The Biology of Dwarf Mistletoes (*Arceuthobium* spp.) in Manitoba

by

Jeannie Anne Gilbert

A thesis
presented to the University of Manitoba
in partial fulfillment of the
requirements for the degree of
Master of Science
in
Botany

Winnipeg, Manitoba, 1984

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A thesis submitted to the Faculty of Graduate Studies of the University of Manitoba in partial fulfillment of the requirements of the degree of

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ABSTRACT

Three coniferous species growing in Manitoba are attacked by dwarf mistletoes. Arceuthobium americanum Nutt. ex Engelm. parasitizes Pinus banksiana Lamb., while A. pusillum Pk. occurs on its principal hosts, Picea mariana Pk. and P. glauca (Moench) Voss. The phenology and the pollination biology of A. americanum were investigated at Belair Provincial Forest, Manitoba, while a survey was undertaken of the mycoflora associated with all three dwarf mistletoe-host associations at sites in the north and south of the province. The flowering period starts about the third week in April, although blooms were seen as early as 5 April after a mild winter. The ratio of male to female plants of A. americanum was found to be 2:1. While the percentage of flowers fertilized was low in 1981 and 1982, there was a higher rate of pollination success in 1983. Dead brooms were numerous after a hot dry summer in 1983. Five genera of ascomycetes and 15 genera of Hyphomycetes were isolated, most of which had been observed in an earlier Manitoba study. Eight genera of Coelomycetes are reported in association with dwarf mistletoe tissue for the first time, two of which, Coniothyrium sp. 1 and a Colletotrichum sp. may hold some potential as biological control agents. Only minor differences were found in the mycoflora associated with each dwarf mistletoe-host association, from both the northern and southern sites. A. americanum is thought to be both entomophilous and anemophilous. A Bradysia sp. (Diptera) and Formica spp. (Hymenoptera) are probably involved in chance pollination of A. americanum. Among the Coleoptera, Hyperaspis

binotata Say (Coccinellidae) and Cyphon sp. (Helodidae) were frequently found bearing mistletoe pollen grains on both male and female brooms and although they are generally destructive plant visitors they probably also effect a limited amount of pollination. Where female brooms were isolated from male brooms only 8.75% of the insects trapped bore pollen, while 79% of the flowers were pollinated. These data, together with the recovery of airborne pollen at least 400 m from a source, indicate that anemophily is probably also a significant pollinating mechanism.

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Dr. T. Galloway of the Department of Entomology took over the identification of the insects and provided me with the preliminary list. Dr. B. Johnston of the Department of Statistics gave help in the initial stages of the project and Mr. K. Knowles, Coordinator of Pest Management, Department of Natural Resources gave valuable advice about the suitability of study sites in Belair Provincial Forest. Ms. B. Lindsay is thanked for her careful typing and retyping and retyping of the manuscript. In particular, sincere thanks go to Dr. L. Sernyk of the Department of Plant Science, who gave unstintingly of his time to advise me and aid in the statistical analysis of the data. Their help is gratefully acknowledged.

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INTRODUCTION

Dwarf mistletoes (Arceuthobium spp.; Viscaceae) are highly specialized, dioecious, angiosperm parasites of Pinaceae and Cupressaceae. Of the 35 known taxa, 28 are found in the New World (Hawksworth and Wiens, 1972) and two attack jack pine and spruce in Manitoba. The damage they inflict on their hosts results in extensive commercial loss to the forest industry (Hawksworth and Wiens, 1972; Baranyay and Smith, 1972). At the point of infection fusiform swellings develop and as the endophytic system of the parasite ramifies through the cortex of the host branch a witches' broom develops (Plate 1a). The mistletoe has a chlorophyllous endosperm but also appropriates host photosynthate (Rediske and Shea, 1961; Hull and Leonard, 1964). The infection results in distorted, retarded growth of the host and in many cases early mortality.

The province of Manitoba is close to the eastern and western limits of the range of Arceuthobium americanum Nutt. ex Engelm. and A. pusillum Pk., respectively. Arceuthobium americanum can parasitize a number of spruce and pine species including lodgepole and ponderosa pine, but in Manitoba it is confined to jack pine, Pinus banksiana Lamb. Arceuthobium pusillum occurs only on its principal hosts Picea mariana Pk. and P. glauca (Moench) Voss in Manitoba, although elsewhere rare hosts include pine and larch species. During the last two decades the role of dwarf mistletoes as destructive forest pathogens has been realized and an extensive literature containing some 5500 titles has developed (Player, 1977). However,

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Plate 1.

a. Jack pine with witches' brooms caused by dwarf mistletoe, Arceuthobium americanum, infection.

b. A. americanum: male flowers. Central cushion (arrow).

c. A. americanum: new female shoots and fruits ready for discharge.

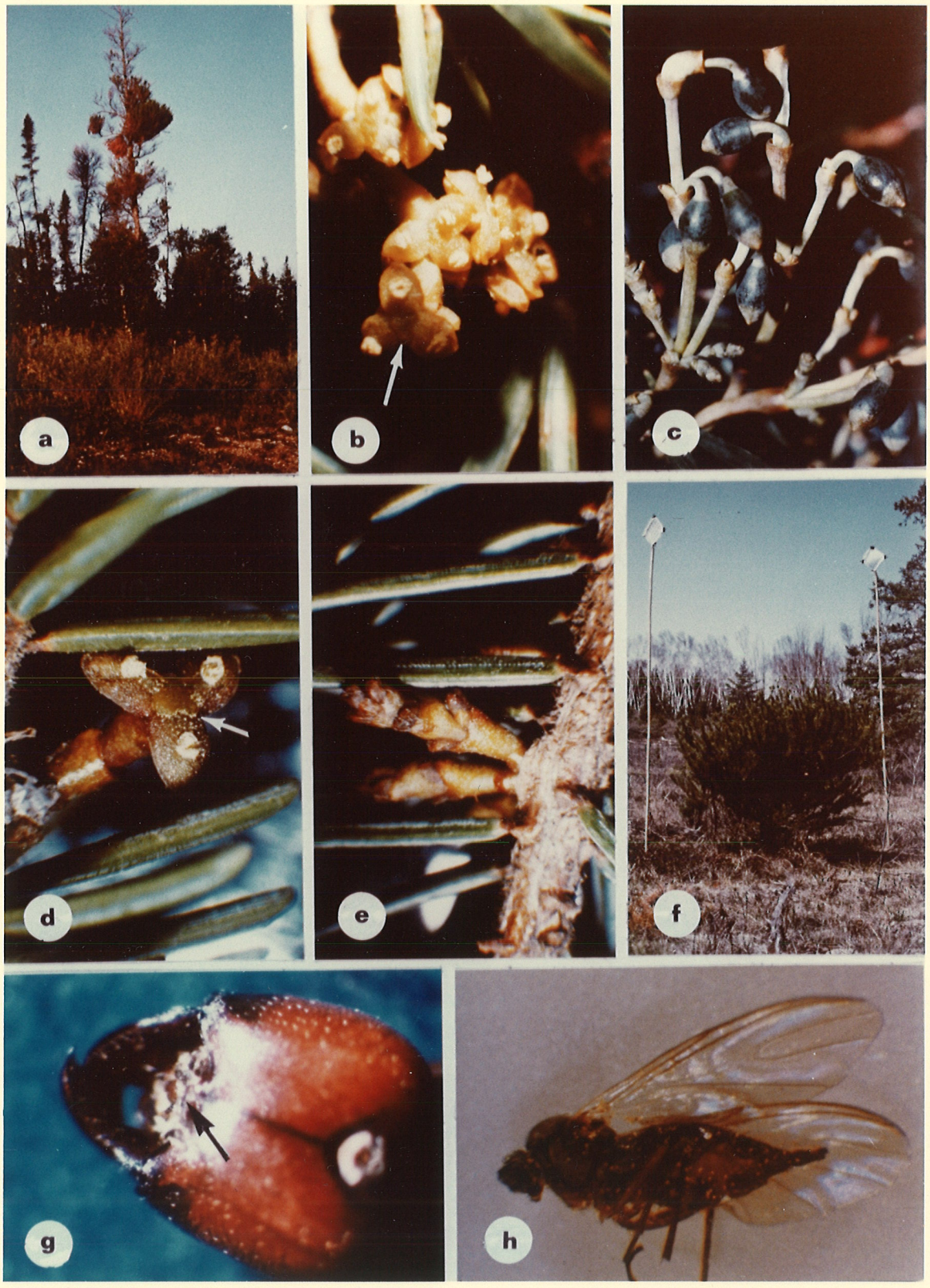
d. A. pusillum: male flower. Central cushion (arrow).

e. A. pusillum: unfertilized female flower.

f. Airborne pollen traps beside jack pine seedling infected with A. americanum.

g. Ant head with pollen of A. americanum clustered about mouth parts. Formica sp. rufa group.

h. Small dipteran with pollen grains of A. americanum adhering to body and wings. Bradysia sp. (Sciaridae).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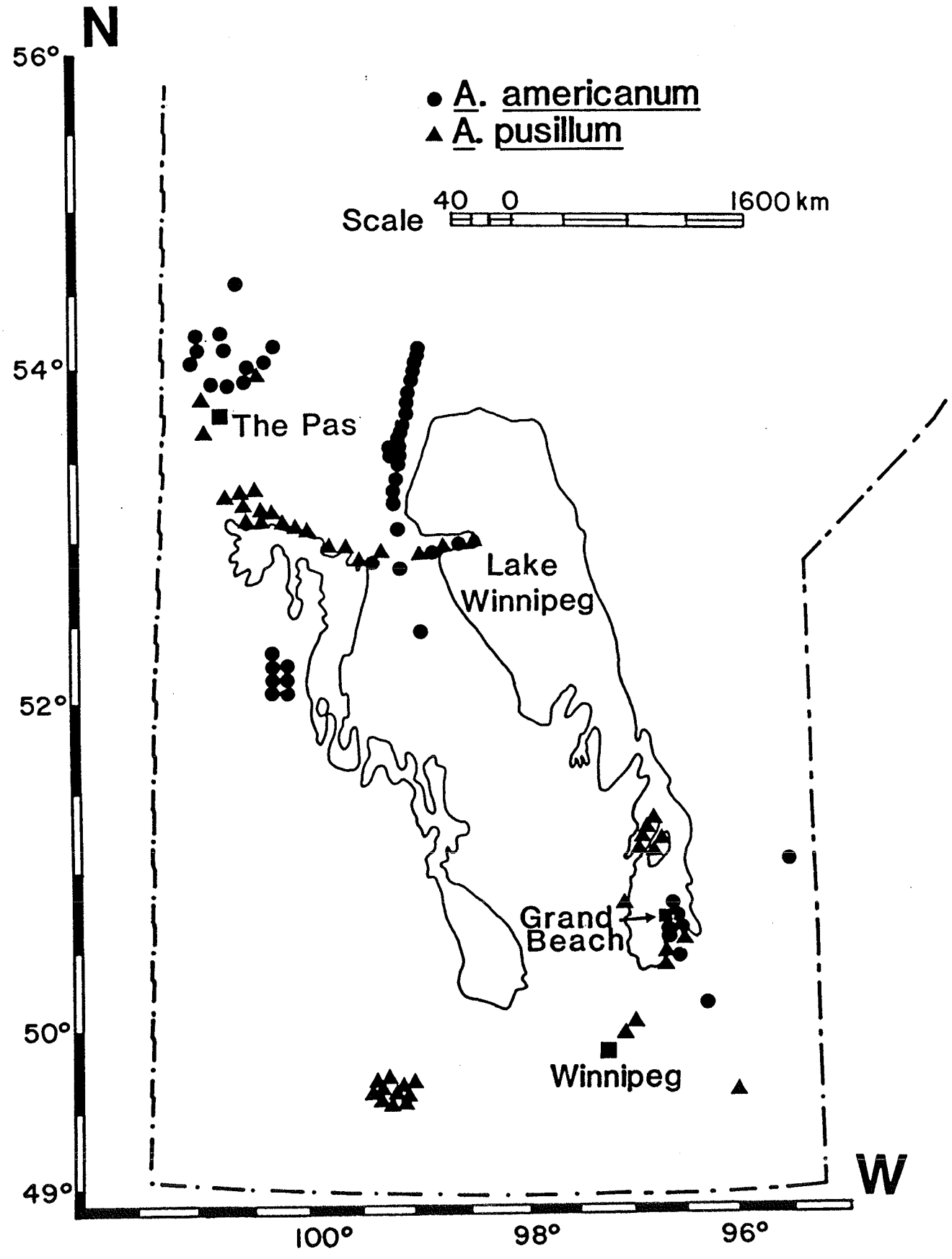
few studies have been conducted on mistletoes in Manitoba, and some biological phenomena remain poorly understood. While phenological observations were made on A. americanum at Belair Provincial Forest, Manitoba, during the course of the study, two aspects of its biology were considered of particular interest: the fungi associated with the parasite and the pollination mechanism, both of which might be of significance in a control program. No complete survey of the fungi attacking both Arceuthobium species in all dwarf mistletoe-host combinations has been undertaken and previous studies have resulted in conflicting evidence and conclusions concerning the importance of entomophily or anemophily as the primary pollinating mechanism. The possibility of control of Arceuthobium by a parasitic fungus or a decrease in viable seed production through control of a pollination vector have yet to be investigated in Manitoba. The fungal associations on all dwarf mistletoe-host combinations at the northern extreme of the range of Arceuthobium in Manitoba and at a southern site on the south shore of Lake Winnipeg were examined (Fig. 1). Fungi were isolated from both sexes of mistletoe, and healthy and moribund tissue sampled at different times during the growing season of 1981. Studies were also conducted in 1981, 1982, and 1983, to examine the insect fauna associated with A. americanum on jack pine in Belair Provincial Forest and to determine to what extent wind and/or insects are the principal vectors of pollen transfer.

Fig. 1. Known distribution of dwarf mistletoes, Arceuthobium spp., in Manitoba.


N
56°
54°
52°
50°
49°
100°
98°
96°
W
● A. americanum
▲ A. pusillum
Scale 40 0 1600 km
The Pas
Lake Winnipeg
Grand Beach
Winnipeg

Chapter 1

PHENOLOGICAL OBSERVATIONS

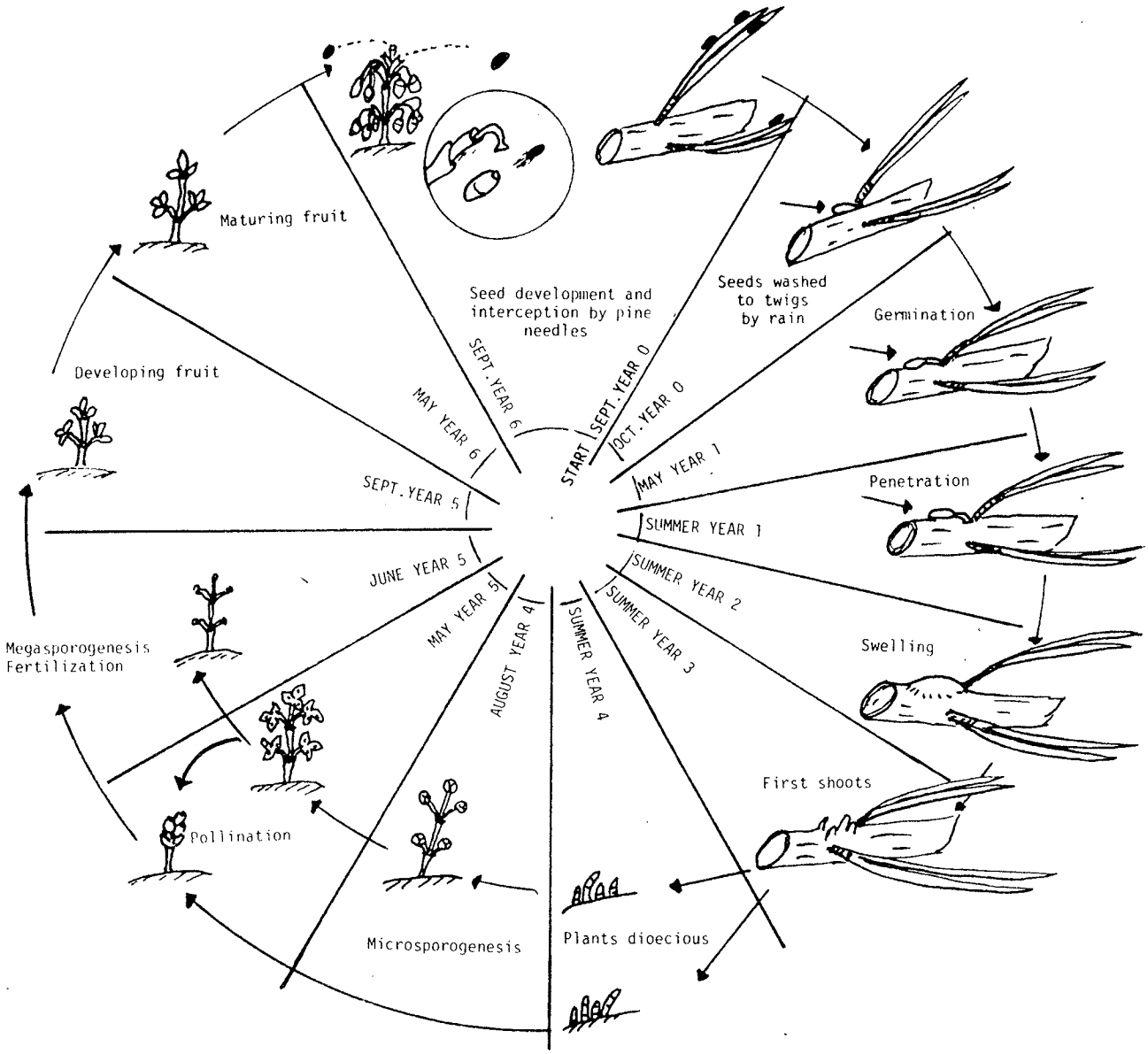
Literature Review

The biology of the dwarf mistletoes has been extensively reviewed by Hawksworth and Wiens (1972). The life cycle may take up to five or six years to complete (Fig. 2a). For two years after germination of the seed and penetration of the host, a rootlike endophytic system composed of cortical strands and sinkers develops (Fig. 3). Shoots emerge in the third year and continue to enlarge in the fourth year. In the fall of year four microsporogenesis takes place while anthesis and pollination occur the following spring. The fruits may take one season to reach maturity and be discharged (e.g. A. pusillum), or two seasons (e.g. A. americanum, Fig. 2b).

Gill (1935) found that the blooming time of dwarf mistletoes appeared to show little response to climatic or other environmental factors, although it varies for individual species (Hawksworth and Wiens, 1972). Baranyay and Smith (1972) state that in British Columbia A. americanum flowers in April and May. In Alberta, Dowding (1929) reported that small female A. americanum flower buds emerge in early May either on the base of stems with older flowers and fruits or on new stems. The male flowers open about 15 May, the pollen is dispersed by 23 May and the perianths of old male flowers are shed by the end of the first week in June. In certain years the flowering period may be considerably longer; in 1980, Gilbert

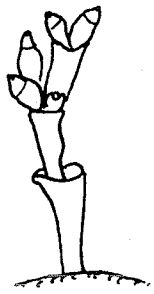
Fig. 2a. Generalized life cycle of Arceuthobium americanum (Modified from Hawksworth and Wiens, 1972: p. 6).

Fig. 2b. Semi-diagrammatic representation of fruit development in Arceuthobium americanum.



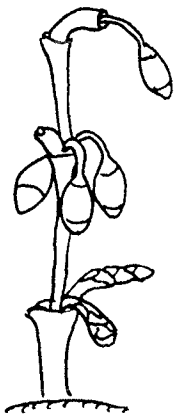
MAY YEAR 1

Newly fertilized flower



SEPT.YEAR 1

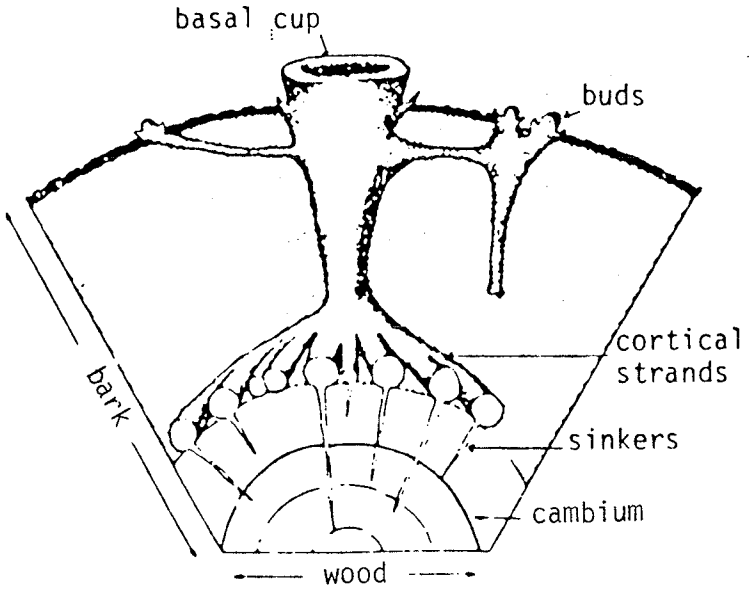
Developing fruit



SEPT.YEAR 2

Mature fruit

Fig. 3. Diagrammatic cross section of an infected branch showing the major structures of dwarf mistletoe (Baranyay and Smith, 1972).


basal cup
buds
cortical strands
sinkers
cambium
bark
wood

(1981) observed a few male flowers in Belair Provincial Forest, Manitoba, each week from the end of May until 8 July. At Victoria Beach, Manitoba, female flowers collected by Dowding for sectioning on 8 May 1931, contained pollen tubes in the stylar canals indicating that pollination had occurred earlier than reported for Alberta.

Dowding (1929) reported that seed dispersal of A. americanum in Alberta occurred between September 10-20, although Muir, cited by Baranyay (1970), suggested a longer period of seed dispersal for that province, extending from mid-August to mid-September. Gilbert (1981) found that the majority of A. americanum seeds in Belair Provincial Forest, Manitoba, were discharged in a single night of heavy continuous rain September 3-4, 1980.

Damage to Arceuthobium shoots by birds and animals has been reported (Gill, 1935; Kuijt, 1955). Birds have been known to choose witches' brooms as nesting sites and Arceuthobium berries as food (Kuijt, 1955; Gill and Hawksworth, 1961). Rodents and deer eat the shoots of Arceuthobium (Gill and Hawksworth, 1961), and the young mistletoe-induced swellings on host trees with their abundance of starch appear to be the preferred food of porcupines and squirrels (Gill, 1935; Kuijt, 1955). However, the effects on dwarf mistletoe populations of such activities appear to be minor (Hawksworth and Wiens, 1972).

Climatic factors affect dwarf mistletoe shoots (Hawksworth and Wiens, 1972) but few studies have been conducted. Baranyay and Smith (1974) experimented with the effect of low temperatures on mature fruits of A. americanum and A. tsugense (Rosendahl) G. N. Jones. They found that only 4% of the mature fruits of A. ameri-

canum exposed to 2.3 hours of -3.9°C temperatures remained two weeks after the experiment. Developing fruits on the same trees exposed to similar conditions were apparently undamaged and seen to mature normally the following year. They concluded that early frosts reduce the current year's seed crop and may also be a factor in the range limitation of dwarf mistletoes. Temperature extremes and winter drying affect Arceuthobium shoots but no experimental data are available for examination (Hawksworth and Wiens, 1972).

Methods

Observations began early in April at Belair Provincial Forest near Grand Beach, Manitoba (Fig. 1) and were continued at weekly intervals until open male flowers of A. americanum were first observed.

In 1981 25 infected trees were selected at random and plants counted to obtain the male to female ratio. For the purpose of the study all the shoots emerging at a node were counted as a single plant. Developing shoots at the tip of a branch were assumed to be the same sex as those at the node immediately below. In those rare cases where plants, usually male, emerged in the internodes all the shoots within the internode were counted as a single plant. On 27 May 1981, the female shoots on one broom from each of the three sites (described in Chapter 3) were examined to determine the ratio of unfertilized flowers to developing fruits. Two more brooms were analyzed in August of the same year when the ratio of unfertilized flowers to developing fruits to maturing fruits could be obtained. In September 1982, a similar count of 809 female flowers, taken from

a tree 17 m from the nearest male infection, was recorded. In 1983, as part of an experiment designed to determine the pollination success and vector(s) of A. americanum the female flowers on 30 plants from 6 trees were counted in April and again in August and the ratio of newly emerged flowers to unfertilized flowers to developing fruits and mature fruits monitored.

The effects of an exceptionally hot and dry July and August on dwarf mistletoe and witches' brooms were observed in 1983.

Results

The date on which open male flowers were first seen varied considerably for the three years. In 1981, after an unusually mild winter and a warm, dry spring, a few flowers were open as early as 5 April, although full anthesis was not observed until about three weeks later. Open flowers were not found until 4 May in 1982 whereas in 1983 opening occurred between 19 April and 26 April.

The numbers of male and female plants counted on 25 trees revealed a ratio of approximately 2:1 in favour of males (Table 1). It was not unusual for the trees to have brooms induced by mistletoe of both sexes although one sex generally dominated.

Comparatively few developing fruits were recorded from brooms collected in May 1981 at any of the three sites (Table 2), and a similar trend was expected and observed from the two brooms examined in August of the same year (Table 3). The mature fruits ready for dispersal were only 5% and 0%, respectively, of the total. The same trend was observed in the single broom sampled in 1982 in which only 4% of the count was composed of mature fruits (Table 3).

Table 1. Numbers of male and female plants of *Arceuthobium americanum* on 25 randomly selected infected *Pinus banksiana* trees, in Belair Provincial Forest, Manitoba, 1981.

Tree #	Male	Female
1	969	55
2	69	331
3	25	0
4	130	133
5	392	51
6	25	2
7	140	5
8	19	231
9	107	46
10	73	72
11	365	345
12	133	206
13	149	0
14	30	16
15	64	0
16	0	59
17	33	60
18	228	0
19	38	4
20	40	0
21	0	49
22	249	0
23	40	17
24	4	10
25	0	99
Total	3322	1791
%	65	35
Ratio	2	1

Table 2. Comparison of numbers of unfertilized flowers and developing fruits counted on brooms from each of three sites in Belair Provincial Forest, Manitoba, in May 1981.

Site	Unfertilized Flowers	%	Developing Fruits	%
1	3432	97	97	3
2	2113	92	193	8
3	895	99	8	1

Table 3. Comparison of numbers of unfertilized flowers, developing fruits and maturing fruits counted on two brooms in August 1981, and one broom in September 1982, from Belair Provincial Forest, Manitoba.

Date	Broom	Unfertilized Flowers	%	Developing Fruits	%	Maturing Fruits	%
1981	1	5236	42	6612	53	610	5
1981	2	2203	80	561	20	0	0
1982	1	502	62	276	34	31	4

The data for the pollination experiment conducted in 1983 are reported in detail in Chapter 3 but in April the number of fertilized flowers totalled 176 of which only 50 (28.4%), remained by the middle of August. The data cannot be compared directly with 1981 and 1982 when whole brooms or branches were examined but again the numbers were low even at the beginning of the season, many of the tagged plants bearing no developing fruits at all. Between July 7, when the plots were examined, and August 28 when the second count was made, considerable damage occurred. A number of tags were chewed, presumably by rodents, and several stems of mistletoe either eaten or dislodged. Some tags were chewed through and had fallen off making it impossible to make the second count on several plants. One entire tree and several tagged plants had died from other causes. Of the original 30 plants, second counts were obtained from only 15. The number of developing fruits on these 15 plants totalled 272, averaging 4 per stem.

In September 1983 many witches' brooms appeared to be dead or dying while the host trees remained healthy. The months of July and August 1983 were notable for exceptionally high average temperatures, 22.2^{o}C and 22.5^{o}C, respectively, compared with norms of 19.6^{o}C and 18.3^{o}C, respectively. Little precipitation in July, 29.8 mm versus norms of 75.9 mm, clearly compounded the problem.

Discussion

Floral opening is presumably influenced by early spring temperatures. After a comparatively mild winter in 1981, flowers were seen in bloom as early as 5 April, whereas in 1982 and 1983

flowers did not open until late April to early May. Dowding (1929) noted that flowers generally opened about 15 May in Alberta, although in her work at Victoria Beach, Manitoba, she observed pollen tubes in the stylar canals of flowers taken for sectioning on 8 May, 1931, indicating that floral opening and pollen transfer had occurred in late April or the first week of May (Dowding, 1931b). Gill (1935) suggested that blooming time was not affected by climate but the difference of a month between 1981 and 1982 when male flowers were first seen open refutes this.

Hawksworth and Wiens (1972) state that female and male plants occur in approximately equal numbers where the sex ratio has been investigated. This ratio was not supported by the findings in Belair Provincial Forest where males outnumbered females approximately 2:1. However, direct comparison of methods used is not possible as Hawksworth and Wiens (1972) do not outline their methods. One argument against an anemophilous pollination system in Arceuthobium spp. is the comparatively small number of pollen grains produced in each flower, approximately 11,300 for A. americanum (Penfield et al., 1976). Should the sex ratio of two male plants for each female be found to be a widespread phenomenon rather than restricted to the sample investigated in Belair Provincial Forest, this could possibly be a compensatory factor for the small numbers of pollen grains produced.

Unfortunately, in the present study, the number of brooms on each tree was not noted at the time the plants were counted. Consequently, it is not possible to determine whether female as opposed to male infection has the effect of more rapidly reducing

host vigour and resulting in fewer plants per broom. Dowding (1929) made the observation that the host needles on female brooms were frequently shorter and yellowish in comparison to those on male brooms. She concluded that seed production was a greater drain on the host than male infection. It is of interest that twice as many trees, 6/25, had no female infections as trees with no male infections, 3/25. The significance of this cannot be ascertained from these data and further observations are necessary to resolve the question.

The percentage of flowers fertilized differs considerably from Weir's (1915) account in which he describes most members of Arceuthobium as "prolific seed producers". There appears to be considerable variation between years and perhaps between locations in the number of fruits reaching maturity. This may well be due to climatic factors affecting pollination success. Penfield et al. (1976) observed that open flowers of A. americanum closed when temperatures fell to about 1-2^{o}C, especially during the early part of the pollination period. Overnight lows as cool as this and frequently colder are known in the latitude of Belair Provincial Forest and may be assumed to affect the pollen transfer. Evidence indicates that pollination may also be effected in part by insects and unusually dry spring weather, such as encountered in 1981, would therefore influence entomophilous pollen transfer.

There were 55% more developing fruits found in August 1983 than maturing fruits in May 1983 on half the initial number of experimental plants. The data are possibly indicative of a higher rate of pollination in 1983 as opposed to 1982 although a final

comparison cannot be made until the spring and fall of 1984 when these fruits have overwintered and reached maturity.

Hawksworth and Wiens (1972) state that squirrels, porcupines, birds and other animals eat dwarf mistletoe shoots which is supported by gnawed tape and lost plants on the experimental plot at Belair in 1983. However, it is not known how commonly such damage occurs or its influence on the overall numbers of viable seeds reaching maturity.

It is known that temperature extremes affect dwarf mistletoe shoots (Hawksworth and Wiens, 1972) and large numbers of brooms succumbed during the hot dry conditions that prevailed during July and August of 1983, while the host trees survived. The brooms on dwarf mistletoe-infected jack pine are frequently notable for their luxuriant and dense growth; Dowding (1929) also remarks on "the healthy appearance" of infected trees. The greater water loss from such dense growth emanating from single lateral branches may be the cause of the death of the brooms. The host trees may have survived because of the smaller stress of transpiration from the more sparse foliage of the remainder of the tree.

Chapter 2

FUNGAL ASSOCIATIONS

Literature Review

There are no comprehensive accounts of the fungi growing on Arceuthobium. The only extensive survey of the mycoflora associated with a specific dwarf mistletoe and its host concerns the fungi associated with the cankers on branch swellings of Tsuga heterophylla (Raf.) Sarg. caused by Arceuthobium tsugense. Baranyay (1966) found a high ratio of ascomycetes to imperfect fungi (9:2). Imperfect fungi were isolated rarely; Epicoccum purpurascens Ehr. (syn. Epicoccum nigrum Lk.) twice and Truncatella truncata (Lev.) Stey. once. The study was extended by Funk et al. (1973), Funk and Baranyay (1973) and Funk and Smith (1981) to include eight more fungi, five of which were found occasionally or only rarely. The sixth, Botryosphaeria tsugae Funk occurred frequently in the Cowichan Valley, South Vancouver Island (Funk and Baranyay, 1973). Potebniamyces gallicola sp. nov. was added to the list recently although its pathogenicity has still to be tested (Funk and Smith, 1981). Nectria macrospora (Wr.) Ouellete was commonly isolated from open, resinous, dwarf mistletoe cankers throughout the range of A. tsugense in British Columbia during 1968 to 1970. Such characteristics as selectivity for dwarf mistletoe-infected host tissue, proven pathogenicity, ability to invade without host wounding, rapid canker production and abundant spore production indicated that there might be promise of a biological control of A. tsugense using N. macrospora (Funk et al.,

1973). However, spray inoculations of a spore suspension of the fungus did not significantly increase the level of colonization of cankers by the fungus, although cankers that were successfully colonized showed reduced production and growth of aerial shoots three years post inoculation (Smith and Funk, 1980).

A second Nectria species, N. fuckeliana Booth, has been described as pathogenic on dwarf mistletoe-infected pine tissue, while remaining only weakly parasitic on healthy tissue (Byler and Cobb, 1972). Cylindrocarpon sporodochia, apparently identical to those of the imperfect stage on N. fuckeliana, were observed on dead and dying Arceuthobium occidentale (Engelm.) and A. abietinum (Engelm.) Hawks. and Wiens in California (Byler and Cobb, 1972). Cylindrocarpon cylindroides Wollenw. was also isolated from 29% of dwarf mistletoe-infected branches on true firs in a study in west-central Oregon (Filip et al., 1979).

Two species of Pestalotia have been recorded on dwarf mistletoe. Pestalotia heterocornis Guba was isolated from Arceuthobium bicarinatum Urban, a parasite of Pinus occidentalis von Turckheim in the Dominican Republic. Its significance with respect to dwarf mistletoes is unknown (Hawksworth et al., 1977). Inoculations on living dwarf mistletoe shoots have shown the second Pestalotia species, P. maculiformans Guba & Zeller to be parasitic, but it has been recorded only once, from Arceuthobium tsugense (Wicker & Shaw, 1968; Hawksworth et al., 1977).

Cytospora cankers on white fir (Abies concolor Lindl. and Gord.) and red fir (A. magnifica A. Murr.) in California were first observed in 1929 (Wright, 1942). Subsequent studies revealed that

the fungus was semi-parasitic requiring weakened host tissue as an infection court. Cytospora abietis Sacc. was frequently found associated with branch swellings caused by the dwarf mistletoe, A. campylopodum Engelm. f. abietinum (Englem.) Gill, on red fir (Wright, 1942). Although the association between dwarf mistletoe and Cytospora on white fir was not initially observed, Scharpf (1969) found that only 4% of C. abietis isolations were made from red and white fir branches that were not infected with dwarf mistletoe. A later study using media prepared from dwarf mistletoe-infected versus non-infected red fir branch tissue provided no evidence that nutrient conditions or other growth factors present in autoclaved mistletoe material would favour the growth of C. abietis in culture (Scharpf, 1983). However, in the earlier study more than 20% of dwarf mistletoe-infected branches of red and white fir were attacked by the fungus (Scharpf, 1969). This represented a considerably higher percentage than Filip et al. (1979) obtained in their west-central Oregon study. Two other fungi, Cryptosporium pinicola and Cylindrocarpon cylindroides were more frequently associated with dwarf mistletoe-infected branches, 29% and 32%, respectively, than C. abietis which was only isolated from 8% of dwarf mistletoe-infected branches. Pathogenicity on dwarf mistletoe-infected branches of true firs has been reported for C. cylindroides and for C. abietis but not for A. pinicola. Its prevalence led Filip et al. (1979) to conclude that it may contribute to branch mortality.

There is a single report of the Loculoascomycete, Metasphaeria wheeleri Linder from A. campylopodum. The fungus attacks and girdles the stems killing the portion distal to the infection

(Linder, 1938). However, the absence of further reports of M. wheeleri perhaps indicates that its occurrence is rare and its control of A. campylopodum limited. Hawksworth et al. (1983) recently reported the association between A. americanum and a rust fungus Peridermium bethelii Hedgc. and Long, that girdles and kills mistletoe-infected branches. P. bethelii has for many years been considered synonymous with Cronartium comandrae Pk., but attempts to infect Comandra umbellata (L.) Nutt., a telial host of C. comandrae, with P. bethelii failed and no alternative hosts for the latter were found. The taxonomic status of P. bethelii and the basis for the association of the rust and A. americanum remain to be established (Hawksworth et al., 1983).

Fungi were isolated from the aerial shoots of A. americanum and from the swellings caused by the mistletoe in the branches of the host, Pinus banksiana (Gilbert, 1981). Striking differences were observed between the fungal flora isolated from A. tsugense on western hemlock (Baranyay, 1966; Funk et al., 1973; Funk and Baranyay, 1973; Funk and Smith, 1981) and Gilbert's (1981) study. In the latter only three Pyrenomycetes were isolated from dwarf mistletoe-infected wood (Chaetomium sp., Sporormia sp. and Ceratocystis sp.) while six were isolated from mistletoe (Wallrothiella arceuthobii (Pk.) Sacc. Melanospora sp., Chaetomium sp., Coniochaeta sp., Gelasinospora sp., and Sordaria sp.). All of the Pyrenomycetes from the cankers of A. tsugense on western hemlock were isolated from wood. A great disparity exists between the number of imperfect fungi isolated in the two studies; two in British Columbia (Baranyay, 1966) and 24 in Manitoba (Gilbert, 1981). The only species common

to both Arceuthobium species was Epicoccum purpurascens (E. nigrum). The genera of imperfect fungi represented in the Manitoba study typically comprised either saprophytic fungi or weak parasites and, except for Penicillium spp. and several pycnidial species, generally occurred more frequently on the aerial shoots of the mistletoe than on the wood. Gilbert (1981) concluded that none of the commonly isolated fungi showed much promise as biological control agents.

Hawksworth et al. (1977) reviewed the fungal parasites of the aerial shoots of dwarf mistletoes. Three of these, Cylindrocarpon gillii (Ellis) J. A. Muir (Septogloeum gillii Ellis), Colletotrichum gloeosporioides Penz. and Wallrothiella arceuthobii have been commonly associated with A. americanum. Only W. arceuthobii has been reported from Manitoba and this is the only one known to occur in association with A. pusillum.

Cylindrocarpon gillii was first described, but not named, by Gill (1935). The white eruptions of the stems, especially at the nodes, and the conspicuous masses of hyaline, cylindrical to fusiform spores were described by Ellis (1946) and the name Septogloeum gillii published. On the basis of conidiophore morphology and spore formation, Muir (1973) transferred the fungus to the genus Cylindrocarpon. He proposed that the new combination Cylindrocarpon gillii (Ellis) J. A. Muir be adopted (Muir, 1973).

The range of C. gillii was extended to include A. americanum and the western provinces of Canada (Bourchier, 1954; 1955a; 1955b) although it was initially found on A. campylopodum Engelm. (Gill, 1935; Hawksworth et al., 1977). In 1959, Mielke conducted inoculation experiments in which he used C. gillii, isolated from A. divari-

catum Engelm., to inoculate A. americanum. The fungus failed to become established and was only seen in the test plots for three years after inoculation. It has been suggested that these results were inconclusive as the C. gillii isolate was from a warm, arid climate and inoculated on to A. americanum growing in cool montane forests (Hawksworth et al., 1977). Greater success might have been achieved using an isolate from a similar climatic zone.

The fungus causes anthracnose of A. campylopodum and A. americanum in Canada and may periodically devastate the parasite in some localities (Kuijt, 1963). Kuijt observes that the disease often originates as small blackish warts on the host which later develop into the conspicuous yellowish white lesions with hyaline spores described in the literature. The fungus has not been isolated from Arceuthobium in Manitoba.

Colletotrichum gloeosporioides has also been commonly isolated from Arceuthobium in the U.S.A. and the western provinces of Canada, Saskatchewan, Alberta and eastern British Columbia (Muir, 1967). While different isolates of the fungus from several Arceuthobium species were shown to be culturally distinct in mycelial growth, colony colour, diameter growth and sporulation, cross inoculation experiments demonstrated that the fungal isolates were not host-specific (Scharpf, 1964). C. gloeosporioides causes small necrotic lesions which girdle the shoots and cause shoot die-back or blight (Wicker and Shaw, 1968). The endophytic system is invaded to a certain extent (Parmeter et al., 1959; Wicker & Shaw, 1968; Muir, 1967; 1977), but probably not seriously enough to reduce the numbers of new plants. Female and male plants are attacked in equal numbers

and one study demonstrated that approximately 24% of the shoots were destroyed by the pathogen (Wicker, 1967). The fungus was seen to persist in an area for several consecutive years (Wicker and Shaw, 1968) but more usually the fungus is sporadic in its occurrence and only builds up to high levels of infection when weather conditions are favourable (Hawksworth et al., 1977). Furthermore, while the infection reduces the reproductive potential of the Arceuthobium it appears to have no effect on the establishment of new mistletoe plants. Equal numbers of new plants were observed in infected and non-infected areas (Muir, 1967; 1977).

Wallrothiella arceuthobii attacks only the female flowers of spring flowering Arceuthobium species (Hawksworth et al., 1977). After pollination has occurred the fungus invades the stigma which, in conjunction with the apical portion of the fruit, is replaced by a stroma of the fungus (Dowding, 1931b). All tissues of the fruit internal to the vascular strands may be invaded and destroyed preventing normal fruit development and seed production (Wicker and Shaw, 1968). The fungus is widely distributed and has been reported from the provinces of British Columbia, Alberta, Saskatchewan and Manitoba (Kuijt, 1963). The fungus has a one year life-cycle and depending on how soon after pollination infection occurs there may be some development of the embryo and endosperm (Kuijt, 1969). There are two reasons why the parasite has not been widely used in the biological control of Arceuthobium. In nature, infection may be high one year with up to 80-100% of the female flowers of the mistletoe affected (Weir, 1915; Dowding, 1931b), but the following year almost no infection may occur in the same area (Hawksworth et

al., 1977; Wicker & Shaw 1968). Secondly, it has only recently been grown in culture. Dowding (1931b) germinated ascospores in a mistletoe decoction solution but no growth of the fungus occurred. Parker (1970) demonstrated that germination and mycelial growth could be obtained in glucose-asparagine solution and solid medium to which 2% yeast extract had been added. However, at the end of six months spores had not developed so that, at present, there is no way of increasing the fungus in culture to provide spore suspensions for spray inoculation.

Alternaria alternata (Fries) Keissler (syn. Alternaria tenuis Nees.), Aureobasidium pullulans (de Bary) Arnaud [syn. Pullularia pullulans (de Bary Berkh.], Epicoccum purpurascens and Cladosporium spp. have been implicated as the cause of resin disease in Arceuthobium (Mark et al., 1976). These fungi were frequently isolated from mistletoe plants that were dead and impregnated with resin; hence the name. They were rarely isolated from healthy mistletoe plants and it was therefore postulated that the fungal attack caused the trees to respond with the formation of wound cork and excessive exudation of resin which in turn effectively cut off the mistletoes from their water and nutrient supply in the host. Gilbert's (1981) study does not support this conclusion. The fungi implicated in resin disease were frequently isolated from healthy mistletoe samples as well as the wood of control trees. It is therefore highly improbable that these organisms are the sole cause of resin disease.

No survey of the mycoflora associated with Arceuthobium pusillum has been conducted and the only fungus reported in assoc-

iation with this dwarf mistletoe is Wallrothiella arceuthobii (Hawksworth et al., 1977).

Introduction

Numerous studies have been conducted on specific fungal organisms associated with Arceuthobium, but no general survey of the mycoflora of a dwarf mistletoe species exists. In 1980 a study of the fungi associated with A. americanum on Pinus banksiana in Manitoba was initiated by Gilbert (1981). The scope of the present study was designed to explore the mycofloras associated with all dwarf mistletoe-host associations in Manitoba.

Methods and Materials

Near Cormorant Lake, 10 km north of The Pas, both dwarf mistletoes were collected from all their common hosts; A. americanum from Pinus banksiana, A. pusillum from Picea mariana and P. glauca. From Grand Beach Provincial Park on the southern shore of Lake Winnipeg, A. americanum was sampled from P. banksiana and A. pusillum from P. mariana (Fig. 1). These locations were close to the northern and southern limits of range of dwarf mistletoes in Manitoba. Collections from both sites were made in May (spring), July (summer) and September (fall). As far as possible mistletoes were collected in a random fashion over an area of several hectares. However, the relative scarcity of A. pusillum and the need to obtain both species from the same area made the use of a formal randomized design of collection impracticable.

The mistletoe was surface sterilized in 1% sodium hypochlorite solution, washed in sterile distilled water and 2 mm

segments plated out on to damp sterile sand. As far as possible ten plates were each inoculated with ten 2mm segments of dwarf mistletoe for each host-parasite combination and for the sex (male, female) and condition (healthy, moribund) of the mistletoe. This was not possible for every dwarf mistletoe-host combination at each season. The male plants of A. pusillum fell after the pollination period and new shoots were not found after the spring sampling period until the fall. It is presumed that dead and dying shoots of A. pusillum drop rapidly as moribund tissue was rarely found; consequently the number of plates of moribund A. pusillum ranged from 0 to 5. In September all tissue was plated according to dwarf mistletoe-host combination and condition only.

The mistletoe-sand plates were incubated in a growth chamber under a mixture of white and ultraviolet light, 0.5 watts/m^2, and a 12 hours light/12 hours dark regime at 23^{o}C. The fungi on the mistletoe were either identified and recorded, or isolated on to 1.25% malt extract agar (MA) at Observation Times 1-4: 4 days, 18 days, 2 months and 6 months, respectively, after the sand plates were established. If fruiting failed to occur on MA the fungi were placed on sterile dwarf mistletoe tissue set in plates of MA and/or Sach's medium as a mineral base. The fungi were incubated under the same conditions as the mistletoe tissue.

The data were analyzed by means of SAS ANOVA (SAS Institute Inc., Cary, N. Carolina). Unidentified fungi were sent to Centraal-bureau voor Schimmelcultures, Baarn, Netherlands, for initial identification. Several Coelomycetes will be sent to the Common-wealth Mycological Institute at Kew for more precise identification

while duplicate cultures, stored on 1.25% MA or sterilized dwarf mistletoe in 1.25% MA or Sach's medium, have been deposited in the Department of Botany, University of Manitoba, culture collection.

In 1981 and 1983 small brooms or branches infected with A. americanum were examined to determine the percentage of fruits parasitized by Wallrothiella arceuthobii.

Results and Discussion

Two analyses of variance (ANOVAs) were performed on the most frequently encountered fungi, Alternaria alternata, Coniothyrium sp. 1 and Cladosporium spp. The first ANOVA analyzed the data from a single dwarf mistletoe-host (Dm-H) association (A. americanum on P. banksiana), and one data of sampling (July), as a complete data-set for both locations, healthy and moribund tissue, and male and female plants was available. The second ANOVA was conducted on all the data to determine the effects of location, date of collection, condition and sex for all Dm-H associations. A comparison of the two analyses was made to discern possible effects due to the use of incomplete datasets in the second ANOVA.

Analysis of variance of July dataset. The analysis revealed that while the frequencies of occurrence of A. alternata and Coniothyrium sp. 1 were dependent on environmental factors in July (Appendix A1, A2), the number of isolates of Cladosporium spp. recovered was not.

Location. Location was a highly significant factor in the July analyses (Appendix A1, A2), and consequently the data were

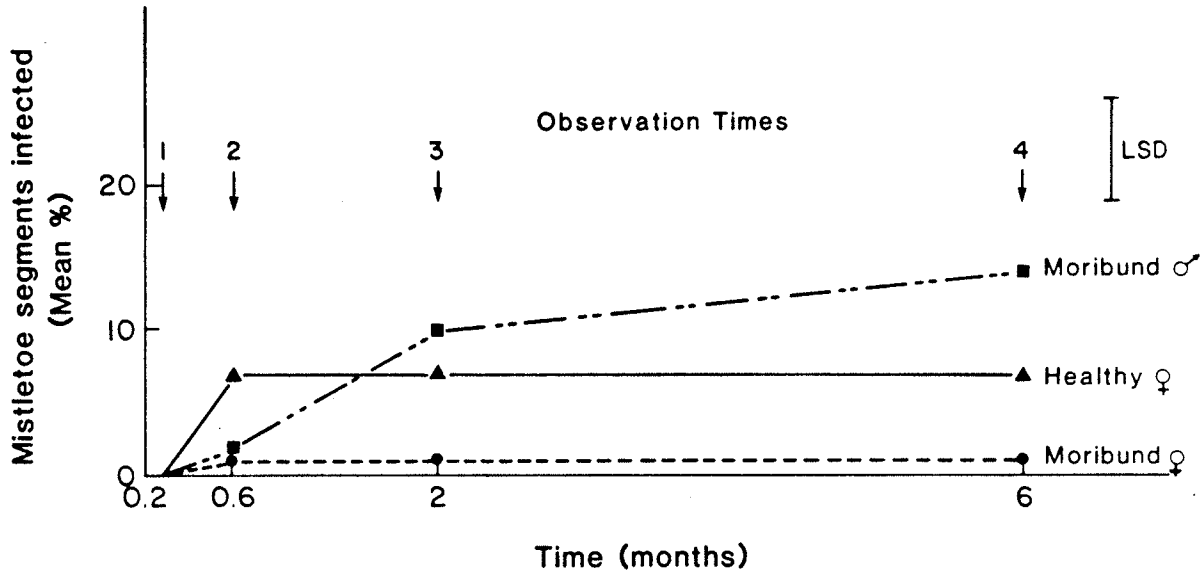
sorted and separate analyses conducted for each site. At Grand Beach both A. alternata and Coniothyrium sp. 1 were found to vary significantly in response to the factors analyzed while at The Pas the analysis proved to be significant for only Coniothyrium sp. 1 (Appendix A3a, A3b, A3c).

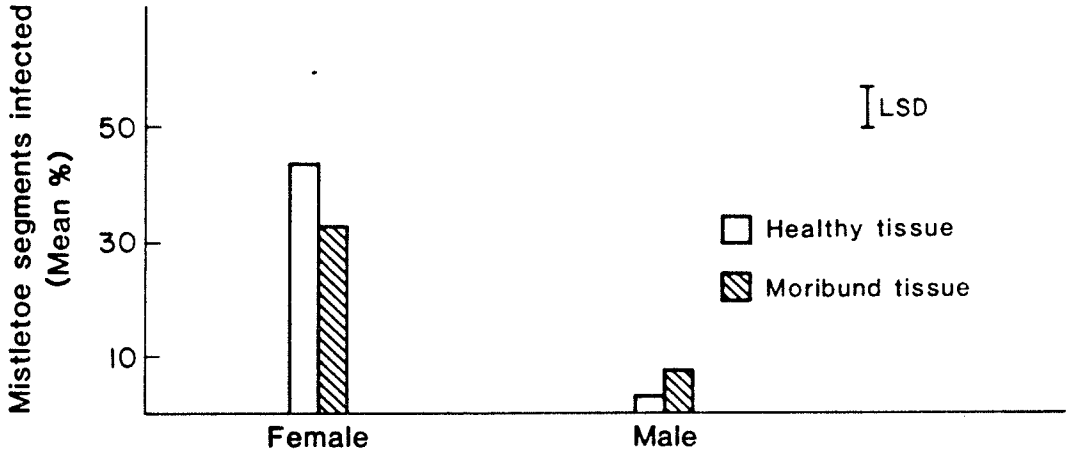
Interactions. One three-way and two two-way interactions were found to be significant for Coniothyrium sp. 1 in the July ANOVA (Appendix A3b, A3c). The three-way interaction of observation* condition*sex of A. americanum on frequency of detection of Coniothyrium sp. 1 at Grand Beach (Fig. 4a) revealed that by observation 3, significant differences between isolations from healthy and moribund male tissue (0% and 10%, respectively) and moribund female and moribund male tissue (1% and 10%, respectively) had become apparent. By observation 4 significantly more Coniothyrium sp. 1 had also been detected on moribund male than healthy female tissue. It would appear from these data that the influences of condition and sex of the mistletoe were not determining the number of isolations of Coniothyrium sp. 1 as both healthy and moribund, and male and female tissues were represented in the two highest frequencies. Observation time was a highly significant factor in every ANOVA revealing that significant changes in frequency of detection of the fungi were apparent by observations 2 and 3 (18 days and 2 months, respectively). After 4 days (observation 1) little fungal development was evident and after 2 months little more occurred. On two occasions only, a significant difference between isolations from different mistletoe tissues was noticed for the first time at observation 4 (e.g. Fig.

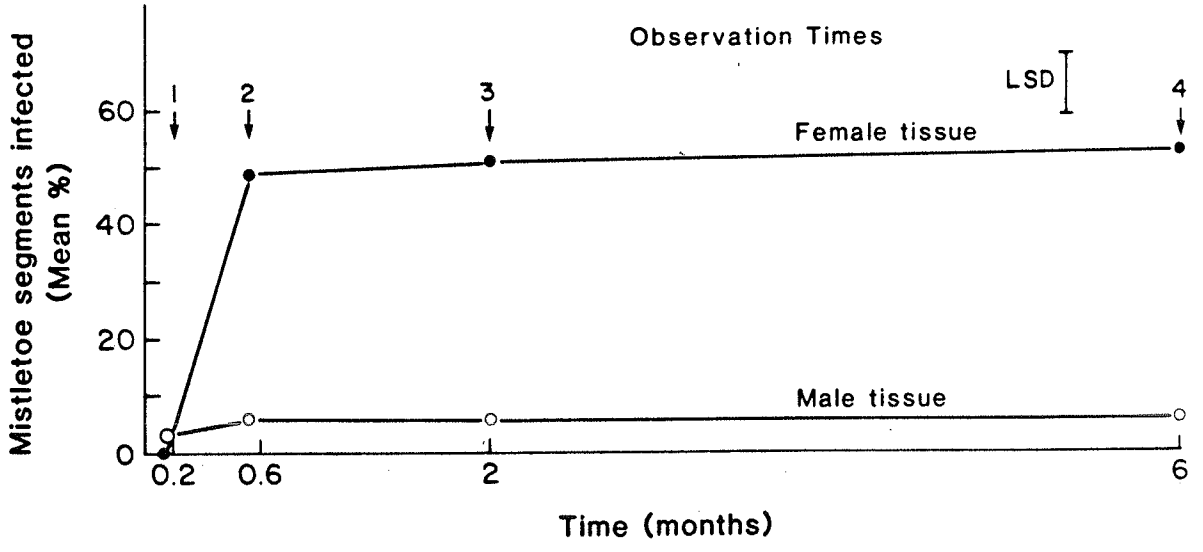
Fig. 4a. Interaction of observation time*condition*sex of Arceuthobium americanum on frequency of detection of Coniothyrium sp. 1 at Grand Beach. July, 1981.

Fig. 4b. Interaction of condition*sex of Arceuthobium americanum on frequency of isolation of Coniothyrium sp. 1 at The Pas. July, 1981.

Fig. 4c. Interaction of observation time*sex of Arceuthobium americanum on frequency of detection of Coniothyrium sp. 1 at The Pas. July, 1981.


Mistletoe segments infected (Mean %)
Observation Times
1
2
3
4
LSD
20
10
0
Moribund ♂
Healthy ♀
Moribund ♀
0.2
0.6
2
6
Time (months)


Mistletoe segments infected (Mean %)
LSD
50
30
10
Healthy tissue
Moribund tissue
Female
Male


Mistletoe segments infected (Mean %)
Observation Times
1
2
3
LSD
4
60
40
20
0
Female tissue
Male tissue
0.2
0.6
2
6
Time (months)

4a). Clearly, the second and third examinations were sufficient to reveal the commonly occurring fungi and the majority of the rarer organisms were detected before observation 4.

While more Coniothyrium sp. 1 was recovered from moribund male tissue than from healthy female tissue at Grand Beach (Fig. 4a), the response was almost reversed at The Pas (Fig. 4b) where the greatest difference was found in the number of Coniothyrium sp. 1 isolations from female versus male mistletoe, irrespective of condition of the tissue (Fig. 4b). The interaction of observation*sex at The Pas is also the result of the highly significant effect of sex for Coniothyrium sp. 1 (Fig. 4c). At observation 1 little Coniothyrium sp. 1 was detected from dwarf mistletoe of either sex. The majority had, however, developed by observation 2, mostly on female dwarf mistletoe (Fig. 4c).

There were no interactions between factors influencing frequency of detection and isolation of A. alternata at Grand Beach (Appendix A3a). The pattern of detection of A. alternata followed that outlined above. More of the fungus was obtained from healthy than moribund tissue, although A. alternata was isolated more frequently from all tissues than either Coniothyrium sp. 1 or Cladosporium isolates.

Analysis of variance of complete data. The analysis of variance for all the fungi were highly significant.

Location. As for the July dataset, location was a highly significant factor, so the data were sorted and separate analyses performed for each of the sites (Appendix A4a, A4b, A5a, A5b, A6a,

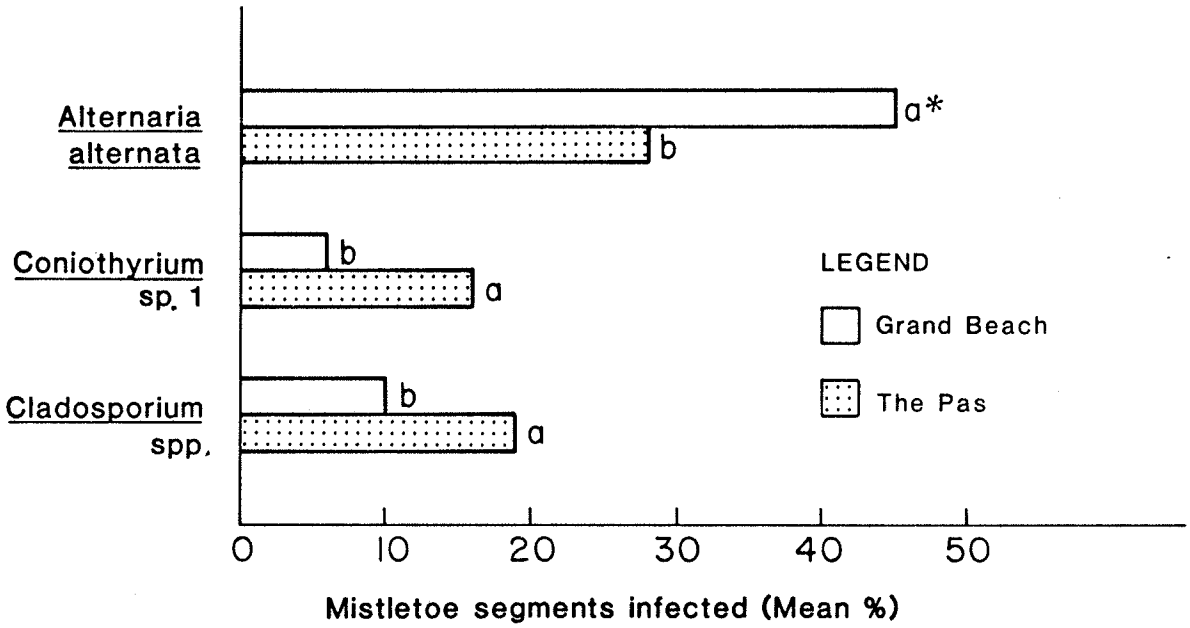
A6b). In order to show the significance of location on the differences in levels of isolation of the principal fungi the main factor effects have been described first. The frequency of isolation of all the fungi differed significantly at the two sites (Fig. 5). A. alternata was more abundant at Grand Beach whereas the other fungi were obtained more frequently from the northern site.

Significantly more A. alternata was recovered in spring and fall at both locations than during the summer (Figs. 6a, 6b). Both Coniothyrium sp. 1 and Cladosporium spp. were isolated most frequently in the spring and significantly less in the summer and fall at the two sites. A flush of spring growth after the winter may account for the high spring levels of isolation. Both A. alternata and Cladosporium spp. are phylloplane organisms and the loss of male A. pusillum shoots after the pollination period may influence their numbers. Alternatively the variation in levels may be a direct response of these fungi to climatic influences.

At the two sites the frequency of detection of all the fungi followed the same pattern as in the analysis of the July dataset (Fig. 4c). Significant increases occurred between observation times 1 and 2 and 2 and 3. Comparatively few identifications were possible at observation 1 and no significant increase occurred between observation 3 and 4 (Figs. 7a, 7b).

Alternaria alternata was found more frequently on A. americanum at Grand Beach than The Pas. However, the frequency of isolation of this fungus from A. pusillum on P. mariana was the same at both the northern and southern sites (Figs. 8a, 8b). The amount of Coniothyrium sp. 1 identified on each Dm-H association differed

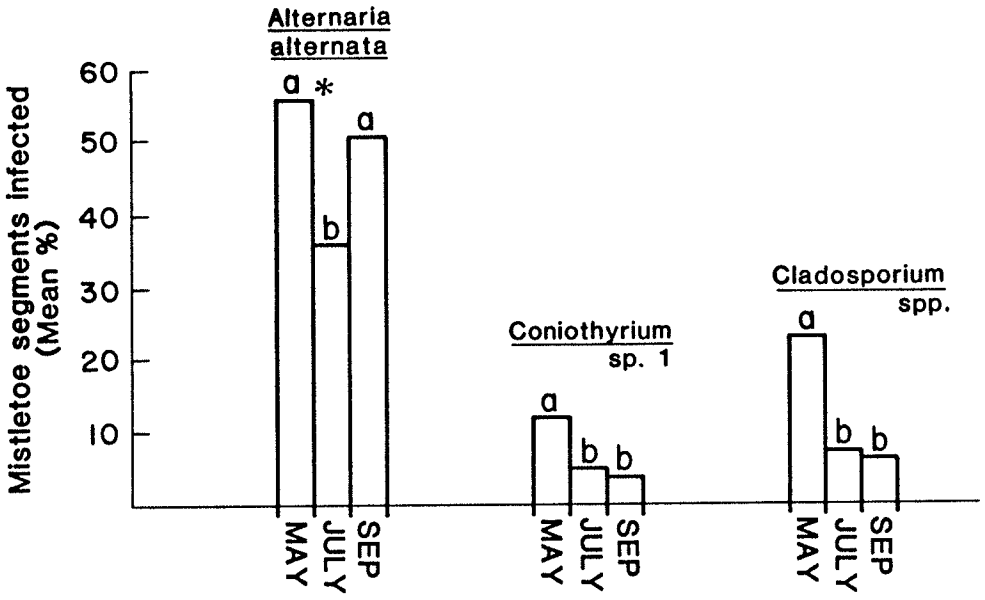
Fig. 5. Frequency of isolation of principal fungi from *Arceuthobium americanum* and *A. pusillum* at Grand Beach and The Pas, 1981.



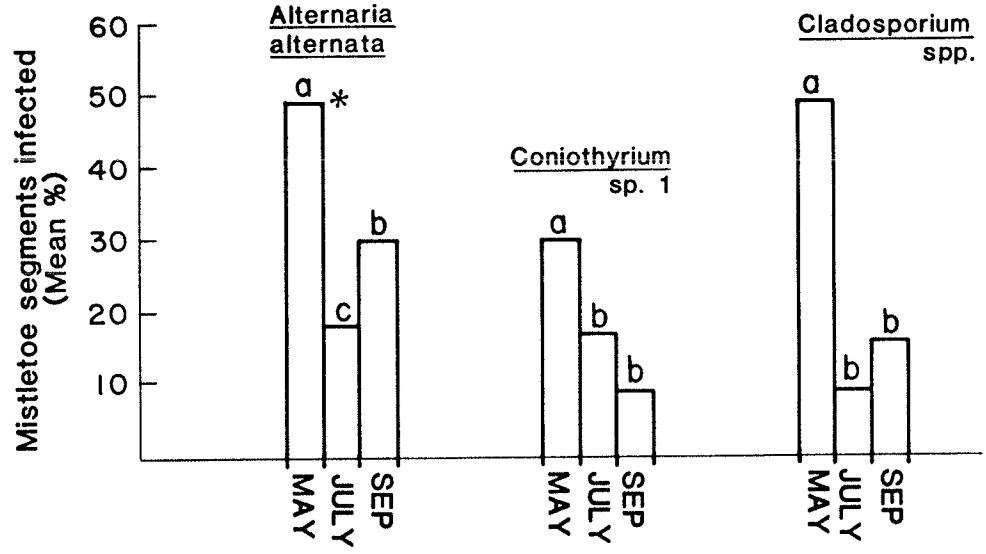
*. Bars representing different fungi followed by the same letter are not significantly different at α=0.05. Duncan's Multiple Range Test.

Fig. 6a. Frequency of isolation of principal fungi from *Arceuthobium americanum* and *A. pusillum* in spring (May), summer (July), and fall (September). Grand Beach, 1981.

Fig. 6b. Frequency of isolation of principal fungi from *Arceuthobium americanum* and *A. pusillum* in spring (May), summer (July), and fall (September). The Pas, 1981.



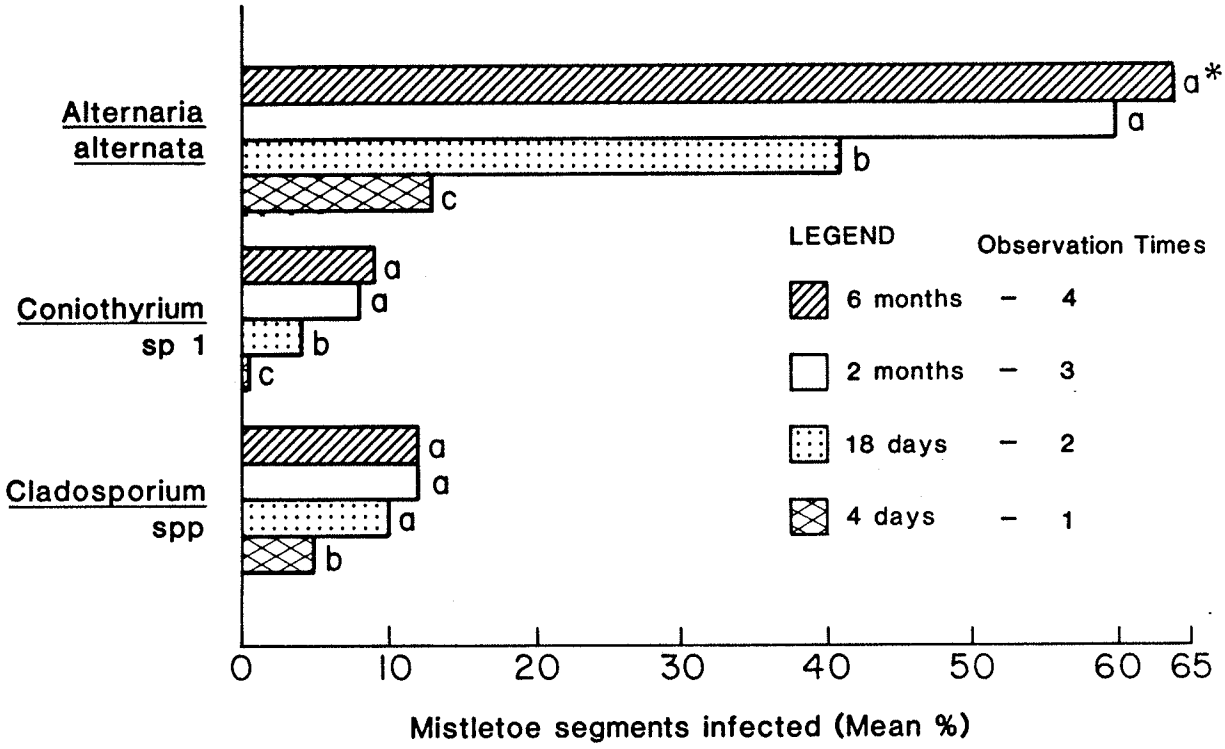
*Bars representing different fungi followed by the same letter are not significantly different at $\alpha = 0.05$. Duncan's Multiple Range Test.



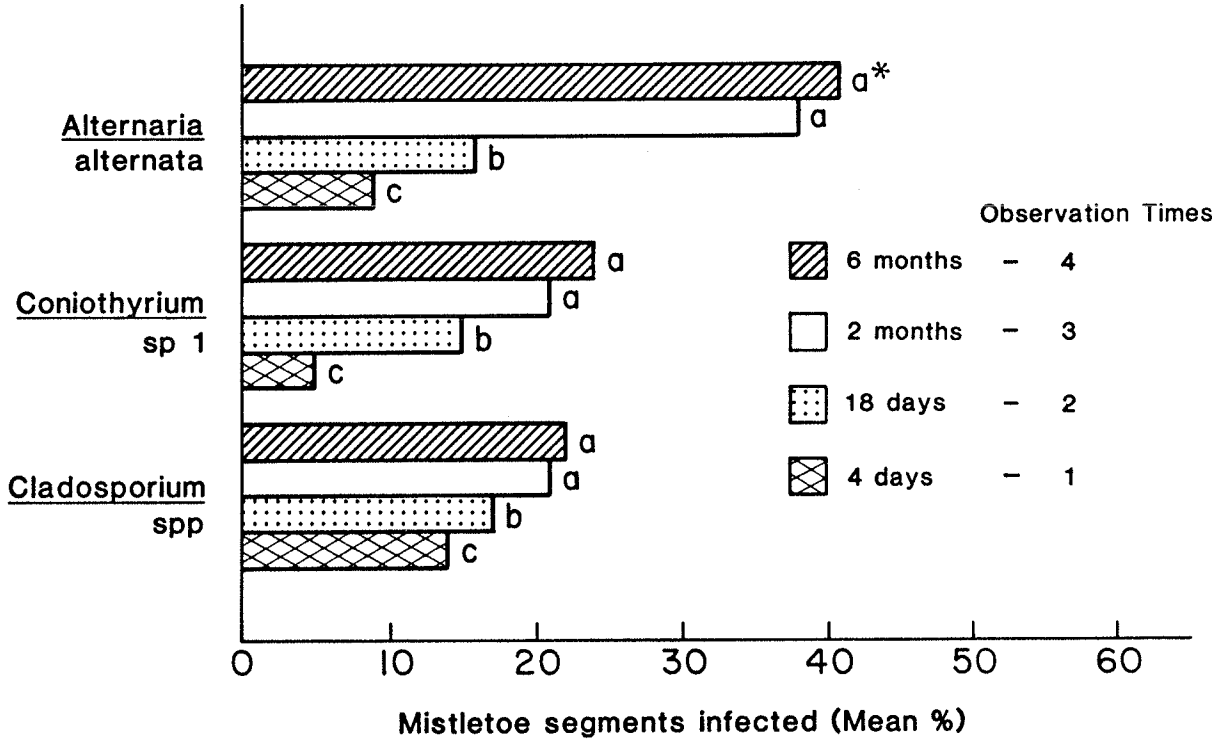
*
Bars representing different fungi followed by the same letter are not significantly different at $\alpha = 0.05$. Duncan's Multiple Range Test.

Fig. 7a. Frequency of detection of principal fungi on Arceuthobium americanum and A. pusillum after progressively longer periods of incubation. Grand Beach, 1981.

Fig. 7b. Frequency of detection of principal fungi on Arceuthobium americanum and A. pusillum after progressively longer periods of incubation. The Pas, 1981.



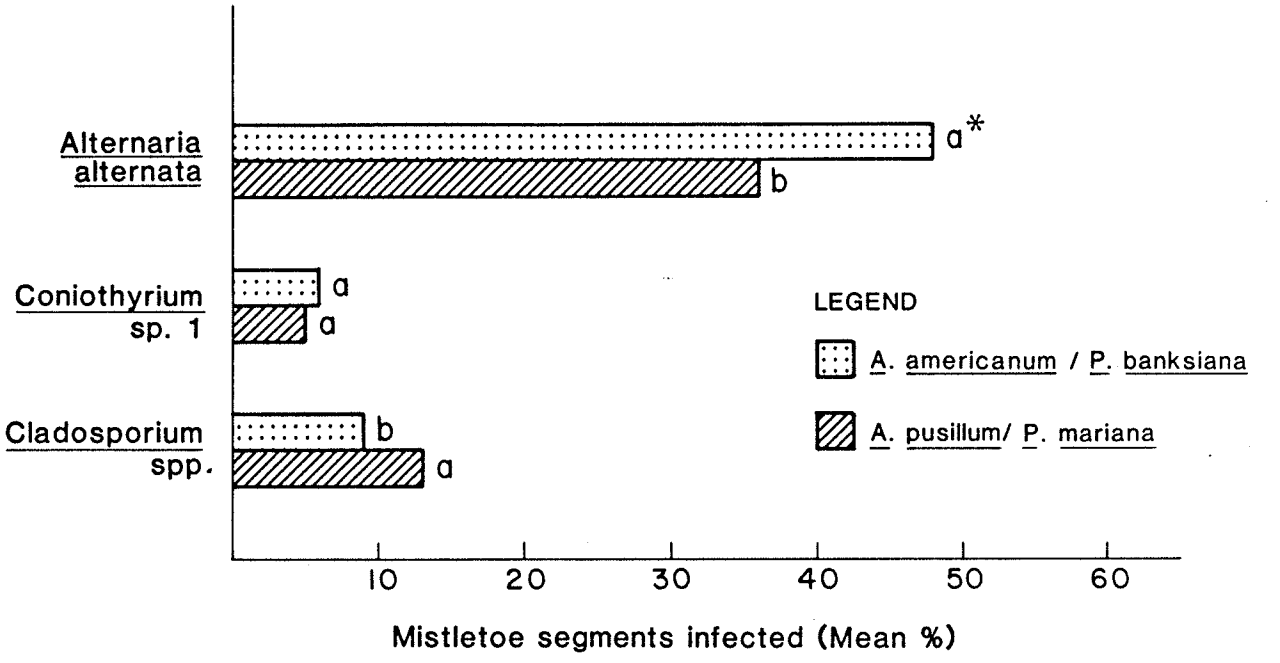
* Bars representing different fungi followed by the same letter are not significantly different at α=0.05. Duncan's Multiple Range Test.



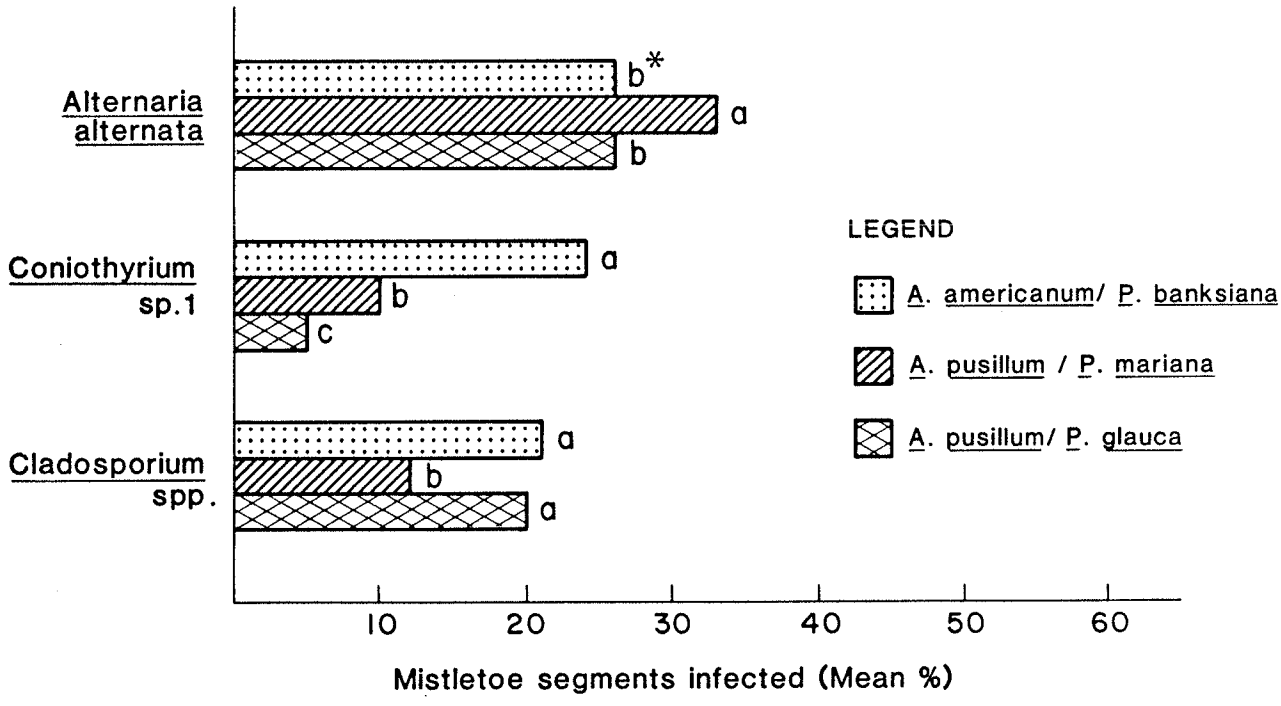
* Bars representing different fungi followed by the same letter are not significantly different at α=0.05. Duncan's Multiple Range Test.

Fig. 8a. Frequency of isolation of principal fungi from *Arceuthobium americanum* on *Pinus banksiana* and *A. pusillum* on *Picea mariana*. Grand Beach, 1981.

Fig. 8b. Frequency of isolation of principal fungi on *Arceuthobium americanum* on *Pinus banksiana* and *A. pusillum* on *Picea mariana* and *P. glauca*. The Pas, 1981.



* Bars representing different fungi followed by the same letter are not significantly different at $\alpha = 0.05$. Duncan's Multiple Range Test.



* Bars representing different fungi followed by the same letter are not significantly different at $\alpha = 0.05$. Duncan's Multiple Range Test.

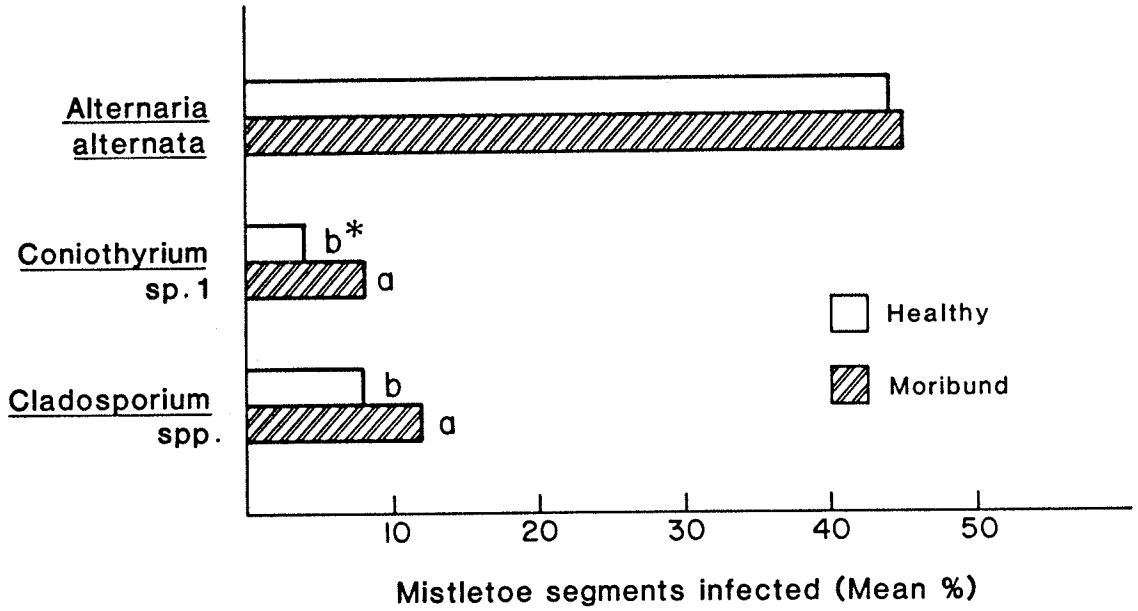
significantly at The Pas, where most was observed on A. americanum. Less Coniothyrium sp. 1 was found at Grand Beach and there was no significant difference in frequency of detection on A. americanum versus A. pusillum there. More Cladosporium isolates were recovered from A. americanum at The Pas than at Grand Beach but the number of isolations from A. pusillum on P. mariana were the same at the two sites. There was no consistent pattern to these data; for example, there was more A. alternata on A. americanum at Grand Beach than The Pas but similar frequencies observed for the same fungus on P. mariana ruling out the possibility of a simple climatic effect. Similarly the number of Cladosporium isolates was the same from A. pusillum on P. mariana at the two sites, but considerably fewer on A. americanum at Grand Beach than The Pas. No infected P. glauca was present at the site at Grand Beach so no geographical comparisons could be made for this host.

Condition of the mistletoe was significant only for Coniothyrium sp. 1 and Cladosporium spp. over all the data (Fig. 9a, 9b); both were isolated more frequently from moribund than from healthy tissue. No difference in frequency of detection of A. alternata was observed from healthy and moribund tissue suggesting that A. alternata has a greater tendency towards parasitism than the other fungi which may be saprophytic in nature.

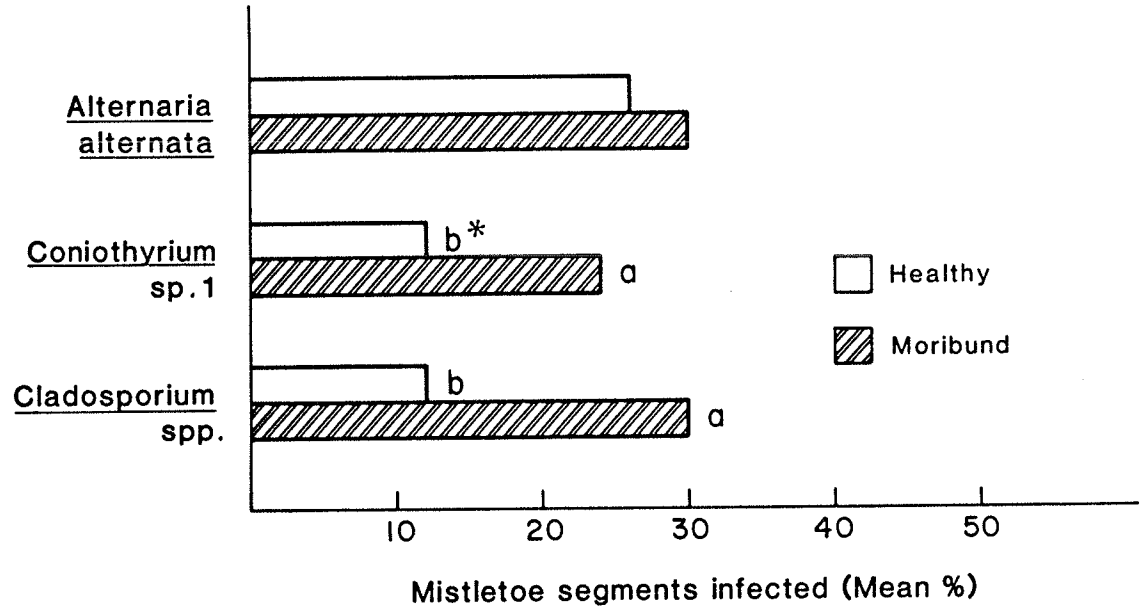
At Grand Beach, the sex of the mistletoe tissue appeared to have no effect on the frequency of isolation of Coniothyrium sp. 1 (Fig. 10a), although significantly more was recovered from female dwarf mistletoe at The Pas. Comparatively little of the fungus occurred at Grand Beach indicating possible effects of both location

Fig. 9a. Frequency of isolation of principal fungi on *Arceuthobium americanum* and *A. pusillum* in healthy and moribund condition. Grand Beach, 1981.

Fig. 9b. Frequency of isolation of principal fungi on *Arceuthobium americanum* and *A. pusillum* in healthy and moribund condition. The Pas, 1981.



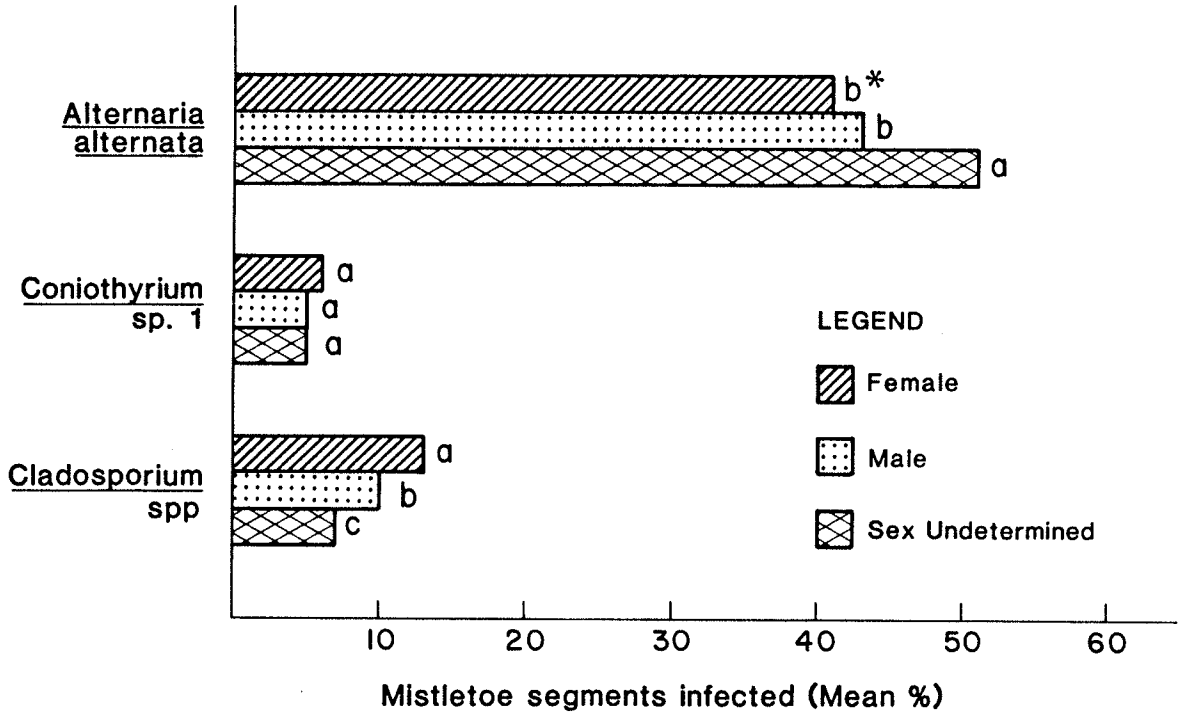
* Bars representing different fungi followed by the same letter are not significantly different at α=0.05. Duncan's Multiple Range Test.



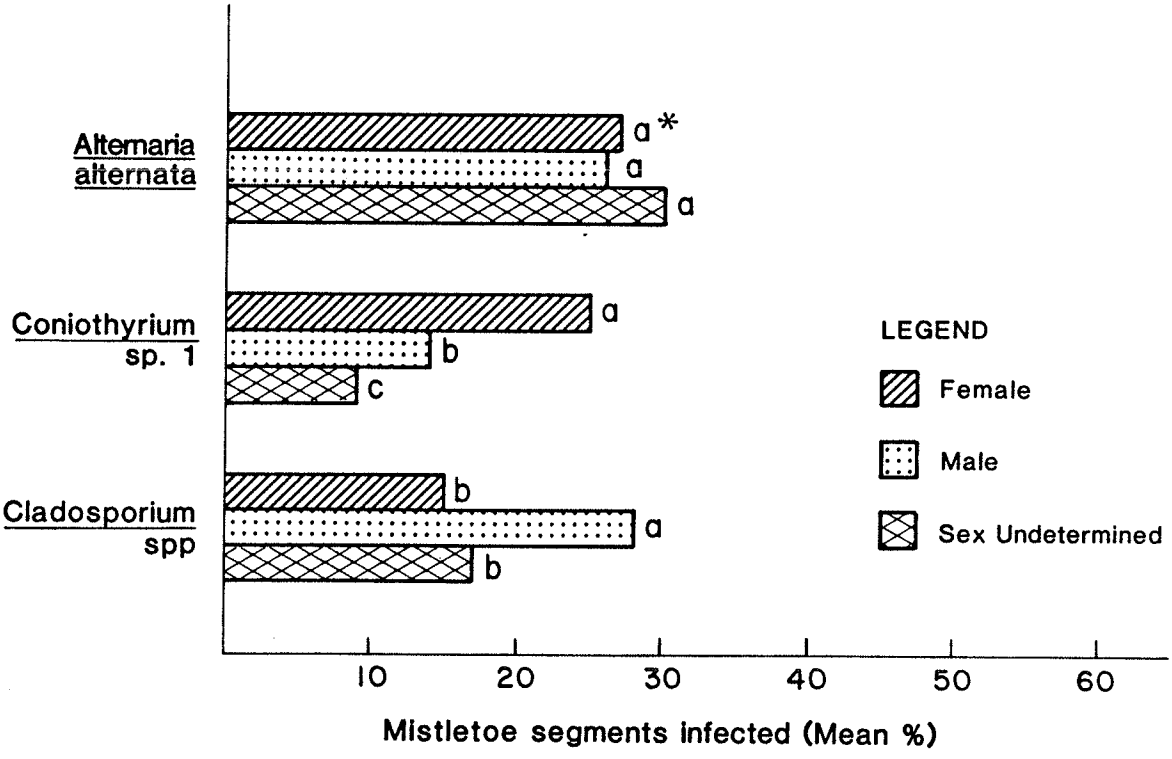
* Bars representing different fungi followed by the same letter are not significantly different at α=0.05. Duncan's Multiple Range Test.

Fig. 10a. Frequency of isolation of principal fungi recovered from male, female, and sexually undifferentiated tissue of Arceuthobium americanum and A. pusillum. Grand Beach, 1981.

Fig. 10b. Frequency of isolation of principal fungi recovered from male, female, and sexually undifferentiated tissue of Arceuthobium americanum and A. pusillum. The Pas, 1981.



* Bars representing different fungi followed by the same letter are not significantly different at α=0.05. Duncan's Multiple Range Test.



* Bars representing different fungi followed by the same letter are not significantly different at α=0.05. Duncan's Multiple Range Test.

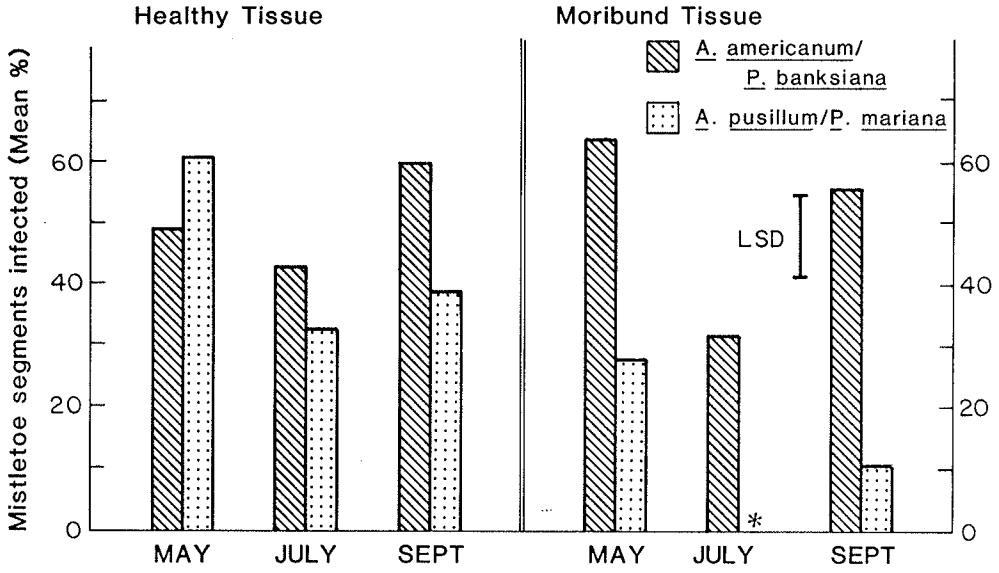
and sex of the tissue. It is unlikely that the available nutrients in male and female tissue would be sufficiently different to favour infection of female versus male tissue by Coniothyrium sp. 1. The loss of male mistletoe shoots after pollination reduced the number of male segments available in the summer sampling and it is more likely this effect that caused female tissue to appear to be favoured as a substrate.

In contrast, significantly greater numbers of isolates of Cladosporium spp. were recovered from male tissue at The Pas but comparatively more from female tissue at Grand Beach. Exceptionally high numbers of Cladosporium isolates were detected on male A. pusillum on P. glauca in the May sample (Figs. 27, 31). The effect of this was seen in Fig. 10b in which the mean percentage of all male mistletoe segments infected with Cladosporium spp. appeared high. Cladosporium isolates were generally more frequent from The Pas than Grand Beach (Figs. 8a, 8b), indicating a possible variation in geographical distribution of these fungi.

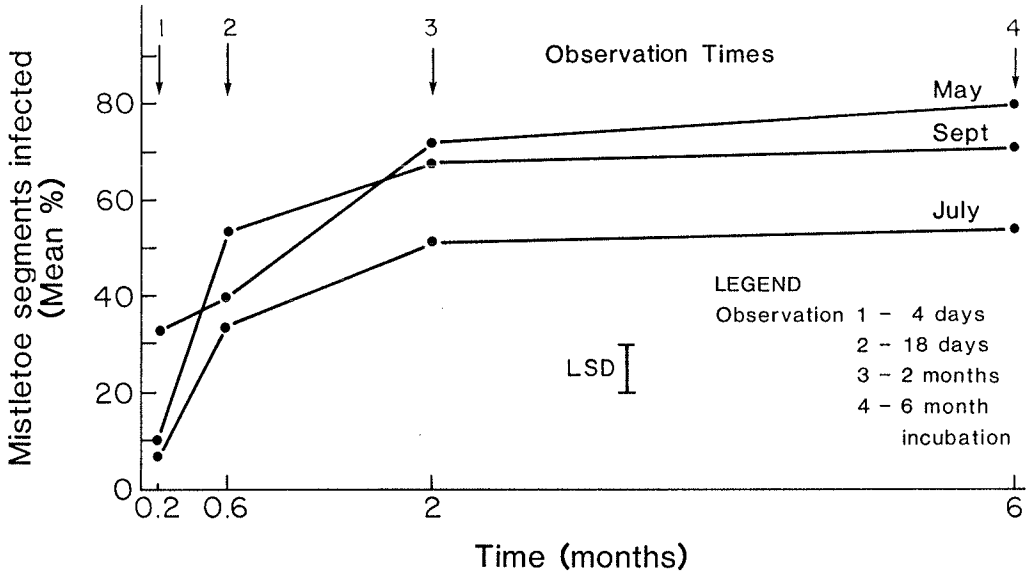
Interactions. At Grand Beach the interaction of date*Dm-H* condition on frequency of observation of A. alternata was the only significant three-way interaction (Fig. 11). Similar frequencies of the fungus on A. americanum on P. banksiana were observed from both healthy and moribund tissue in July and September although significantly more was recovered from moribund tissue in May. More A. alternata was recovered from healthy than moribund tissue of A. pusillum on P. mariana in May and September. The levels of isolation of A. alternata from both mistletoe species were consistently higher

Fig. 11. Interaction of date*dwarf mistletoe-host association* condition of Arceuthobium americanum on Pinus banksiana and A. pusillum on Picea mariana and P. glauca on frequency of isolation of Alternaria alternata. Grand Beach, 1981.

Fig. 12. Interaction of date*observation time of Arceuthobium americanum and A. pusillum on frequency of detection of Alternaria alternata. Grand Beach, 1981.



*No material in this category



in spring and fall than for the summer sample. The two-way interaction, date*observation time (Fig. 12), revealed again that the most useful observation times were 2 and 3 with no significant changes occurring between observation 3 and 4. As observed in the three-way interaction more A. alternata was recovered in spring and fall and significantly less in the summer.

The three-way interaction of Dm-H association*condition*sex on levels of A. alternata at The Pas (Fig. 13) revealed no significant difference in level of colonization between healthy and moribund tissue of either male or female material of A. americanum on P. banksiana, or of sexually undifferentiated material of A. americanum and A. pusillum on P. glauca. Significantly more A. alternata was recovered from healthy female tissue of A. pusillum on P. mariana and from moribund tissue of sexually undifferentiated material. Frequency of recovery of A. alternata was also significantly greater from moribund versus healthy female tissue of A. pusillum on P. glauca (Fig. 13). The interaction reveals that A. alternata has the capacity to parasitize both healthy and moribund material of all Dm-H associations and both sexes.

At The Pas several significant two-way interactions occurred. In the interaction of date*Dm-H association (Fig. 14) levels of colonization of A. americanum on P. banksiana by A. alternata followed the same trend as at Grand Beach (Fig. 11), but much less was recognized in July than May and September. The frequency of isolation of this fungus from A. pusillum was different from A. americanum. Less was found in May from A. pusillum on P. mariana and there was no significant difference in the number of isolations

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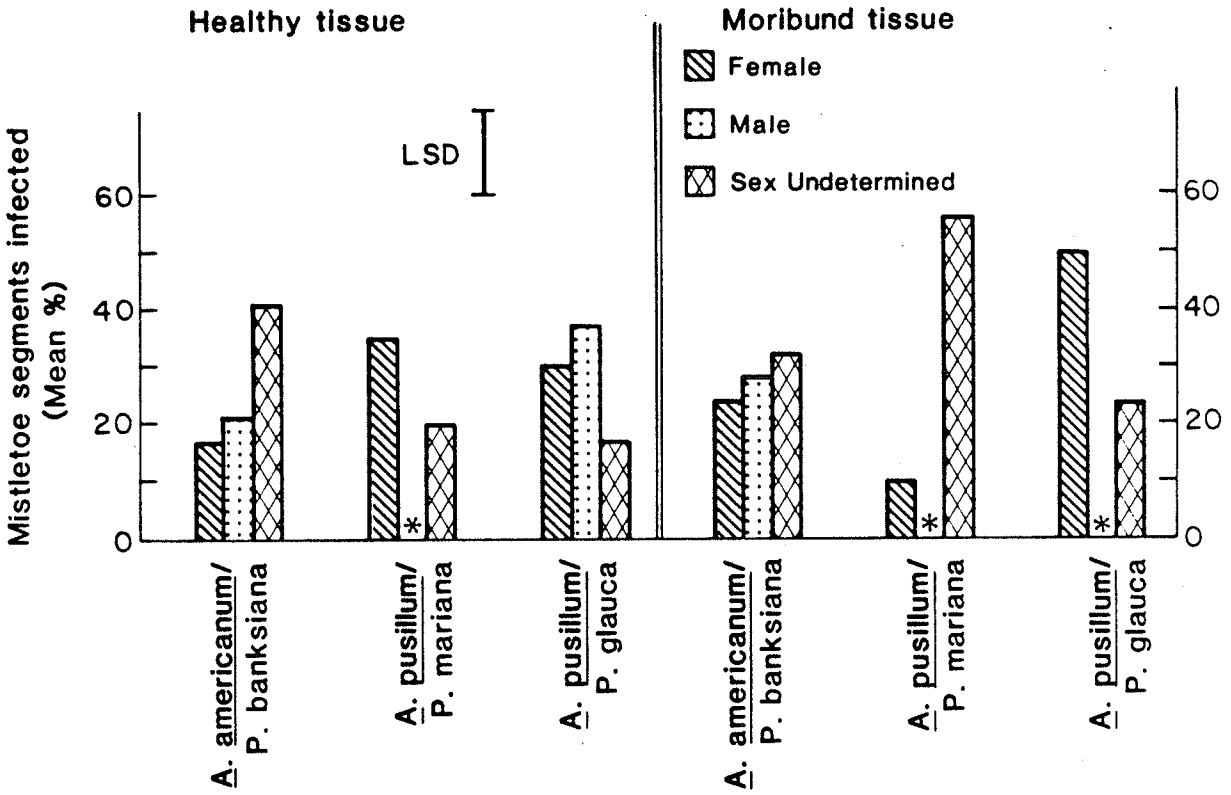
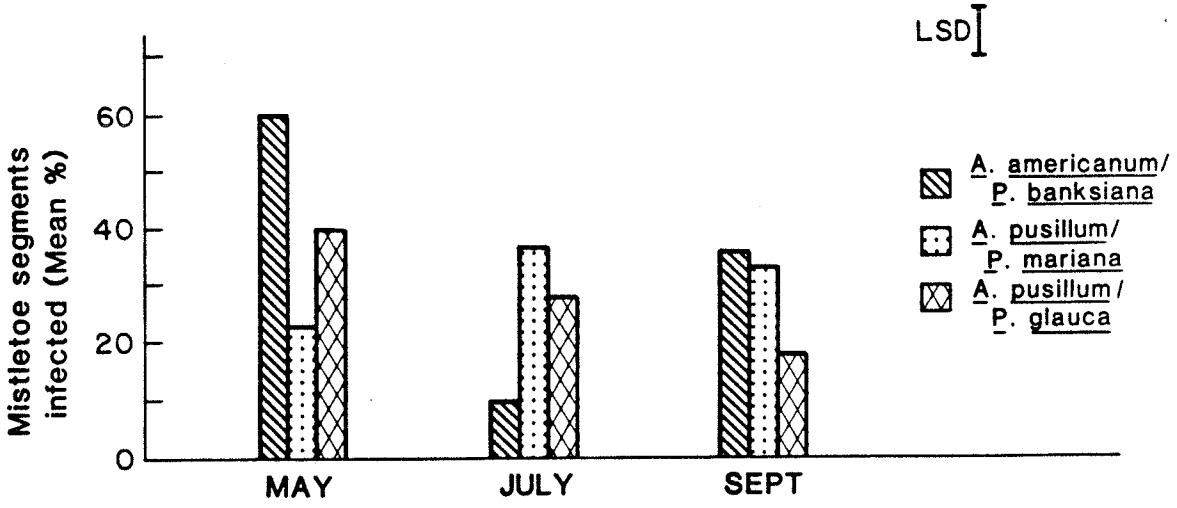
Fig. 13. Interaction of dwarf mistletoe-host association* condition*sex of Arceuthobium americanum on Pinus banksiana and A. pusillum on Picea mariana and P. glauca on frequency of isolation of Alternaria alternata. The Pas, 1981.

Fig. 14. Interaction of date*dwarf mistletoe-host association of Arceuthobium americanum on Pinus banksiana and A. pusillum on Picea mariana and P. glauca on frequency of isolation of Alternaria alternata. The Pas, 1981.



*No material in these categories.



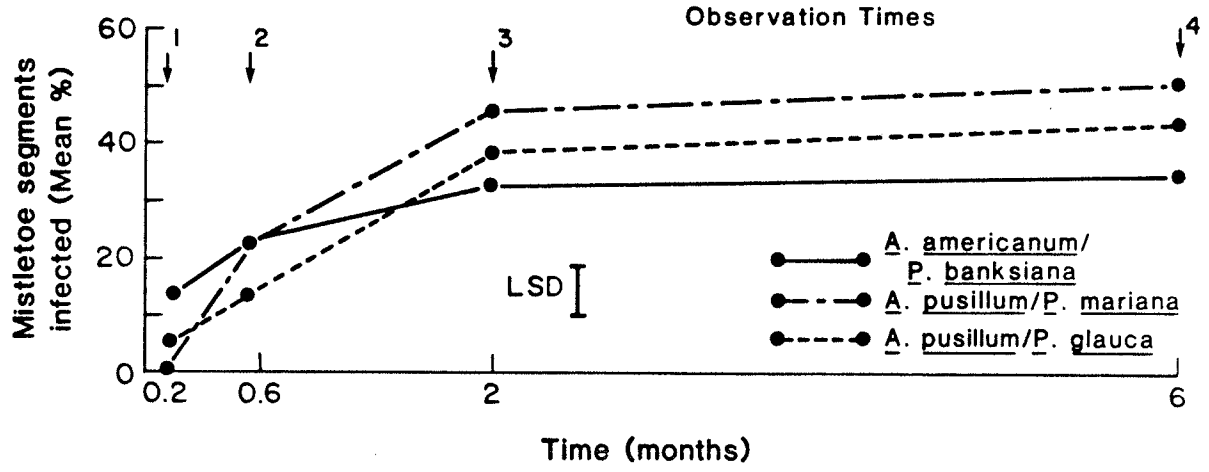
in July and September. Most A. alternata isolated from A. pusillum on P. glauca was recovered in May with significantly less in both July and September.

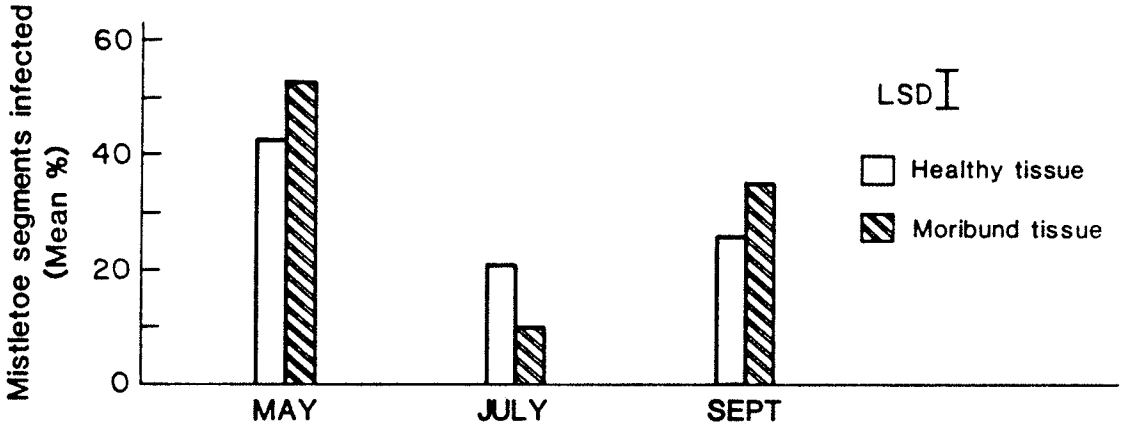
The interaction of observation*Dm-H association on isolations of A. alternata at The Pas (Fig. 15) revealed that significantly less was obtained from A. americanum on P. banksiana than from A. pusillum on either of its hosts. The very low levels found from A. americanum on P. banksiana in July (Fig. 14) affect the interaction of observation*Dm-H association, although there is no obvious explanation for the comparative scarcity of A. alternata from this Dm-H association in July at The Pas. Significantly more A. alternata was observed on moribund tissue in May and September while more was recovered from healthy tissue in July (Fig. 16). In the September sample the mistletoe was not divided according to sex; consequently the interaction of observation*sex of mistletoes on the frequency of detection of A. alternata at The Pas (Fig. 17) also reflects the influence of the September date of sampling. There was significantly more A. alternata isolated in the fall than in summer, though less than in spring (Fig. 6b). More A. alternata was taken from tissue that was not sexually differentiated than from female or male (Fig. 17). However, one plate of tissue, sexually undifferentiated, from the May sample had 75% of its segments infected with A. alternata by observation 4. Further, if the means of A. alternata infected segments from May and July (representing material divided according to sex) (Fig. 14) are compared with the frequency of isolation of A. alternata in September (sexually undifferentiated material), it is clear that the differences between male, female and sexually

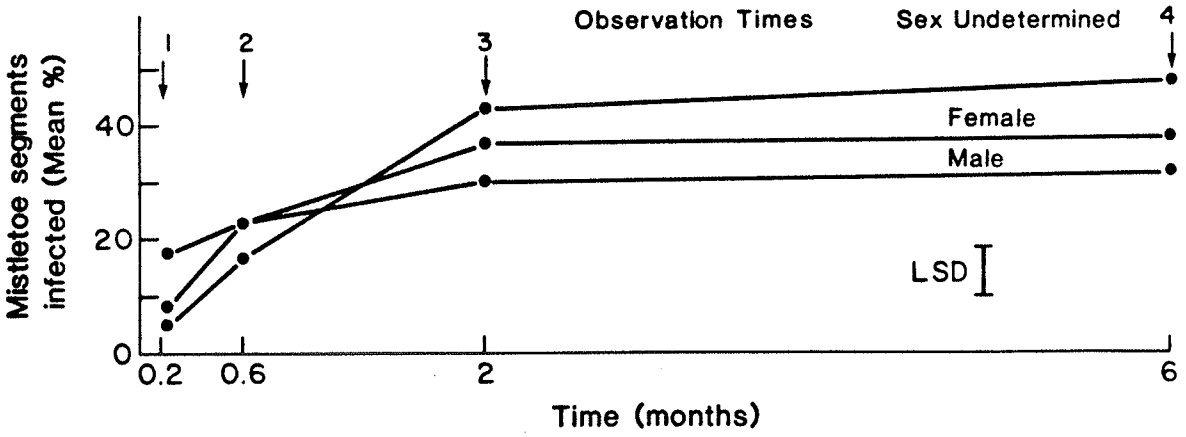
Fig. 15. Interaction of observation time*dwarf mistletoe-host association of Arceuthobium americanum on Pinus banksiana and A. pusillum on Picea mariana and P. glauca on frequency of detection of Alternaria alternata. The Pas, 1981.

Fig. 16. Interaction of date*condition of Arceuthobium americanum and A. pusillum on frequency of isolation of Alternaria alternata. The Pas, 1981.

Fig. 17. Interaction of observation time*sex of Arceuthobium americanum and A. pusillum on frequency of detection of Alternaria alternata. The Pas, 1981.


Observation Times
1
2
3
4
Mistletoe segments infected (Mean %)
60
40
20
0
LSD
A. americanum/ P. banksiana
A. pusillum/P. mariana
A. pusillum/P. glauca
0.2
0.6
2
6
Time (months)


Mistletoe segments infected (Mean %)
60
40
20
0
LSD
Healthy tissue
Moribund tissue
MAY
JULY
SEPT

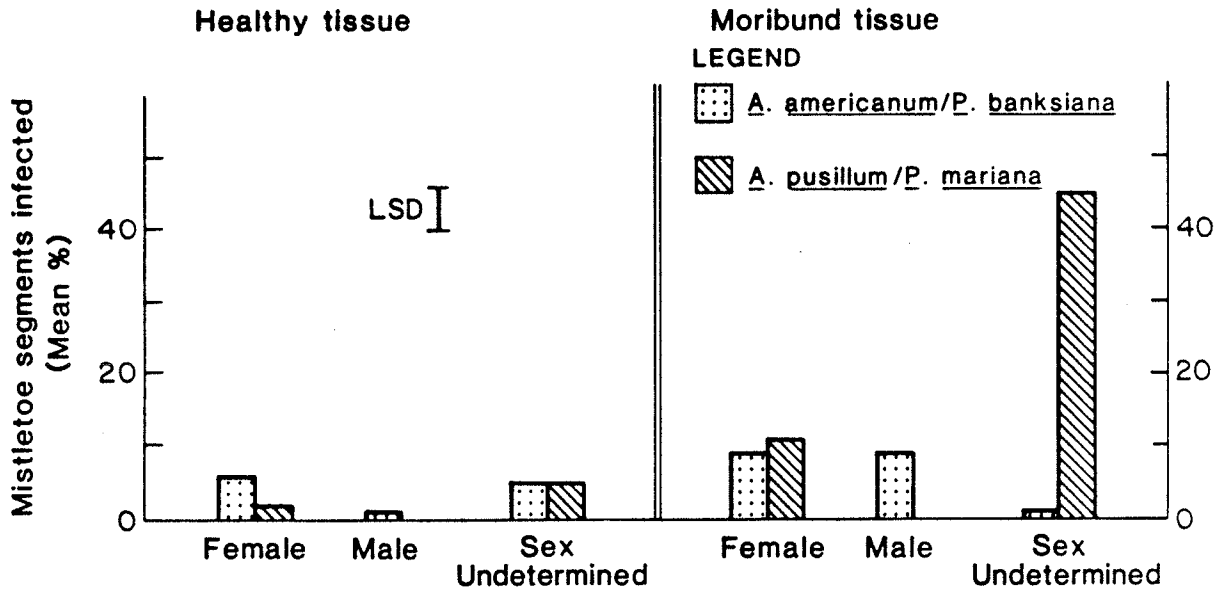

Observation Times
Sex Undetermined
1
2
3
4
Mistletoe segments infected (Mean %)
40
20
0
Female
Male
LSD
0.2
0.6
2
6
Time (months)

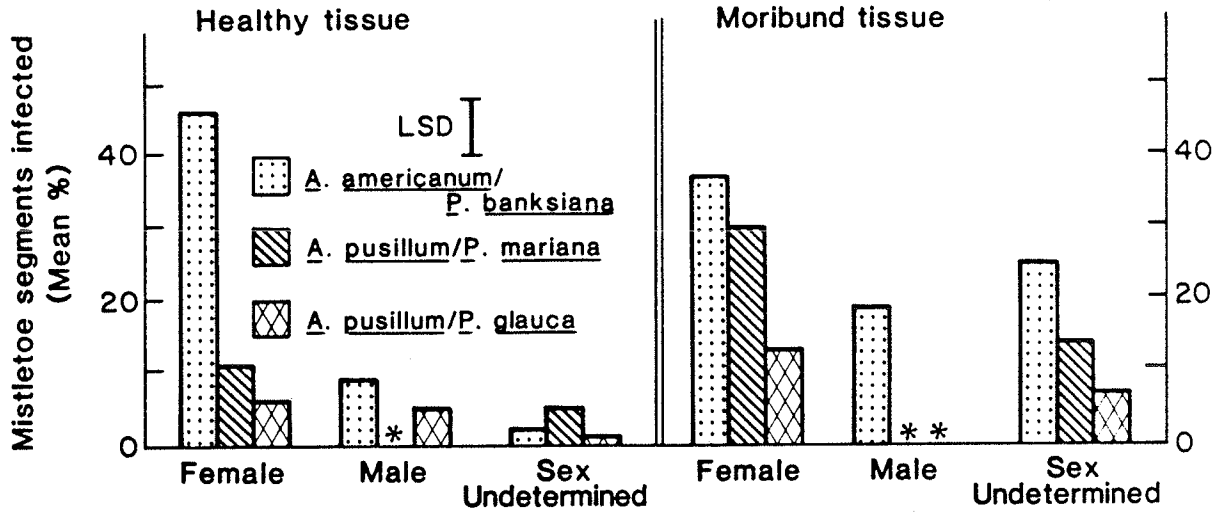
undifferentiated tissue were less significant than they appeared in Fig. 17.

Significant three- and two-way interactions on the frequency of isolation of Coniothyrium sp. 1 were more numerous at both locations. The three-way interaction of Dm-H association*condition*sex was significant at both Grand Beach and The Pas (Figs. 18, 19). Generally, little Coniothyrium sp. 1 was recovered at Grand Beach in comparison with The Pas except from A. pusillum tissue that was not classified according to sex, the majority of which came from the September sample (Fig. 18). There were no significant differences in the amount of Coniothyrium sp. 1 obtained from either Dm-H association on healthy tissue or moribund female tissue at Grand Beach (Fig. 18). Significant differences, however, occurred between healthy and moribund female A. pusillum tissue and male A. americanum tissue (Fig. 18). With one exception, considerably more Coniothyrium sp. 1 was discovered on all Dm-H associations at The Pas regardless of the sex and condition of the mistletoe (Fig. 19); less was obtained from the sexually undifferentiated A. pusillum on Picea mariana which, however, constituted only one plate and may not be representative. Except from healthy female A. americanum more Coniothyrium sp. 1 was observed on moribund tissue at The Pas and more was recovered from female tissue than either male or mixed material (Fig. 19). No Coniothyrium sp. 1 was identified on male A. pusillum, healthy or moribund, from Grand Beach. No male tissue of A. pusillum on P. mariana or male, moribund tissue of A. pusillum on P. glauca was collected at The Pas. As observed above, with the exception of healthy, female A. americanum on P. banksiana, moribund

Fig. 18. Interaction of dwarf mistletoe-host association* condition*sex of Arceuthobium americanum on Pinus banksiana and A. pusillum on Picea mariana on frequency of isolation of Coniothyrium sp. 1. Grand Beach, 1981.

Fig. 19. Interaction of dwarf mistletoe-host association* condition*sex of Arceuthobium americanum on Pinus banksiana and A. pusillum on Picea mariana and P. glauca on frequency of isolation of Coniothyrium sp. 1. The Pas, 1981.





*No Mistletoe collected in these categories.

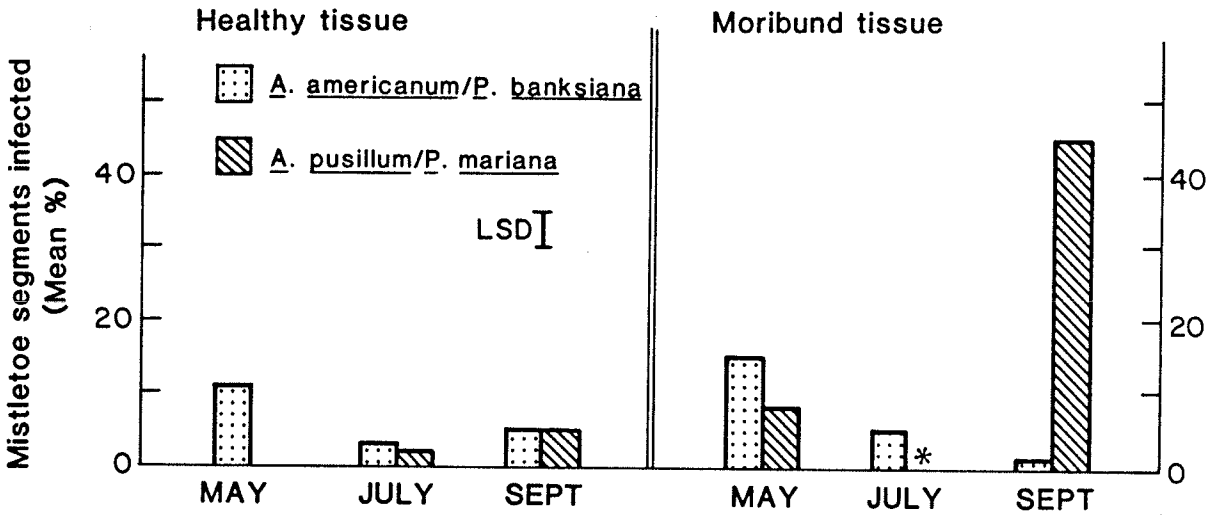
female Arceuthobium tissue appeared to be favoured by Coniothyrium sp. 1.

The three-way interaction of date*Dm-H association*condition was also significant at both locations. In general most Coniothyrium sp. 1 was isolated in May with lower frequencies observed in July and September (Figs. 20, 21). The exception was the level of isolation from moribund A. pusillum on P. mariana in the fall at Grand Beach (Fig. 20). However, moribund A. pusillum was not frequently encountered. This value was derived from incubation of a single sand plate with 14 segments which was not necessarily a representative sample. The presence of more Coniothyrium sp. 1 on moribund as opposed to healthy tissue was noted but for A. americanum on P. banksiana the difference was significant only for the September sample at The Pas (Fig. 21). The difference was significant for A. pusillum on P. mariana wherever both healthy and moribund tissue was represented. The same trend was apparent for A. pusillum on P. glauca although the differences were not significant.

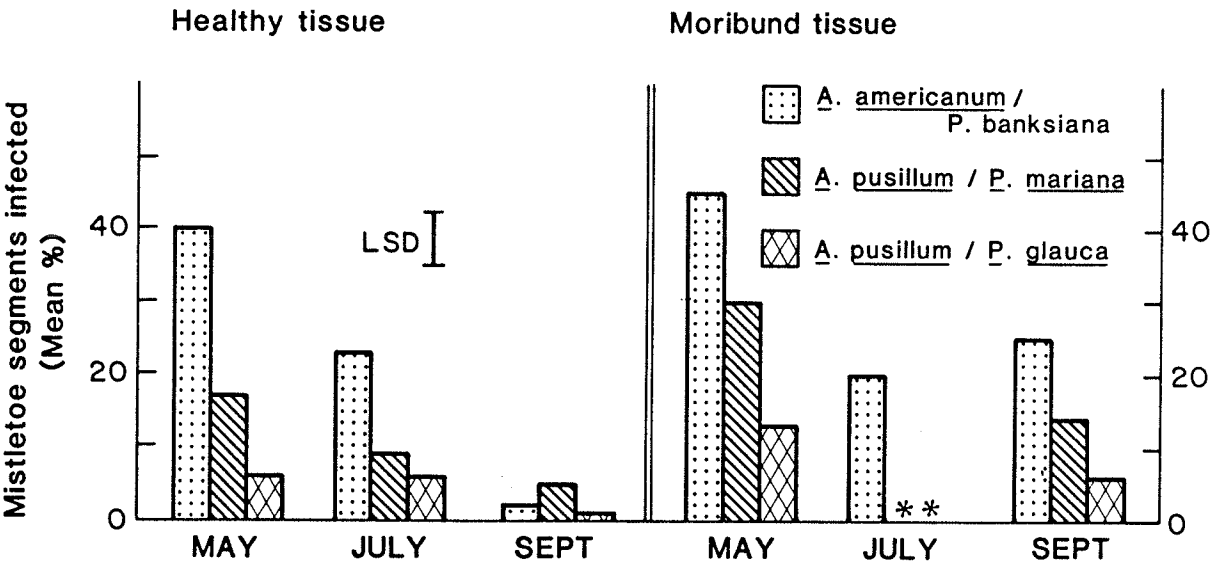
The three-way interaction for observation time*Dm-H association*sex was also significant at The Pas where more Coniothyrium sp. 1 was usually detected on female tissue (Figs. 22a-c). The difference was, however, significant only for observations 2 to 4 of A. americanum on P. banksiana (Fig. 22a). After observation 1 significantly more Coniothyrium sp. 1 was isolated from A. americanum on P. banksiana than from A. pusillum, on either of its hosts, and at observations 3 and 4 significantly more was identified on A. pusillum on P. mariana than P. glauca (Figs. 22b, c).

Fig. 20. Interaction of date*dwarf mistletoe-host association* condition of Arceuthobium americanum on Pinus banksiana and A. pusillum on Picea mariana and P. glauca on frequency of isolation of Coniothyrium sp. 1. Grand Beach, 1981.

Fig. 21. Interaction of date*dwarf mistletoe-host association* condition of Arceuthobium americanum on Pinus banksiana and A. pusillum on Picea mariana and P. glauca on frequency of isolation of Coniothyrium sp. 1. The Pas, 1981.



*No material in this category.



* No material in these categories

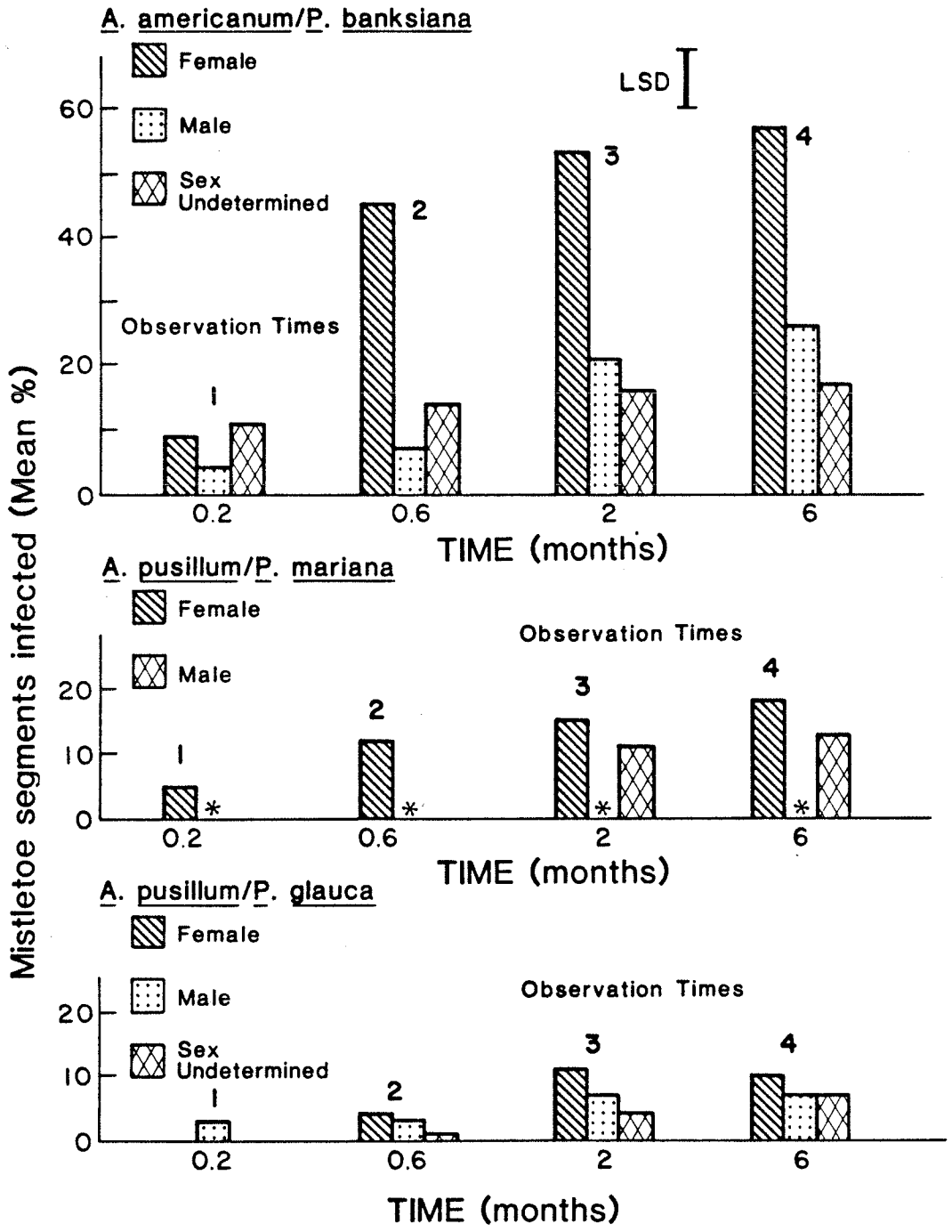
Fig. 22. Interaction of observation time*dwarf mistletoe-host association*sex of

a. Arceuthobium americanum on Pinus banksiana,

b. A. pusillum on Picea mariana, and

c. A. pusillum on P. glauca

on frequency of detection of Coniothyrium sp. 1. The Pas, 1981.



*No material in this category.

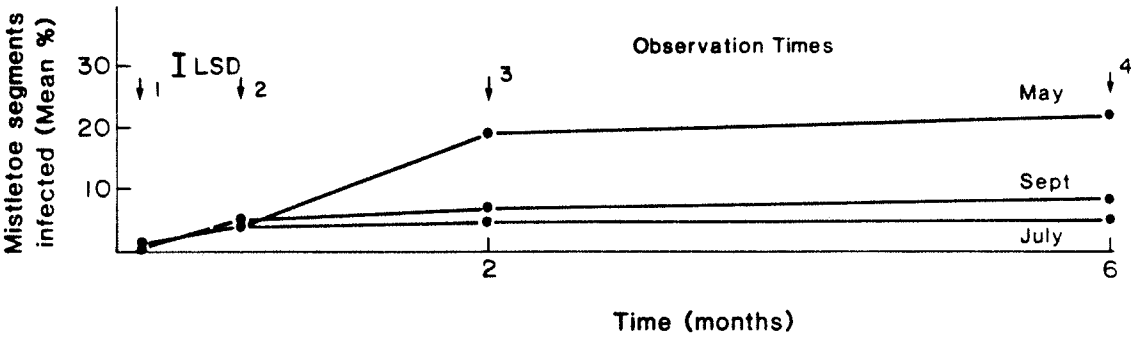
At Grand Beach two two-way interactions occurred which have not been accounted for by the three-way interactions. There were significantly more isolations of Coniothyrium sp. 1 from the May sample than from either the September or the July sample (Fig. 23). Similarly, levels of recovery were higher from female tissue than from either male or mixed material in May (Fig. 24). The two-way interaction of date*observation for Coniothyrium sp. 1 was also significant at The Pas. The trend was similar at both locations. More Coniothyrium sp. 1 was detected on the May sample but the difference between all three sampling dates was significant after observation 2 (Fig. 25). These results indicate that Coniothyrium sp. 1 pycnidia develop after two to eight weeks of incubation of Arceuthobium host tissue and this fungus is detected most frequently in spring.

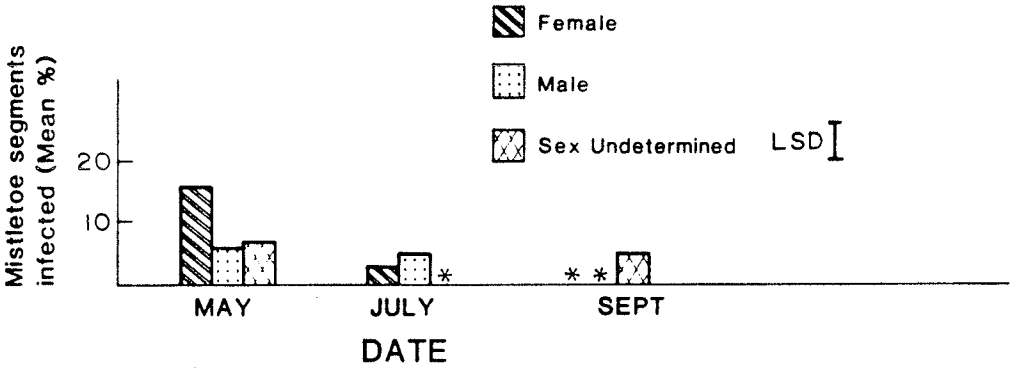
The three-way interaction of Dm-H*condition*sex was significant for Cladosporium spp. at both Grand Beach and The Pas. More of these fungi were recovered from moribund A. americanum than healthy; the differences were significant only for female mistletoe at Grand Beach, but for male and sexually undifferentiated tissue at The Pas (Figs. 26, 27). From A. pusillum on P. mariana at Grand Beach isolations were much more abundant from moribund female material than from healthy female, but none was obtained from male nor from mixed moribund material (Fig. 26). In the three-way interaction of Dm-H association*condition*sex on the number of isolates of Cladosporium spp. at The Pas (Fig. 27) no male A. pusillum on P. mariana was found and only healthy male A. pusillum on P. glauca. Where comparisons can be made, significantly more isolates were

Fig. 23. Interaction of date*observation time of Arceuthobium americanum and A. pusillum on frequency of detection of Coniothyrium sp. 1. Grand Beach, 1981.

Fig. 24. Interaction of date*sex of Arceuthobium americanum and A. pusillum on frequency of isolation of Coniothyrium sp. 1. Grand Beach, 1981.

Fig. 25. Interaction of date*observation time of Arceuthobium americanum and A. pusillum on frequency of detection of Coniothyrium sp. 1. The Pas, 1981.





*No material in these categories

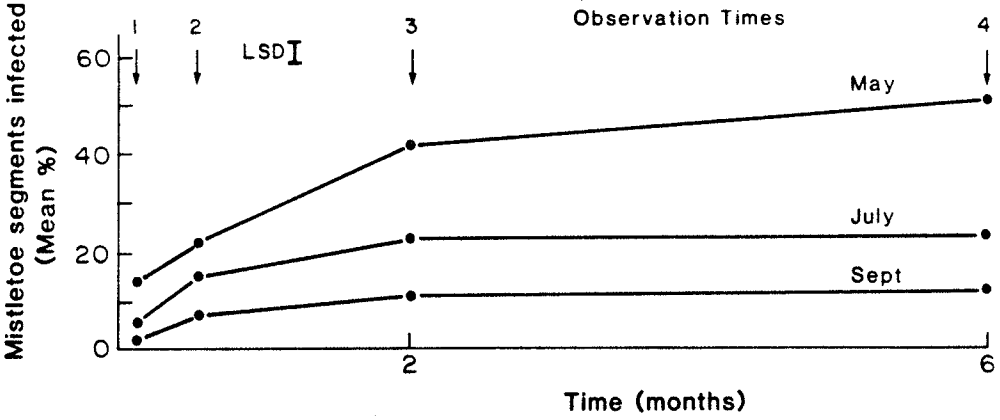
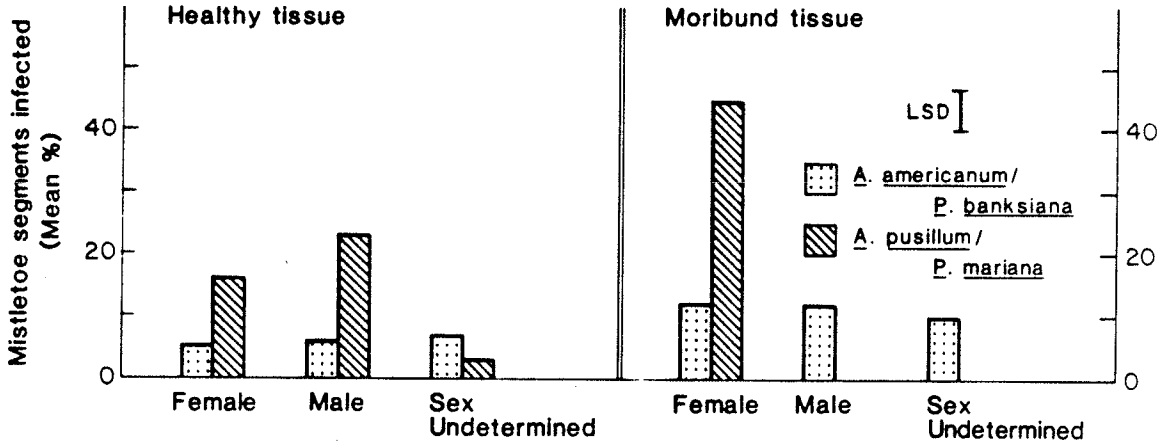
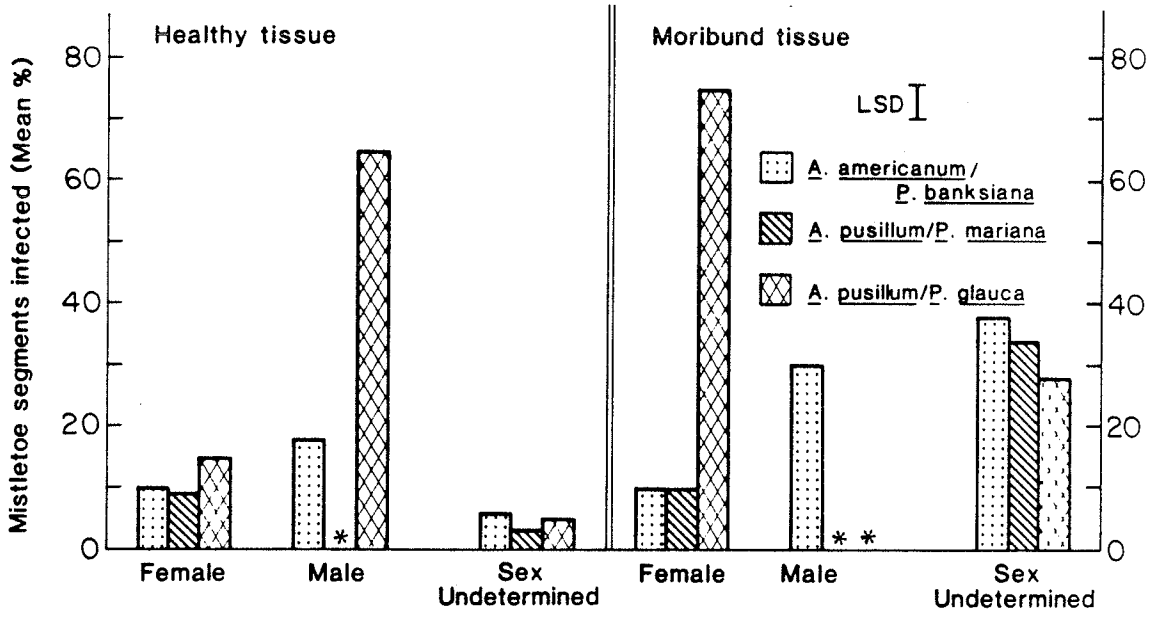


Fig. 26. Interaction of dwarf mistletoe-host association* condition*sex of Arceuthobium americanum on Pinus banksiana and A. pusillum on Picea mariana on frequency of isolation of Cladosporium spp. Grand Beach, 1981.

Fig. 27. Interaction of dwarf mistletoe-host association* condition*sex of Arceuthobium americanum on Pinus banksiana and A. pusillum on Picea mariana and P. glauca on frequency of isolation of Cladosporium spp. The Pas, 1981.





*No material in these categories.

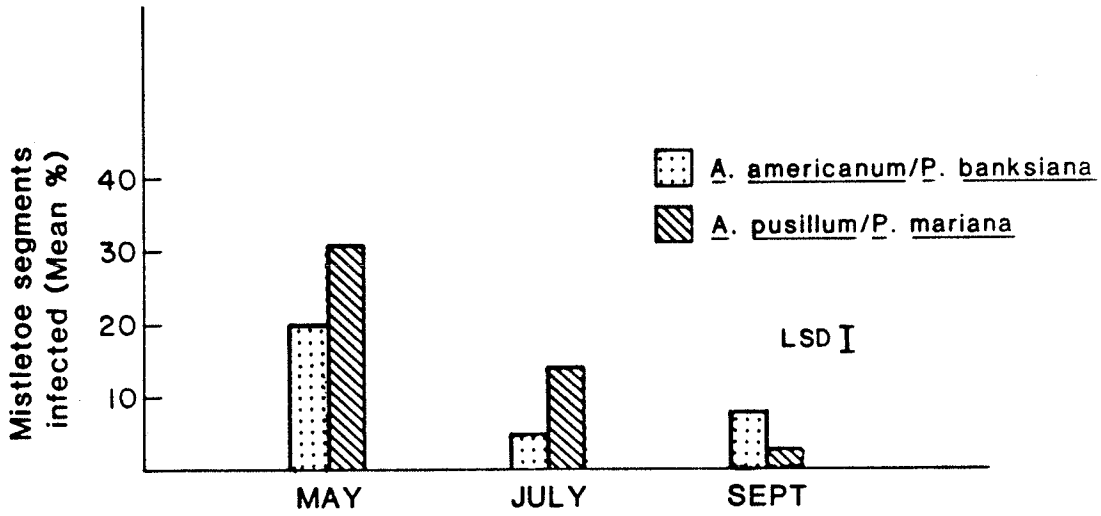
recovered from moribund tissue in all cases except between female tissue of A. americanum on P. banksiana and A. pusillum on P. mariana where condition seemed to be of no importance (Fig. 27). The three records in Figs. 26 and 27 that revealed high levels of isolation of Cladosporium spp. are not necessarily representative as only a few plates of male and moribund A. pusillum material were available; female moribund tissue of A. pusillum on P. mariana (Fig. 26), two plates, and male healthy and female moribund tissue of A. pusillum on P. glauca (Fig. 27), three plates and one plate, respectively.

The two-way interaction of date*Dm-H association was significant at both locations. Fewer isolates of Cladosporium spp. were recognized on A. americanum at Grand Beach than from The Pas, although the trend was similar at both sites (Figs. 28, 29). Most was isolated in May, less and September and least in July. The same trend was also noted in the numbers of isolates of Cladosporium spp. from A. pusillum at The Pas with exceptionally high frequencies for May on A. pusillum from P. glauca (Fig. 29). At Grand Beach significantly fewer isolates of Cladosporium spp. were detected on A. pusillum on P. mariana at each successive sampling date (Fig. 28).

At The Pas there were two other significant two-way interactions involving date. More isolates of Cladosporium spp. were recovered from moribund than healthy tissue with significant differences between the two conditions for all seasons (Fig. 30). Significantly more of these fungi were isolated in the spring than in summer or fall (Fig. 31) from all tissues regardless of sex.

Fig. 28. Interaction of date*dwarf mistletoe-host association of Arceuthobium americanum on Pinus banksiana and A. pusillum on Picea mariana on frequency of isolation of Cladosporium spp. Grand Beach, 1981.

Fig. 29. Interaction of date*dwarf mistletoe-host association of Arceuthobium americanum on Pinus banksiana and A. pusillum on Picea mariana and P. glauca on frequency of isolation of Cladosporium spp. The Pas, 1981.


Mistletoe segments infected (Mean %)
40
30
20
10
A. americanum/P. banksiana
A. pusillum/P. mariana
LSD I
MAY
JULY
SEPT

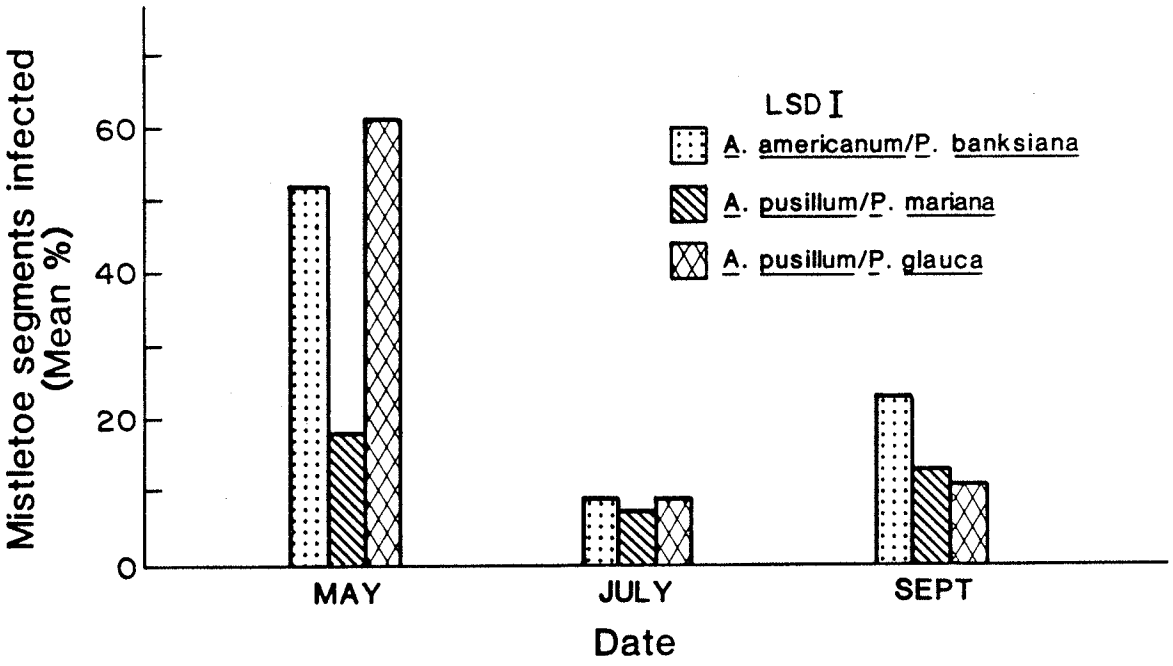
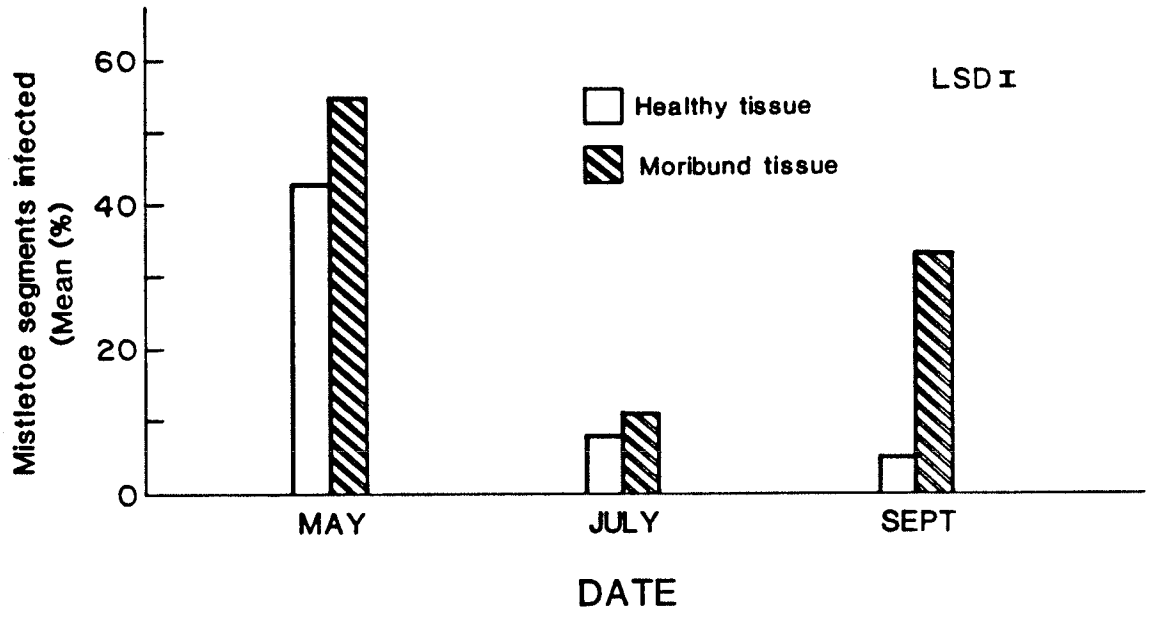
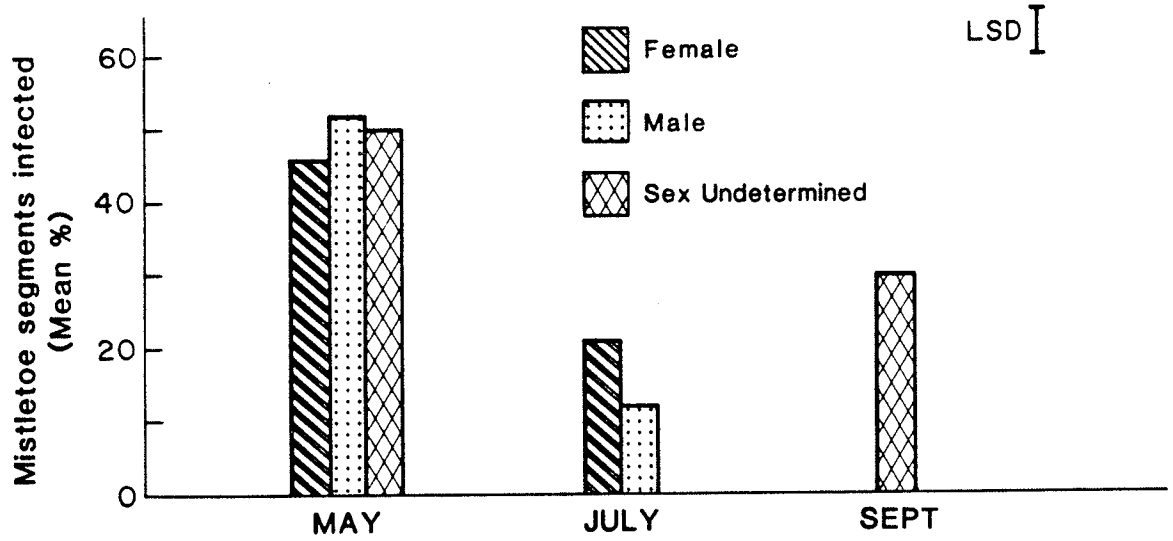

Mistletoe segments infected (Mean %)
60
40
20
0
LSD I
A. americanum/P. banksiana
A. pusillum/P. mariana
A. pusillum/P. glauca
MAY
JULY
SEPT
Date

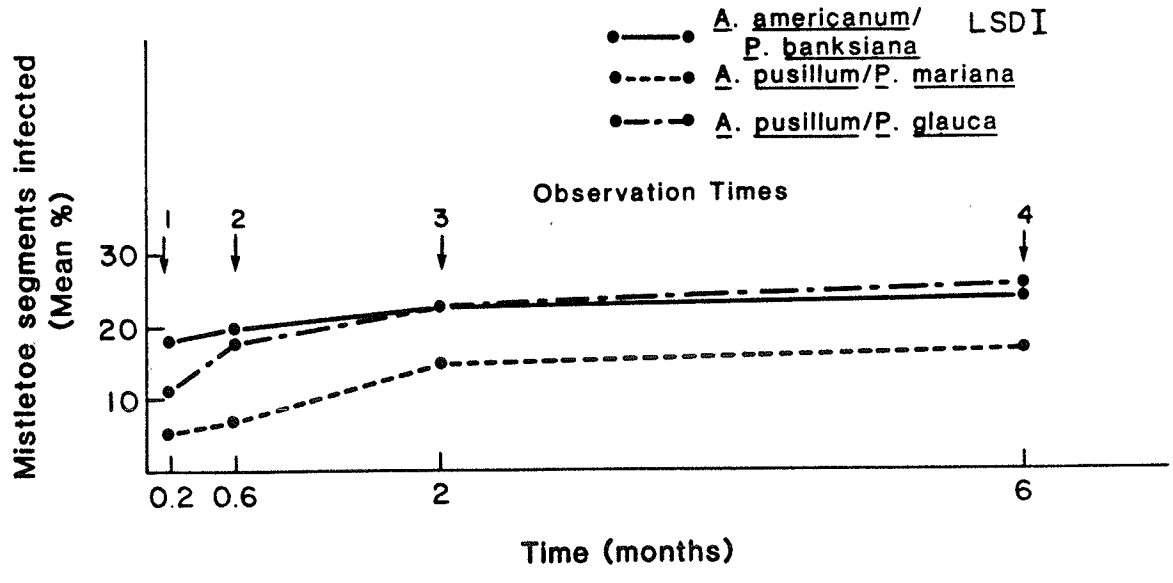
Fig. 30. Interaction of date*condition of Arceuthobium americanum and A. pusillum on frequency of isolation of Cladosporium spp. The Pas, 1981.

Fig. 31. Interaction of date*sex of Arceuthobium americanum and A. pusillum on frequency of isolation of Cladosporium spp. The Pas, 1981.

Fig. 32. Interaction of observation time*dwarf mistletoe-host association of Arceuthobium americanum on Pinus banksiana and A. pusillum on Picea mariana and P. glauca on frequency of detection of Cladosporium spp. The Pas, 1981.


Mistletoe segments infected
(Mean (%)
60
40
20
0
LSD I
Healthy tissue
Moribund tissue
MAY
JULY
SEPT
DATE


Mistletoe segments infected
(Mean %)
60
40
20
0
LSD I
Female
Male
Sex Undetermined
MAY
JULY
SEPT


Mistletoe segments infected
(Mean %)
A. americanum/ P. banksiana
A. pusillum/P. mariana
A. pusillum/P. glauca
LSD I
Observation Times
1
2
3
4
30
20
10
0.2
0.6
2
6
Time (months)

Significantly more were recovered from female tissue in July but if isolations from female and male material are summed there appears to have been no significant difference in frequency between July and September. The preceding interactions (Figs. 28, 29, 30, 31) indicated that significantly more isolates of Cladosporium spp. were recovered in spring than in summer or fall. However, the number of plates for moribund and male A. pusillum were few (0-5), and these data may not be representative. The interaction of observation*Dm-H association showed that by observation 4 the majority of isolates of Cladosporium spp. were detected on A. pusillum on P. glauca though the difference between frequencies of isolation from this Dm-H association and A. americanum on Pinus banksiana was not significant after observation 1 (Fig. 32). Significantly fewer Cladosporium isolates were recovered from A. pusillum on P. mariana (Fig. 32).

Comparison of analysis of July dataset with overall data. In the July dataset only three significant interactions occurred (Figs. 4a-c). Coniothyrium sp. 1 was frequently isolated from female Arceuthobium tissue and each of the significant interactions involved the sex of the mistletoe. In comparison, with the addition to the analysis of the factors date and Dm-H association, the number of significant interactions was greatly increased and only one out of 22 did not involve either one or both of these factors justifying the analysis of the total set of data. However, the lack of complete datasets in the overall analysis may sometimes have resulted in interactions that are of questionable significance; for example,

the effect of date on frequency of isolation of Cladosporium spp. (Figs. 28-31) in interactions involving date of collection of A. pusillum. It is usual to analyze a study with unbalanced data using a GLM procedure in SAS; it was found, however, that GLM required too much memory for this project and failed to run even at the lowest priority rating. However, the number of plates of mistletoes in each category was generally large enough so that while the statistical figures might differ the interpretation of the data would be the same. Difficulties have arisen where interactions occurred involving date of collection of A. pusillum, for which male and moribund material was scarce. During the early stages of the analysis it appeared that sex was not an important factor and consequently material was not differentiated according to sex in the September sample. It was later found to be significant for at least one of the commonly isolated fungi, and for that reason the analysis would have been improved had the factor not been dropped.

Rarely Isolated Fungi

The number of genera represented as a percentage of the total was 64% at Grand Beach and 61% at The Pas, but more isolates of rarely encountered fungi were recovered from The Pas than Grand Beach; 462 versus 208, respectively (Table 4). The greatest differences in frequency of isolation occurred for Colletotrichum sp., Seimatosporium lichenicola (Corda) Shoemaker and Muller, Truncatella sp. and Aureobasidium pullulans, all of which were recovered only, or more often, from the northern site. However, at Grand Beach

Table 4. Rarely isolated fungi from Arceuthobium americanum and A. pusillum at Grand Beach and The Pas, 1981

Fungi	Grand Beach 2 Dm-H associations	The Pas 3 Dm-H associations
Pyrenomycetes		
Ascomycetes (Unid.)	1	3
Chaetomium sp.	2	0
Chaetomium elatum Kunze	5	0
Sordaria spp.	1	0
Loculoascomycetes		
Pleospora sp.	1	0
Coelomycetes		
Colletotrichum gloeosporioides	0	4
Colletotrichum sp.	24	75
Coniothyrium sp. 2	12	30
Coniothyrium sp. 3	1	0
Coniothyrium sp. 4	1	1
Cryptosporiopsis sp.	0	2
Cytospora sp.	5	9
Naemospora sp.	1	0
Phoma sp.	10	21
Pycnidiella resinae	1	0
Pycnidial sp. (Unid.)	1	1
Seimatosporium lichenicola	0	21
Truncatella sp.	0	38
Hyphomycetes		
Hyphomycetes (Unid.)	0	8
Arthrinium phaeospermum	2	19
Aspergillus sp.	1	0
Aureobasidium pullulans	34	127
Drechslera sp.	6	7
Epicoccum purpurascens	28	25
Fusarium sp.	0	2
Monodyctis sp.	3	0
Nigrospora sp.	2	8
Penicillium thomii	0	1
Penicillium spp.	14	2
Stachybotris atra	0	5
Ulocladium sp.	3	0
Mycelia sterilia (Unid.)	49	50
Actinomycetes (Unid.)	1	1
Total Isolations	208	462
% Genera Represented	64	61

only two dwarf mistletoe-host associations were represented versus three at The Pas, which accounts at least in part for the difference noted.

The majority of isolations, 60%, were from A. americanum on Pinus banksiana as opposed to A. pusillum on either of its hosts (Table 5, Appendix A8, A9, A10), a fact that may reflect the scarcity of male and moribund A. pusillum rather than a host preference for one of the mistletoes. Most of the rarely isolated fungi were recovered in July, 51%, (Table 5) with 19% and 30% recovered in May and September, respectively. This is in contrast to the three principal fungi which were generally isolated more frequently in May, less in September, and least in July. It is possible that competition from A. alternata, Coniothyrium sp. 1 and Cladosporium spp. prevented the establishment of rare fungi in spring and accounted for their decline again in the fall.

A list of the fungal associations reported for A. pusillum on P. mariana and P. glauca is given as well as a list of fungi associated with A. americanum on P. banksiana (Table 6). The differences in genera associated with A. americanum and A. pusillum in Manitoba are slight in comparison with the different mycofloras associated with Arceuthobium species in Manitoba and British Columbia suggesting that the fungi are more dependent on climatic and environmental factors than on the Arceuthobium host.

Eight genera of fungi from the Ascomycotina were isolated from A. americanum and A. pusillum, the same number reported in an earlier study in Manitoba (Gilbert, 1981). However, only Sordaria sp. and Chaetomium sp. were represented in both studies. A survey

Table 5. Frequency of isolation of rarely encountered fungi from *Arceuthobium americanum* on *Pinus banksiana* and *A. pusillum* on *Picea mariana* and *P. glauca* at Grand Beach and The Pas in May, July, and September, 1981.

Date	*A. americanum*/ *P. banksiana*	*A. pusillum*/ *P. mariana*	*A. pusillum*/ *P. glauca*	%
May	87	18	25	19
July	243	72	25	51
September	73	73	54	30
%	60	24	16	

Table 6. Survey of fungi from three dwarf mistletoe-host associations in Manitoba, 1981.

Fungus	*Arceuthobium americanum*/ *Pinus banksiana*	*A. pusillum*/ *Picea mariana*	*A. pusillum*/ *Picea glauca*
Pyrenomycetes			
Chaetomium elatum	+	-	-
Chaetomium sp.	+	+	-
Sordaria spp.	+	-	-
Wallrothiella arceuthobii	+	+	+
Loculoascomycetes			
Pleospora sp.	+	+	-
Coelomycetes			
Colletotrichum gloeosporioides	+	-	-
Colletotrichum sp.	+	+	+
Coniothyrium sp. 1	+	+	+
Coniothyrium sp. 2	+	+	+
Coniothyrium sp. 3	-	+	-
Coniothyrium sp. 4	+	-	-
Cryptosporiopsis sp.	-	-	+
Cytospora sp.	+	+	+
Naemospora sp.	-	+	-
Phoma sp.	+	+	+
Seimatosporium lichenicola	+	-	+
Truncatella sp.	-	+	+
Hyphomycetes			
Acremonium charticola (Lindau) K. W. Gams	-	+	-
Alternaria alternata	+	+	+
Arthrinium phaeospermum	+	+	+
Aspergillus sp.	+	-	-
Aureobasidium pullulans	+	+	+
Cladosporium spp.	+	+	+
Drechslera sp.	+	+	+
Epicoccum purpurascens	+	+	+
Fusarium sp.	+	-	-
Monodyctis sp.	+	-	+
Nigrospora sp.	+	-	+
Penicillum thomii	-	-	+
Penicillum spp.	+	+	-
Stachybotris atra	+	+	-
Ulocladium sp.	+	-	-

of mycoflora associated with the wood of dwarf mistletoe cankers on western hemlock in British Columbia revealed different fungi from the Ascomycotina and very few imperfect fungi (Baranyay, 1966; Funk et al., 1973; Funk and Baranyay, 1973; Funk and Smith, 1981).

The present study has identified a number of Coelomycetes reported on Arceuthobium species in Manitoba for the first time. The pycnidia of the four Coniothyrium species are morphologically similar, but the spores differ in terms of size, colour and thickness of the spore wall. Coniothyrium sp. 1 was frequently recovered from A. americanum and occasionally from the wood associated with A. americanum cankers in Manitoba (Gilbert, 1981). Cryptosporiopsis sp., Naemospora sp., Phoma sp. and Seimatosporium lichenicola are reported in association with dwarf mistletoes for the first time. A Truncatella species, T. truncata, was recovered from the cankers of A. tsugense on western hemlock in British Columbia (Baranyay, 1966) and Cytospora abietis was isolated frequently from red and white firs that were infected with A. campylopodum (Scharpf, 1969). However, this is the first report of Truncatella sp. from A. pusillum and of Cytospora sp. isolated from tissue of dwarf mistletoe itself.

Colletotrichum gloeosporioides, reported from A. americanum in Manitoba for the first time, has been associated with anthracnose of dwarf mistletoes for many years (Wright, 1942). Of interest is the second Colletotrichum sp. which occurred much more frequently than C. gloeosporioides and which was also reported in Gilbert's (1981) earlier study. Colletotrichum sp. appeared to respond to climatic stimuli as it was isolated rarely in spring (1), frequently in summer (74), and less in the fall (24). The majority of isola-

tions of the fungus were from moribund tissue but a significant number were from healthy tissue suggesting parasitic capabilities and potential as a biological control agent. Pycnidiella resinae (Fr. ex Fr.) Höhnel was recorded rarely in both the present and the earlier study (Gilbert, 1981).

A number of plurivorous Hyphomycetes (Ellis, 1971) apart from the commonly isolated A. alternata and Cladosporium spp. were isolated. These included Arthrinium phaeospermum (Corda) M. B. Ellis, Aureobasidium pullulans, Epicoccum purpurascens, Drechslera sp., Nigrospora sp., Ulocladium sp. and Stachybotris atra Corda. A. pullulans and E. purpurascens were comparatively common although less so than A. alternata and Cladosporium spp., but these four comprise the genera that were implicated in resin disease (Mark et al., 1976). Resin impregnated A. americanum has been observed during the present study, but the fungi have been isolated from both healthy and moribund tissue and are unlikely to be the sole cause of resin disease. The present study includes most of the Hyphomycetes recovered in the earlier study (Gilbert, 1981), while extending the number of known genera associated with A. americanum in Manitoba.

The percentage of fruits of A. americanum parasitized by Wallrothiella arceuthobii was 50% in 1981 and 39% in 1983 (Table 7). The broom counted in 1981 had 467 developing fruits of which 233 were infected with the fungus. In 1983, 73 of 185 developing fruits were parasitized. On both occasions examinations were made because W. arceuthobii appeared to be abundant. Brooms with such a high percentage of infected flowers were not commonly seen during the investigation.

Table 7. Fruits of *Arceuthobium americanum* parasitized by *Wallrothiella arceuthobii* in Belair Provincial Forest, 1981 and 1983.

Date	Developing fruits	Fruits infected with *W. arceuthobii*	%
1981	467	233	50
1983	185	73	39

The specificity of W. arceuthobii for female flowers of spring flowering Arceuthobium species and its apparent abundance, initially led to hopes that the fungus might be used to control dwarf mistletoes. Weir (1915) saw 100% of the 400 fruits on a small broom attacked and Dowding (1931b) found stands of Pinus banksiana at Victoria Beach, Manitoba, in which at least 80% of the fruits were parasitized. However, the sporadic nature of the buildup of W. arceuthobii to such abundance has resulted in its dismissal as a reliable control agent (Hawksworth et al., 1977; Wicker & Shaw, 1968). Occasionally, over the three seasons of investigation, branches of dwarf mistletoe heavily infested with W. arceuthobii have been found but neither consistently nor to the extent reported by Weir (1915) and Dowding (1931b).

General Discussion

Some of the differences in the frequency of isolation of the principal fungi revealed by the statistical analyses, are resolved when a closer examination of the data is made. The relatively small number of sand plates with male and moribund A. pusillum, for example, probably distorted the analysis in terms of sex and condition for all the principal fungi on this host. The analysis of Cladosporium spp. may have been especially affected. The July dataset indicated that the frequency of isolation of these fungi was not dependent on the factors under examination. The overall dataset indicated that a number of significant interactions were occurring but this was probably due to the small sample size of A. pusillum (Figs. 26, 27) and the real abundance of Cladosporium

spp. in May.

Other complicating factors include the possibility of intra-plate contamination by densely sporulating colonies of A. alternata and Cladosporium spp. It is possible that the increase generally noted between observation times 2 and 3 was due to spread of these fungi between segments versus infections that were already established but which took two months to become evident. The observation of rarely isolated fungi was no doubt influenced by the presence of A. alternata which formed a dense mat over the mistletoe segment making detection and isolation of other fungi difficult. The presence of four different Coniothyrium species was not initially discerned and although every effort was made to correct the record it is possible that some anomalous results stem from this confusion.

These factors may in some part explain the inconsistencies noted in the pattern of isolation of the principal fungi. However, the following observations are probably more real than apparent. More Coniothyrium sp. 1 was isolated from female, moribund material at The Pas (Fig. 19). Sex was not a significant factor at Grand Beach (Fig. 18); the high levels found on sexually undifferentiated material of A. pusillum on P. mariana are not necessarily representative as these isolations resulted from a single plate of incubated mistletoe. More Coniothyrium sp. 1 was isolated from moribund material at the two sites suggesting that the fungus is in fact a saprophyte with facultative parasitic capabilities.

The date at which the Arceuthobium tissue was collected was a significant factor influencing the levels of isolation of both the principal fungi and the rarely isolated fungi. The principal

fungi were most frequently recovered in the spring at both Grand Beach and The Pas (Figs. 6a, 6b). In the same season the number of isolations of rare fungi was lowest (Table 5). Conversely, in July the number of rarely isolated fungi reached their height, especially from A. americanum for which most tissue was available. Simultaneously, isolations of A. alternata and Cladosporium spp. were at their lowest, suggesting possible competition between fungi for available host nutrients.

Many of the Coelomycetes isolated from A. americanum and A. pusillum in Manitoba are either from genera that are poorly known, e.g. Naemospora or that have not been reported in association with Arceuthobium species before, e.g. Coniothyrium. Coniothyrium sp. 1 was frequently isolated and Coniothyrium sp. 2 relatively so. Three more Coelomycetes were isolated with comparative frequency; Colletotrichum sp., Truncatella sp. and Seimatosporium lichenicola. The majority of Colletotrichum sp. was recovered from moribund tissue of both A. americanum and A. pusillum at the two sites. Truncatella sp. was recovered only from A. pusillum at the northern site while S. lichenicola was taken from both Arceuthobium species at The Pas. Coniothyrium sp. 1 (reported but not identified) and Colletotrichum sp. were also relatively frequently isolated from A. americanum in an earlier Manitoba study (Gilbert, 1981). The value of these fungi as possible biological control agents is presently unknown. Their relative abundance on moribund tissue versus healthy indicates that they are primarily saprophytic; their isolation from healthy mistletoe suggests that they are also facultative parasites. Further research to test the pathogenicity of these fungi on Arceuthobium

species may be of value in the search for a means of controlling dwarf mistletoes.

The specificity of the mycoflora associated with Arceuthobium species is brought into question by this study. The genera of fungi associated with A. americanum on P. banksiana and A. pusillum on P. mariana and P. glauca in Manitoba (Table 6) vary to a small degree, but they are quite different from those associated with cankers on western hemlock infected with A. tsugense in British Columbia (Baranyay, 1966; Funk et al., 1973; Funk and Baranyay, 1973; Funk and Smith, 1981). The studies are only remotely comparable as the wood associated with the dwarf mistletoe was sampled in the British Columbia study as opposed to mistletoe tissue. However, the similarity between the mycofloras of A. americanum and A. pusillum indicate a greater dependence of the fungi on climatic and environmental factors than on the specific Arceuthobium host.

Chapter 3

POLLINATION BIOLOGY

Literature Review

The mode of pollination of the genus Arceuthobium, in which the flowers are remarkably uniform (Cohen, 1968; 1970), has been investigated since the beginning of the century. The male flowers have a single whorl of perianth parts; on each segment a single sessile anther is centrally positioned (Plate 1b, d). The female flowers are characterized by a single dimerous whorl of reduced, scale-like perianth parts which flank the slightly protruding stigma (Plate 1c, e). Gill and Hawksworth (1961), and in greater detail Player (1977), cite the work of Heinricher who studied the pollination of A. oxycedri (DC.) M. Bieb. Heinricher listed a number of floral characteristics that suggested entomophily as the mode of pollination. These included sessile anthers, spined pollen grains, the presence of "mucous balls" holding the pollen grains together, the clumping of pollen in clusters of 20-40 grains, low pollen production, non-plumose stigma, visual prominence of the male inflorescence and the presence of a glistening stigmatic exudate. However, in spite of the entomophilous features of Arceuthobium flowers Heinricher later modified his views after observing greenhouse plants which had considerable seed set with no noticeable insect visitors. He concluded that anemophily was the primary pollinating mechanism in Arceuthobium with insects playing a minor role (Gill & Hawksworth, 1961).

Additional entomophilous characteristics have, however,

been noted. Dowding (1931a) made reference to the presence of a central cushion (Plate 1b) in the male flowers of A. americanum which bears pairs of glandular cells suggesting nectaries. However, Cohen (1968) in his study of the staminate flower observed nothing to support this conclusion. Gregor et al. (1974) describe the "pungent, citric-like odor" of both male and female flowers of A. americanum which present olfactory cues to insect visitors. Anthocyanins are found in all species of Arceuthobium with dark shoots and in nore than half of the light-coloured ones (Hawksworth and Wiens, 1972). In the outer portions of living male flowers of A. americanum and A. douglasii Engelm. a light magenta colour pattern occurs which resembles the anthocyanin bands isolated chromatographically from their shoots. Hawksworth and Wiens (1972) suggest that anthocyanins function as visual attractants to dipteran pollinators. The stigmatic exudate of A. abietinum Engelm. was analyzed by Brewer et al. (1974) by thin-layer and gas-liquid chromatography. Mistletoe nectar was found to be similar to that of most other plants in that the major component sugars are glucose, fructose, and sucrose. Flowers produced large (0.24 μl) droplets of highly concentrated nectar (52-92%) which Brewer et al. (1974) concluded was probably a strong insect pollinator attractant.

Reports of insects associated with A. americanum were made by Weir (1915) who observed hymenopterous insects visiting Arceuthobium species and reported that in 1914 great numbers of grasshoppers emerged from Hangman Creek Valley near Spokane and were seen to feed on male dwarf mistletoe flowers. Pollen that had adhered to their bodies was deposited on the female flowers as the

insects swarmed over them. There is, however, no other record of the involvement of grasshoppers in the pollination of Arceuthobium species. Dowding (1931b) reported that small flies and ants are the pollinators of A. americanum and Kuijt (1955) too observed ants on the male inflorescences of A. americanum. Following these observations systematic studies of the insect fauna associated with Arceuthobium species were conducted.

Stevens and Hawksworth (1970) in a review of the literature concerning the insects and mites associated with dwarf mistletoes suggested that "some wind pollination may occur, but only within a meter or so". The most common insect pollinator associated with A. vaginatum subsp. cryptopodum (Engelm.) Hawksworth and Wiens was a thrips of the genus Frankliniella, whereas on A. americanum small flies such as Bradysia sp. (Sciaridae) were common early in the season and succeeded by ants towards the end of the flowering period. The number of possible insect pollinators of A. americanum was extended by Gregor et al. (1974). Their studies included the collection of insects from the immediate vicinity of the inflorescences and the trapping of air-borne pollen on microscope slides coated with petroleum jelly. The slides were exposed from 3 hours to 7 days at various distances from male flowers. The majority of insects collected belonged to the orders Hymenoptera and Diptera and were considered to be the most important pollinators. No attempt, however, was made to determine the pollination potential of the different insects. Of the four species of ants collected, only one, Tapinoma sessile (Say) was also reported by Stevens and Hawksworth (1970). One other insect, a small fly, Philygria debilis

Loew, had also been collected on a previous occasion from A. americanum. Most of the airborne pollen grains were collected on slides between 2.5 and 30 cm from male flowers and none was recorded from slides more than one meter away. However, Gregor et al. (1974) cite the work of Estella B. Leopold in which Arceuthobium pollen was trapped 15 km south of the nearest source. Potter and Rowley (1960) similarly report finding a single Arceuthobium pollen grain 5 km from the nearest source.

Penfield et al. (1976) also investigated the insect fauna associated with three Arceuthobium species and used vaseline coated microscope slides to measure air-borne pollen concentrations. More than 200 insect species bearing pollen were collected but relatively few species were trapped from mistletoe of both sexes. Only 13 species were considered important and these differed to some extent for each Arceuthobium species. The pollinators of A. americanum included the ant, Formica fusca L. (Formicidae) and the Dipterans Philygria debilis, Protophormia terraenovae (R.-D.) (Calliphoridae), and several Hylemya species, H. ceralis (Gillette), H. cinerella (Faller) and H. platura (Meigen) (Anthomyiidae). The vaseline coated slides trapped pollen of A. cyanocarpon Coulter and Nelson up to distances of 151 m from the nearest male flowers. Similar quantities of A. americanum and A. cyanocarpon pollen were trapped over their respective flowering periods but almost five times as much pollen from A. vaginatum was trapped. Penfield et al. (1976) concluded that both wind and insects effected pollination but suspected entomophily of being the primary pollinating system. This conclusion was based on the relatively low counts of Arceuthobium (4,000 to

11,000) pollen grains per flower and the tendency for the pollen to be released in clusters.

Baker (1981) conducted a number of exclusion experiments, using screen bags of 0.8, 2.2 and 4.0 mm mesh and uncovered plants for controls, to determine the mode of pollination for A. pusillum. Vaseline coated slides were used to investigate air-borne pollen concentrations at distances up to 128 m from the centre of the Arceuthobium infestation. A rotorod sampler was also used within 2 m of staminate infections. Insects were trapped from female witches' brooms, on screen traps and sticky board traps. Greater fruit set was recorded on plants covered with 4.0 mm mesh than on branches with smaller screens. Low numbers of air-borne pollen grains (0.4/ cm^2/year) were trapped within 5 m of male flowers. Of the 332 insects examined, 42% had at least one pollen grain. Several of the insect genera trapped were earlier reported from studies of insects associated with A. americanum (Gregor et al., 1974; Penfield et al., 1976) including Hylemya, Phora, Bradysia, Syrphus, Bradysia (Diptera) and Tapinoma (Hymenoptera). Baker (1981) concluded that A. pusillum has primarily an entomophilous pollination system with a minimal role for wind pollination based on the relative abundance of pollen-bearing insects and the low airborne pollen concentrations measured.

Player (1977) studied the pollination of A. douglasii and A. strictum Hawksworth and Wiens and found insect visitors were rare to the female flowers of both these species. On the other hand laboratory studies indicated that pollen was easily liberated by wind. For continuous trapping of pollen the use of square rods was

preferred, These had a calculated sampling efficiency of 80 to 95% with wind velocities between 3 and 10 m/sec. compared with the theoretical sampling efficiency of microscope slides of 0.0% at 1 m/sec and 46.0% at 10 m/sec. Dispersal of pollen was measured up to 7 m from the male flowers but not tested beyond that distance. There was relatively low seed set (2% or less) on female plants screened with mesh 0.5 mm and 1.0 mm in comparison with 11 to 62.5% seed set on uncovered plants. Player concluded that a large component of the wind with its pollen load would likely be forced around the cages. Plants bagged to prevent access of pollen either by insect or wind had 0.0% fruit set ruling out the possibility of apomixis. Player (1977) argued that the pollination of Arceuthobium is principally an anemophilous system and based his conclusions on the lack of insect visitors and the relative abundance of air-borne pollen.

A. Insects

Introduction

Recent attempts to identify the pollination mechanism of Arceuthobium have not resolved the question. Most experimental work has assumed the genus to be primarily insect pollinated on the basis of the entomophilous characteristics of the flowers. However, in studies in the United States no specialized and few regular insect visitors have been found, while in Manitoba no observations have been conducted on the insect fauna associated with dwarf mistletoes since the 1930s.

Methods and Materials

To determine the insect fauna associated with A. americanum on P. banksiana in southern Manitoba and its role in pollination, insects were trapped from dwarf mistletoe brooms for three consecutive years, 1981-1983. A pyrethrin spray, beat net and kill jar containing ethyl acetate fumes were used in the first two seasons when each broom was sampled just once. The spray was used to stun the insects before the broom was beaten. To catch the insects as they fell from the broom, a square of cheesecloth was placed over the net which could be labelled and folded thus isolating insects from each broom sampled. The folded cheesecloth was placed in the kill jar until examination and identification of the insects could be made. Even with the use of the pyrethrin spray some ants escaped and a few small flying insects (Diptera and Hymenoptera) recovered and flew away before the cheesecloth was folded. It was felt, however, that a representative sample was saved. In the final season as the same brooms were sampled repeatedly over the course of the pollination period, pyrethrin spray was not used. The number of insects lost without use of the spray was fewer than expected and little different from previous years. Insects were examined under a dissecting microscope for preliminary identification and for presence of pollen.

In 1981 three sites were chosen so that insects could be sampled from different environments:

1. Trees in an exposed location at Lester Beach, near

Grand Beach Provincial Park, on the shore of Lake Winnipeg.

2. Trees in a sheltered environment within Belair Provincial Park.
3. Trees in open forest close to the highway at Victoria Beach.

At each site, insects were trapped from female and male brooms at three times, morning (10.00 a.m. to 12.00 noon), noon (12.00 noon to 2.00 p.m.), and afternoon (2.00 p.m. to 4.00 p.m.), during the course of three days, 10, 12, and 13 May, 1981. Air temperature, sex of witches' broom and time and date were recorded for each broom sampled. In 1981, 155 brooms were sampled; 86 male and 69 female.

A preliminary analysis indicated that the number of insects trapped by site, day and time of sampling was not significantly different, whereas a significant difference existed between the number of insects trapped from male and female brooms. Insects bearing pollen and trapped from female brooms were of most interest in the study, therefore in 1982 more female than male brooms were sampled, 73 female as opposed to 30 male. Insects were sampled from the three sites established in 1981 on 13, 14, 20, 21, and 25 May, 1982.

Within the forest, where male and female brooms were in close proximity, insects with pollen adhering to them were trapped from brooms of both sexes. To identify pollen-bearing insects that might seek and pollinate female plants of A. americanum, five young jack pines with female dwarf mistletoe infections that were situated

at least 10 m from the nearest male infection were sampled in the final season. Insects were trapped at weekly intervals from the start of the pollination period 26 April until the male flowers were shed, 31 May.

Insects of the family Formicidae (Hymenoptera) were identified by Mr. G. L. Ayre of Agriculture Canada Research Station, Winnipeg, and all others were identified at least to the family by Dr. T. Galloway, Department of Entomology, University of Manitoba, before being sent to the Biosystematics Research Institute, Agriculture Canada, for more precise identification. Representative insect species will be preserved in the Department of Entomology as a permanent record of the insect fauna associated with A. americanum in Manitoba.

Results and Discussion

The data for insects collected in 1981 and 1982 (total number of insects and insects with pollen grains adhering to them) were combined and analyzed to discover what, if any, relationship existed between number of insects trapped and air temperature. Analysis employing a general linear model (GLM) indicated that for these data numbers of insects trapped were not dependent on air temperature. However, at Site 2, the majority of insects trapped at high temperatures, 27^{o}-28^{o}C, were the coleopteran Hyperaspis binotata Say (23/33). Ants were especially numerous at Sites 2 and 3 at temperatures ranging from 20^{o}C to 22^{o}C while dipterans were frequently collected on the coolest day, 13.5^{o}C (28/36), up

to temperatures of 20°C (45/56) at Sites 1 and 3.

The numbers of insects collected from male and female brooms at the three sites in 1981 and 1982 are recorded in Table 8. A preliminary analysis of variance of the 1981 data showed that the number of insects collected did not differ significantly in terms of site, day or time of collection, although significantly different numbers of insects were found on male and female brooms (Appendix A7). The data of 1982 were analyzed to determine the effect of site and sex of dwarf mistletoe on insect numbers with similar results; significantly more insects were trapped from male dwarf mistletoe brooms than from female (Table 9). This result is partly explained, however, by the fact that more female than male brooms yielded no insects (Table 10). In general, fewer insects were collected on brooms in 1982 than in 1981 and different trends were noted at Sites 1 and 3 (Table 9). The mean number of insects on female brooms was greater at Site 1 and little difference was observed between numbers of insects trapped from brooms of both sexes at Site 3. Many small beetles, Cyphon sp., were found at Site 1 in 1982 constituting nearly 25% of all the insects trapped from female brooms. The apparently high number of insects trapped from male brooms at Site 2 in 1982 was the result of one broom swarming with ants (Formica sp. rufa group). For unknown reasons 12 of the 25 female brooms sampled at Site 2 yielded no insects at all and resulted in the unusually low mean number of insects in this category (Tables 9, 10). In 1981 several of the brooms sampled were swarming with ants which resulted in a higher mean number of insects trapped from male brooms at Site 3. This phenomenon was

Table 8. Numbers of insects collected from brooms of Pinus banksiana induced by male and female Arceuthobium americanum at Belair Provincial Forest, Manitoba, 1981 and 1982.

Year	Site 1		Site 2		Site 3		Total Brooms	Total Insects
	B*	I**	B	I	B	I		
1981	24	63	30	117	32	136	M 86	316
	25	47	22	64	22	57	F 69	168
Totals	49	110	52	181	54	193	155	484
1982	10	15	10	31	10	15	M 30	61
	23	48	25	19	25	35	F 73	102
Totals	33	63	35	50	35	50	103	163

*Brooms

**Insects

Table 9. Mean number of insects collected from brooms of Pinus banksiana induced by Arceuthobium americanum at three sites in Belair Provincial Forest, 1981 and 1982.

		Mean Number Insects/Broom			
		1981		1982	
Site Description	Site #	M	F	M	F
Exposed lakeshore	1	2.6	1.9	1.5	2.1
Sheltered within forest	2	3.9	2.9	3.1	0.8
Open forest	3	4.3	2.6	1.5	1.4

Table 10. Percentage of brooms of Pinus banksiana caused by male and female Arceuthobium americanum in Belair Provincial Forest which yielded no insects in 1981 and 1982.

	Site 1		Site 2		Site 3		% of all
Year	M	F	M	F	M	F	brooms
1981	8	20	13	14	6	18	13
1982	30	13	30	48	30	24	29
1983							17

not observed at Site 3 in 1982. A preliminary list of the insects trapped from A. americanum is given in Table 11. The four orders Diptera, Hymenoptera, Coleoptera and Hemiptera comprised almost 95% of the insects trapped. Thysanopterans were found relatively frequently in 1981 (28, 5.7%) but only once in 1982 and not at all in 1983. Four were found each with a single pollen grain. In 1981 three insects belonged to the order Homoptera, in 1982 none and in 1983 two. Two microlepidopterans were trapped in both 1982 and 1983. These orders, Thysanoptera, Homoptera, and Microlepidoptera have been omitted from further analysis on account of their scarcity.

In 1981 and 1983 insects of the orders Diptera and Hymenoptera were trapped most frequently (Figs. 33, 35) while the orders Hymenoptera and Coleoptera were represented more frequently in 1982 (Fig. 34). In all three seasons the majority of the dipterans were Bradysia sp. (Sciaridae); 1981 55%, 1982 36% and 1983 54%, whereas Formicidae, Formica spp. (fusca and rufa groups) and Tapinoma sessile comprised most of the Hymenoptera; 1981 70%, 1982 61% and 1983 48%. The coccinellid, Hyperaspis binotata Say was especially abundant at Site 2 in 1981 and comprised 38% of all the coleopterans trapped. Other insect taxa included in the list of insects associated with A. americanum were isolated less frequently.

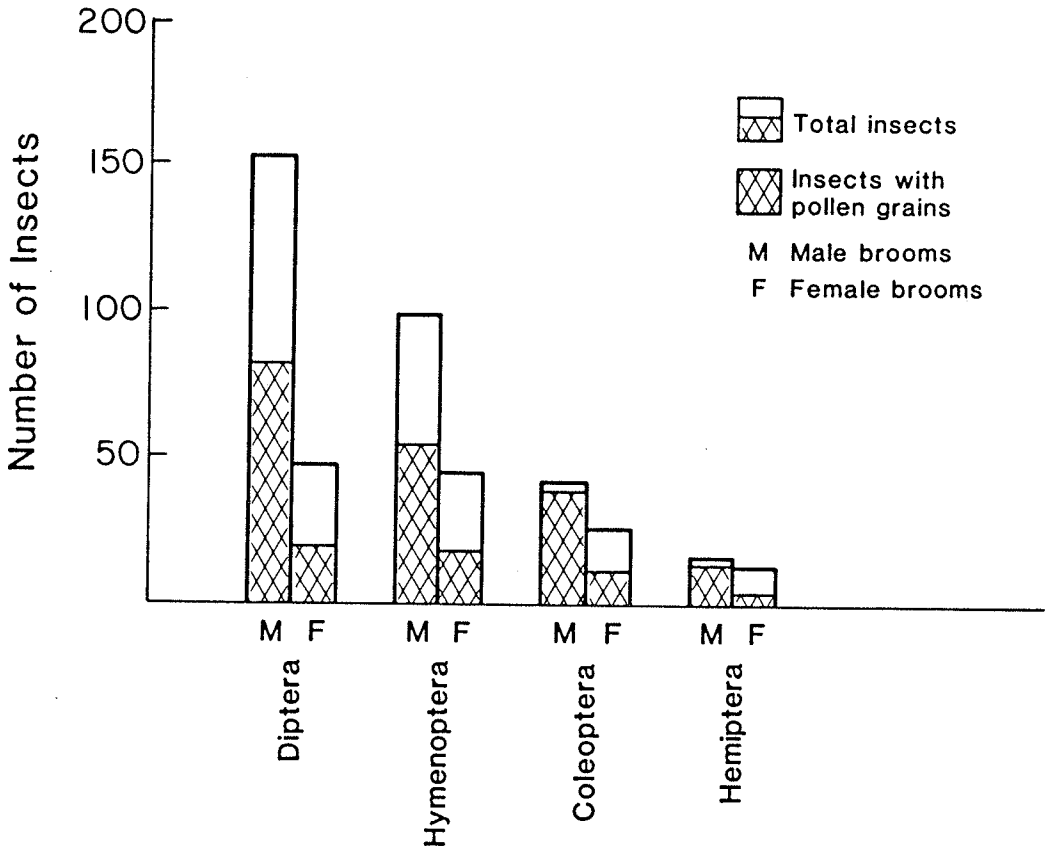
In both years more than 50% of all the insects trapped from male and female brooms combined bore at least one pollen grain, although the majority of pollen bearing insects were trapped from male brooms (Table 12). Of the insects trapped on male brooms in 1981 and 1982, 60% and 72% respectively carried pollen, whereas

Table 11. Preliminary list of insects collected from brooms of *Pinus banksiana* induced by *Arceuthobium americanum* in Belair Provincial Forest, Manitoba, 1981-1983.

				1981	1982	1983
DIPTERA	UNIDENTIFIED		6 specimens	-	+	-
	CECIDOMYIIDAE		2 specimens	-	-	+
	CHIRONOMIDAE		2 specimens	-	-	+
	CHLOROPIDAE		1 specimen	+	-	-
	EPHYDRIDAE		3 specimens	-	-	+
		Phylygria debilis Lw.		+	+	+
		Psilopsa olga Cresson		+	+	-
	MUSCIDAE	*Musca domestica* L.		+	-	-
	MYCETOPHILIDAE		1 specimen	-	-	+
	SCIARIDAE	*Bradysia* sp.		+	+	+
		Corynoptera sp.		+	-	-
		Lycoriella sp.		+	-	-
	TEPHRITIDAE	*Tephritis* sp. *araneosa* (Coquillet)?		+	-	-
HYMENOPTERA	UNIDENTIFIED		15 specimens	-	+	-
	CHALCIDOIDEA		3 specimens	+	-	+
	CHALCIDIDAE		1 specimen	-	-	+
	ENCYRTIDAE		1 specimen	+	-	-
	PTEROMALIDAE		5 specimens	+	+	+
	BRACONIDAE		3 specimens	+	-	+
	FORMICIDAE	*Camponotus herculeanus* (Linne)		+	-	-
		Dolichoderus taschenbergi (Mayr)		+	-	-
		Formica sp., *fusca* group		+	+	+
		Lasius sitkaensis Pergande		+	-	-
		Tapinoma sessile (Say)		-	-	+
	SCELIONIDAE		1 specimen	+	-	-
	TENTHREDINIDAE		2 specimens	-	+	+
	XYELIDAE		1 specimen	+	-	-
COLEOPTERA	UNIDENTIFIED		5 specimens	-	+	+
	BUPRESTIDAE	*Chrysobothris* sp.		+	-	-
	CHRYSOMELIDAE	*Calligrapha* sp.		-	+	-
	COCCINELLIDAE	*Coccinella* sp.		-	+	-
		Coccinella transversoguttata Fald.		-	+	+
		Hippodamia tridecimpunctata (L.)		+	+	-
		Hyperaspis binotata Say		+	-	-
		Mulsantina hudsonica Casey		+	-	-
		Scymnus (*Pullus*) *lacustris* Lec.		+	+	-
	CURCULIONIDAE		1 specimen	+	-	-
	ELATERIDAE	*Ctenicera triundulatus* (Rand.)		+	+	+
	HELODIDAE	*Cyphon* sp.		-	+	+
	LATHRIDIIDAE	*Corticariini* sp.		+	+	-
	MELYRIDAE	*Amecocerus* sp.		+	+	-
HEMIPTERA	LYGAEIDAE	*Kleidocerys resedae* (Parzer)		+	+	-
		Ischnorrhyncus sp.		-	+	-
		Nysius ericae (Schilling)		-	+	-
	MIRIDAE	*Lygus* sp.		-	-	+
HOMOPTERA	CICADELLIDAE		1 specimen	-	-	+
	PSYLLIDAE	*Trioza obtusa* Patch		+	-	-
		T. tripunctata (Fitch)		+	-	-
MICROLEPIDOPTERA	UNIDENTIFIED			-	+	+
THYSANOPTERA	UNIDENTIFIED			+	+	-

Fig. 33. Diptera, Hymenoptera, Coleoptera, and Hemiptera trapped from brooms of Pinus banksiana induced by 86 male and 69 female infections of Arceuthobium americanum in Belair Provincial Forest, Manitoba, 1981.

Fig. 34. Diptera, Hymenoptera, Coleoptera, and Hemiptera trapped from brooms of Pinus banksiana induced by 30 male and 73 female infections of Arceuthobium americanum in Belair Provincial Forest, Manitoba, 1981.


200
150
100
50
Number of Insects
Total insects
Insects with pollen grains
M Male brooms
F Female brooms
M F
Diptera
Hymenoptera
Coleoptera
Hemiptera

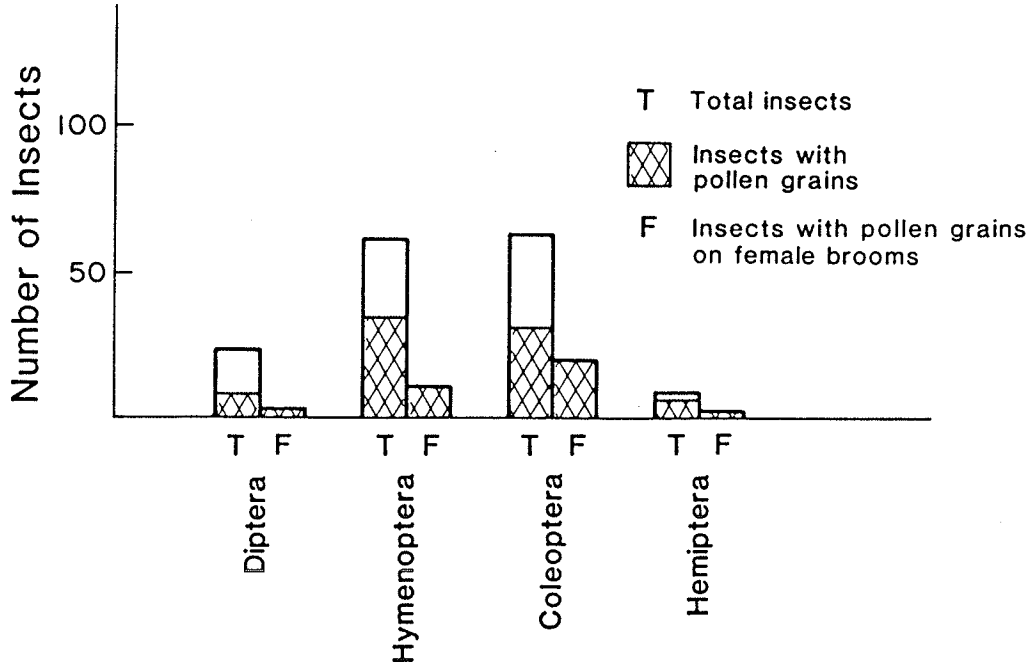
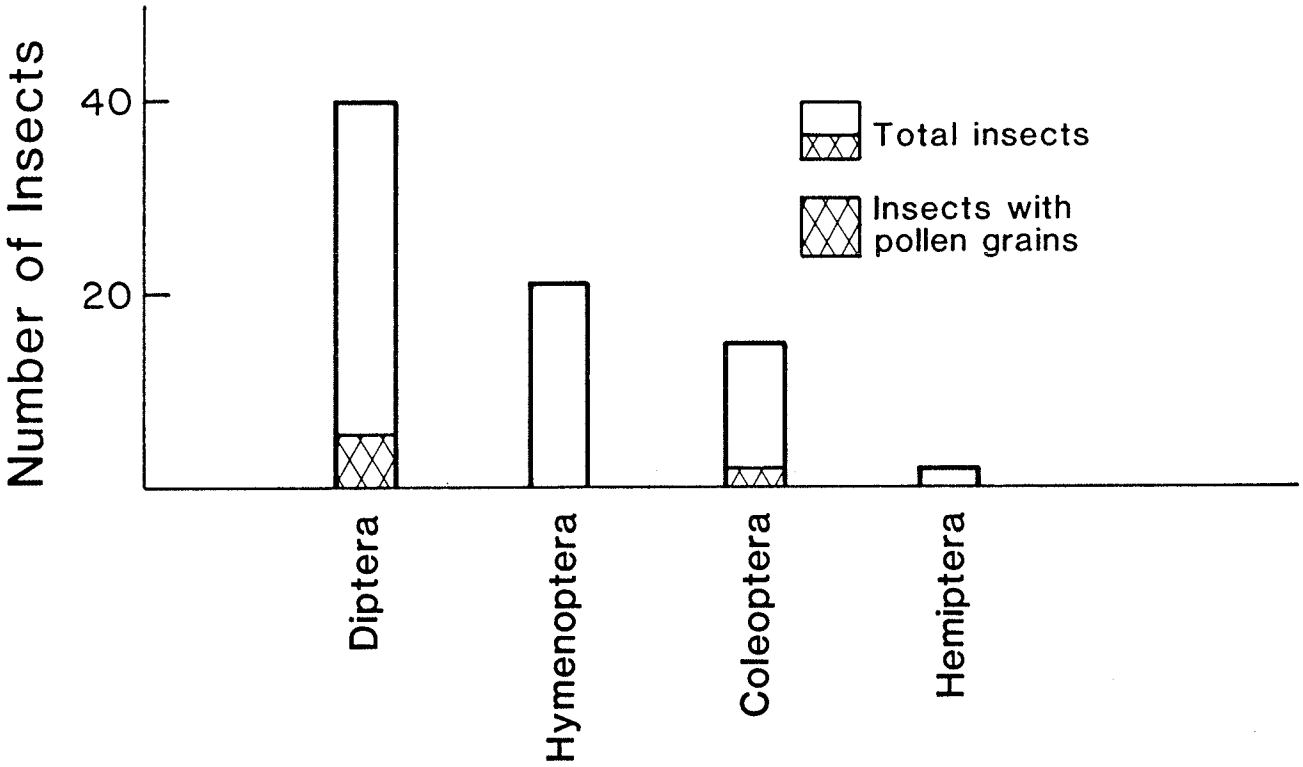

100
50
Number of Insects
T Total insects
Insects with pollen grains
F Insects with pollen grains on female brooms
T F
Diptera
Hymenoptera
Coleoptera
Hemiptera

Fig. 35. Diptera, Hymenoptera, Coleoptera, and Hemiptera trapped from five brooms of Pinus banksiana induced by female Arceuthobium americanum in Belair Provincial Forest, Manitoba, at six weekly intervals in 1983.


Number of Insects
40
20
Total insects
Insects with pollen grains
Diptera
Hymenoptera
Coleoptera
Hemiptera

for the same seasons, 34% and 39% respectively of insects trapped on female brooms bore pollen (Table 12). In 1983 the number of pollen-bearing insects trapped on female brooms was considerably lower, 8.75% (Table 13), than in either 1981 or 1982. Fewer brooms were sampled in 1983 but the mean number of insects per broom was 2.6, which was comparable to the numbers collected in 1981 (Tables 9, 13).

Several of the insect families collected in Manitoba were represented in earlier studies in the United States (Gregor et al., 1974; Penfield et al., 1976). Of the Diptera, Mycetophilidae (Fungus-gnats; one specimen trapped), was the only family represented in the Manitoba survey that had not been associated with A. americanum in earlier studies (Gregor et al., 1974; Penfield et al., 1976). The majority of the Diptera trapped belonged to families characterized by sucking mouthparts (Cecidomyiidae, Chironomidae, Ephydridae, Mycetophilidae and Sciaridae). The flowers commonly visited by these dipterans are flat or bowl-shaped with well exposed or partly concealed nectar. Nectarless flowers are thought to be visited for their pollen, grains of which can be taken up in the saliva that reaches almost to the apex of the proboscis (Proctor and Yeo, 1972). The small fly Bradysia sp. (Sciaridae) was collected most frequently from both male and female brooms in Manitoba and was not uncommonly well dusted with pollen (Plate 1h). Sciaridae has been described as the chief anthophilous family (Proctor and Yeo, 1972).

The families Braconidae, Encyrtidae, Pteromalidae, Scelionidae, and Tenthredinidae (Hymenoptera) were poorly represented in the Manitoba study, but have also been found in association with

Table 12. Percentage of insects bearing mistletoe pollen from brooms induced by Arceuthobium americanum in Belair Provincial Forest, Manitoba, 1981 and 1982.

Year	% Insects from Male brooms	Female brooms	% Total Insects
1981	60	34	51
1982	72	39	52

Table 13. Insects collected from brooms of Pinus banksiana induced by female Arceuthobium americanum in Belair Provincial Forest, Manitoba, 1983.

Number of Brooms	Number of Insects	Mean Number of Insects per Broom	Number of Insects with Pollen	% Insects with Pollen
30	80	2.6	7	8.75

A. americanum in Utah or Colorado (Gregor et al., 1974; Penfield et al., 1976). Females of the Tenthredinidae (sawflies) often take floral foods, nectar, pollen stamens and petals, especially from flowers in which the nectar and pollen are well exposed (Proctor and Yeo, 1972). The superfamily, Chalcidoidea and family Chalcididae plus the family Xyelidae are reported in this association for the first time. Chalcid wasps have been recorded at flowers (Proctor and Yeo, 1972), and larvae of the Xyelidae are known to feed on the staminate cones of pines (Rose and Lindquist, 1973). However, the family in the Hymenoptera best represented was the Formicidae. They regularly collect nectar from flowers but are unlikely to effect cross-pollination as the worker-ants, responsible for nectar collection, are wingless and have to reach flowers by crawling up the trunks of trees and stems of flowers (Proctor and Yeo, 1972). Several genera (Lasius, Camponotus, Formica) and two species (Formica sp. fusca group, Tapinoma sessile) have been trapped in the United States as well as in Canada. In a few cases ants have been identified as principal pollen vectors but in the main they are liable to be harmful visitors and plants may form impassable barriers (for example, sticky zones on the upper parts of some Silene species) to exclude the ants' passage (Proctor and Yeo, 1972). Many ants were found covered with A. americanum pollen or with it clustered about the mouthparts (Plate 1g), but pollen was not observed on ants trapped from female dwarf mistletoe that was isolated from male infections in 1983 (Fig. 35).

Among the Coleoptera, Coccinellidae, Elateridae and Melyridae were collected in both the United States and Canada; the Melyridae

is the one exclusively anthophilous family (Proctor and Yeo, 1972). Many specimens of Ctenicera triundulatus (Elateridae) were found with abundant pollen adhering to them, but the family is known to feed destructively on flowers offsetting the value of any chance pollination effected, by the damage they cause (Proctor and Yeo, 1972). Different species of the genera Ctenicera (Elateridae), Mulsantina and Scymnus (Coccinellidae) have been reported from both Colorado and Utah, United States, and from Manitoba, Canada. Coccinella transversoguttata represents the one coleopteran species that is presently known as a denizen of A. americanum-infected pine in the United States (Utah) and Manitoba. Ladybird beetles (Coccinellidae) were not considered important pollinators of dwarf mistletoe by Gregor et al. (1974) or Penfield et al. (1976); however, Hyperaspis binotata and Cyphon sp. (Helodidae) were two of the most common insect visitors to A. americanum in Manitoba, and pollen grains were frequently found about the mouthparts and adhering to the ventral surface. As a family the Coccinellidae are primarily an entomophagous group but nectar and pollen also commonly provide an alternate food source when insect food is scarce, permitting survival and immediate resumption of oviposition when insect prey reappear (Hagen, 1962; Hodek, 1973).

Kleidocerys resedae was the only hemipteran recorded with any frequency from A. americanum in Manitoba; the family (Lygaeidae) and genus have not been recorded in this association elsewhere. Members of this order have often been recorded at other flowers (Proctor and Yeo, 1972). The piercing sucking mouthparts suck up the juices of plants but the bugs may become dusted with pollen and

effect chance pollination as they visit from flower to flower (Proctor and Yeo, 1972). K. resedae, well dusted with pollen, were trapped from both male and female brooms from Site 1 in 1981 (Fig. 33).

A number of insects reported as anthophilous and implicated in the pollination of flowers were found in the immediate vicinity of A. americanum in Belair Provincial Forest. While the majority of insects, including those that were well dusted with pollen, were trapped on male brooms, a significant number were taken from female brooms that were in close proximity to male brooms (Figs. 33, 34). However, insects with pollen were rarely trapped from female brooms that were isolated from male brooms (Fig. 35).

B. Wind

Introduction

The majority of studies of air-borne pollen concentrations have employed microscope slides coated with petrolatum to form an adhesive surface. The levels of air-borne Arceuthobium pollen measured with this method have been low. Moreover, most dwarf mistletoe pollen trapped on slides has been in the immediate vicinity of male flowers while reports of long distance travel of pollen have been rare. In the present study concentrations of air-borne dwarf mistletoe pollen and long distance transfer were investigated using cheesecloth traps.

Methods and Materials

In 1982 and 1983 cheesecloth traps were used to collect air-borne pollen. Cheesecloth was stretched over a square wire frame

15 x 15 cm and supported by 2 m bamboo poles (Plate 1f). A 9 x 9 cm square from the centre of each trap was later scanned under a dissecting microscope for evidence of air-borne pollen. Sizes of pollen clusters and total numbers of grains per trap were recorded.

In 1982 two sites were chosen where stands of dwarf mistletoe-infected jack pine flanked areas which had been clear cut. Traps (3 replicates) were erected at 25 m, 50 m, and 100 m, from the pollen source. The cheesecloth was replaced at six 24-hour intervals and two 4-day intervals. Before the male flowers opened in 1983, traps were erected 100 m, 200 m, 300 m, and 400 m from the pollen source at two similar sites. The cheesecloth traps were examined at the end of the seven week pollination period, 7 June 1983.

Although the effective distance of pollen travel and the environmental conditions which control it were the main focus of this study, preliminary observations were made to determine the importance of air-borne transport in short-range transfer of pollen. For this purpose seven traps were erected below or beside exposed male brooms on three selected trees in the Belair Provincial Forest. These traps were placed at heights of 1-2 m above ground and at distances of 0-3 m from the brooms; four were bent to expose a horizontal surface, three presented a vertical surface.

In 1983 five young jack pines bearing female dwarf mistletoe brooms and established in a clear cut area were selected and marked. Two traps were erected by each tree on 19 April, 1983 and changed at weekly intervals for the duration of the pollination period. Insects were trapped at weekly intervals from the same trees. At

the start of the pollination period the number of developing fruits on 5 mistletoe plants on each tree plus one control tree from which insects were not trapped, were counted. In August 1983, the same plants were examined to determine the number of flowers fertilized in the spring of 1983.

Results and Discussion

i. Distance

Total pollen counts and number of clusters of pollen (dispersal units) trapped at 25 m, 50 m, and 100 m from the source (1982) varied greatly, but with no consistent pattern, between sites, ranging from 0 to 60 for total pollen count per 24 hour period and 0 to 18 for number of dispersal units over a similar interval of time (Table 14). Considerable variation between sites and traps was also observed in 1983 (Table 15). However, analysis of variance to determine the effect of site and distance revealed that the number of pollen grains and dispersal units trapped at each distance did not vary significantly between the two sites so the data were combined. Although the numbers of dispersal units (each of which can only effect the pollination of a single female flower) were found to increase slightly with distance from the source, the concentration of air-borne pollen was relatively uniform over the distance measured. However, the percentage of single pollen grains was greater at 50 m and 100 m (Fig. 36). At 25 m, 64% of the dispersal units were single grains whereas at 50 m and 100 m 79% and 71% respectively were single grains. An ANOVA to determine the effect of site and distance on the number of pollen grains trapped

Table 14. Total counts of pollen grains and dispersal units of Arceuthobium americanum recorded for Sites 1 and 2 at increasing distances from the source in Belair Provincial Forest, Manitoba, 12-25 May 1982.

Date May 1983	Total Pollen Count							Dispersal Units					
	25 m Site		50 m Site		100 m Site			25 m Site		50 m Site		100 m Site	
	1	2	1	2	1	2	Total	1	2	1	2	1	2
12	0	34*	26	4	9	1	74	0	3	2	4	4	1
13	10	0	2	12	0	60	84	1	0	2	3	0	1
14	3	11	4	7	4	2	31	3	10	4	7	4	2
15-18	9	56	33	50	50	51	249	8	34	16	45	35	43
19	3	2	0	1	0	2	8	3	2	0	1	0	2
20	20	14	13	36	11	19	113	4	9	5	15	6	16
21	10	11	4	8	53	21	107	5	6	3	8	18	12
22-25	184	61	89	63	249	88	734	65	30	52	34	56	25
Totals	239	189	171	181	376	244		89	94	84	118	123	102
Mean number per trap	80	63	57	60	125	81		30	31	28	39	41	34

*Sum of 3 replicates.

Table 15. Total counts of pollen grains and dispersal units of Arceuthobium americanum recorded for Sites 1 and 2 at increasing distances from the source in Belair Provincial Forest, Manitoba, 19 April to 7 June 1983.

Total Pollen Count								Dispersal Units							
100 m		200 m		300 m		400 m		100 m		200 m		300 m		400 m	
Site		Site		Site		Site		Site		Site		Site		Site	
1	2	1	2	1	2	1	2	1	2	1	2	1	2	1	2
13	17*	48	41	59	37	10	6	5	11	4	15	15	18	9	5

*Count for one trap

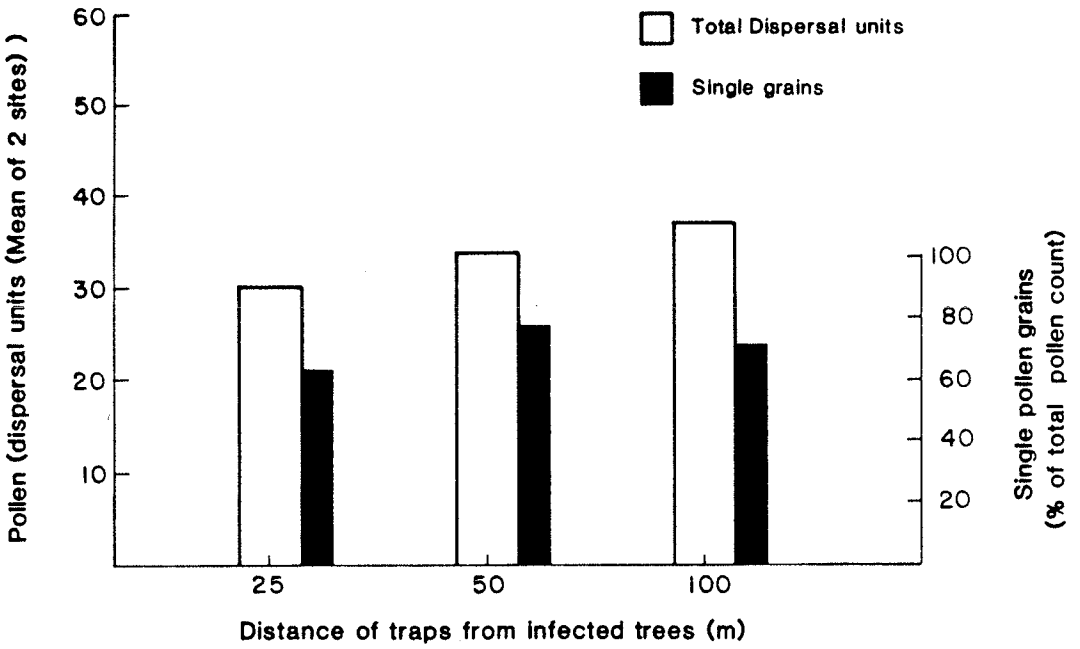
at 100 m to 400 m in 1983 revealed that significantly more pollen was trapped from Site 1, exposed to sources both to the north and east, than at Site 2 where pollen was dispersed from the east alone. Significantly more pollen clusters were trapped at 200 m and 300 m at both sites, although the highest percentage, 73%, of single pollen grains occurred in traps farthest from the source (Fig. 37). From 100 m to 300 m the percentage of single grains was lower, ranging from 24-35% (Fig. 37).

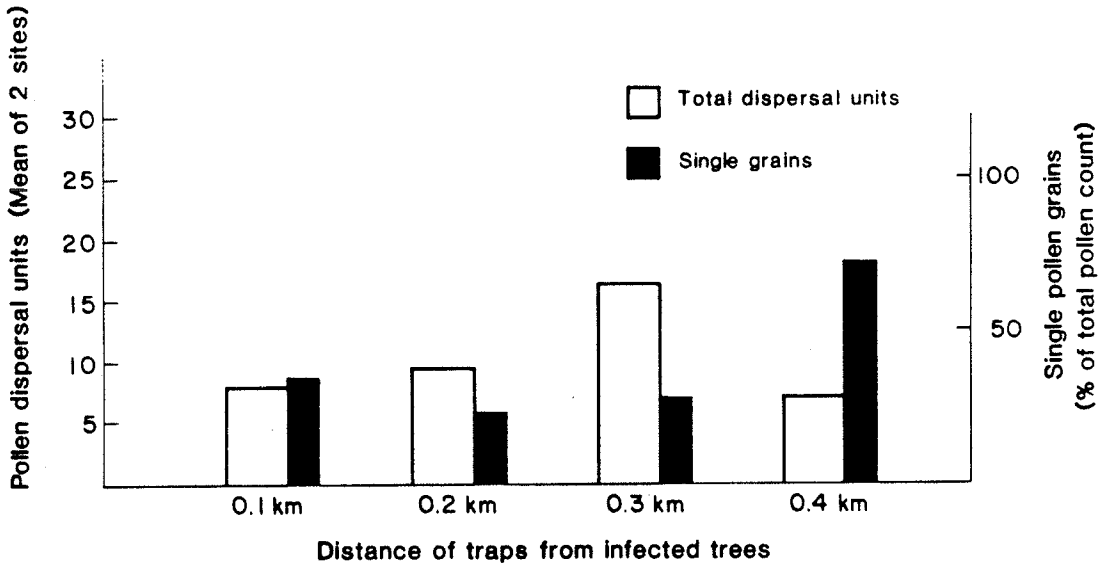
Air-borne pollen of A. americanum was found at greater distances from the source in the present study than might have been expected from previous studies (Gregor et al., 1974; Baker, 1981). Player (1977) did not measure pollen dispersal beyond 7 m but Gregor et al. (1974) found no A. americanum pollen more than 1 m from source. Baker (1981) concluded that the numbers of air-borne pollen grains of A. pusillum (0.4/cm^2/year) trapped within 5 m of male flowers were too low to support the hypothesis of an anemophilous pollination mechanism. Penfield et al. (1976), however, trapped pollen of A. cyanocarpon up to 151 m from the nearest male flowers.

The number of dispersal units increased up to 300 m from the pollen source but was lower again at 400 m (Fig. 37). An examination of the pollen trapped at 200 m and 300 m in 1983 (Table 15) reveals that the mean number of pollen grains was only slightly higher at 300 m than at 200 m (48 and 45 grains respectively). However, the pollen grains were clustered into smaller dispersal units at 300 m than at 200 m. This suggests that the smaller pollen clusters travel a greater distance than larger ones or alternatively

Fig. 36 Dispersal of Arceuthobium americanum pollen in Belair Provincial Forest, Manitoba, 1982.

Fig. 37 Dispersal of Arceuthobium americanum pollen in Belair Provincial Forest, Manitoba, 1983.


Total Dispersal units
Single grains
Pollen (dispersal units (Mean of 2 sites))
Single pollen grains (% of total pollen count)
60
50
40
30
20
10
100
80
60
40
20
25
50
100
Distance of traps from infected trees (m)


Total dispersal units
Single grains
Pollen dispersal units (Mean of 2 sites)
Single pollen grains (% of total pollen count)
30
25
20
15
10
5
100
50
0.1 km
0.2 km
0.3 km
0.4 km
Distance of traps from infected trees

that clusters of pollen break apart in flight. Single grains made up a large proportion of the dispersal units at 400 m (Figs. 36, 37); higher numbers of small clusters are expected as distance increases but their numbers may also have risen as a result of the disintegration of dispersal units.

Higher numbers of dispersal units were trapped in 1982 in a two week period, in which sampling was conducted at several 24-hour intervals and two 4-day intervals, than in 1983 when the traps were exposed for the entire pollination period (Figs. 36, 37). A possible explanation of the disparity in the pollen counts between 1982 and 1983 is the washing of pollen from the traps by rain during the course of the seven week exposure.

ii. Throughfall

Slightly more than 60% of the pollen was caught on horizontal traps at 0 m (Tree 1, Trap 1, 241; Tree 2, Trap 1, 462) (Table 16). Of the remaining 40%, 23.1% was trapped at 1 m (3 traps), 11.4% at 2 m (1 trap) and 5.4% at 3 m (1 trap). The number of single pollen grains represented in the total pollen counts averaged 33% per trap at 0 m and increased to 69% per trap at 1 m and 50% and 51% at 2 m and 3 m, respectively. Univariate plot analysis revealed that the data were extremely non-normal and transformations (square root, log (X+0.5)) failed to give means and variances that were not highly correlated. Consequently the untransformed data were analyzed using a general linear model (GLM) procedure. The data, while biased, revealed no significant differences between the trees and the traps.

Table 16. Air-borne pollen of Arceuthobium americanum trapped close to brooms of Pinus banksiana in Belair Provincial Forest, Manitoba, 1982.

Tree	Trap	Plane of Trap	Height of Trap Above Ground	Horizontal Distance from Broom	Total Pollen	Dispersal Units	% Single Grains
1	1	Horizontal	1 m	0 m	241	90	37
	2	Vertical	2 m	1 m	85	60	71
2	1	Horizontal	1 m	0 m	462	133	29
	2	Horizontal	2 m	1 m	107	79	74
	3	Vertical	2 m	2 m	134	67	50
3	1	Horizontal	2 m	1 m	79	49	62
	2	Vertical	2 m	3 m	63	32	51
Totals	7				1171	510	

A single flower trapped on day 7 of the sampling period accounted for 87% of the day's pollen count, when this was omitted the plot of the combined data (Fig. 38) showed a similar trend to the pollen trapped in the open (Fig. 39) in which a significant dip in the pollen count followed by an increase occurred on days 7 and 8 of the pollination period. Unlike the total pollen count recorded in the open (Fig. 39) the airborne pollen concentrations within the forest decreased soon after the male flowers had absissed. Wind speeds within the forest obtained with the use of a hand-held anemometer ranged from 0 to 1.2 m/sec and presumably pollen did not remain airborne under such conditions.

iii. Relationship with Climate

In both 1982 and 1983 there were dips in the total pollen recorded. In 1983 (Fig. 40) an early peak (day 14) was followed by a low count (day 21) and a gradual rise to a second peak (day 42). It has been observed that the male flowers of A. americanum close during cold weather during which time no pollen is discharged (Penfield et al., 1976). The spring of 1983 was marked by unusually low temperatures for part of the season (days 9 to 19, Fig. 40). It would appear that the lows preceding the weekly pollen collection affected the quantity of pollen trapped. A relatively high low ($7^{o}C$) on day 6 may have been responsible for the initial peak after the male flowers opened. The relatively cool lows ($-3^{o}C$ to $-9^{o}C$) on days 9 to 16 were thought to have affected the flowers, causing them to close and drastically reducing the concentration of airborne pollen. There were several relatively warm lows over days 21 to 35

Fig. 38. Air-borne pollen of *Arceuthobium americanum* trapped in the immediate vicinity of brooms of *Pinus banksiana* induced by male infections of *A. americanum* within Belair Provincial Forest, Manitoba, 1982.

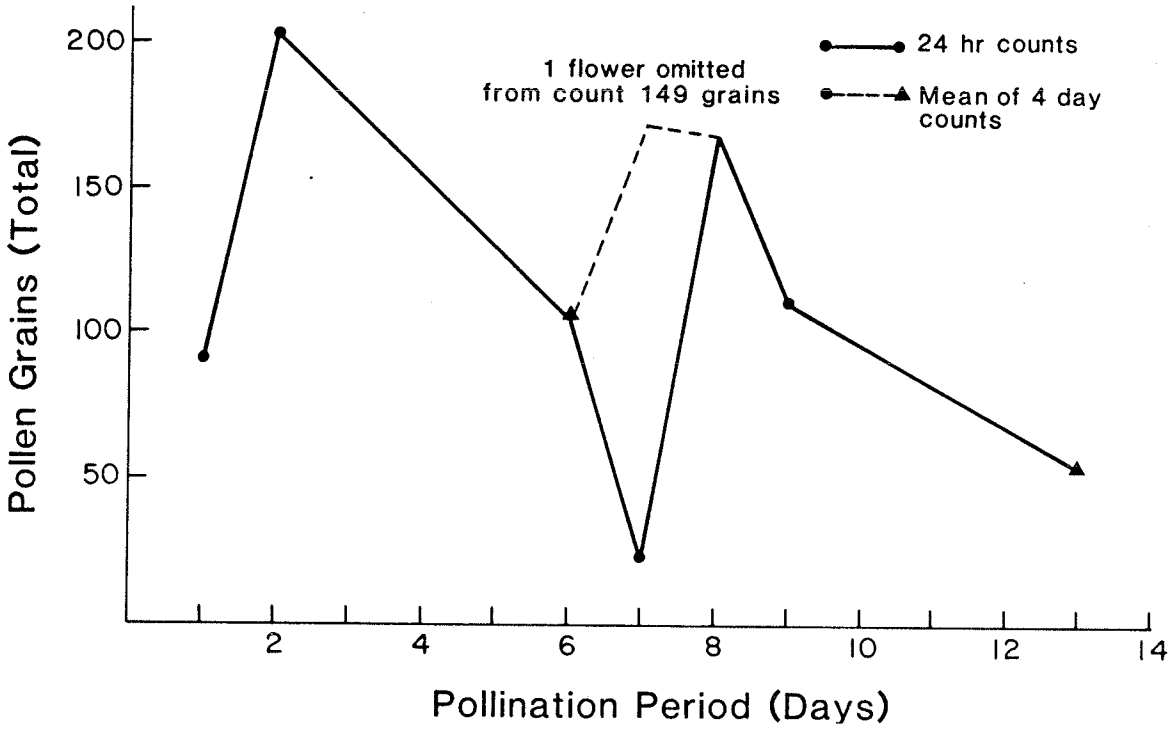

200
150
100
50
Pollen Grains (Total)
1 flower omitted
from count 149 grains
24 hr counts
Mean of 4 day
counts
2
4
6
8
10
12
14
Pollination Period (Days)

Fig. 39. Relationship between air-borne pollen of Arceuthobium americanum and temperature in Belair Provincial Forest, Manitoba, 1982.

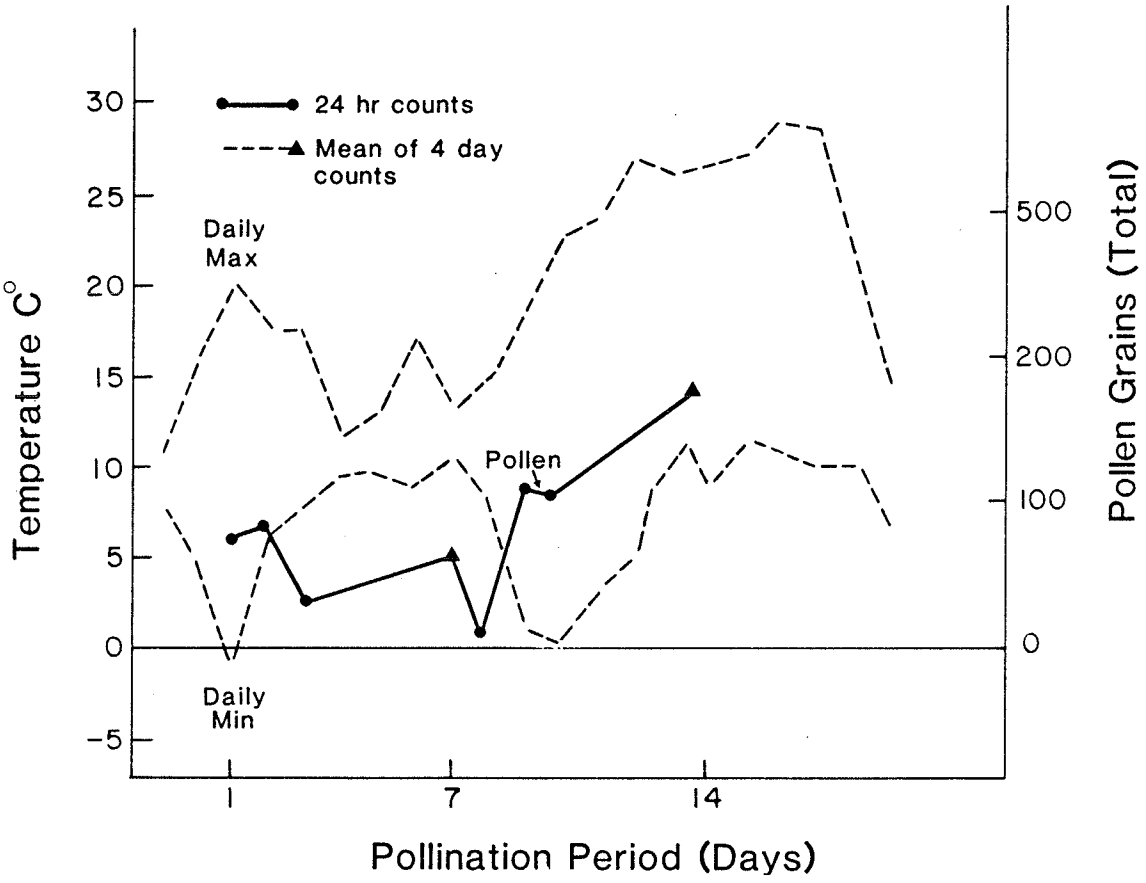
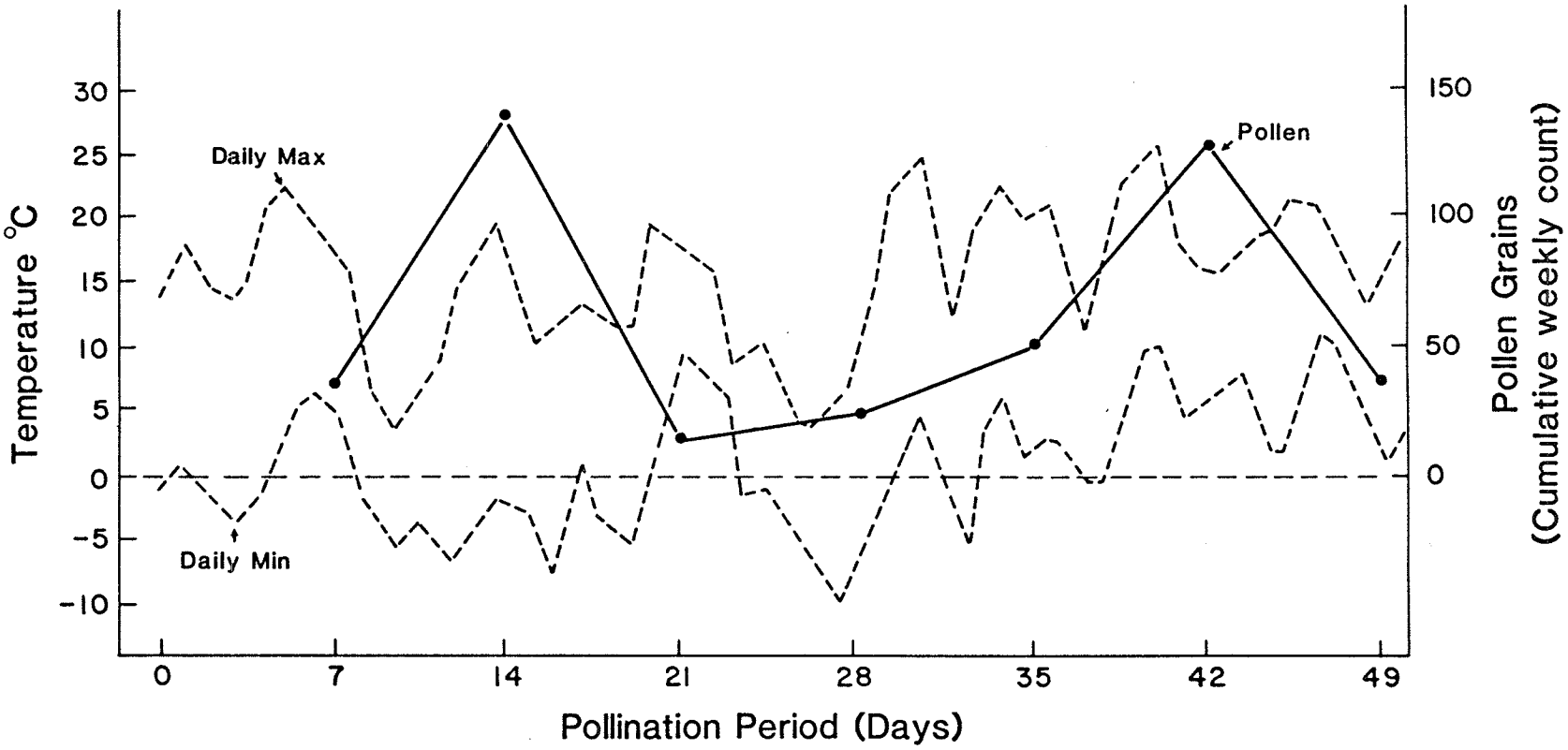

24 hr counts
Mean of 4 day counts
Daily Max
Daily Min
Pollen
Temperature C°
Pollen Grains (Total)
30
25
20
15
10
5
0
-5
500
200
100
0
1
7
14
Pollination Period (Days)

Fig. 40. Relationship between air-borne pollen of Arceuthobium americanum and temperature in Belair Provincial Forest, Manitoba, 1983.


Temperature °C
30
25
20
15
10
5
0
-5
-10
Daily Max
Daily Min
Pollen
150
100
50
0
Pollen Grains
(Cumulative weekly count)
0
7
14
21
28
35
42
49
Pollination Period (Days)

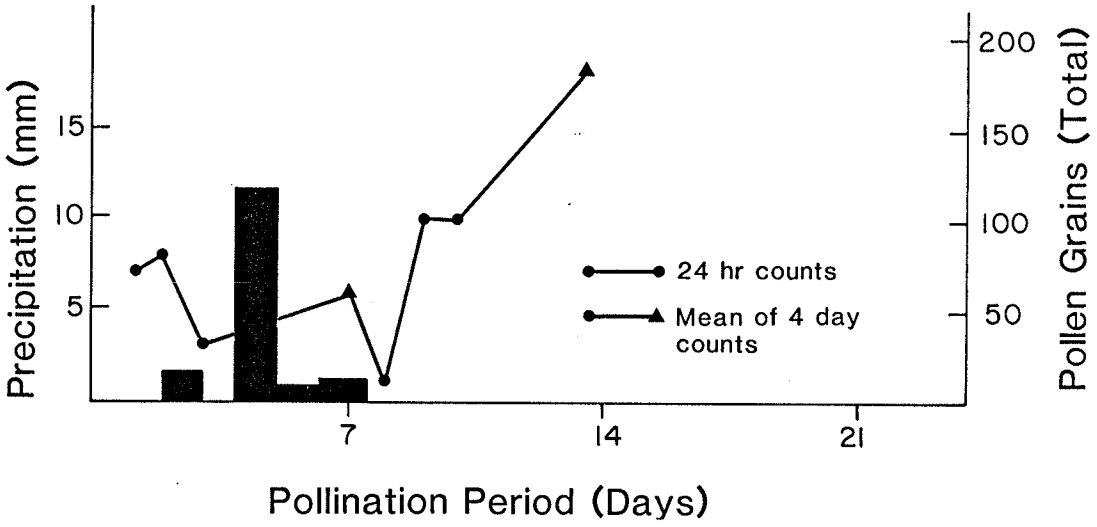
and pollen counts increased up to a second peak on day 42. All flowers had dishcarged their pollen and absissed by day 42, although low concentrations remained a week later (day 49).

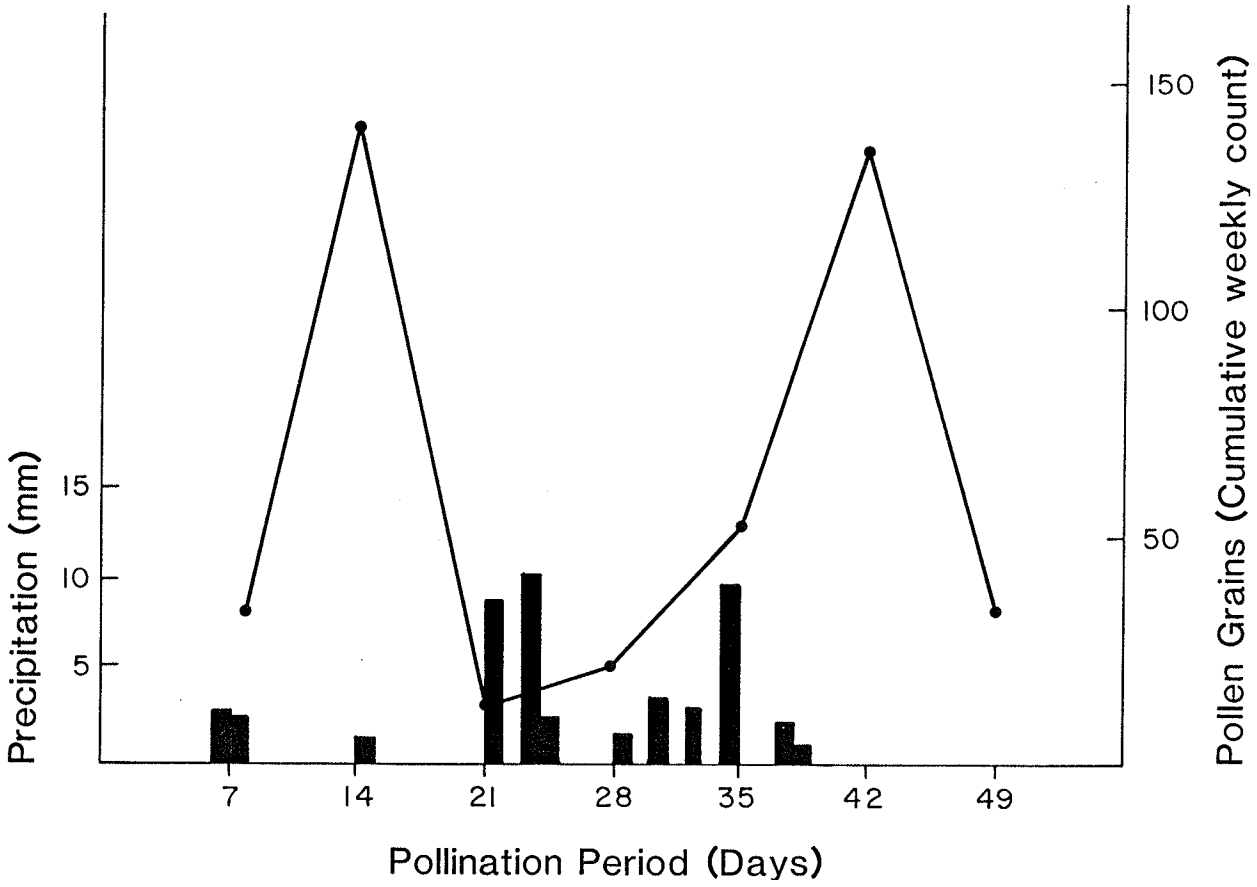
When temperature and pollen counts were compared for 1982 (Fig. 39) a relatively low minimum ($-1^{o}C$) on the first day of sampling may have accounted for the first dip, but the second dip precedes the second period of low minimum temperatures (days 8, 9) and the pollen count increased before the temperatures recovered their earlier values. Temperature may be one factor influencing pollen discharge but it does not explain all the variations in air-borne pollen concentrations observed in this study. In 1983, it was found that some pollen remained air-borne a week after floral abscission. Sampling was terminated when the flowers were shed in 1982 and consequently the decrease in total pollen count at the end of the pollination period was missed.

Dips in the pollen count of A. americanum were noted by Penfield et al. (1976). It was suggested that a continuous 3-day rain might be responsible for the lower values. In 1982 rain occurred the day before the first dip (Fig. 41), but values appeared to be rising during the rainy weather (days 4 to 6) before the second major dip (day 8). As the count for days 4 to 7 is a mean, it is possible that varying daily values around the substantial rain of day 5 are obscured, but the second dip in the pollen count remains unexplained (Fig. 41). In 1983, when counts were made on a weekly basis, substantial rain fell on day 21 when the dip occurred (Fig. 42). The weather remained unsettled for the following two weeks and although pollen counts were low they were rising by day

Fig. 41. Relationship between air-borne pollen of Arceuthobium americanum and precipitation in Belair Provincial Forest, Manitoba, 1982.

Fig. 42. Relationship between air-borne pollen of Arceuthobium americanum and precipitation in Belair Provincial Forest, Manitoba, 1983.


Precipitation (mm)
15
10
5
200
150
100
50
Pollen Grains (Total)
24 hr counts
Mean of 4 day counts
7
14
21
Pollination Period (Days)


Precipitation (mm)
15
10
5
150
100
50
Pollen Grains (Cumulative weekly count)
7
14
21
28
35
42
49
Pollination Period (Days)

35. The dips and peaks observed in the concentration of air-borne pollen in 1982 and 1983 suggest that release is not uniform or continuous over the pollination period. The climatic data available failed to implicate either temperature or precipitation as the sole cause for arrest or retardation of pollen discharge. However, the sites were close to Lake Winnipeg, a large body of water which would no doubt influence local temperature and precipitation, while the study had to rely on the climatic records of Environment Canada Meteorological Office for Pine Falls, the closest meteorological station to the study sites and some 16 km distant. This may have obscured the relationship between air-borne pollen concentrations and temperature and/or precipitation.

Pollination Success

The experiment to determine the number of successfully pollinated flowers on trees isolated from male dwarf mistletoe infections was disturbed in a number of ways as outlined in Chapter 1. Only 14 of the original twenty-five marked plants on the experimental trees and one of the five on the control tree (from which no insect collection was attempted) remained at the time of the second count (Table 17). On the 15 surviving plants just 50% of the developing fruits counted in April reached maturity. However, considerably more flowers appeared to have been pollinated in the spring of 1983 (272) than 1982 (99) (Table 17), although a direct comparison cannot be made until the developing fruits have overwintered and reached maturity. Approximately 21% of the flowers with receptive stigmas in spring 1983 were not pollinated.

Table 17. Pollination success of tagged plants of female Arceuthobium americanum infected Pinus banksiana isolated from male infections in Belair Provincial Forest, Manitoba, 1983.

Tree	Plant	First Count (April 1983) Developing Fruits ('81)[1]	Second Count (August 1983) Mature Fruits ('81)	Developing Fruits ('82)	Unfert-ilized Flowers ('82)	Newly emerged Flowers ('83)
1	1	2	0	32	0	46
	2	0	0	15	0	15
	3	0	0	43	0	0
	4	0	0	24	0	28
	5	0	0	6	0	34
3	1	3	0	13	0	3
	2	18*	2*	1	6	0
	3	7	0	1	5	0
	4	0	0	2	13	0
	5	4	1	2	2	0
4	1	1	1	0	0	3
5	2	45	35	31	6	15
	3	0	0	68	30	12
	5	19	11	22	11	0
CONTROL	2	0	0	12	0	16
TOTALS	15	99	50	272	73	172

*Some pedicels remained suggesting that maturing fruits had perhaps been eaten by birds or trampled by rodents.

[1]Year of floral initiation.

General Discussion

There is evidence that both entomophily and anemophily play a role in the pollination of A. americanum.

Members of several anthophilous insect families, some well dusted with pollen, were found associated with dwarf mistletoe flowers. Ants of the genus Formica and Bradysia sp. (Sciaridae) have commonly been reported as insect pollinators of A. americanum in earlier studies (Gregor et al., 1974; Penfield et al., 1976). In Manitoba, two coleopterans, Hyperaspis binotata (Coccinellidae) and Cyphon sp. (Helodidae), were frequently trapped and may effect a degree of pollination. However, the scarcity of H. binotata after 1981 and the absence of Cyphon sp. in the first year of sampling is perhaps indicative of a local and erratic population buildup in some insect species. Presumably, flowers such as A. americanum with no special adaptations to specific insect pollinators are placed at advantage if such a population explosion occurs in a pollinating insect species. None of the insects reported showed specific adaptations for the pollination of A. americanum; rather it would appear that a number of unspecialized insect visitors are responsible for chance pollen transfer in conjunction with nectar and/or pollen predation. However, in 1983 insects bearing pollen and trapped from female A. americanum isolated from male brooms were few, 8.75% of the total, although an appreciable percentage,79%, of flowers with receptive stigmata were fertilized. The experiment had been disturbed, but the pollination success was high, suggesting that the wind as a pollination mechanism of A. americanum was effective.

Exclusion experiments, designed to prevent the entry of insect visitors to female flowers and to determine whether the pollination mechanism is entomophilous and anemophilous have resulted in low seed set and conflicting interpretations of the data (Player, 1977; Baker, 1981). Screens of small mesh (0.5 mm and 1.0 mm) gave 2% or less seed set in comparison with a range of 11% to 62.5% seed set in uncovered plants (Player, 1977). Baker (1981) observed considerable seed set in plants screened with 4.0 mm mesh, which, however, failed to exclude insects, but there was also some fruits set on branches covered with screens of smaller mesh (0.8 mm and 2.2 mm). Player (1977) reasoned that the low seed set observed in his experiment was due to the airstream with its pollen load passing around the mesh bags. Baker (1981) concluded that while anemophily must play at least a minimal role in pollination, low seed set was due to exlcusion of insects. It is also possible that the pollen carries a small electrical charge sufficient to attract it to the mesh screens rather than permitting entry to the flowers inside the bag. Gregory (1973) cites a number of studies which indicate that some spores do carry a charge, and that some carry different charges under different conditions. The present study has revealed the presence of air-borne pollen up to 400 m from a source and that anemophily is an effective mode of pollination. It would be of great interest to determine whether or not the cause for low seed set in screened Arceuthobium flowers is due to opposite electrical charges on spores and screen obstructing passage of the spore to the flowers inside.

Pollen was trapped up to 400 m from the source over a

clear cut area and provides evidence that, in spite of its entomophilous characteristics, presence of spines and tendency to cluster, it is easily transported by the wind. At approximately 20μ diam., A. americanum pollen falls within the size range of the pollen grains possessed by most wind-pollinated species (Whitehead, 1969). Moreover, in sheltered areas of the forest where male and female brooms are encountered on the same tree the indication is that, at low wind speed or in the absence of wind, gravity deposition occurs effecting a certain degree of pollination.

Efficiency of trapping air-borne pollen

Most studies have concluded that both insects and wind are effective pollinators of A. americanum; the divergence of opinion stems from which is considered the primary pollinating mechanism (Baker, 1981; Gregor et al., 1974; Penfield et al., 1976; Player, 1977). Microscope slides, coated with vaseline or petrolatum, have been commonly used to trap air-borne spores and pollen and were employed by the supporters of an entomophilous pollination syndrome (Baker, 1981; Gregor et al., 1974; Penfield et al., 1976). However, microscope slides have poor impaction efficiency at the low wind speeds observed within a forest, especially when the spores in question are small (Gregory, 1973), and it is most probable that the method has led to an underestimation of the air-borne pollen load.

Using petrolatum covered microscope slides Potter and Rowley (1960) found that the pollen concentration on weekly slides was not 7X but usually only 3 or 4X higher than slides exposed for

one day. The reason for this was assumed to be a decrease in the adhesiveness of the slide as the surface became covered with pollen and dust (Potter and Rowley, 1960). Some mistletoe studies (e.g. Penfield et al., 1976) have exposed slides for periods of a week compounding the problem of underestimating air-borne pollen concentrations.

The cheesecloth traps used in the present study avoided some of the problems associated with sticky slides. Air passes through the cloth trapping a proportion of the spined pollen grains on the cheesecloth fibres. The pollen grains of A. americanum are small (20μ) and probably carried in the airstream around a microscope slide unless the wind speed is high enough to give momentum sufficient for impaction of the spores. While the cheesecloth traps can only give an indication of the relative concentrations of pollen in the air it is felt that they give a better estimation than the microscope slides.

There is strong evidence that past studies have underestimated the role of wind in the pollination of A. americanum. Some of the features that have been described as characteristics of insect pollinated flowers may in fact aid an anemophilous pollination mechanism. Player (1977) suggested that the spines on the pollen, which are unusual in wind pollinated species may serve as an arresting mechanism when conditions are unfavourable for dispersal. The anther is open and exposed and provides no other means of holding pollen back, although the male flowers commonly close when temperatures are low, especially in early spring (Penfield et al., 1976). Feathery stigmata, which increase the efficiency of impaction

of spores, are frequently associated with anemophiles (Whitehead, 1969). The stigma of A. americanum is not at all characteristic of wind pollinated flowers but the highly concentrated stigmatic exudate may have a dual purpose; to provide necessary adhesiveness to increase pollen retention after deposition and to serve as an insect attractant, as proposed by Brewer et al. (1974).

The specifically entomophilous features of fragrance and nectaries may be vestigial as found in other anemophilous plants, for example Urtica (Faegri and van der Pijl, 1979). Player (1977) has observed that secretions are emitted from the central cushion of male Arceuthobium flowers, and the organ has been interpreted as a nectary by Dowding (1931a) and others (Gregor et al., 1974; Penfield et al., 1976). Ants have been observed probing the central cushion and it may have the advantage of distracting insect pollen predators. However, it should be noted that observations of A. americanum in the present study support the conclusions of Cohen (1968) who, in his detailed examination of the development of male flowers of this species found no evidence of glandular cells or nectaries.

The decussate arrangement of male flowers (ensuring that some always face the wind), sexual dimorphism, a reduction in seed number (A. americanum has two embryo sacs but only one seed develops) and a flowering time that is temporally separated from the coniferous host are features of Arceuthobium (Player, 1977) which indicate it is well suited to an anemophilous mode of pollination. Moreover, in Manitoba, flowers of A. americanum are the first to open followed by Carex richardsonii R. Br. and Salix spp. resulting

in little competition for space from foreign pollen on the stigmata of A. americanum.

In conclusion, there is sufficient evidence to suggest that both entomophily and anemophily are important pollination mechanisms of A. americanum depending on the local environment in which pollen transfer is taking place. Anemophily is most likely to be of significance in open forest and for long distance transfer of pollen while within closed forest chance visits by unspecialized insect visitors will effect a degree of pollination; that is, "some plants make the best of both worlds" (Gregory, 1973).

SUMMARY AND CONCLUSIONS

Phenological Observations

Floral opening generally starts in the third week of April to the first week of May in Belair Provincial Forest, Manitoba. However, after a mild winter in 1981 flowers were seen in bloom as early as 5 April reflecting the strong influence of climatic factors.

A male to female ratio of 2:1 was found in plants counted on 25 dwarf mistletoe-infected trees. Twice as many trees, 6/25, had no female infections as trees with no male infections, 3/25. Further observations are necessary to assess the significance of this ratio.

The percentage of developing fruits found in May 1981 was low, 1-8%, A higher percentage of flowers were fertilized in spring 1981, 20-53%, and the following spring 1982, 34%. However, the highest percentage of successfully pollinated flowers, 79%, was recorded in 1983. The reason for such variation in pollination success from year to year needs further study.

The hot, dry summer of 1983 is thought to have caused the death, due to water stress, of numerous witches' brooms.

The loss of 50% of the tagged plants in one experiment in 1983 leads one to question whether such losses were exceptional or typical of any year, and what was responsible.

Fungal Associations

Wallrothiella arceuthobii was found in comparative abundance, but only locally, parasitizing a maximum of 50% of the developing fruits on a small broom.

A comparison of the ANOVA of the July dataset with the ANOVA of the entire data revealed that date of collection and dwarf mistletoe-host association were significant factors influencing the abundance of the principal fungi, A. alternata, Coniothyrium sp. 1 and Cladosporium spp. The analyses were complicated by the scarcity of moribund A. pusillum and by the loss of male shoots of this species after pollination. A. alternata was observed as often on healthy mistletoe tissue as moribund, revealing both parasitic and saprophytic capabilities. Coniothyrium sp. 1 and Cladosporium spp. were more frequently associated with moribund tissue suggesting that they are generally saprophytic in nature.

The commonly observed fungi were most abundant in spring. While rarely isolated fungi were in greater evidence in summer, the principal fungi, especially A. alternata, increased in number in the fall again, although not to spring levels. Climatic effects and competition for available host nutrients are thought to influence the abundance of different fungal species.

The majority of Pyrenomycetes and Hyphomycetes had previously been identified in association with A. americanum in Manitoba; however, a number of genera of Coelomycetes are reported for Arceuthobium for the first time. These include four Coniothyrium species, Cryptosporiopsis sp., Seimatosporium lichenicola, Naemospora sp., Cytospora sp., Phoma sp., and Colletotrichum sp. Colletotrichum gloeosporioides is reported on dwarf mistletoe from Manitoba for the first time.

The surveys of mycoflora identify a distinct similarity between the fungi associated with A. americanum on P. banksiana and

and A. pusillum on Picea mariana and P. glauca.

Two fungi once considered as possible control agents were isolated in the present study, W. arceuthobii and C. gloeosporioides. Both of these species have characteristics that lower their value as control agents. Colletotrichum gloeosporioides mainly attacks the aerial shoots of dwarf mistletoe reducing the current year's seed crop but having no effect on the number of new plants. The abundance of W. arceuthobii varies widely and inexplicably on a year to year basis. Another Colletotrichum sp., found more frequently than Colletotrichum gloeosporioides and Coniothyrium sp. 1, may have some potential as biological control agents, but their pathogenicity on Arceuthobium has first to be proven.

Pollination Biology

There is evidence to support the presence of both entomophilous and anemophilous pollination mechanisms in A. americanum. Bradysia sp. (Diptera) and Formica spp. (Hymenoptera) account for the majority of insects collected each year and are successful pollinators where brooms of both sexes are in close proximity. Hyperapsis binotata and Cyphon sp. were frequently trapped from both male and female brooms. Although coleopterans are generally known as destructive insect visitors a limited amount of chance pollination is attributed to them.

Where female brooms were isolated from male brooms, few pollen-bearing insects were collected although a high percentage, 79%, of flowers were fertilized. Moreover, air-borne dwarf mistletoe pollen was trapped up to 400 m from the source. These phenomena

indicate that pollen transfer is primarily effected by wind.

Mistletoe pollen is not released uniformly or continuously, although the stimulus or mechanism that arrests or retards pollen release is at present unknown. There is no evidence of a direct correlation between pollen discharge and temperature or rainfall. However, on-the-spot and continuous records are needed before the impact of climatic forces on pollen release can be properly assessed.

BIBLIOGRAPHY

Baker, F. A. 1981. Biology and control of the eastern dwarf mistletoe. Ph. D. Diss., University of Minnesota, 254 pp. Unpubl.

Baranyay, J. A. 1966. Fungi from dwarf mistletoe infections in western hemlock. Canadian Journal of Botany 44: 597-604.

_____. 1970. Lodgepole pine dwarf mistletoe in Alberta. Dept. of Fisheries & Forestry, Canadian Forestry Service, Publication No. 1286. Pamphlet.

_____ and R. B. Smith. 1972. Dwarf mistletoes in British Columbia and recommendations for their control. Pacific Forest Research Centre. BC-X-72.

_____ and _____. 1974. Low temperature damage to dwarf mistletoe fruit. Canadian Journal of Forest Research 4: 361-365.

Bourchier, R. J. 1954. Septogloeum gillii on lodgepole pine mistletoe. Canada Dept. Agriculture Science Service, Forest Biology Division. Bimonthly Progress Report 10: 3.

_____. 1955a. New host relationships for fungus parasites of the lodgepole pine mistletoe. Canada Dept. Agriculture Science Service, Forest Biology Division. Bimonthly Progress Report 11: 2.

_____. 1955b. Parasites of dwarf mistletoe. In Annual Report of the Forest Insect and Disease Survey. Canada Dept. Agriculture. 1954. p.111.

Brewer, J. W., K. J. Collyard and C. E. Lott, Jr. 1974. Analysis of sugars in dwarf mistletoe nectar. Canadian Journal of Botany 52: 2533-2538.

Byler, J. W. and F. W. Cobb, Jr. 1972. The occurrence and pathogenicity of Nectria fuckeliana on dwarf mistletoe in California. Canadian Journal of Botany 50: 1162-1163.

Cohen, L. I. 1968. Development of the staminate flower in the dwarf mistletoes, Arceuthobium. American Journal of Botany 55: 187-193.

_____. 1970. Development of the pistillate flower in the dwarf mistletoes, Arceuthobium. American Journal of Botany 57: 477-485.

Dowding, E. S. 1929. The vegetation of Alberta. III. The Sandhill areas of central Alberta with particular reference to the ecology of Arceuthobium americanum Nutt. Journal of Ecology 17: 82-105.

_____. 1931a. Floral morphology of Arceuthobium americanum. Botanical Gazette 41: 42-54.

_____. 1931b. Wallrothiella arceuthobii, a parasite of the jackpine mistletoe. Canadian Journal of Research 5: 219-230.

Ellis, D. E. 1946. Anthracnose of dwarf mistletoe caused by a new species of Septogloeum. Elisha Mitchell Scientific Society Journal 62: 25-50.

Ellis, M. B. 1971. Dematiaceous Hyphomycetes. Commonwealth Mycological Institute. Commonwealth Agricultural Bureaux.

Faegri, K. and L. van der Pijl. 1979. The Principles of Pollination Ecology. Pergamon Press Ltd.

Filip, G. M., J. S. Hadfield and C. Schmitt. 1979. Branch mortality of true firs in west-central Oregon associated with dwarf mistletoe and canker fungi. Plant Disease Reporter 63: 189-193.

Funk, A. and J. A. Baranyay. 1973. Additional fungi and a gall disease of dwarf mistletoe swellings in western hemlock. Canadian Plant Disease Survey 53: 182.

_____ and R. B. Smith. 1981. Potebniamyces gallicola n. sp. from dwarf mistletoe infections in western hemlock. Canadian Journal of Botany 59: 1610-1612.

_____, R. B. Smith and J. A. Baranyay. 1973. Canker of dwarf mistletoe swellings on western hemlock caused by Nectria fuckeliana var. macrospora. Canadian Journal of Forest Research 3: 71-74.

Gilbert, J. 1981. The fungi associated with the dwarf mistletoe Arceuthobium americanum that attacks jack pine, Pinus banksiana in Manitoba. B. Sc. Hons. Thesis, Department of Botany, University of Manitoba, 47 pp. Unpubl.

Gill, L. S. 1935. Arceuthobium in the United States. Transactions of the Connecticut Academy of Arts & Science. Vol. 32, p. 111-245.

_____ and F. G. Hawksworth. 1961. The Mistletoes. A Literature Review. United States Department of Agriculture. Technical Bulletin #1242.

Gregor, S., D. Wiens, R. E. Stevens and F. G. Hawksworth. 1974. Pollination studies of Arceuthobium americanum in Utah and Colorado. The Southwestern Naturalist 19: 65-73.

Gregory, P. H. 1973. Microbiology of the atmosphere. 2nd Ed. Leonard Hill. Aylesbury, England. 377 pp.

Hagen, K. S. 1962. Biology and ecology of predaceous Coccinellidae. Annual Review of Entomology 7: 289-326.

Hawksworth, F. G. and D. Wiens. 1972. Biology and classification of the dwarf mistletoes (Arceuthobium). United States Department of Agriculture.Forest Service.Agriculture Handbook No. 401.

_____, C. S. Dixon and R. G. Krebill. 1983. Peridermium bethelii: A rust associated with lodgepole pine dwarf mistletoe. Plant Disease 67: 729-733.

_____, E. F. Wicker and R. F. Scharpf. 1977. Fungal parasites of dwarf mistletoes. United States Department of Agriculture Forest Service General Technical Report RM-36. 1976.

Hodek, I. 1973. Biology of the Coccinellidae. Dr. W. Funk. The Hague. pp. 260.

Hull, R. J. and O. A. Leonard. 1964. Physiological aspects of parasitism in mistletoes (Arceuthobium and Phoradendron). I. The Carbohydrate Nutrition of Mistletoe. Plant Physiology. pp. 996-1007.

Kuijt, J. 1955. Dwarf mistletoes. The Botanical Review 21: 569-626.

_____. 1963. Distribution of dwarf mistletoes and their fungus hyperparasites in western Canada. National Museum of Canada Bulletin 186: 134-148.

_____. 1969. Observations on Wallrothiella arceuthobii, a fungus parasite of dwarf mistletoes. Canadian Journal of Botany 47: 1359-1365.

Linder, D. H. 1938. New California fungi. Mycologia 30: 664-671.

Mark, W. R., F. G. Hawksworth and N. Oshima. 1976. Resin Disease: a new disease of lodgepole pine dwarf mistletoe (A. americanum). Canadian Journal of Forest Research 6: 415-424.

Mielke, J. L. 1959. Infection experiments with Septogloeum gillii, a fungus parasitic on dwarf mistletoe. Journal of Forestry 57: 925-926.

Muir, J. A. 1967. Occurrence of Colletotrichum gloeosporioides on dwarf mistletoe (Arceuthobium americanum) in western Canada. Plant Disease Reporter 51: 798-799.

_____. 1973. Cylindrocarpon gillii, a new combination for Septogloeum gillii on dwarf mistletoe. Canadian Journal of Botany 51: 1997-1998.

_____. 1977. Effects of the fungal hyperparasite Colletotrichum gloeosporioides of dwarf mistletoe (Arceuthobium americanum) on young lodgepole pine. Canadian Journal of Forest Research 7 (4): 579-583.

Parker, A. K. 1970. Growth of Wallrothiella arceuthobii on artificial media. Canadian Journal of Botany 48 (5): 837-839.

Parmeter, J. R., Jr., J. R. Hood and R. F. Scharpf. 1959. Colletotrichum blight of dwarf mistletoe. Phytopathology 49: 812-815.

Penfield, F. B., R. E. Stevens and F. G. Hawksworth. 1976. Pollination ecology of three Rocky Mountain dwarf mistletoes. Forest Science 22: 473-484.

Player, G. 1977. Some aspects of wind pollination with emphasis on the pollination of Arceuthobium. Ph. D. Diss., Department of Biology, University of Utah, 81 pp. Unpubl.

Potter, L. D. and J. Rowley. 1960. Pollen rain and vegetation, San Augustin Plains, New Mexico. Botanical Gazette 122: 1-25.

Proctor, M. and P. Yeo. 1972. The Pollination of Flowers. Taplinger Publ. Co., Inc. New York, New York. 418 pp.

Rediske, J. H. and K. R. Shea. 1961. The production and translocation of photosynthate in dwarf mistletoe and lodgepole pine. American Journal of Botany 48: 447-452.

Rose, A. H. and O. H. Lindquist. 1973. Insects of Eastern pines. Dept. of the Environment. Canadian Forestry Service. Publication 1313.

Scharpf, R. F. 1964. Cultural variation and pathogenicity of the Colletotrichum blight fungus of dwarf mistletoe. Phytopathology 54: 905-906.

_____. 1969. Cytospora abietis associated with dwarf mistletoe on true firs in California. Phytopathology 59: 1657-1658.

_____. 1983. Growth of Cytospora abietis on media made from dwarf mistletoe-infected and uninfected branch tissues of red fir. Plant Disease 67: 656-657.

Smith, R. B. and A. Funk. 1980. Assessing Nectria macrospora as a biological control agent for hemlock dwarf mistletoe. Environment Canada Forestry Service. Bi-monthly Research Notes 36: 11.

Stevens, R. E. and F. G. Hawksworth. 1970. Insects and mites associated with dwarf mistletoes. United States Department of Agriculture. Forest Service Research Paper RM-59.

Weir, J. R. 1915. Wallrothiella arceuthobii. Journal of Agricultural Research 4: 369-376.

Whitehead, D. R. 1969. Wind pollination in the angiosperms: evolutionary and environmental considerations. Evolution 23: 28-35.

Wicker, E. F. 1967. Appraisal of biological control of Arceuthobium campylopodum f. campylopodum by Colletotrichum gloeosporioides Plant Disease Reporter 51: 311-313.

_____ and C. G. Shaw. 1968. Fungal parasites of dwarf mistletoes. Mycologia 60: 372-383.

Wright, E. 1942. Cytospora abietis, the cause of a canker of true firs in California and Nevada. Journal of Agricultural Research 65: 143-153.

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Table A1. Analysis of variance of frequency of isolation of *Alternaria alternata* from *Arceuthobium americanum* (parasitic on *Pinus banksiana*) at Grand Beach and The Pas, July 1981.

Source of Variation	Df.	Sum square	Mean square	F value
Location	1	60006.0	60006.0	142.36**
Observation time	3	44938.8	14979.6	35.54**
Condition	1	2300.5	2300.5	5.46*
Sex	1	5.5	5.5	0.01
Loc*Observ	3	17552.8	5850.9	13.88**
Loc*Cond	1	1891.5	1891.5	4.49*
Observ*Cond	3	1784.3	594.8	1.41
Loc*Sex	1	987.0	987.0	2.34
Observ*Sex	3	75.3	25.1	0.06
Cond*Sex	1	19.0	19.0	0.05
Loc*Observ*Cond	3	81.3	27.1	0.06
Loc*Observ*Sex	3	1147.8	382.6	0.91
Loc*Cond*Sex	1	127.5	127.5	0.30
Observ*Cond*Sex	3	515.8	171.9	0.41
Loc*Observ*Cond*Sex	3	315.3	105.1	0.25
Error	288	121393.2	421.5	
Total	319	253142.0		

*Significant at α = .05

**Highly significant at α = .01

Table A2. Analysis of variance of frequency of isolation of *Coniothyrium* sp. 1 from *Arceuthobium americanum* (parasitic on *Pinus banksiana*) at Grand Beach and The Pas, July 1981.

Source of Variation	Df.	Sum square	Mean square	F value
Location	1	25027.8	25027.8	154.70**
Observation time	3	14598.4	4866.1	30.07**
Condition	1	15.3	15.3	0.09
Sex	1	19687.8	19687.8	121.65**
Loc*Observ	3	7665.9	2555.3	15.79**
Loc*Cond	1	750.3	750.3	4.64*
Observ*Cond	3	268.4	89.5	0.55
Loc*Sex	1	23977.8	23977.8	148.16**
Observ*Sex	3	7665.9	2555.3	15.79**
Cond*Sex	1	4277.8	4277.8	26.43**
Loc*Observ*Cond	3	393.4	131.1	0.81
Loc*Observ*Sex	3	8805.9	2935.3	18.14**
Loc*Cond*Sex	1	15.3	15.3	0.09
Observ*Cond*Sex	3	985.9	328.6	2.03
Loc*Observ*Cond*Sex	3	78.4	26.1	0.16
Error	288	46610.0	161.8	
Total	319	160824.7		

*Significant at α = .05

**Highly significant at α = .01

Table A3a. Analysis of variance of frequency of isolation of *Alternaria alternata* from *Arceuthobium americanum* (parasitic on *Pinus banksiana*) at Grand Beach, July 1981.

Source of Variation	Df.	Sum Square	Mean Square	F value
Observation time	3	59246.7	19748.9	32.07**
Condition	1	4182.0	4182.0	6.79**
Sex	1	570.0	570.0	0.93
Observ*Cond	3	1160.7	386.9	0.63
Observ*Sex	3	890.7	296.9	0.48
Cond*Sex	1	24.0	24.0	0.04
Observ*Cond*Sex	3	788.7	262.9	0.43
Error	144	88673.2	615.8	
Total	159	155536.0		

*Significant at α = .05

**Highly significant at α = .01

Table A3b. Analysis of variance of frequency of isolation of *Coniothyrium* sp.1 from *Arceuthobium americanum* (parasitic on *Pinus banksiana*) at Grand Beach, July 1981.

Source of Variation	Df.	Sum square	Mean square	F value
Observation time	3	561.9	187.3	3.15*
Condition	1	275.6	275.6	4.64*
Sex	1	105.6	105.6	1.78
Observ*Cond	3	36.9	12.3	0.21
Observ*Sex	3	36.9	12.3	0.21
Cond*Sex	1	1890.6	1890.6	31.84**
Observ*Cond*Sex	3	561.9	187.3	3.15*
Error	144	8550.0	59.4	
Total	159	12019.4		

*Significant at α = .05

**Highly significant at α = .01

Table A3c. Analysis of variance of frequency of isolation of *Coniothyrium* sp. 1 from *Arceuthobium americanum* (parasitic on *Pinus banksiana*) at The Pas, July 1981.

Source of Variation	Df.	Sum square	Mean square	F value
Observation time	3	21702.5	7234.2	27.37**
Condition	1	490.0	490.0	1.85
Sex	1	43560.0	43560.0	164.81**
Observ*Cond	3	625.0	208.3	0.79
Observ*Sex	3	16435.0	5478.3	20.73**
Cond*Sex	1	2402.5	2402.5	9.09**
Observ*Cond*Sex	3	502.5	167.5	0.63
Error	144	38060.0	264.3	
Total	159	123777.5		

*Significant at $\alpha = .05$

**Highly significant at $\alpha = .01$

Table A4a. Analysis of Variance[1] of frequency of isolation of *Alternaria alternata* from *Arceuthobium americanum* and *A. pusillum*, at Grand Beach, 1981.

Source of Variation	Df.	Sum square	Mean square	F value
Date	2	28484.2	14242.1	7.2**
Plate (date)[2]	32	63183.7	1974.5	4.2**
Observation time	3	164851.4	54950.5	116.0**
Dm-H[3]	1	10348.8	10348.8	21.8**
Condition	1	45.2	45.2	0.1
Sex	2	6917.6	3458.8	7.3**
Date*Observ	6	9176.2	1529.4	3.2**
Date*Dm-H	2	8749.5	4374.7	9.2**
Date*Dm-H*Cond	1	9431.5	9431.5	19.9**
Error	349	165329.1	473.7	
Total	399	437455.6		

r^2 = .7

[1]All single factor effects, but only highly significant (= .01) interactions given.

[2]Error term for Date is MS of Plate (date).

[3]Dwarf mistletoe-host association.

*Significant at = .05.

**Highly significant at = .01.

Table A4b. Analysis of variance[1] of frequency of isolation of Alternaria alternata from Arceuthobium americanum and A. pusillum, at The Pas, 1981.

Source of Variation	Df.	Sum square	Mean square	F value
Date	2	67455.5	33727.8	17.0**
Plate (date)[2]	31	61367.7	1979.6	4.6**
Observation time	3	88585.8	29528.6	69.0**
Dm-H[3]	2	4055.3	2027.7	4.7*
Condition	1	1585.4	1585.4	3.7
Sex	2	1534.9	767.4	1.8
Date*Dm-H	4	56636.0	14159.0	33.1**
Observ*Dm-H	6	11952.1	1992.0	4.7**
Date*Cond	2	12689.1	6344.6	14.8**
Observ*Sex	6	11513.3	1918.9	4.5**
Dm-H*Sex	3	14073.6	4891.2	11.0**
Dm-H*Cond*Sex	2	12000.0	6000.0	14.0**
Error	483	206784.9	428.1	
Total	531	492030.3		

$r^2 = .7$

[1] All single factor effects, but only highly significant (= .01) interactions given.

[2] Error term for Date is MS of Plate (date).

[3] Dwarf mistletoe-host association.

* Significant at = .05.

** Highly significant at = .01.

Table A5a. Analysis of variance[1] of frequency of isolation of Coniothyrium sp. 1 from Arceuthobium americanum and A. pusillum, at Grand Beach, 1981.

Source of Variation	Df.	Sum square	Mean square	F value
Date	2	3732.3	1866.2	7.1**
Plate (date)[2]	32	8402.1	262.6	3.6**
Observation time	3	4671.1	1557.0	21.4**
Dm-H[3]	1	2.9	2.9	0.04
Condition	1	1609.8	1609.8	22.2**
Sex	2	146.6	73.3	1.0
Date*Observ	6	3523.4	587.2	8.1**
Date*Dm-H	2	2590.7	1295.4	17.8**
Dm-H*Cond	1	1461.3	1461.3	20.1**
Date*Sex	1	1762.6	1762.6	24.3**
Dm-H*Sex	2	2026.2	1013.1	13.9**
Date*Dm-H*Cond	1	4004.5	4004.5	55.1**
Dm-H*Cond*Sex	2	4185.4	2092.7	28.8**
Error	343	24924.5	72.7	
Total	399	55491.7		

r^2 = .7

[1]All single factor effects, but only highly significant (= .01) interactions given.

[2]Error term for Date is MS of Plate (date).

[3]Dwarf mistletoe-host association.

*Significant at = .05.

**Highly significant at = .01.

Table A5b. Analysis of variance[1] of frequency of isolation of *Coniothyrium* sp. 1 from *Arceuthobium americanum* and *A. pusillum* at The Pas, 1981.

Source of Variation	Df.	Sum square	Mean square	F value
Date	2	30638.9	15319.5	7.6**
Plate (date)[2]	31	62459.5	2014.8	12.1**
Observation time	3	28205.4	9401.8	56.5**
Dm-H[3]	2	38691.4	19345.7	116.4**
Condition	1	19212.6	19212.6	115.6**
Sex	2	28509.7	14254.9	85.7**
Date*Observ	6	18728.3	3121.4	18.8**
Observ*Dm-H	6	7749.9	1291.6	7.8**
Date*Cond	2	2837.9	1418.9	8.5**
Observ*Sex	6	11994.7	1999.1	12.0**
Dm-H*Sex	3	19712.4	6570.8	39.5**
Cond*Sex	2	6495.1	3247.6	19.5**
Date*Dm-H*Cond	2	4167.9	2083.9	12.5**
Observ*Dm-H*Sex	9	4939.4	548.8	3.3**
Dm-H*Cond*Sex	2	5343.7	2671.8	16.7**
Error	452	75151.7	166.3	
Total	531	326566.4		

r^2 = .9

[1]All single factor effects, but only highly significant (= .01) interactions given.

[2]Error term for Date is MS of Plate (date).

[3]Dwarf mistletoe-host association.

*Significant at = .05.

**Highly significant at = .01.

Table A6a. Analysis of variance[1] of frequency of isolation of Cladosporium spp. from Arceuthobium americanum and A. pusillum, at Grand Beach, 1981.

Source of Variation	Df.	Sum square	Mean square	F value
Date	2	16567.3	8283.6	14.5**
Plate (date)[2]	32	18313.8	572.3	7.4**
Observation time	3	3503.4	1167.8	15.0**
Dm-H[3]	1	1050.9	1050.9	13.5**
Condition	1	2014.7	2014.7	25.9**
Sex	2	2464.5	1232.2	15.9**
Date*Dm-H	2	3683.8	1841.9	23.7**
Dm-H*Cond	1	2002.9	2002.9	25.8**
Dm-H*Sex	2	4864.1	2432.1	31.3**
Dm-H*Cond*Sex	2	5160.4	2580.2	33.2**
Error	351	27277.8	77.7	
Total	399	76899.2		

r^2 = .7

[1]All single factor effects, but only highly significant (= .01) interactions given.

[2]Error term for Date is MS of Plate (date).

[3]Dwarf mistletoe-host association.

*Significant at = .05.

**Highly significant at = .01.

Table A6b. Analysis of variance[1] of frequency of isolation of Cladosporium spp. from Arceuthobium americanum and A. pusillum, at The Pas, 1981.

Source of Variation	Df.	Sum square	Mean square	F value
Date	2	112370.4	56185.2	32.5**
Plate (date)[2]	31	53582.6	1728.5	24.8**
Observation time	3	5912.1	1970.7	28.3**
Dm-H[3]	2	7278.3	3639.2	52.3**
Condition	1	37809.8	37809.8	542.9**
Sex	2	15278.4	7639.2	109.7**
Date*Dm-H	4	18019.5	4504.9	64.7**
Observ*Dm-H	6	2200.2	366.7	5.3**
Date*Cond	2	3322.2	1661.1	23.9**
Date*Sex	1	4133.5	4133.5	59.3**
Dm-H*Sex	3	16632.2	5544.1	79.6**
Cond*Sex	2	9291.9	4645.9	66.7**
Dm-H*Cond*Sex	2	8161.6	4080.8	58.6**
Error	470	32734.1	69.6	
Total	531	278990.1		

r^2 = .9

[1]All single factor effects, but only highly significant (= .01) interactions given.

[2]Error term for Date is MS of Plate (date).

[3]Dwarf mistletoe-host association.

*Significant at = .05.

**Highly significant at = .01.

Table A7. Analysis of variance for the study of insects associated with dwarf mistletoe, Arceuthobium americanum, in Belair Provincial Forest, Manitoba, 1981.

Source	Df.	Sum Square	Mean Square	F value
Site	2	6.07	3.04	
Day	2	0.47	0.24	
Time	2	111.20	55.60	
Latin Sq. Error	2	110.86	55.43	
Latin Sq. Total	8	228.60		
Gender	1	64.18	64.18	6.3*
Gender*Site	2	4.28	2.14	0.2
Gender*Day	2	15.08	7.54	0.7
Gender*Time	2	49.42	24.71	2.4
Error	74	750.04	10.13	
Total	89	1111.60		

*Significant at α = .01.

RARELY ENCOUNTERED FUNGI

TABLE		PAGE
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Table A8. Rarely encountered fungi from Arceuthobium americanum and A. pusillum at Grand Beach and The Pas. May, 1981.

	Grand Beach									The Pas										
	1*				2					1				2				3				
	H**		M		H		M			H		M		H		M		H		M		
	♂	♀	♂	♀	♂	♀	♂	♀	Total	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	Total
PYRENOMYCETES																						
Ascomycetes (Unid.)									0													0
Chaetomium sp.									0													0
Chaetomium elatum				1					1													0
Sordaria spp.				1					1													0
LOCULOASCOMYCETES																						
Pleospora sp.									0													0
COELOMYCETES																						
Colletotrichum gloeosporioides									0			4										4
Colletotrichum sp.			1						1													0
Coniothyrium sp. 2			1	1					3		1	8	7									16
Coniothyrium sp. 3									0													0
Coniothyrium sp. 4			1						1			1										1
Cryptosporiopsis sp.									0													0
Cytospora sp.		1				1			2													0
Naemospora sp.									0													0
Phoma sp.			1						1			3	3					3				9
Pycnidiella resinae									0													0
Pycnidial sp. (Unid.)									0													0
Seimatosporium lichenicola									0				10									10
Truncatella sp.									0						2			2			3	7
HYPHOMYCETES																						
Hyphomycetes (Unid.)									0										1			1
Arthrinium phaeospermum									0											1		1
Aspergillus sp.									0													0
Aureobasidium pullulans		1	5	3	1	1		1	12	1		1	1		1		1	2	1			8
Drechslera sp.	2		1	1					4													4
Epicoccum purpurascens		3	3		3			3	12				4					1				5
Fusarium sp.									0				1									1
Monodyctis sp.		1	1						2													0
Nigrospora sp.									0													0
Penicillium thomii									0											1		1
Penicillium spp.									0													0
Stachybotris atra									0													0
Ulocladium sp.									0													0
Mycelia sterilia	2		4	4		2	1		13			2	1	1				1				5
ACTINOMYCETES (Unid.)									0										1			1

*1 A. americanum/Pinus banksiana 2 A. pusillum/Picea mariana 3 A. pusillum/P. glauca **H Healthy mistletoe tissue M Moribund mistletoe tissue

Table A9. Rarely encountered fungi from *Arceuthobium americanum* and *A. pusillum* at Grand Beach and The Pas. July, 1981

	Grand Beach									The Pas									
	1*				2					1				2				3			
	H**		M		H		M			H		M		H		M		H		M		
	♂	♀	♂	♀	♂	♀	♂	♀	Total	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	Total
PYRENOMYCETES																						
Ascomycetes (Unid.)									0	2	1											3
Chaetomium sp.									0													0
Chaetomium elatum		1		3					4													0
Sordaria spp.									0													0
LOCULOASCOMYCETES																						
Pleospora sp.									0			1										1
COELOMYCETES																						
Colletotrichum gloeosporioides									0													0
Colletotrichum sp.	1		1	1		9			12	1	1	19	40						1			62
Coniothyrium sp. 2		4				3			7		5	1	2			2			1			10
Coniothyrium sp. 3						1			1													0
Coniothyrium sp. 4									0													0
Cryptosporiopsis sp.		1							0													0
Cytospora sp.									1		2	3	1						1			7
Naemospora sp.									0													0
Phoma sp.	1	3	2			2			8		4				2				2			8
Pycnidiella resinae				1					1						1							0
Pycnidial sp. (Unid.)				1					1													1
Seimatosporium lichenicola									0			2	2		6							10
Truncatella sp.									0						7				8			15
HYPHOMYCETES																						
Hyphomycetes (Unid.)									0			1	1		4				1			7
Arthrinium phaeospermum						1			1													0
Aspergillus sp.		1							1													0
Aureobasidium pullulans	2	1	3	3		3			12	30	8	43	7		3				1			92
Drechslera sp.						1			1										1			1
Epicoccum purpurascens	9	1		3		1			14	1	2	1			10							14
Fusarium sp.									0			1										1
Monodyctis sp.				1					1										1			1
Nigrospora sp.		2							2	1		1										2
Penicillium thomii									0													0
Penicillium spp.		3				7			10													0
Stachybotris atra									0						2							2
Ulocladium sp.		1	2						3													0
Mycelia sterilia		4	3	6		4			17		1		1		5				8			17
ACTINOMYCETES (Unid.)									0													0

*1 *A. americanum*/*Pinus banksiana* 2 *A. pusillum*/*Picea mariana* 3 *A. pusillum*/*P. glauca* **H Healthy mistletoe tissue M Moribund mistletoe tissue

Table A10. Rarely encountered fungi from Arceuthobium americanum and A. pusillum at Grand Beach and The Pas. September, 1981.

	Grand Beach						The Pas									
	1*		2				1		2		3					
	H**	M	H	M	Total		H	M	H	M	H	M	Total			
PYRENOMYCETES																
Ascomycetes (Unid.)			1		1								0			
Chaetomium sp.	1		1		2								0			
Chaetomium elatum					0								0			
Sordaria spp.					0								0			
LOCULOASCOMYCETES																
Pleospora sp.					0				1				1			
COELOMYCETES																
Colletotrichum gloeospioides					0								0			
Colletotrichum sp.		10	1		11			12				1	13			
Coniothyrium sp. 2			2		2		1	1	1	1			4			
Coniothyrium sp. 3					0								0			
Coniothyrium sp. 4					0								0			
Cryptosporiopsis sp.					0						2		2			
Cytospora sp.	1		1		2			1		1			2			
Naemospora sp.			1		1								0			
Phoma sp.			1		1		2					2	4			
Pycnidiella resinae					0								0			
Pycnidial sp. (Unid.)					0								0			
Seimatosporium lichenicola					0							1	0			
Truncatella sp.					0				2	6	6	2	16			
HYPHOMYCETES																
Hyphomycetes (Unid.)					0					1			1			
Acremonium charticola (Lindau) K. W. Gams					0					1			1			
Arthrinium phaeospermum		1			1		1			2	10	5	18			
Aspergillus sp.					0								0			
Aureobasidium pullulans	1	8	1		10		7	12	5	3			27			
Drechslera sp.		1			1				1	1			2			
Epicoccum purpurascens	1		1		2			1		1		4	6			
Fusarium sp.					0								0			
Monodyctis sp.					0								0			
Nigrospora sp.					0		2	2				1	5			
Penicillium thomii					0								0			
Penicillium spp.		2			2		1	1					2			
Stachybotris atra					0		1		1				3			
Ulocladium sp.					0								0			
Mycelia sterilia (Unid.)	5	6	8		19		2	9	7	6	10	2	30			
ACTINOMYCETES (Unid.)	1				1								0			

*1 A. americanum/Pinus banksiana 2 A. pusillum/Picea mariana 3 A. pusillum/P. glauca **H Healthy mistletoe tissue M Moribund mistletoe tissue