 8-10), all new host records, were recorded previously (Table 6). Sitka spruce, a rare host in nature, was not infected in this study.

The regularity of shoot production by each dwarf mistletoe varied with the host. In this respect, western larch proved to be a very incompatible host. Only one of 38 infections produced aerial shoots up to 1973. Shoots appeared on this infection (Fig. 5) but were dead by early 1969 (6) and no new shoots appeared until late 1973. Also, in 1973, small new shoots were observed on two other infections on the same tree. The three larch infections which bore aerial shoots were produced by *A. tsugense* from western hemlock. None of the swellings on western larch caused by *A. tsugense* from shore pine produced aerial shoots.

Another very incompatible combination was *A. tsugense* collected

Table 5. Percentages of infection and aerial shoot production resulting from all combinations of dwarf mistletoe and host

Dwarf mistletoe species and host-tree source	Tree species inoculated												
	Ponderosa pine	Lodgepole pine	Western larch	Interior Douglas-fir	White pine	Engelmann spruce (B.C.)	Engelmann spruce (Montana)	White spruce	Sitka spruce	Grand fir	Coastal Douglas-fir	Western hemlock	Amabilis fir
	% a/												
A. americanum (lodgepole pine)	3.9/100.0	12.5/100.0	0/0	0/0	0/0	0/0	0/0	0/0	0/0	0/0	0/0	0/0	0/0
A. campylopodum (ponderosa pine)	15.0/100.0	-/-	-/-	-/-	-/-	-/-	-/-	-/-	-/-	-/-	-/-	0/0	-/-
A. douglasii (interior Douglas-fir)	0/0	0/0	0/0	8.1/100.0	0/0	0/0	0/0	0/0	0/0	0/0	1.3/100.0	0/0	0/0
A. laricis (western larch)	0.7/100.0	6.2/100.0	27.1/100.0	0/0	0/0	2.8/100.0	3.5/40.0	3.5/100.0	0/0	0/0	0/0	0/0	1.4/50.
A. laricis (lodgepole pine)	0/0	0/0	6.7/100.0	0/0	0/0	0/0	0/0	0/0	0/0	0/0	0/0	0/0	0/0
A. laricis (white pine)	0/0	0/0	0/0	0/0	0/0	0/0	0/0	0/0	0/0	0/0	0/0	0/0	0/0
A. tsugense (western hemlock)	1.9/100.0	5.0/100.0	6.9/21.4	0.6/0.0	0/0	8.3/46.1	9.4/73.3	6.0/100.0	0/0	0/0	0/0	22.5/100.0	0.6/100.
A. tsugense (shore pine)	4.4/100.0	13.1/100.0	16.9/0.0	3.1/40.0	3.1/60.0	14.4/69.6	5.6/55.5	8.8/50.0	0/0	1.9/66.7	0/0	0.6/0.0	1.3/50.

a/ ○/○ — upper: % of seeds resulting in infection; lower: % of infections producing aerial shoots

TABLE 6. Summary of new host records for dwarf mistletoes native to British Columbia resulting from artificial inoculations at Victoria, British Columbia

Dwarf mistletoe species	Tree species	Location of inoculation[a]	Literature reference[b]
A. laricis	Amabilis fir	P	9
	White spruce	P	R
A. tsugense	Douglas-fir (interior provenance)	P	8
	Engelmann spruce	P	5
	Lodgepole pine (interior provenance)	G,P	4,R
	Monterey pine (*Pinus radiata* D. Don)	G	7
	Norway spruce (*Picea abies* (L.) Karst)	G	4
	Ponderosa pine	G,P	7,7
	Scots pine (*Pinus sylvestris* L.)	G	7
	Western hemlock (interior provenance)	G	4
	Western larch	P	6
	White spruce	G,P	4,R

[a] P = Plantation; G = Greenhouse

[b] Numbers refer to literature cited at end of this report; R = This report

from shore pine on western hemlock. Only one definite swelling was produced (Fig. 6) and no aerial shoots appeared. A cross-section of this swelling revealed considerable disruption of the xylem in the third annual ring from the cambium, including occluded cells and enlarged rays containing disintegrating dwarf mistletoe sinker elements (Fig. 7A, B). The outside two annual rings appeared normal. In contrast to this abortive type of infection, *A. tsugense* collected from western hemlock produced 36 swellings on western hemlock each with aerial shoots. This represented 22.5% of the seeds used in the inoculations.

Aerial shoot production of *A. tsugense* on the spruces was relatively low, occurring on about 65% of all swellings of this combination (Table 5).

Rate of Enlargement of Branch Swellings

Extension of the endophytic system was estimated by the rate of enlargement of branch swellings, or with systemic infection (*A. douglasii* and *A. americanum*) by both swelling enlargement and the length of systemically infected branches. The following comparisons of growth rates are restricted to local swelling enlargement.

Growth rates were generally highest when a dwarf mistletoe was on its principal host (shown as solid lines in Figs. 11-18). However, exceptionally high growth rates were obtained by A. *tsugense* parasitizing ponderosa pine, an unnatural host (Fig. 14).

There was a marked difference between the rate of growth for A. *tsugense* collected from hemlock and that for A. *tsugense* collected from shore pine. The former grew more rapidly than the latter on western hemlock (Fig. 12), western larch (Fig. 13), ponderosa pine (Fig. 14), interior Douglas-fir (Fig. 15) and the spruces (Fig. 16), and less rapidly than the latter on lodgepole pine (Fig. 11) and amabilis fir (Fig. 17).

Swellings resulting from parasitism by dwarf mistletoes of their principal hosts were generally less globose (high length to width ratio) than those resulting from less common combinations (Table 7). Notable exceptions were swellings caused by A. *tsugense* from western hemlock on larch and A. *americanum* on ponderosa pine. These were less globose than the ones produced on the principal hosts, western hemlock and lodgepole pine, respectively. A. *tsugense* from shore pine generally produced more globose (low length to width ratio) swellings than A. *tsugense* from hemlock; amabilis fir was the only notable exception.

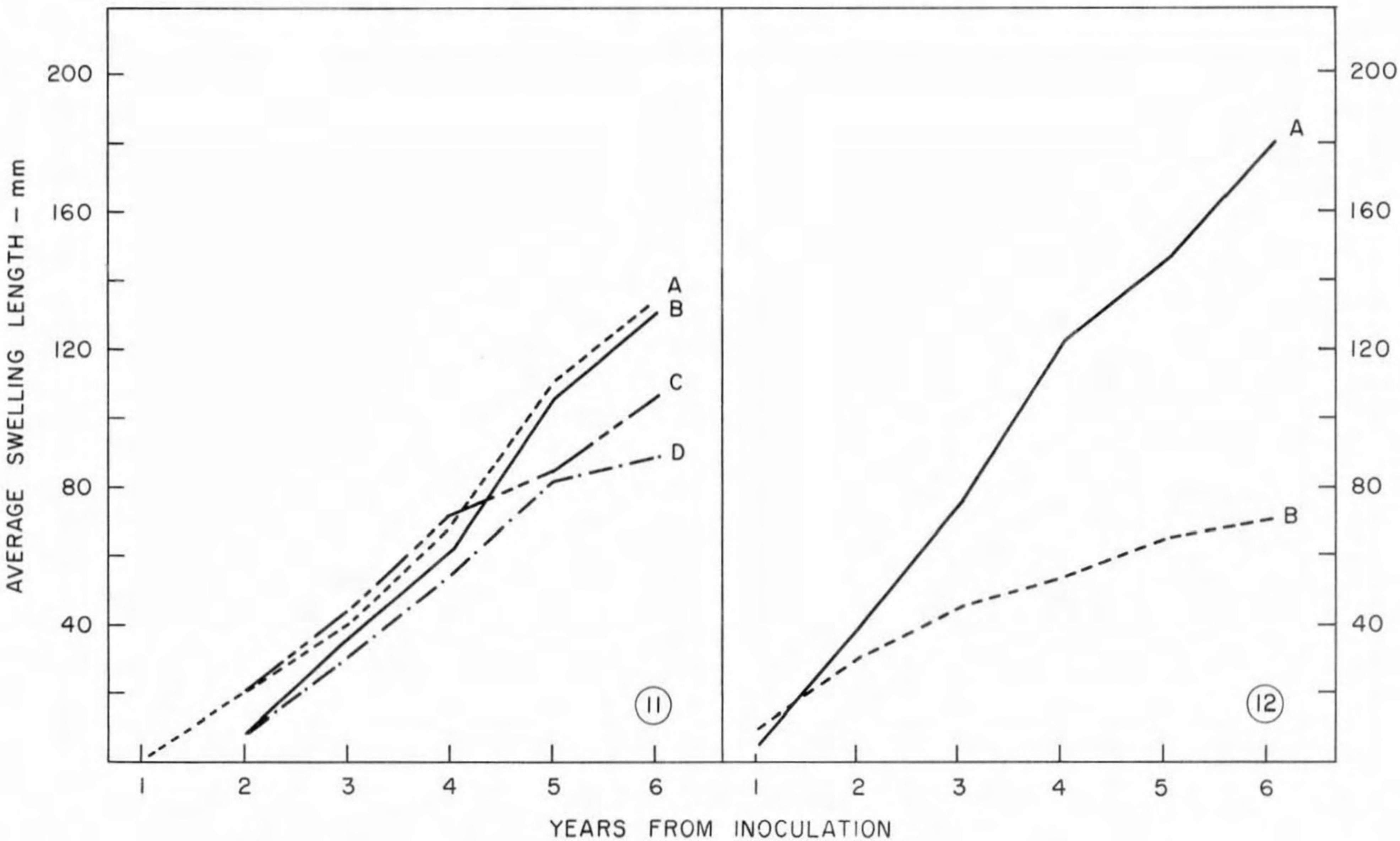
Flower and Fruit Production

Once aerial shoots were produced, flowers developed in almost all cases. For A. *tsugense* and A. *laricis*, fruit maturation followed female flower production normally. Large crops of fruit were produced by A. *tsugense* (from shore pine) on ponderosa and lodgepole pine, A. *tsugense* (from hemlock) on ponderosa pine and western hemlock, A. *laricis* on western larch and A. *campylopodum* on ponderosa pine. No fruit were produced by A. *douglasii* even though female flowers developed on several infections and male flowers on several others. Only one of 10 female A. *americanum* infections had produced fruit up to the last observation in 1973.

Brooming

Excessive branch proliferation (witches' broom formation) was associated with either systemic infection, in which case the mistletoe endophytic system kept pace with branch elongation, or local branch infection, in which case the endophytic system was restricted to the swollen portion of the branch. All combinations of host and dwarf mistletoe produced local infections, while systemic infections were only produced by A. *douglasii* and A. *americanum*. The largest and densest brooms resulted from systemic infection, but local infection by A. *tsugense* on ponderosa pine occasionally resulted in a dense proliferation of branches that closely resembled the systemic type (Figs. 8-10). However, unlike systemic infections, aerial shoots of A. *tsugense* were confined to the visibly swollen portion of the infection.

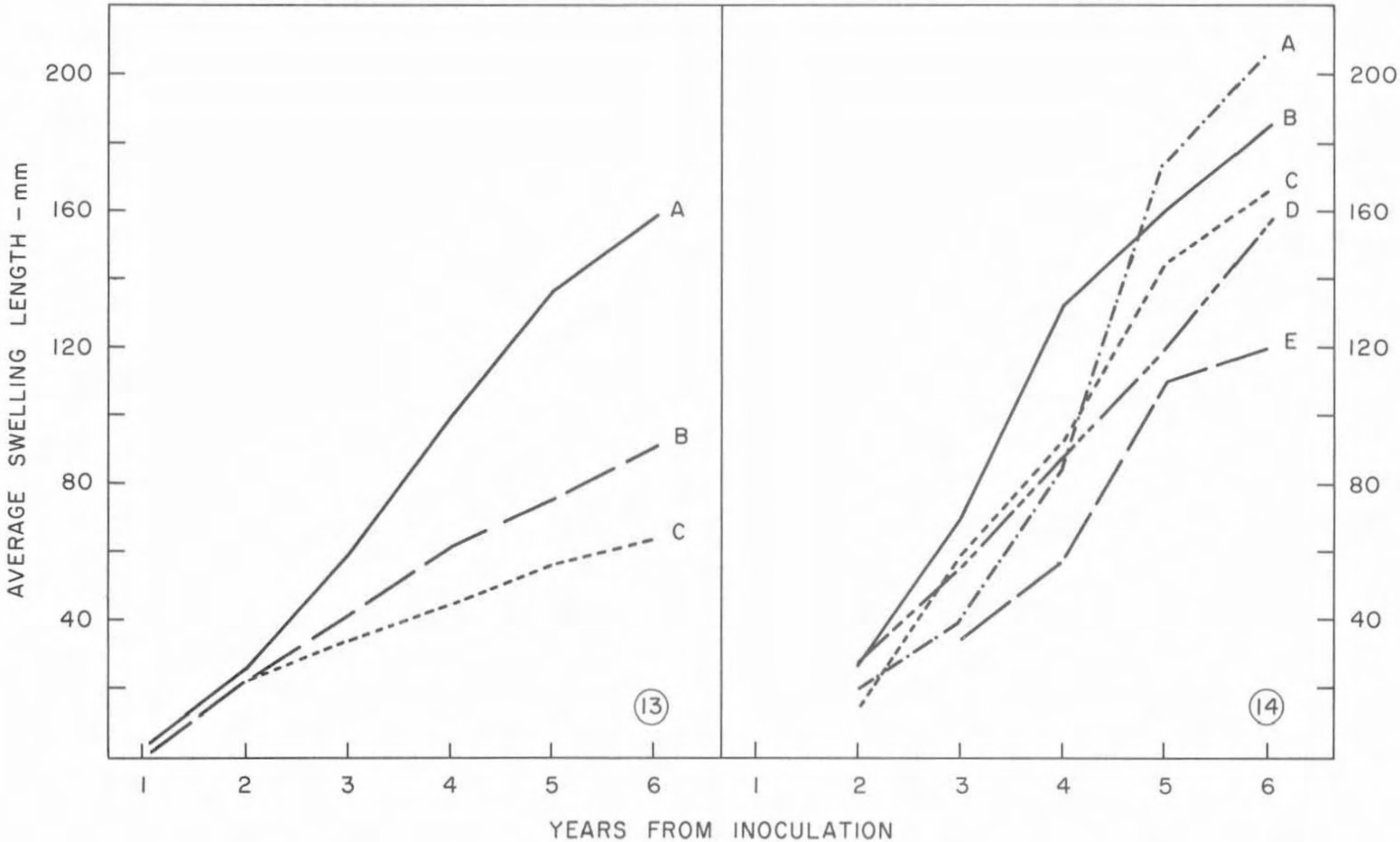
All A. *americanum* infections on ponderosa pine produced systemic brooms, while only a few of the infections on lodgepole pine became systemic. Most A. *douglasii* infections resulted in systemically infected



Figs. 11-12. Rates of swelling enlargement. Combinations of dwarf mistletoes and their principal hosts are shown in solid lines.

Fig. 11. Lodgepole pine: A. A. *tsugense* (from shore pine); B. A. *americanum*; C. A. *tsugense* (from western hemlock); D. A. *laricis*.

Fig. 12. Western hemlock: A. A. *tsugense* (from western hemlock); B. A. *tsugense* (from shore pine).



Figs. 13-14. Rates of swelling enlargement. Combinations of dwarf mistletoes and their principal hosts are shown in solid lines.

Fig. 13. Western larch: A. A. *laricis*; B. A. *tsugense* (from western hemlock); C. A. *tsugense* (from shore pine).

Fig. 14. Ponderosa pine: A. A. *americanum*; B. A. *campylopodum*; C. A. *tsugense* (from western hemlock); D. A. *tsugense* (from shore pine); E. A. *laricis*.

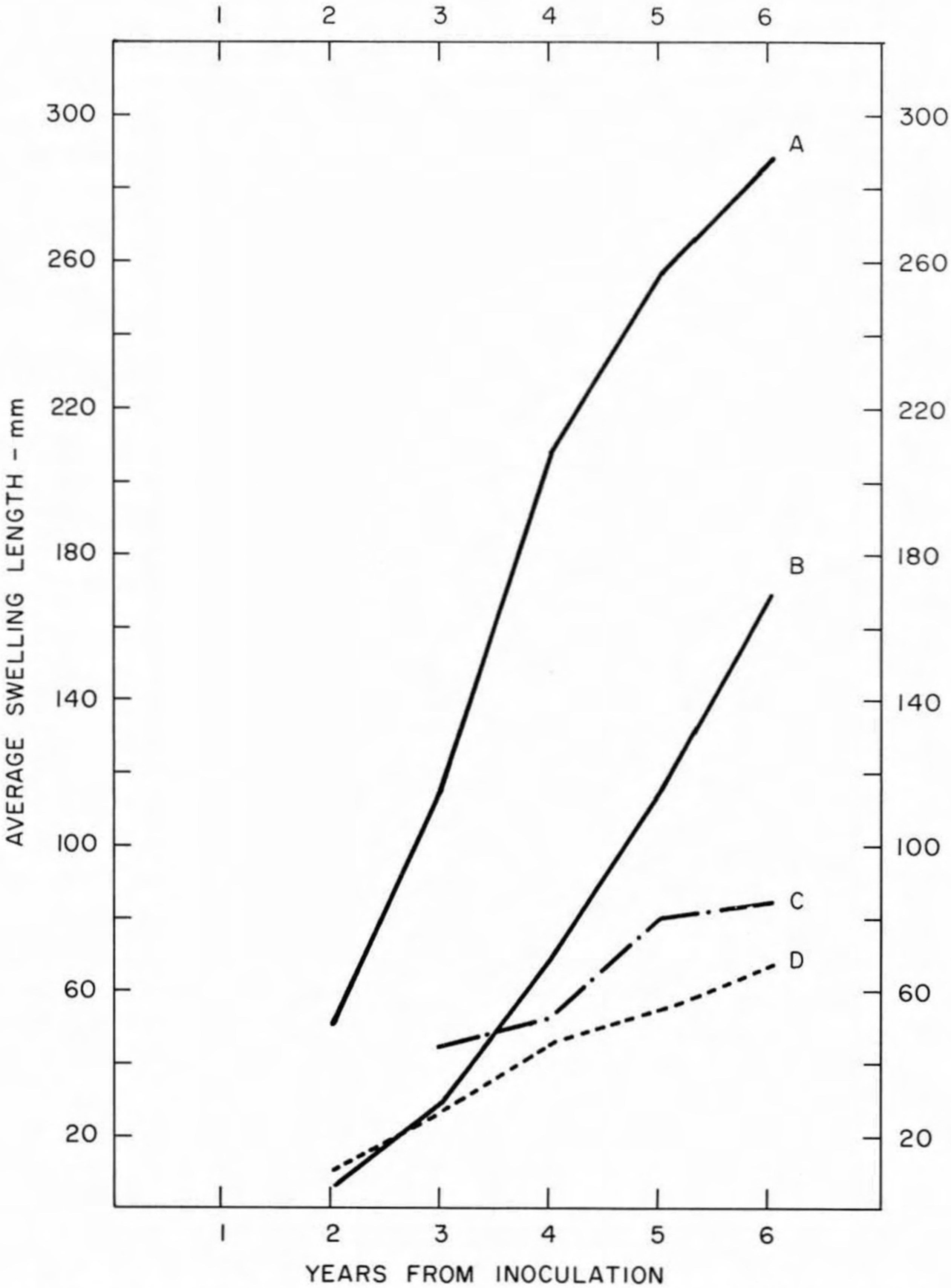
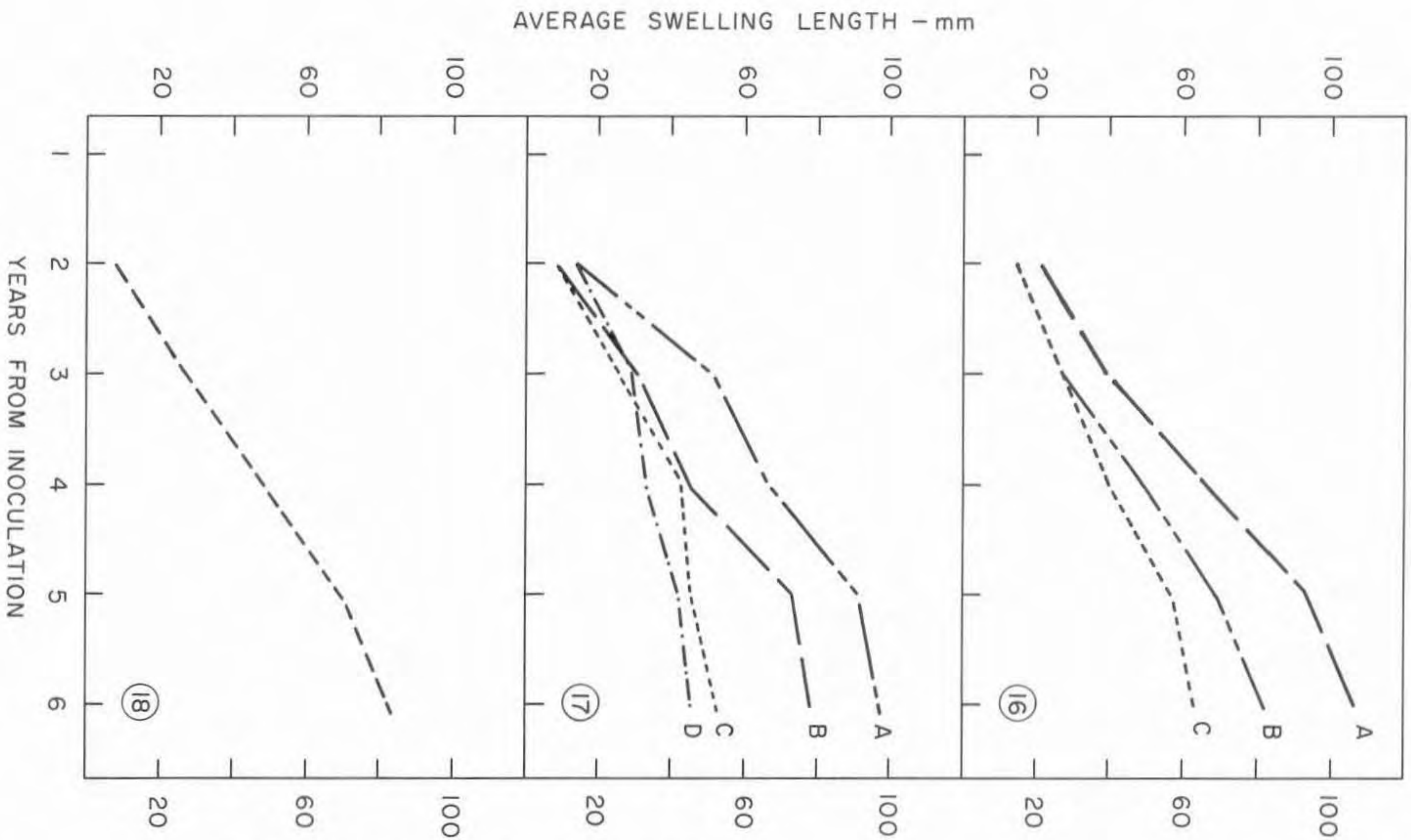


Fig. 15. Rates of swelling enlargement. Combinations of dwarf mistletoes and their principal hosts are shown in solid lines. A. *A. douglasii* on coastal Douglas-fir; B. *A. douglasii* on interior Douglas-fir; C. *A. tsugense* (from western hemlock) on interior Douglas-fir; *A. tsugense* (from shore pine) on interior Douglas-fir.



Figs. 16-18. Rates of swelling enlargement.

Fig. 16. Spruce (all species combined): A. *A. tsugense* (from western hemlock); B. *A. laricis*; C. *A. tsugense* (from shore pine).

Fig. 17. True firs: A. *A. tsugense* (from shore pine) on grand fir; B. *A. tsugense* (from shore pine) on amabilis fir; C. *A. laricis* on amabilis fir; D. *A. tsugense* (from western hemlock) on amabilis fir.

Fig. 18. *A. tsugense* (from shore pine) on white pine.

TABLE 7. Length to width ratios for dwarf mistletoe induced swellings measured 6 years after inoculation[a]

Dwarf mistletoe species	Ponderosa pine	Lodgepole pine	Western larch	Douglas-fir (coast & interior)	White pine	Spruces	Grand fir	Amabilis fir	Western hemlock
A. *americanum*	5.7	5.0	-	-	-	-	-	-	-
A. *campylopodum*	4.5	-	-	-	-	-	-	-	-
A. *douglasii*	-	-	-	6.2	-	-	-	-	-
A. *laricis*	3.9	3.0	6.4	-	-	4.4	-	4.2	-
A. *tsugense* (hemlock)	3.7	3.9	7.2	4.5	-	3.7	-	3.8	6.1
A. *tsugense* (shore pine)	2.9	3.3	4.6	3.4	2.5	2.9	2.1	5.6	6.4

[a] Ratios for combinations of dwarf mistletoe and principal host are underlined

branches. Branches of Douglas-fir systemically infected by *A. douglasii* and those of ponderosa and lodgepole pine systemically infected by *A. americanum* were up to 1 m in length at the time of the final measurement. Some systemic brooms were so dense that observations of aerial shoots and local swelling enlargement became difficult. In one instance, the systemically infected broomed lateral branch of an interior Douglas-fir tree had forced the original leader into a subdominant role.

Several combinations of parasite and host resulted in local swellings without witches' broom formation or without even minor branch proliferation. These were *A. laricis* on lodgepole pine and white spruce, *A. tsugense* (from hemlock) on ponderosa and lodgepole pine and *A. tsugense* (from shore pine) on lodgepole pine, western larch, white pine and grand fir.

DISCUSSION AND CONCLUSIONS

Mechanisms that produce differing degrees of resistance of conifers to dwarf mistletoes operate at several stages in the life cycle of the parasite. The capability of dwarf mistletoe seeds to remain attached to branches over the winter affects the number of chances for infection to occur. Spruces retain a large percentage of seeds as a result of their densely packed needles. Low seed retention on western larch may result in part from its deciduous nature, and on pines, particularly ponderosa, from their open, often drooping foliage. Retardation of germination of interior dwarf mistletoe seeds (*A. laricis*, *A. americanum* and *A. douglasii*) on the spruces was sufficiently consistent over 4 years to point to an inhibitory substance or substances in spruce needle or bark tissue. The depressing effect of white pine on the germination of interior dwarf mistletoe seeds and its neutral or enhancing effect on seeds of *A. tsugense* are indications that there is a variation in response to such inhibition among dwarf mistletoe species.

After germination, resistance may take the form of a low percentage of infection, e.g., *A. laricis* on ponderosa pine and *A. tsugense* on amabilis fir and Douglas-fir. After infection, there may be a low rate of endophytic growth, e.g., *A. tsugense* on larch and Douglas-fir, or a sparse production or complete absence of aerial shoots, e.g., *A. tsugense* on western larch and *A. tsugense* (from shore pine) on western hemlock. Other suggested signs of resistance are swellings with a low length to width ratio, e.g., *A. tsugense* on white pine and the spruces, and the absence of even minor host branch proliferation or brooming, e.g., *A. laricis* on lodgepole pine.

Seven new host records, five involving *A. tsugense*, were obtained from the inoculations. Including studies during the same period on potted trees in a greenhouse (Table 6), a total of eight completely new host records plus the interior provenances of lodgepole pine and western hemlock were obtained for *A. tsugense*. Along with previous field observations, the results of these inoculations allow a rating of the four dwarf mistletoes native to British Columbia on the basis of host specificity. *A. douglasii* is most host specific, followed in order by *A. americanum*, *A. laricis* and *A. tsugense*. Hosts of *A. tsugense* occur within six genera of the family Pinaceae (*Tsuga, Abies, Larix, Picea, Pinus* and *Pseudotsuga*), the highest number of host genera known for any dwarf mistletoe species. The difference between *A. tsugense* and other closely related species, such as *A. laricis*, in terms of hosts is the ability of *A. tsugense* to infect both *Tsuga* and *Pseudotsuga*. It is, in fact, the only dwarf mistletoe known capable of infecting western hemlock.

Objections to these inoculation results might be raised on the basis that many of the hosts and most of the dwarf mistletoes were growing in an unnatural environment, including possible microfloral differences affecting seed viability and radicle growth. The failure to achieve some combinations of host and parasite found in nature may have been the result of an unnatural environment. The absence of fruit on *A. douglasii* plants and the low numbers on *A. americanum* plants probably resulted from an absence or insufficiency of pollinating insects during flowering or a low incidence of pollen sources. Likewise, some of the new host records may have been stimulated by the unnatural environmental conditions. However, I maintain that results of the inoculations indicate when infection can be expected, either when dwarf mistletoe and host are naturally sympatric or when they come in contact as a result of exotic tree establishment. *A. tsugense*, for example, was found to infect Engelmann spruce quite readily in the plantation, indicating that similar infection could be found in nature. It was not surprising, therefore, to receive the first report of *A. tsugense* parasitizing Engelmann spruce in Oregon where the host and parasite are sympatric (5). Infection of Douglas-fir by *A. tsugense* in the plantation spurred a search for the combination in nature. If *A. tsugense* infection does exist in nature on Douglas-fir, it is unlikely to be a serious disease problem or it would have been reported earlier. Much more serious problems might arise from the introduction of exotic tree species in areas of dwarf mistletoe infection. For instance, movement of ponderosa pine into coastal areas in contact with *A. tsugense* should be avoided.

The inoculations provide data on the adaptability of dwarf mistletoes to unnatural climates. *A. americanum, A. campylopodum, A. douglasii* and *A. laricis* all were able to become established and grow vigorously in the plantation well away from their natural habitats. Extensions of their ranges is thus quite possible and accidental introductions must be prevented.

The very low rate of infection of western hemlock by *A. tsugense* collected from shore pine and the lack of aerial shoots when infection does occur suggest that two populations of *A. tsugense* exist in coastal British Columbia with differing physiologies -- one on western hemlock, the other on shore pine. A less plausible explanation is that growth on lodgepole pine imparts to the seed a property which inhibits or represses infection of western hemlock. An absence of or low degree of cross-infection from shore pine to western hemlock in mixed stands was observed earlier (3) in the same area on Vancouver Island from which seeds for these inoculations were collected. Differences in endophytic growth rates of individuals of the two *A. tsugense* populations on the same host species found in this study support the contention of differing physiologies. The reverse, infection of lodgepole pine by *A. tsugense* (from western hemlock) was obtained, but at a rate less than that by *A. tsugense* (from shore pine) on lodgepole pine. The lodgepole pine used in the trials was from an interior origin. Field inoculations and morphological and ecological studies, which should more clearly define these population differences, are currently being conducted in shore pine stands.

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