

Yasuyuki Hiratsuka
and John M. Powell

Pine Stem Rusts of Canada

Forestry Technical Report 4



**Yasuyuki Hiratsuka
and John M. Powell**

Pine Stem Rusts of Canada

**Northern Forest Research Centre,
Edmonton, Alberta**

**Identification, hosts, distribution,
morphology, life cycle, cytology,
damage, epidemiology, and control**

**Department of the Environment
Canadian Forestry Service
Forestry Technical Report 4**

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Among the diseases of pines (*Pinus* spp.) the stem rusts are most destructive and dangerous (Boyce 1961). Damage caused by this group of fungi (species of *Cronartium* and *Endocronartium*) tends to increase by intensive and extensive cultivation of pines. Rust fungi prefer to attack vigorously growing trees of all ages rather than weakened ones. Several species kill trees by girdling them; others severely deform trees or reduce their rate of growth. To some extent, blister rusts may act as thinning agents in extremely dense natural stands. Stem rusts have been the limiting factor for the successful establishment and management of certain pine species, especially in areas where white pine blister rust is common. Damage caused by native pine stem rusts has not always been considered a major problem in Canada, but it will become increasingly important should intensive and extensive cultivation of pines be undertaken.

About 20 species of stem rusts of pine are known (Peterson 1962b, 1967, 1973); six are found in Canada. Most species belong to the genus *Cronartium* and require alternate host plants to complete their life cycles. The imperfect (spermogonial and aecial) states, which in this genus occur on pines, are included in the form genus *Peridermium*. The other states (uredinial and telial) occur on the alternate hosts. Several species of pine stem rusts, however, are able to reinfect pines directly and do not have alternate hosts. These are classified in the genus *Endocronartium* (Hiratsuka 1969).

The results of recent taxonomical, nomenclatural, cytological and life history studies have clarified much of the past confusion of this group of rusts (Peterson 1962b, 1967, 1973; Hiratsuka 1969; Ziller 1970, 1974). We have had the opportunity to examine and annotate all the major Canadian pine stem rust material held in

North American herbaria. Taxonomical and nomenclatural remarks for each species are included in the section on "Hosts and distribution". In Canada the following six pine stem rusts are recognized:

- White pine blister rust
Cronartium ribicola J. C. Fisch.
ex Rabh.,
- Stalactiform blister rust
Cronartium coleosporioides Arth.,
- Comandra blister rust
Cronartium comandrae Pk.,
- Sweet fern blister rust
Cronartium comptoniae Arth.,
- Eastern gall rust
Cronartium quercuum (Berk.)
Miyabe ex Shirai,
- Western gall rust
Endocronartium harknessii
(J. P. Moore) Y. Hiratsuka.

White pine blister rust occurs on soft pines (subgenus *Strobus*)¹ and was introduced into North America at the end of the nineteenth century. The other five species are native to North America and occur on hard pines (subgenus *Pinus*).

There is a single persistent record of the Scotch-pine blister rust, *Cronartium flaccidum* (Alb. & Schw.) Wint., collected in 1925 on *Impatiens balsamina* L. from Charlottetown, Prince Edward Island (Arthur 1934; Wehmeyer 1950; Hurst 1957; Connors 1967). A recent re-examination of the original collection (PUR 43561) at the Arthur Herbarium, Purdue University, Lafayette, Indiana, by Dr. R. S. Peterson, however, revealed that the host plant was not *Impatiens balsamina* as reported, but a cultivated species of Onagraceae. The rust was identified as

¹Scientific and common names for the genus *Pinus* follow Critchfield and Little (1966).

Puccinastrum epilobii Otth. We examined the same specimen and agreed with Peterson.

The present work includes the up-to-date information on identification, morphology, life cycle, cytology, damage, epidemiology, hosts, distribution, and control of the pine stem rusts in Canada. It is based on a literature review and data gathered since 1962 during the authors' personal research on pine stem rusts. Distribution data are based mostly on herbarium specimens, although in a few cases literature reports have been used where the identification of the rust species was not in doubt.

A. Cankers on soft pines.

- C. ribicola*

E. harknessii

C. quercuum

C. comptoniae

C. coleosporioides

C. comandrae

Microscopic Key to Aecia on Hard Pines:

- A. Aeciospores pear-shaped with elongated tails, without smooth area, processes not annulated (Figs. 16, 17).
 - A.A. Aeciospores (or peridermioid teliospores) globose to subglobose, with conspicuous smooth areas, processes annulated (6-7 annulations). (Figs. 12, 14, 19, 22).
 - B. Aecia (or peridermioid telia) on globose or hemispherical galls.
 - C. Germ-tube of aeciospores non-septate, variable in shape; growth indeterminate.
 - C.C. Germ-tube of peridermioid teliospores septate, straight; growth determinate.
 - B.B. Aecia not on globose or hemispherical galls.
 - C. Processes of aeciospores uneven, much larger at the opposite side of the smooth areas (Figs. 13, 14).
 - C.C. Processes of aeciospores more or less even (Figs. 18, 19).
- C. *comandrae*
- C. *quercuum*
- E. *harknessii*
- C. *coleosporioides*
- C. *comptoniae*

Identification of Pine Stem Rusts on the Alternate Hosts (Non-Pine Hosts):

The alternate hosts for each pine stem rust are specific to that rust; therefore accurate identification can be achieved if one is able to identify the alternate host. However, in many cases, other groups of non-coniferous rusts parasitize the same plants, and one must be able to distinguish the pine stem rusts (*Cronartium* spp.) from the other rusts. Presence of the characteristic columnar telia (Figs. 32, 34, 37) always proves that the rust is a species of *Cronartium*. Following is a list of the alternate host plants with the pine stem rust occurring on them, and the other rust fungi which are known to occur on these hosts. Brief descriptions of distinguishing characteristics of each rust are given.

Castilleja spp. (paint-brush, Indian paint-brush). (Figs. 31, 32)

Cronartium coleosporioides Arth. (stalactiform blister rust) Uredinia scattered, cone-shaped with central pores, hypophyllous, yellow. Urediniospores singly on pedicels, echinulate. Telia hypophyllous. Teliospores in brown hair-like columns.

Puccinia andropogonis Schw. Spermogonia amphigenous, in groups. Aecia cup-shaped, in groups, mostly hypophyllous, with whitish bordering peridium. Aeciospores in chains, verrucose (heteroecious; uredinia and telia on grasses).

Comandra umbellata (L.) Nutt. ssp. *umbellata* and ssp. *pallida* (A.DC.) Piehl (comandra, bastard toad-flax). (Figs. 33, 34)

Cronartium comandrae Pk. (comandra blister rust) Uredinia scattered, cone-shaped with central pores,

hypophyllous and caulicolous. Urediniospores singly on pedicels, echinulate. Telia hypophyllous. Teliospores in brown hair-like columns.

Puccinia andropogonis Schw.

Spermogonia amphigenous, in groups. Aecia cup-shaped, in groups, mostly hypophyllous. Aeciospores in chains, verrucose (heteroecious; uredinia and telia on grasses).

Puccinia comandrae Pk.

Telia blackish-brown mostly hypophyllous. Teliospores, pedicellate, two-celled, dark brown (autoecious).

Comptonia peregrina (L.) Coult. (sweet fern). (Figs. 36, 37)

Cronartium comptoniae Pk. (sweet fern blister rust)

No other rust is known on the host in Canada (*Gymnosporangium ellisii* is known in U.S.).

Geocaulon lividum (Richardson) Fernald (northern bastard toad-flax). (Fig. 35)

Cronartium comandrae Pk. (comandra blister rust). See *Comandra*.

Puccinia comandrae Pk. See *Comandra*.

Melampyrum lineare Desr. (cow-wheat).

Cronartium coleosporioides Arth. (stalactiform blister rust). See *Castilleja*.

Puccinia andropogonis Schw. See *Castilleja*.

Myrica gale L. (sweet gale). (Fig. 38)

Cronartium comptoniae Arth. (sweet fern blister rust)

No other rust is known on the host in Canada (*Gymnosporangium ellisii* is known in U.S.).

Orthocarpus luteus Nutt. (owl-clover).

Cronartium coleosporioides Arth.

(stalactiform blister rust)

No other rust is known on the host.

Pedicularis spp. (louseworts).

Cronartium coleosporioides Arth.

(stalactiform blister rust)

See *Castilleja*.

Puccinia clintonii Pk.

Telia mostly hypophyllous, chestnut brown. Teliospores in open pustules, two-celled, dark brown (resting form) to golden-brown or nearly colorless (germinating form), finely verrucose in striae (autoecious).

Quercus rubra L. (red oak). (Fig. 39)

Cronartium quercuum (Berk.)

Miyabe ex Shirai (eastern gall rust)

No other rust is known on the host.

Quercus velutina Lam. (black oak).

Cronartium quercuum (Berk.)

Miyabe ex Shirai (eastern gall rust)

No other rust is known on the host.

Rhinanthus spp. (yellow-rattle).

Cronartium coleosporioides Arth.

(stalactiform blister rust)

No other rust is known on the host.

Ribes spp. (currant, gooseberry).

(Figs. 29, 30)

Cronartium ribicola J. C. Fisch. ex Rabh.

(white pine blister rust)

Uredinia scattered, cone-shaped with central pores, hypophyllous.

Urediniospores singly on pedicels, orange-yellow, echinulate. Telia hypophyllous. Teliospores in brown hair-like columns.

Melampsora epitea Thuem.

(*M. ribesii-purpurea* Kleb.).

Spermogonia mostly epiphyllous in small groups. Aecia hypophyllous, in small groups on discolored spots.

Aeciospores in chains finely verrucose (heteroecious; uredinia and telia on willows).

Puccinia caricina DC.

Spermogonia epiphyllous in groups.

Aecia mostly hypophyllous, in groups, cup-shaped. Aeciospores one-celled, in chains, finely verrucose (heteroecious; uredinia and telia on sedges).

Puccinia parkerae Diet. & Holw.

Telia hypophyllous and petioliculous. Teliospores in open pustules, two-celled, smooth, chestnut brown (autoecious).

Puccinia ribis DC.

Telia mostly epiphyllous. Teliospores in open pustules, two-celled, verrucose, cinnamon brown (autoecious).

Hosts and distribution in Canada

White Pine Blister Rust

Causal organism:

Cronartium ribicola J. C. Fisch. ex Rabh.

Synonym:

Peridermium strobi Kleb.

Illustrations:

Macroscopic characteristics (Fig. 1)

Microscopic characteristics (Figs. 11, 12, 23, 24, 27)

Nuclear cycle (Fig. 40)

Distribution maps (Maps 1, 2)

Hosts and distribution in Canada:

Spermogonial and aecial states (O, I)

on *Pinus albicaulis* Engelm. (whitebark pine) — Alta., B.C.

P. cembra L. (Swiss stone pine) — B.C., Man.

P. flexilis James (limber pine) — Alta., B.C.

P. lambertiana Dougl. (sugar pine) — B.C.

P. monticola Dougl. (western white pine) — B.C., Ont.

P. strobus L. (eastern white pine) — B.C., Man., N.B., Nfld., N.S., Ont., P.E.I., Que., Sask.

Uredinial and telial states (II, III)

on *Ribes alpinum* L. (alpine currant) — Que.

R. americanum Mill. (*R. floridum* L'Her.) (wild black currant) — Ont., Que.

R. aureum Pursh (golden currant) — B.C., Ont., Que.

R. cereum Dougl. (squaw currant) — B.C.

R. cynosbati L. (prickly gooseberry) — Man., Ont., Que.

R. diacanthum Pall. — Man.

R. divaricatum Dougl. (*Grossularia divaricata* (Dougl.) Cov. & Britt.) (common gooseberry) — B.C.

R. glandulosum Grauer (skunk

currant) — Man., N.B., N.S., Ont., P.E.I., Que.

R. gracile Michx. (*R. missouriense* Nutt.) (Missouri gooseberry) — Ont.

R. grossularia L. (European common gooseberry) — B.C., N.B., Nfld., N.S., Ont., Que.

R. hirtellum Michx. (wild gooseberry) — Alta., N.B., N.S., Ont., Que.

R. howellii Greene (*R. acerifolium* Howell) (maple-leaved currant) — B.C.

R. hudsonianum Richards. (northern black currant) — Alta., B.C. (Fig. 29)

R. inerme Rydb. (white-stemmed gooseberry) — B.C.

R. irriguum Dougl. (Idaho or inland black gooseberry) — B.C.

R. lacustre (Pers.) Poir. (*R. echinatum* Lindl.) (swamp or bristly black currant) — Alta., B.C., Ont., Que. (Fig. 30)

R. laxiflorum Pursh (trailing black currant) — B.C.

R. lobbii Gray (red-flowered gooseberry) — B.C.

R. nevadense Kellogg — B.C.

R. nigrum L. (black currant) — Alta., B.C., Man., N.B., Nfld., N.S., Ont., P.E.I., Que.

R. niveum Lindl. (*Grossularia nivea* (Lindl.) Spach) (snowy gooseberry) — B.C., Ont.

R. odoratum Wendl. (Missouri or Buffalo currant) — Man., N.S., Ont., Que.

R. orientale Desp. — Ont.

R. oxyacanthoides L. (northern or smooth gooseberry) — Alta., B.C., Man., N.B., N.S., Ont., P.E.I., Que.

R. petiolare Dougl. (wild black currant) — B.C.

R. sanguineum Pursh (red-flowered or blood currant) — B.C.

R. sativum Syme (*R. vulgare* Lam.) (red currant) — B.C., N.S., Ont., P.E.I., Que.

R. setosum Lindl. (*Grossularia setosa* (Lindl.) Cov. & Britt. (wild gooseberry) — B.C.

R. triste Pall. (*R. rubrum* L.) (American red currant) — Alta., B.C., Ont., Que.

R. viscosissimum Pursh (sticky currant) — Alta., B.C.

R. watsonianum Koehne (*Grossularia watsoniana* Cov. & Britt.) (Watson gooseberry) — B.C.

Range and other known hosts:

This rust occurs over most of the ranges of the white or soft pines in North America, Europe and Asia. It is considered native to Asia and is thought to have spread to Europe about 1850. It was probably introduced into the north-eastern United States by at least 1898 (Spaulding 1922) and was first found in eastern Canada in 1914 (Howitt and McCubbin 1916). In western North America it was first discovered in September 1921, in Vancouver, British Columbia (Eastham 1922). It now occurs from Newfoundland to southeastern Saskatchewan, south through New England down the Appalachian Mountains to North Carolina, Georgia and Tennessee, and across the Midwest from Ohio to Iowa, South Dakota and Minnesota. In western North America it occurs in British Columbia and south-western Alberta, south through Montana, Wyoming, Idaho, Washington, Oregon to northern California. In the United States it is reported to infect the introduced *Pinus griffithii* McClelland (blue pine), and at least seven other species of white pine in Europe or Asia (Gremmen 1964). No infection has been found in native stands of *P. aristata* Engelm. (bristlecone pine), *P. balfouriana* Grev. & Balf. (foxtail pine), and *P. ayacahuite* Ehvenb. (Mexican white pine), in southwestern North America although these pines have been infected in controlled inoculation tests

(Miller *et al.* 1959; Gremmen 1964). The rust is known to occur on about 200 species of *Ribes* throughout the world, and on over 40 species in North America.

Remarks:

The closely related species *Cronartium occidentale* Hedgc., Bethel & Hunt occurs on several common *Ribes* species in the western United States, and overlaps the range of *C. ribicola* in Washington, Oregon and California. However, pine hosts for *C. occidentale* (*Pinus monophylla* Torr. & Frem. and *P. edulis* Engelm.) do not occur naturally in Canada and one would not expect to find this rust in Canada. The Himalayan form *Peridermium indicum* Colley & Taylor is considered to be the aecial state of *C. ribicola* (Bakshi and Singh 1967), but several authors have considered them as different species (Peterson 1967; Colley and Taylor 1927).

Stalactiform Blister Rust

Causal organism:

Cronartium coleosporioides Arth.

Synonyms:

C. stalactiforme Arth. & Kern nom. nud.

Peridermium stalactiforme Arth. & Kern

Illustrations:

Macroscopic characteristics (Figs. 2, 3, 31, 32)

Microscopic characteristics (Figs. 13, 14, 25, 28)

Nuclear cycle (Fig. 40)

Distribution maps (Maps 3, 4)

Hosts and distribution in Canada:

Spermogonial and aecial states (O, I) on *Pinus banksiana* Lamb. (jack pine) — Alta., Man., Ont., Que., Sask.
P. contorta Dougl. (lodgepole and shore pine) — Alta., B.C., Man., N.W.T. (Mack.)

P. echinata Mill. (shortleaf pine) — N.S.

P. mugo Turra (Mugo or Swiss mountain pine) — Que.

P. ponderosa Laws. (ponderosa pine) — B.C.

P. sylvestris L. (Scotch pine) — B.C., Man.

Uredinial and telial states (II, III)

on *Castilleja angustifolia* Dougl. (paint-brush) — B.C.

C. miniata Dougl. ex Hook. (common red paint-brush) — Alta., B.C. (Fig. 31)

C. occidentalis Torr. (paint-brush) — Alta.

C. raupii Pennell (paint-brush) — Alta.

C. rhexifolia Rydb. (paint-brush) — Alta., Sask.

C. septentrionalis Lindl. (common yellow paint-brush) — Alta.

Melampyrum lineare Desr. (cow-wheat) — Alta., B.C., Man., N.B., Ont., Que., Sask.

Orthocarpus luteus Nutt. (owl-clover) — Alta.

Pedicularis bracteosa Benth. (lousewort) — Alta., B.C.

Rhinanthus crista-gallii L. (*R. borealis* (Sterneck) Chabert) (yellow-rattle) — Alta., B.C., Que.

Range and other known hosts:

Stalactiform blister rust is found across Canada, from Nova Scotia to British Columbia and Yukon, and is especially prominent in western Canada, southward into the Lake States, and in the west to Colorado, Utah and southern California. It has not been collected near the northern limits of pine in western Canada.

A white-spored form of this rust is found in Banff National Park on *Pinus contorta* and on *Castilleja miniata* (Powell 1966). Ziller (1970) has given the name

C. coleosporioides Arth. f. *alba* Ziller to this form. All spore states from this form lack yellow pigment in the cytoplasm.

In addition, stalactiform blister rust was reported on the following pines in the United States: *Pinus halepensis* Mill. (aleppo pine), *P. coulteri* D. Don (Coulter pine), *P. jeffreyi* Grev. & Balf. (Jeffrey pine), and *P. attenuata* Lemm. (knobcone pine) (Peterson 1967). Some additional alternate hosts for *C. coleosporioides* are listed by Arthur (1934) and Peterson (1968) but because of the overlapping range with *Peridermium filamentosum* Pk., in California, Colorado, Utah and Wyoming, it is impossible to give with certainty a thorough list of alternate hosts for this species (see Remarks). In Ontario, *Castilleja coccinea* (L.) Spreng. has been successfully inoculated (Sippell *et al.* 1972).

Remarks:

Until recently, *C. coleosporioides* was considered as a species complex having at least three distinctive forms on pine: *Peridermium filamentosum*, *P. harknessii* J. P. Moore, and *P. stalactiforme* Arth. & Kern (Cummins 1962; Peterson 1962b). These forms are now recognized as separate species with the name *C. coleosporioides* retained for *P. stalactiforme* (Savile 1968; Ziller 1970). "*P. filamentosum*" consists of at least three different races (Peterson 1966b). One race alternates to Indian paint-brush, and resembles *C. coleosporioides* (= *P. stalactiforme*) in life cycle. Two other races are known to carry infection directly from pine to pine. Germ-tube morphology and nuclear condition of germ-tubes of one of these pine-to-pine races are similar to *Endocronartium harknessii* (= *P. harknessii*) (Krebill and Nelson 1970), and it possibly belongs in the genus *Endocronartium*.

Comandra Blister Rust

Causal organism:

Cronartium comandrae Pk.

Synonyms:

C. asclepiadeum var. *thesii* Berk.

C. pyriforme Hedgc. & Long

C. thesii (Berk.) Lagerh.

Peridermium betheli Hedgc. & Long

P. pyriforme Pk.

Illustrations:

Macroscopic characteristics (Figs. 4, 5, 34)

Microscopic characteristics (Figs. 15, 16, 17)

Nuclear cycle (Fig. 40)

Distribution maps (Maps 5, 6)

Hosts and distribution in Canada:

Spermogonial and aecial states (O, I)
on *Pinus banksiana* Lamb. (jack pine) —
Alta., Man., N.B., N.W.T., Ont., Que.,
Sask.

P. contorta Dougl. (lodgepole and
shore pine) — Alta., B.C., Sask.,
Yukon

P. ponderosa Laws. (ponderosa pine)
— B.C.

P. mugo Turra (Mugo or Swiss Moun-
tain pine) — Alta.

P. sylvestris L. (Scotch pine) — Alta.,
Man., Sask.

Uredinial and telial states (II, III)

on *Comandra umbellata* (L.) Nutt. ssp.
umbellata (= *C. umbellata* (L.) Nutt.;
C. richardsoniana Fern.) (comandra,
bastard toadflax) — Man., Ont., Que.,
Sask.

Comandra umbellata (L.) Nutt. ssp.
pallida (A.DC.) Piehl (= *C. pallida*
A.DC.) (comandra, bastard toadflax)
— Alta., B.C., Man., Ont., Sask.
(Fig. 33)

Geocaulon lividum (Richards.) Fern.
(= *C. livida* Richards.) (northern
bastard toadflax) — Alta., B.C., Man.,

N.B., N.W.T., Ont., Que., Sask., Yukon
(Fig. 35)

Range and other known hosts:

Comandra blister rust is found
across North America from New Bruns-
wick to the Yukon, from the northern
limits of pine southward to Tennessee,
Alabama, Mississippi, New Mexico, and
California. It has not been found in
Alaska or Mexico although susceptible
pines occur there (Powell 1970). Besides
the five hard pine species on which the
rust has been reported in Canada (Powell
1970; Powell and Wilkinson 1973) it has
been reported on a further eleven hard
pines in the United States: *Pinus nigra*
Arnold (Austrian pine), *P. taeda* L. (loblolly
pine), *P. jeffreyi* Grev. & Balf. (Jeffrey
pine), *P. attenuata* Lemm. (knobcone
pine), *P. rigida* Mill. (pitch pine), *P. serotina*
Michx. (pond pine), *P. echinata* Mill.
(shortleaf pine), *P. elliotii* Engelm. (slash
pine), *P. pungens* Lamb. (Table Moun-
tain pine), *P. glabra* Walt. (spruce pine),
and *P. virginiana* Mill. (Virginia pine)
(Mielke *et al.* 1968; Cordell *et al.* 1969;
Applegate and Seay 1971; Hepting 1971).

The uredinial and telial states of the
rust have been recorded on *Comandra*
and *Geocaulon* over a similar range to
the spermogonial and aecial states oc-
curring on pine. *Comandra* grows on
open, often sandy sites, and *Geocaulon*
on moist sites in pine or spruce stands.
C. umbellata ssp. *californica* (Eastw.)
Piehl, is the uredinial and telial host in
California, Oregon and Washington. The
other North American subspecies (*um-
bellata* and *pallida*) cover a considerable
range in the United States, but *Geocaulon*
has a northern distribution and only
barely enters the United States (Powell
1970; Packer 1971).

Buckleya distichophylla (Nutt.) Torr.,
was erroneously reported as uredinial
and telial host of the rust by Arthur

(1934). More recently it has been shown to be the host for *Cronartium appalachianum* Hepting, known to occur on *Pinus virginiana* in the southeastern United States (Hepting 1957).

Remarks:

Although this rust is confined to the North American continent at present, it is of potential danger to pines in the Balkan countries where a possible alternate host (*Comandra umbellata* (L.) Nutt., ssp *elegans* (Rchb.f.) Piehl) occurs (Piehl 1965; Mielke *et al.* 1968). Mielke *et al.* (1968) also warned that other genera of the Santalaceae, which occur near hard pines outside North America, may prove to be susceptible alternate hosts, thus every effort should be made to limit the rust to its native range.

Sweet Fern Blister Rust

Causal organism:

Cronartium comptoniae Arth.

Synonym:

Peridermium comptoniae Orton & Adams

Illustrations:

Macroscopic characteristics (Fig. 6)

Microscopic characteristics (Figs. 18, 19, 37)

Nuclear cycle (Fig. 40)

Distribution maps (Maps 7, 8)

Hosts and distribution in Canada:

Spermogonial and aecial states (O, I) on *Pinus banksiana* Lamb. (jack pine) — Alta., Man., N.B., N.W.T., N.S., Ont., Que., Sask.

P. contorta Dougl. (lodgepole and shore pine) — Alta., B.C., N.B., N.W.T. (Mack.), N.S., Que.

P. echinata Mill. (shortleaf pine) — N.S.

? *P. jeffreyi* Grev. & Balf. (Jeffrey pine) — B.C. (DAVFP15460)

P. mugo Turra (Mugo or Swiss mountain pine) — N.B., Que.

P. muricata D. Don (bishop pine) — B.C.

P. nigra Arnold var. *poiretiana* (Ant.) Aschers Graebn. (Corsican pine) — Ont.

? *P. pinaster* Ait. (maritime pine) — B.C. (DAVFP13411)

P. ponderosa Laws. (ponderosa pine) — B.C.

P. radiata D. Don (Monterey pine) — B.C.

P. resinosa Ait. (red pine) — Ont.

P. sylvestris L. (Scotch pine) — N.B., N.S., Ont., Que.

Uredinial and telial states (II, III)

on *Comptonia peregrina* (L.) Coult.

(sweet fern) — N.B., N.S., Ont., Que. (Fig. 36)

Myrica gale L. (sweet gale) — Alta., B.C., N.S., N.W.T. (Mack.), Ont., Que., Sask. (Fig. 38)

Range and other known hosts:

Sweet fern blister rust is found across northern North America from Nova Scotia to British Columbia and Alaska (Hiratsuka and Gautreau 1966), south through New England to North Carolina, and west to Minnesota. To date there are no records from the Yukon. There are isolated records from Iowa and Missouri based on shipments of infected seedlings (Peterson 1966a). On the Pacific Coast of the United States it is known only from Washington and northern Oregon (Peterson 1966a). The rust is reported on the following additional hard pines in the United States: *Pinus tabulaeformis* Carr. (Chinese pine), *P. coulteri* D. Don (Coulter pine), *P. densiflora* Sieb. & Zucc. (Japanese red pine), *P. taeda* L. (loblolly pine), *P. rigida* Mill. (pitch pine), *P. pungens* Lamb. (Table Mountain pine), *P. virginiana* Mill. (Virginia pine) (Peterson 1967; Spaulding

and Hansborough 1932; G. W. Anderson 1963). Although the records of infection on *P. jeffreyi* and *P. pinaster* from British Columbia are questionable, both these species have been found infected in the United States (Spaulding and Hansborough 1932; Gremmen 1964).

Comptonia typically grows on open sandy sites, and *Myrica gale* grows in swampy moist areas. *Comptonia peregrina* is restricted to eastern North America, and *Myrica gale* has a northern distribution especially in western Canada. Although other species of *Myrica* have not been found naturally infected, it is reported that *M. carolinensis* Miller (= *M. pensylvanica* Loisel) and *M. cerifera* L. have been successfully inoculated (Weir and Hubert 1917; Ziller 1967).

Remarks:

Although this rust is confined to the North American continent at the present time, it is potentially dangerous to pines in other areas of the world, because one of the alternate hosts of the rust, *Myrica gale* L., occurs widely in northern Europe and eastern Asia (Hultén 1968) where susceptible pines are also present.

Eastern Gall Rust

Causal organism:

Cronartium quercuum (Berk.) Miyabe ex Shirai.

Synonyms:

C. cerebrum (Pk.) Hedgc. & Long.

C. asclepiadeum quercuum Berk.

Peridermium cerebrum Pk.

P. giganteum Tub.

Illustrations:

Macroscopic characteristics (Figs. 7, 8, 39)

Microscopic characteristics (Fig. 20)

Nuclear cycle (Fig. 40)

Distribution map (Map 9)

Hosts and distribution in Canada:

Spermogonial and aecial states (O, I) on *Pinus banksiana* Lamb. (jack pine) — Ont.

P. sylvestris L. (Scotch pine) — Ont.
Uredinial and telial states (II, III)

on *Quercus rubra* L. (red oak) — Ont.
(Fig. 39)

Q. velutina Lam. (black oak) — Ont.

Range and other known hosts:

Eastern gall rust is found in eastern North America from the northern limits of *Quercus* through southern United States to Florida and Texas, and west through the Lake States to Minnesota. It occurs in eastern Asia in an area bounded by Siberia, Korea, Japan, Philippines, and eastern India.

The rust is reported on the following additional hard pines in the United States: *Pinus nigra* Arnold (Austrian pine), *P. thunbergiana* Franco (Japanese black pine), *P. taeda* L. (loblolly pine), *P. palustris* Mill. (longleaf pine), *P. pinaster* Ait. (maritime pine), *P. rigida* Mill. (pitch pine), *P. serotina* Michx. (pond pine), *P. ponderosa* Laws. (Ponderosa pine), *P. clausa* (Chapm.) Vasey (sand pine), *P. resinosa* Ait. (red pine), *P. echinata* Mill. (shortleaf pine), *P. elliotii* Engelm. (slash pine), *P. glabra* Walt. (spruce pine), *P. pungens* Lamb. (Table Mountain pine), and *P. virginiana* Mill. (Virginia pine) (Anderson, N.A. 1963; Peterson 1967; Hepting 1971). The rust is known to occur on an additional six pine species in Asia (Hiratsuka 1960; Gremmen 1964). In the United States this species is reported on the following additional oaks: *Quercus alba* L. (white), *Q. bicolor* Willd. (swamp white), *Q. coccinea* Muench. (scarlet), *Q. ilicifolia* Wang (bear), *Q. imbricaria* Michx. (shingle or laurel), *Q. macrocarpa* Michx. (bur), *Q. marilandica* Muench. (black jack), *Q. myrtifolia* Willd. (myrtle leaf), *Q. nigra* L. (water),

Q. palustris Muench. (pin), *Q. phellas* L. (willow), *Q. prinus* L. (basket), and *Q. stellata* Wang. (post) (Gremmen 1964). It has also been reported on *Castanea dentata* (Marsh.) Borkh. (American chestnut) and *Castanopsis chrysaphyllas* (Doug.) A.DC. (golden chinkagin), while Hedgcock (1939) reports successful inoculations on *Castanea mollissima* Blume., *C. pumila* (L.) Mill., *C. sativa* Mill., *Castanopsis argentea*, *C. diversifolia* (Kurz) King and *Lithocarpus densiflora* (Hook. & Arn.) Rehd. Other oaks are infected in Europe and Asia and it is found on *Castanea*, *Castanopsis* and *Fagus* spp. in Asia (Hedgcock 1939; Hiratsuka 1960; Gremmen 1964).

Remarks:

This rust has been reported on pines from many locations in eastern Canada, but most of the reports are now considered to be erroneous and should be for *Endocronartium harknessii* rather than of Eastern gall rust (Hiratsuka and Maruyama 1968; Van Sickle and Newell 1968). Arthur (1934) even reports collections from Alberta but this is undoubtedly incorrect. There is still some doubt about the distribution of *C. quercuum* on pine in Canada but it appears to be restricted to southern Ontario (see distribution map, Map 9). Conners (1967) lists *C. cerebrum* separately as occurring in Canada, but adds that the records listed probably concern *E. harknessii* (as *C. coleosporioides*).

Arthur (1934) included *C. fusiforme* Hedgc. & Hunt ex Cumm. and *C. conigenum* Hedgc. & Hunt in his concept of *C. quercuum* but they are generally regarded as distinct species (Peterson 1967; Hedgcock and Siggers 1949). According to Hedgcock and Siggers (1949) the North American *C. quercuum* and the Asian pine-oak rust, which is also called *C. quercuum*, are different.

Since the type specimen of *C. quercuum* is American, the binomial must only be applied to the American fungus (Cummins 1962).

Western Gall Rust

Causal organism:

Endocronartium harknessii (J. P. Moore)
Y. Hiratsuka

Synonyms:

Cronartium harknessii (J. P. Moore)

Meinecke nom. nuda

Peridermium cerebroides Meinecke

P. harknessii J. P. Moore

"Woodgate" - *Peridermium*

Illustrations:

Macroscopic characteristics (Figs. 9, 10)

Microscopic characteristics (Figs. 21, 22)

Nuclear cycle (Fig. 41)

Distribution map (Map 10)

Hosts and distribution in Canada:

Spermogonial and peridermioid telial states (0, III)

on *Pinus banksiana* Lamb. (jack pine)

Alta., Man., N.B., N.W.T.

(Mack.), N.S., Ont., Que., Sask.

P. contorta Dougl. (lodgepole and shore pine) — Alta., B.C., N.B., N.S., N.W.T., Que., Sask., Yukon

P. mugo Turra (mugo or Swiss mountain pine) — Alta., B.C., N.B.

P. muricata D. Don (Bishop pine) — B.C.

P. nigra Arnold (Austrian or Corsican pine) — B.C.

P. pinaster Ait. (maritime pine) — B.C.

P. ponderosa Laws. (ponderosa pine) — B.C., Ont.

P. radiata D. Don (Monterey pine) — B.C.

P. sylvestris L. (Scotch pine) — Alta., B.C., Man., N.B., N.S., Ont., Que.

Range and other known hosts:

Western gall rust is found across Canada from the Yukon to Nova Scotia, southward through New York, the Lake States and Nebraska, and in the west southward to Arizona and northern Mexico. It has not been collected to the limits of pine in the Yukon. It is reported on the following additional hard pines in the United States: *P. halepensis* Mill. (Aleppo pine), *P. canariensis* C. Smith (Canary Island pine), *P. coulteri* D. Don (Coulter pine), *P. sabiniana* Dougl. (Digger pine), *P. thunbergiana* Franco (Japanese black pine), *P. jeffreyi* Grev. & Balf. (Jeffrey pine) and *P. attenuata* Lemm. (knobcone pine), while another eight species have been successfully inoculated (Peterson 1967). An albino race is widely distributed on *Pinus ponderosa* L. var. *scopulorum* Engelm. from northern Colorado to southern New Mexico, westward through Utah to southern Nevada (Mielke and Peterson 1967). In some areas of its range the albino form does not overlap with the normal orange-spored form.

Remarks:

This species has been confused with *Cronartium quercuum* in the eastern part of North America due to morphological similarities; thus there is still some doubt as to the exact range of the two species. Peterson (1967) and others consider that *C. quercuum* and *E. harknessii* cause "morphologically indistinguishable globose galls". At present these two species are best distinguished through their germ-tube morphology and nuclear behavior during germination (Anderson 1965; Anderson and French 1965a, b; Hiratsuka *et al.* 1966; McGrath 1968; Hiratsuka and Maruyama 1968; Hiratsuka 1969). York (1926) described a gall rust on *Pinus sylvestris* near Woodgate, New York, and the rust was called Woodgate-

Peridermium for many years. This is now considered as *E. harknessii* (Boyce 1957; Krebill 1970).

This rust is potentially dangerous in many countries where it has not yet been reported because such important pine species as *P. sylvestris* in Europe, *P. thunbergiana* in Asia, and *P. radiata* in New Zealand, Australia and South Africa, are known to be very susceptible to this rust (Parmeter and Newhook 1967).

Morphology, life cycle and nuclear cycle

Most of these pine stem rusts are heteroecious, i.e. requiring certain unrelated uredinial-telial hosts in alternation with the pine to complete their life cycles. In Canada only *Endocronartium harknessii* is autoecious, with pine as its only host.

Heteroecious species:

In heteroecious species, five different spore states are produced in a life cycle: spermatia, aeciospores, urediniospores, teliospores and basidiospores. Spermatia and aeciospores are produced on pine, and urediniospores, teliospores and basidiospores are produced on the alternate hosts (Fig. 40).

Basidiospores produced on the alternate host initiate infections on pine but the process of infection is not well understood. Most authors claim that basidiospore germ-tubes penetrate directly through the cuticle of the needles (Boyer 1962; Patton and Nicholls 1966; Hirt 1938) but Patton and Johnson (1970) showed stomatal penetration by *Cronartium ribicola*. Although infection usually occurs through needles, there is evidence that much occurs directly on young shoot tissues (Van Arsdel 1968; Hiratsuka, unpublished data), or at the bases of needle fascicles (Colley 1918).

The mycelium in the pine is haploid and monokaryotic. It grows intercellularly into the inner bark and ray cells (Krebill 1968a) forming haustoria in surrounding cells. Haustoria are sac-like thin-walled structures of the fungus by which the fungus obtain nutrients from the host cells.

Spermogonia containing spermatia are formed within two years of infection as extended cushions immediately below the periderm (Fig. 27). Spermatia are monokaryotic, one-celled, hyaline, small ($2\text{--}3\ \mu \times 3\text{--}4\ \mu$) cells (Fig. 15), are produced on the tips of simple spermatio-

phores as phyalospores. Spermatia are deposited in nectar-like fluid which contains high concentration of fructose and glucose. The nectar with spermatia oozes out as orange droplets in summer or early fall (Figs. 5, 7), which dry eventually to dark spots termed spermogonial or pycnial scars. Spermatia are not infective but function in diploidization of the fungus. Many insects are attracted to the nectar and transfer spermatia from one infection to the other (Buller 1950). The transferred spermatia fuse to receptive hyphae of opposite mating type, and the nuclei pass through the receptive hyphae into the base of the mycelium making the cells binucleate. There are some doubts that *C. ribicola* is heterothallic (Hirt 1964). However, from abundant production of spermatia and observations in the field and greenhouse, the authors think that all heteroecious Canadian species are heterothallic.

The binucleate cells divide and develop to form an aecium. Aecia are produced in spring and summer. They originate several cell layers below the spermogonia in the cortex tissue (Fig. 28) and when mature push through the bark as pustules, covered first by a white peridium of sterile cells. Aecia contain orange-yellow, verrucose aeciospores that are produced in chains (Fig. 28). Except for *C. comandrae*, aeciospores are subglobose, have annulated processes, and each spore has a smooth area (Figs. 12, 14, 19). Aeciospores of *C. comandrae* are elongated, pear-shaped, have no smooth area, and have obtuse or cuspidate processes without annulations (Hiratsuka 1971) (Figs. 16, 17).

The pine infection is perennial and in most of the species spermogonia occur on the advancing outer zone of the cankers and aecia on the zone one or more years older; but in *C. quercuum* spermatia and aecia repeat year after

year on the radially-expanding gall tissue.

On the surface of alternate hosts aeciospores germinate and produce appressoria the infection pegs of which penetrate through stomatal openings. Mycelia initiated by aeciospores are dikaryotic and grow intercellularly, and produce intracellular haustoria. After 10 to 14 days of aeciospore infection uredinia are formed. In the uredinia, pedicellate and echinulate urediniospores are formed (Figs. 23, 24, 25). Urediniospores are binucleate and can reinfect the same hosts and initiate further binucleate infections. Infections can be repeated by urediniospores 3 or more times during the growing season of the host plants. Being asexual repeating spore states, urediniospores are equivalent to conidia of many other fungi. Urediniospores are probably the most important spore state responsible for long distance spread of the fungi.

Later in summer, telia are produced on the same dikaryotic infections. Telia are hair-like structures composed of smooth-walled, nearly cylindrical teliospores united in slender columns (Figs. 26, 32, 34, 37). As soon as conditions of temperature and moisture are favorable, the teliospores germinate. Before germination, paired nuclei in the teliospores fuse and then undergo meiotic division as they germinate. Teliospores produce a four-celled basidium, each cell of which bears a basidiospore at the tip of a slenderly pointed sterigma (Fig. 26). The basidiospores are haploid, monokaryotic, and of two mating types. They are forcibly discharged and disseminated by wind. They have thin, hyaline walls, and have a much shorter life and potential dispersal distance than aeciospores and urediniospores (usually less than 1,000 ft.). In some instances basidiospores can be carried by wind 10 to 17

miles from their source (Van Arsdel *et al.* 1961).

Autoecious species:

In contrast to species of *Cronartium*, *Endocronartium harknessii* is autoecious and has a much shortened life cycle with only one spore state, namely teliospores, although spermatia are known to be produced occasionally (Fig. 41). This rust has been confused with *C. coleosporioides* and was stated to be facultatively heteroecious, e.g. the fungus can repeat on pine and also infect an alternate host (Meinecke 1920, 1929; Weir and Hubert 1917; Anderson and French 1965b). However, recent inoculation tests and cytological studies indicate that the fungus is purely autoecious (Ouellette 1965; Wagener 1964; Zalasky and Riley 1963; Hiratsuka *et al.* 1966).

Teliospores of this rust, which are similar to aeciospores of *Cronartium* spp., are orange-yellow, verrucose with annulated processes, and formed in chains (Figs. 21, 22). Spermatia are occasionally produced in late fall in British Columbia (van der Kamp, B. J., personal communication 1970) but it is questionable whether they function.

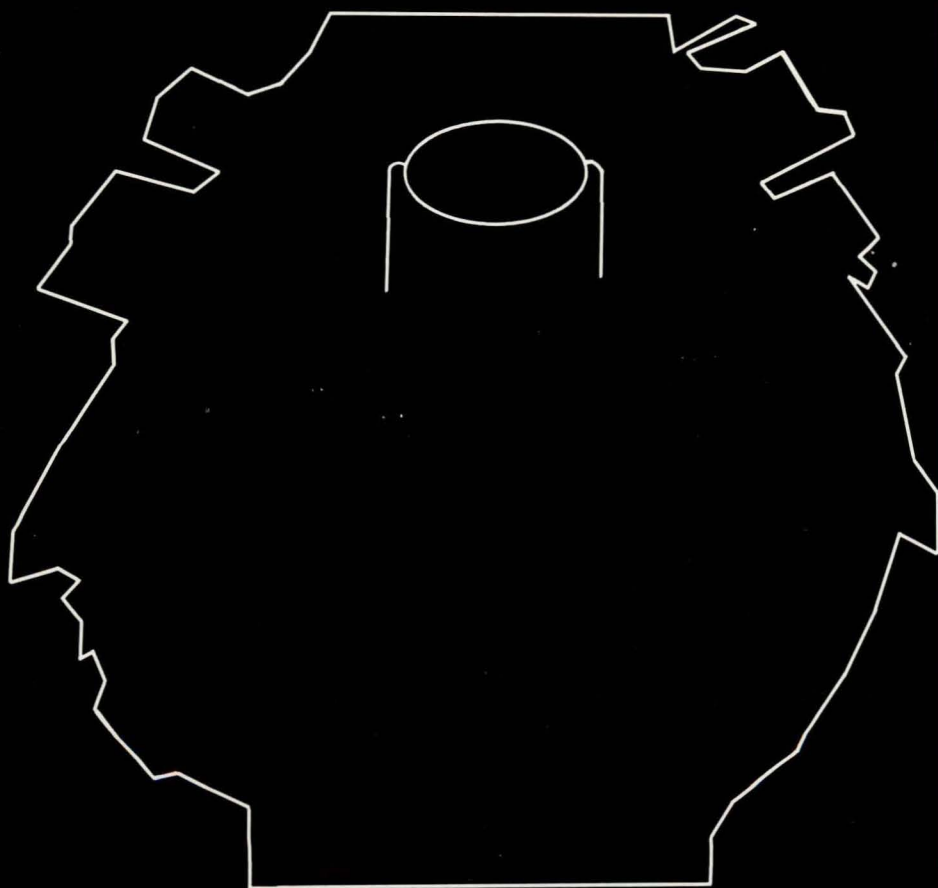
The young teliospores are dikaryotic, but whether of identical nuclei (homokaryotic) or dissimilar nuclei (heterokaryotic) is not known. Nuclear fusion occurs at spore maturity and at germination the nucleus usually divides twice. This appears to be a meiotic division. The germ tubes become septate and typically divided into 4 cells each of which contain one nucleus. This is in contrast with the heteroecious species which produce tortuous, non-septate germ-tubes of indefinite length having two nuclei which migrate toward the tip of the germ tube (Hiratsuka *et al.* 1966; Powell and Hiratsuka 1969).

The germ tubes of *E. harknessii* are

considered as basidia although they do not produce basidiospores (Hiratsuka *et al.* 1966). Basidia producing spores by definition should be called teliospores and it is suggested that this special kind of teliospore be called peridermioid teliospore (Hiratsuka 1973a, b). This type of life cycle is termed endocyclic. Germ tube morphology has been used to distinguish this rust from the gall forming heteroecious species, *C. quercuum*, in eastern North America where both rusts occur together or had been reported to occur together (Anderson and French 1965a; Krebill 1970; Van Sickle and Newell 1968).

Teliospores are effectively spread by the wind. Upon germination, germ tubes or basidia of the fungus penetrate young green tissue of the current year's shoot or needles but the mode of penetration is not clearly known. The mycelium, which is haploid and monokaryotic, stimulates the cambial cells to produce excess xylem and ray parenchyma cells. Dikaryotization occurs in the mycelium in cortex. Dikaryotic cells divide and develop to produce telia. Sporulation occurs year after year in the newly-formed cortex tissue of the expanding gall surface.





1



- 2 Stalactiform blister rust (*Cronartium coleosporioides*) on lodgepole pine (*Pinus contorta*). Note rodent chewing on some cankers.

2



3



4



5



- 6 Sweet fern blister rust (*Cronartium comptoniae*) on jack pine (*Pinus banksiana*). Note rodent chewing on two centre cankers.

6



- 7 Eastern gall rust (*Cronartium quercuum*)
on jack pine (*Pinus banksiana*). Spermatial
drops.
- 8 Aecial state.

7



8





- 10 Western gall rust (*Endocronartium harknessii*) with purple mold (*Tuberculina maxima*).

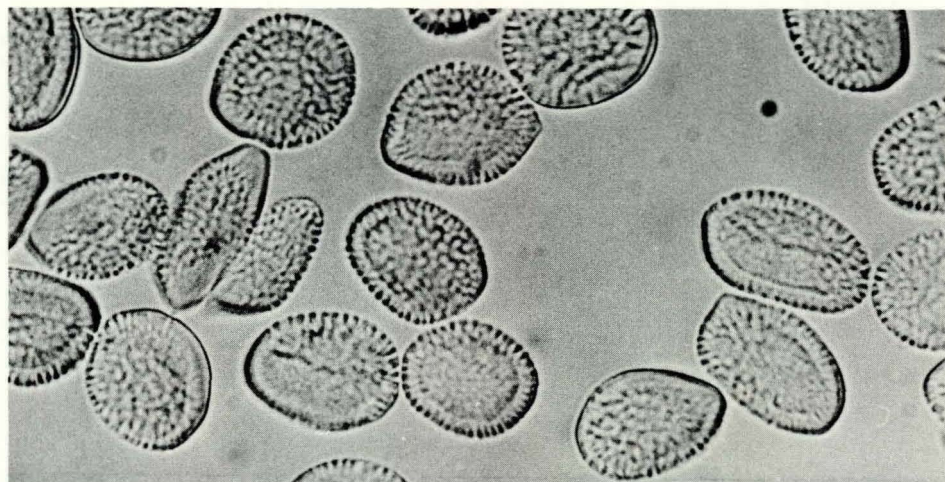
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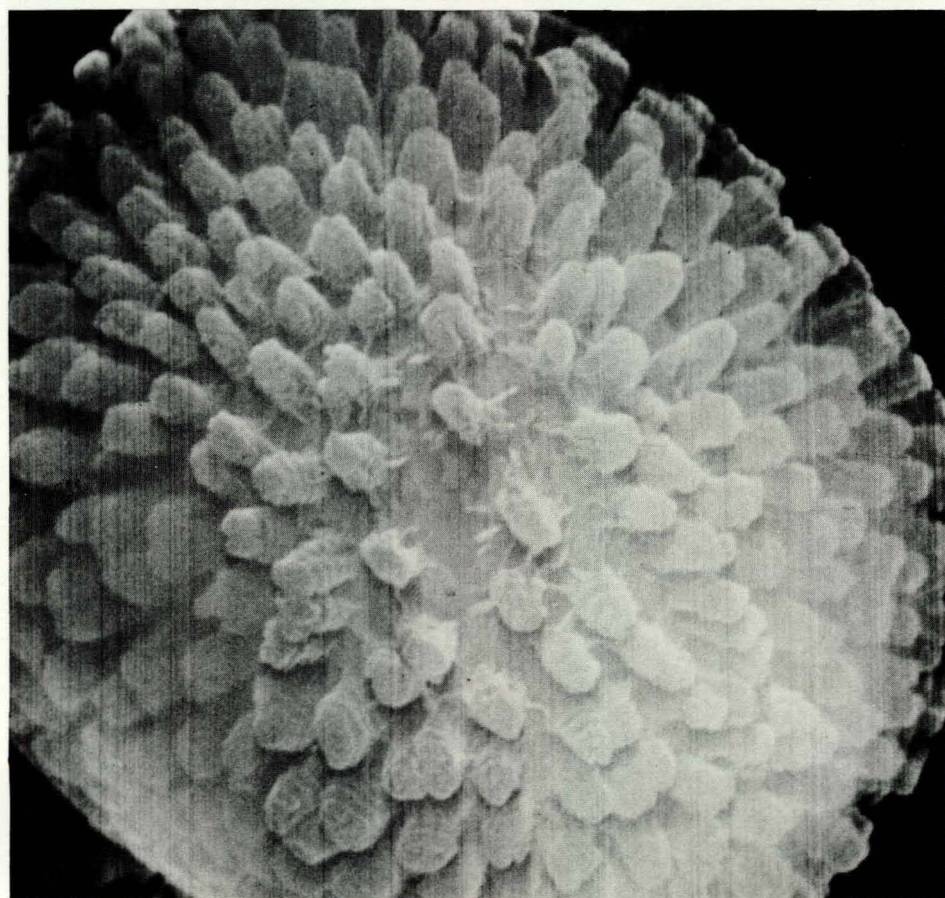
11 Aeciospores of *Cronartium ribicola* X 840.

12 X 7,600. (Scanning electron micrograph = SEM).

11



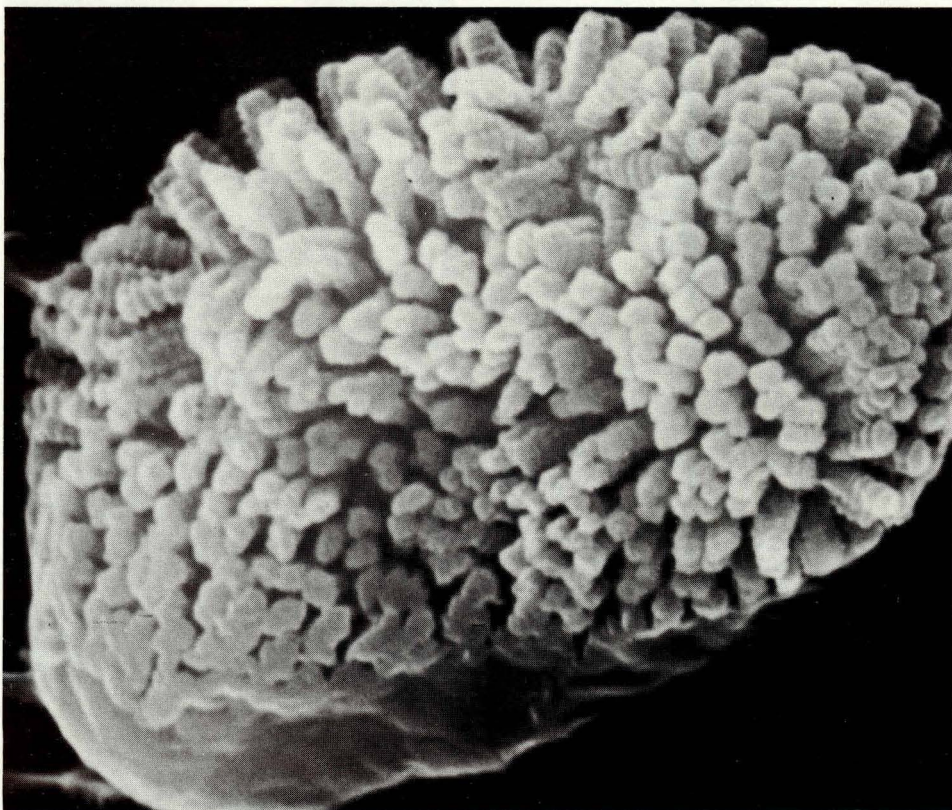
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14

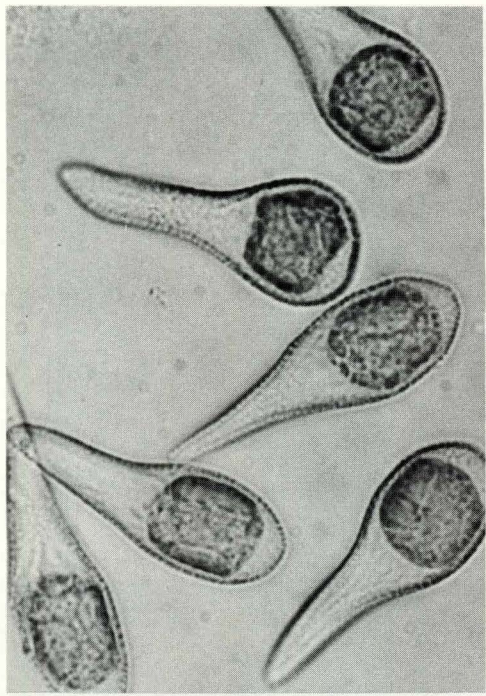


16 Aeciospores of *Cronartium comandrae*.
X 840.

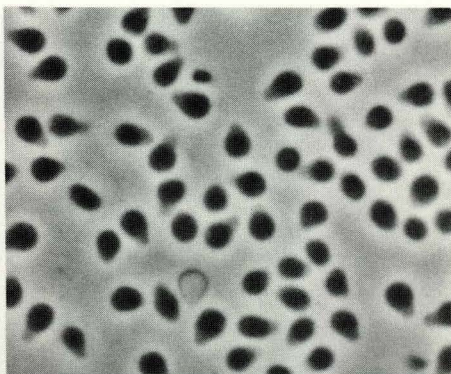
15 Spermatia of *Cronartium comandrae*.
X 2,050.

17 X 4,100 (SEM).

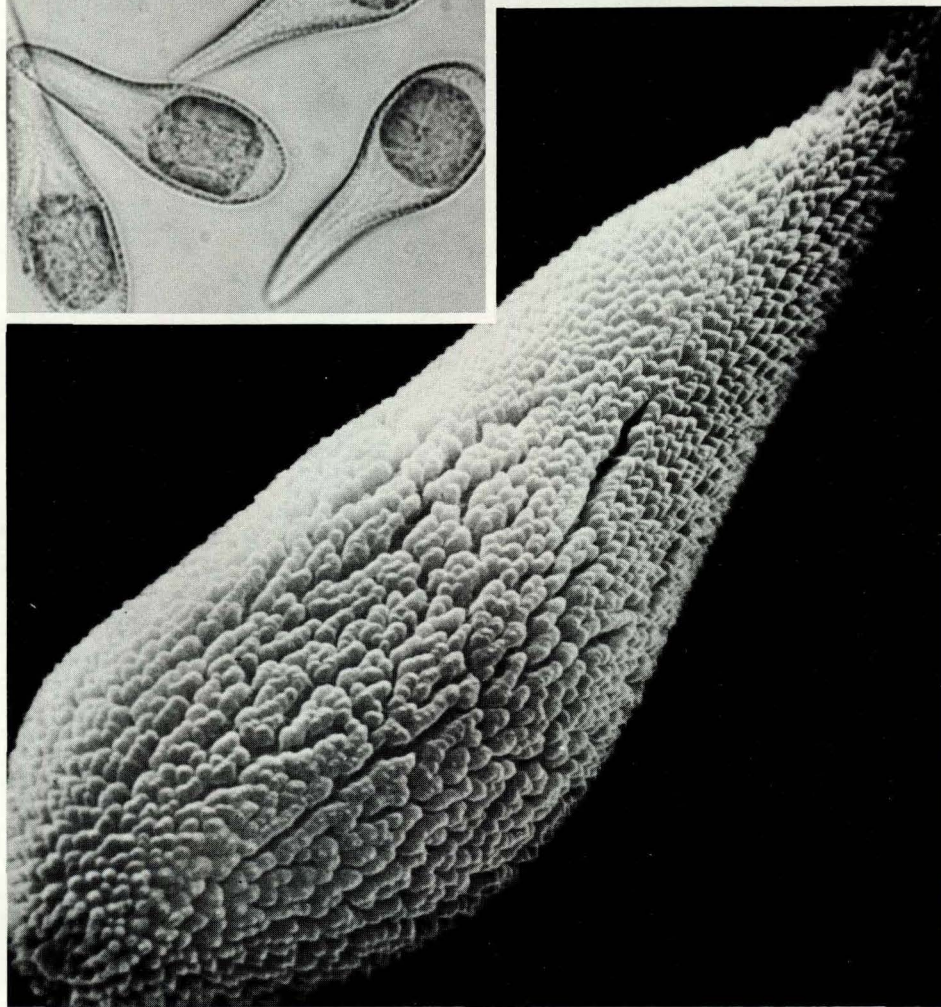
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15



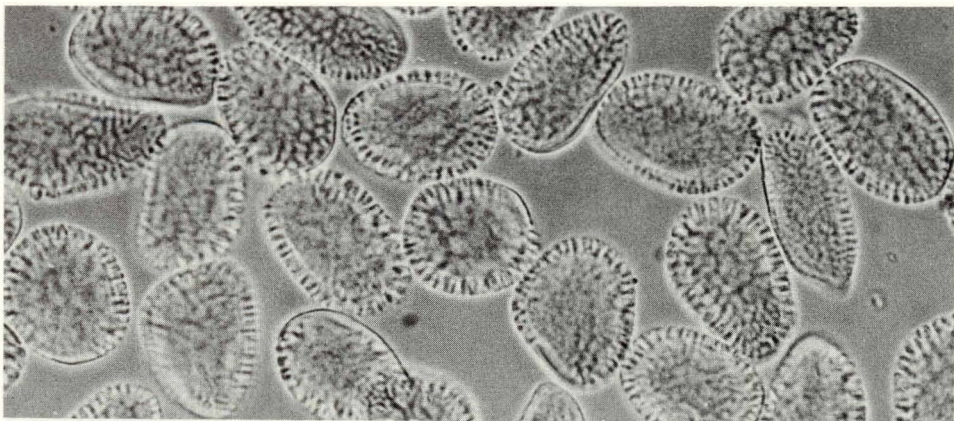
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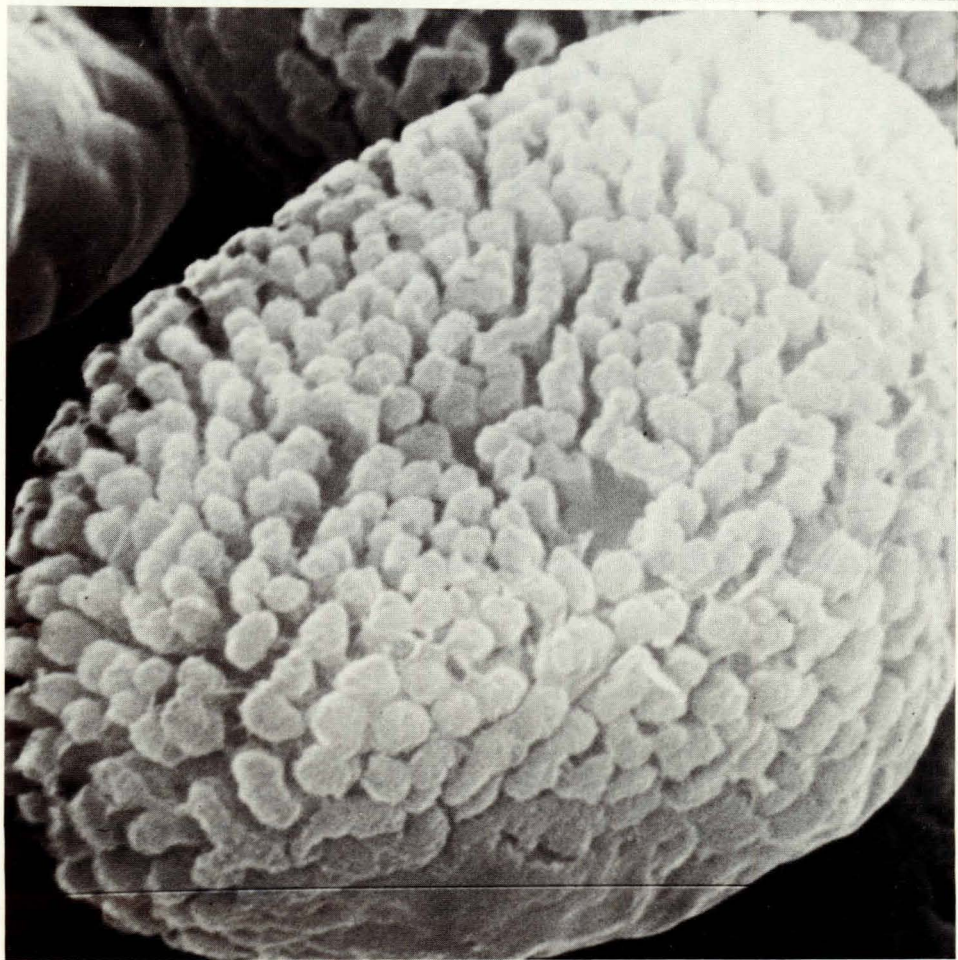
18 Aeciospores of *Cronartium comptoniae*.
X 830.

19 X 7,600 (SEM).

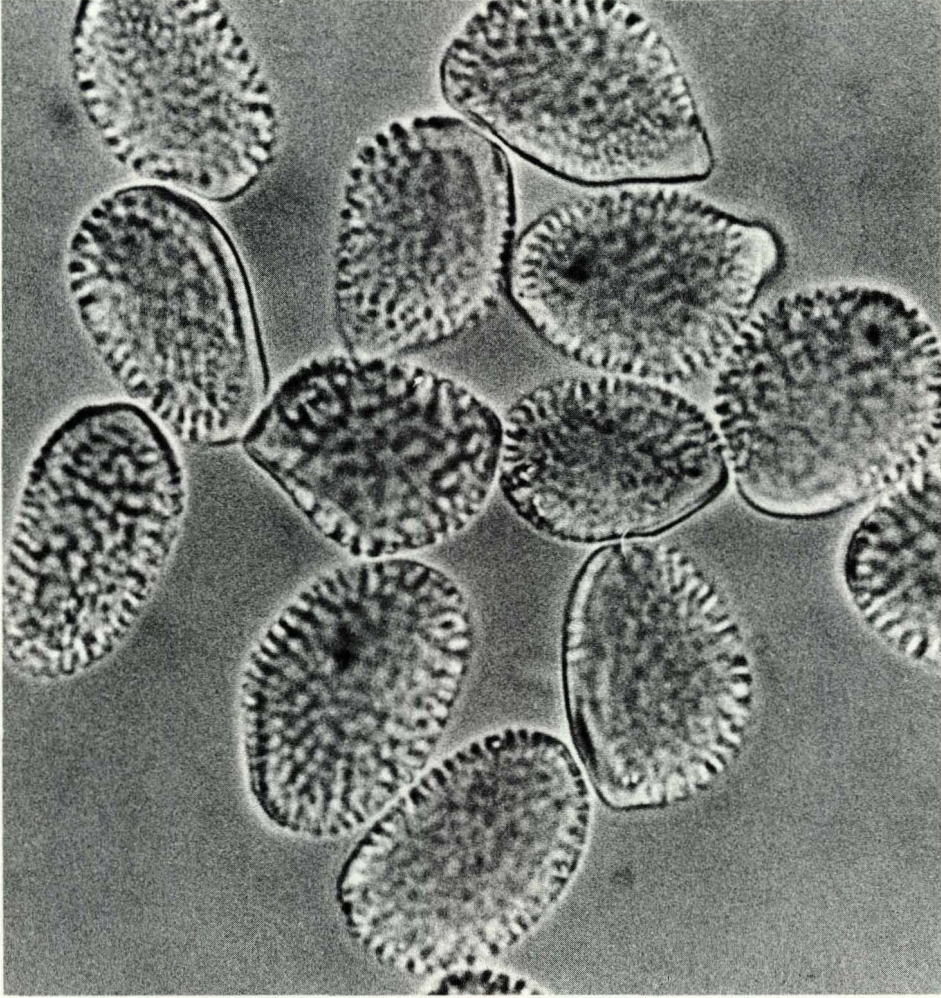
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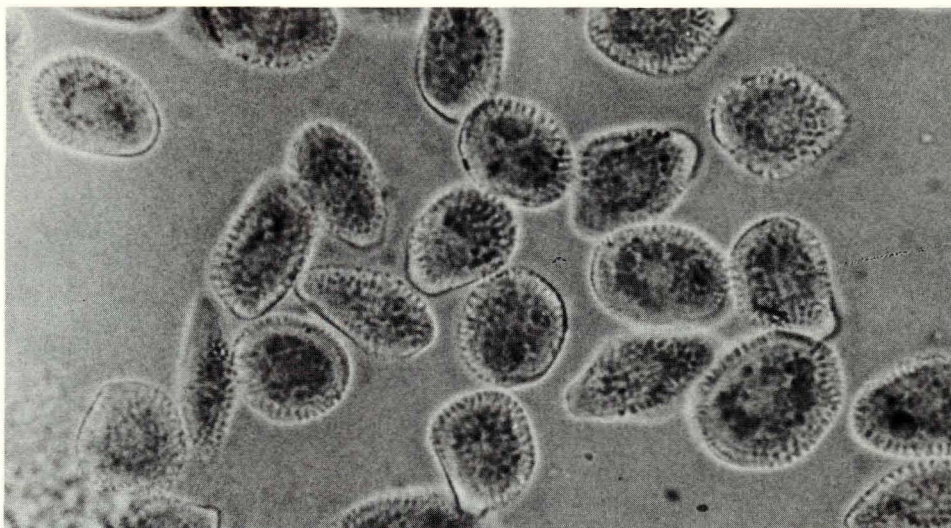
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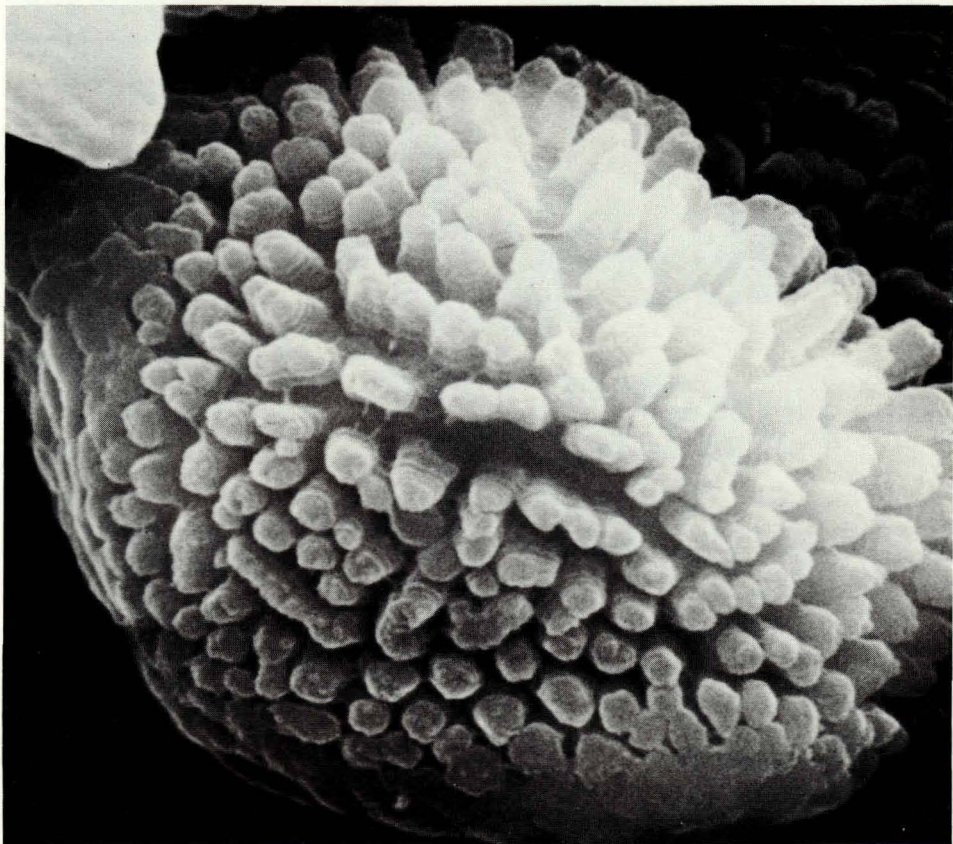
21 Peridermioid teliospores (aeciospores) of
Endocronartium harknessii. X 830.

22 X 7,800 (SEM).

21



22

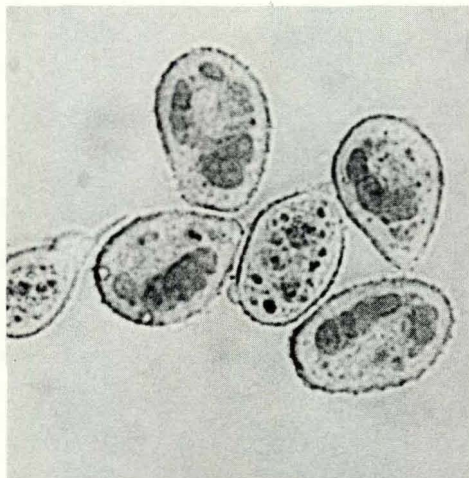


23 Urediniospores of *Cronartium ribicola*.
X 980.

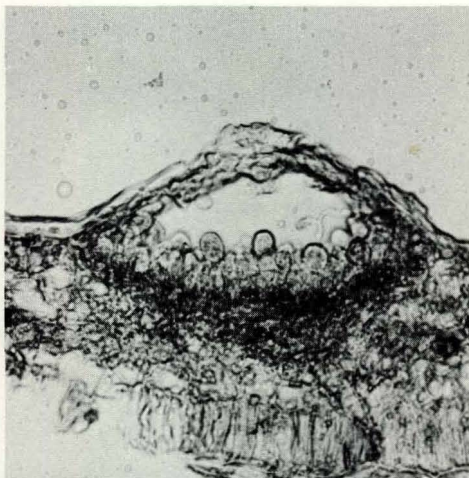
24 Uredinium of *Cronartium ribicola*. X 200.

25 Urediniospores of *Cronartium coleosporioides*. X 3,000 (SEM).

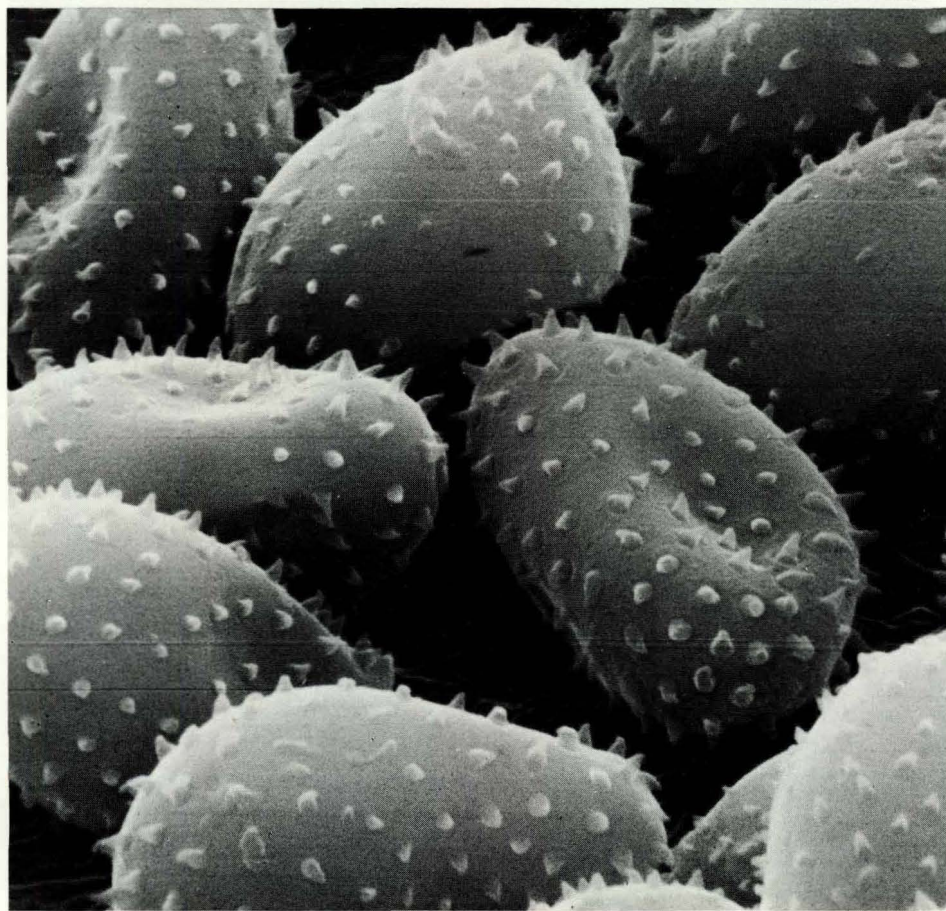
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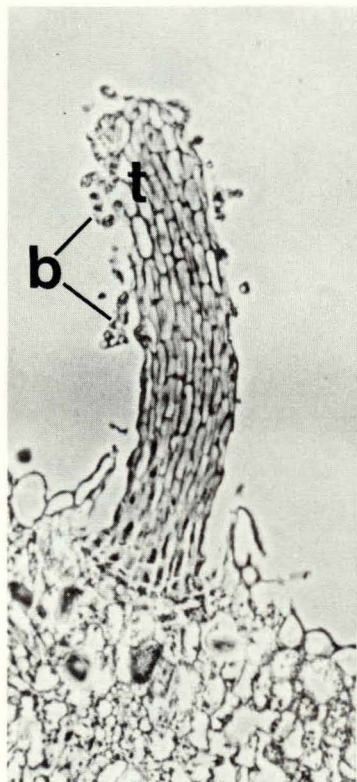
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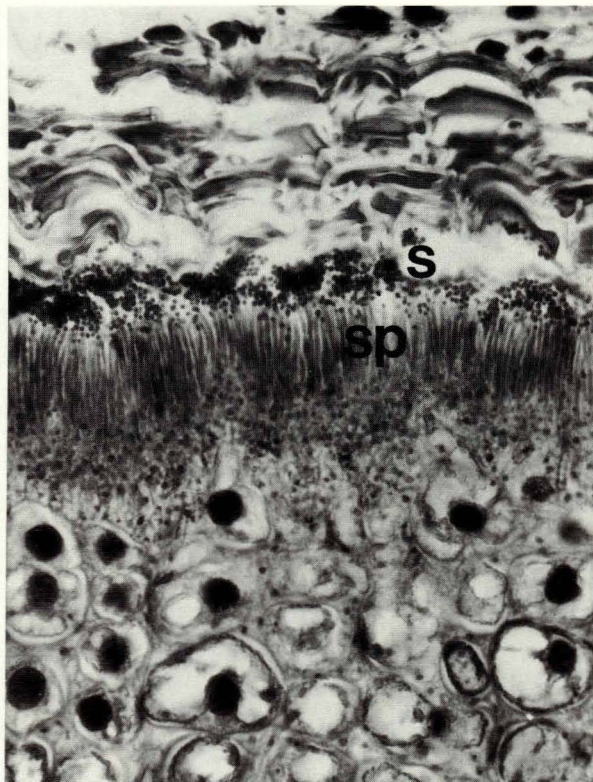
- 26 Germinating telium of *Cronartium coleosporioides*. X 190. t: teliospores, b: basidia and basidiospores.
- 27 Cross section of *Pinus monticola* stem with a spermogonium of *Cronartium ribicola*. X 480. s: spermatia, sp: spermatophores.
- 28 Cross section of a young stem of *Pinus contorta* with an aecium of *Cronartium coleosporioides*. X 80. p: peridium, a: aeciospores.

37

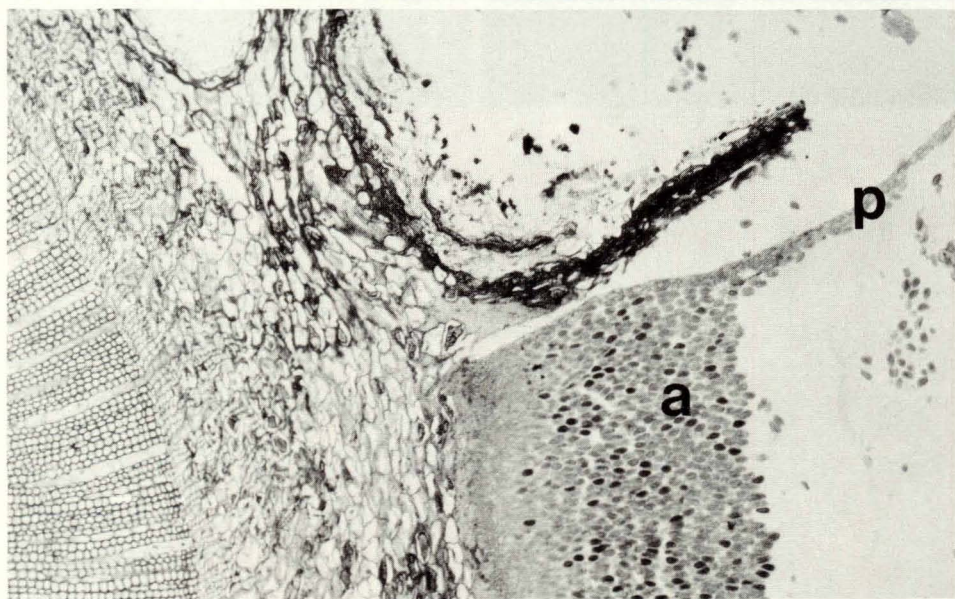
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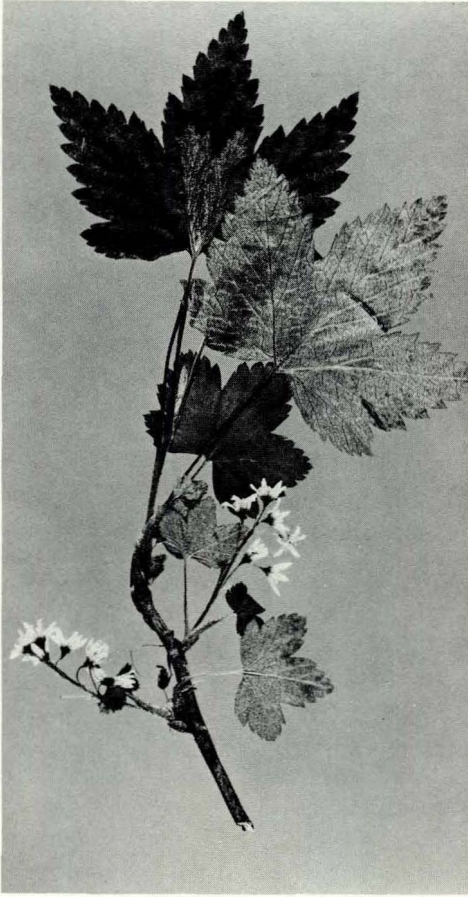


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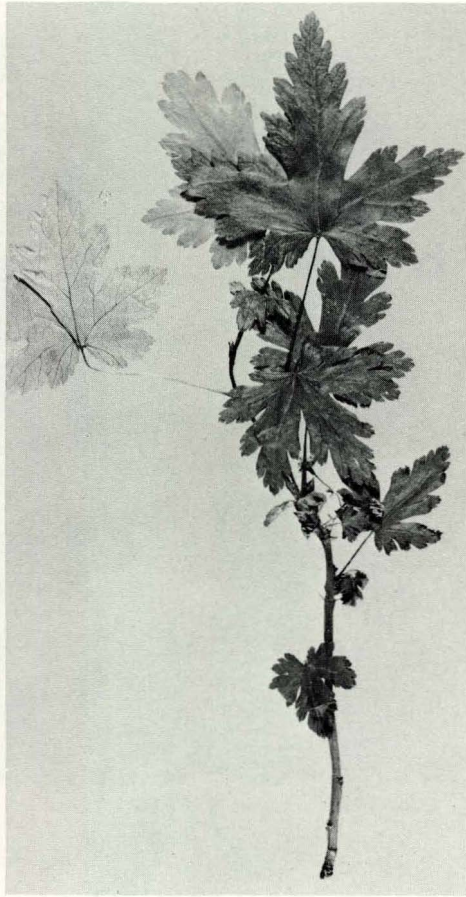


- 29 Northern black currant (*Ribes hudsonianum*), an alternate host of white pine blister rust (*Cronartium ribicola*).
- 30 Swamp or bristly black currant (*Ribes lacustre*), an alternate host of white pine blister rust (*Cronartium ribicola*).

29



30



- 31 Paint-brush (*Castilleja miniata*), an alternate host of stalactiform blister rust (*Cronartium coleosporioides*).
- 32 Close-up of infected leaf of paint-brush (*Castilleja* sp.) with telia of stalactiform blister rust (*Cronartium coleosporioides*).

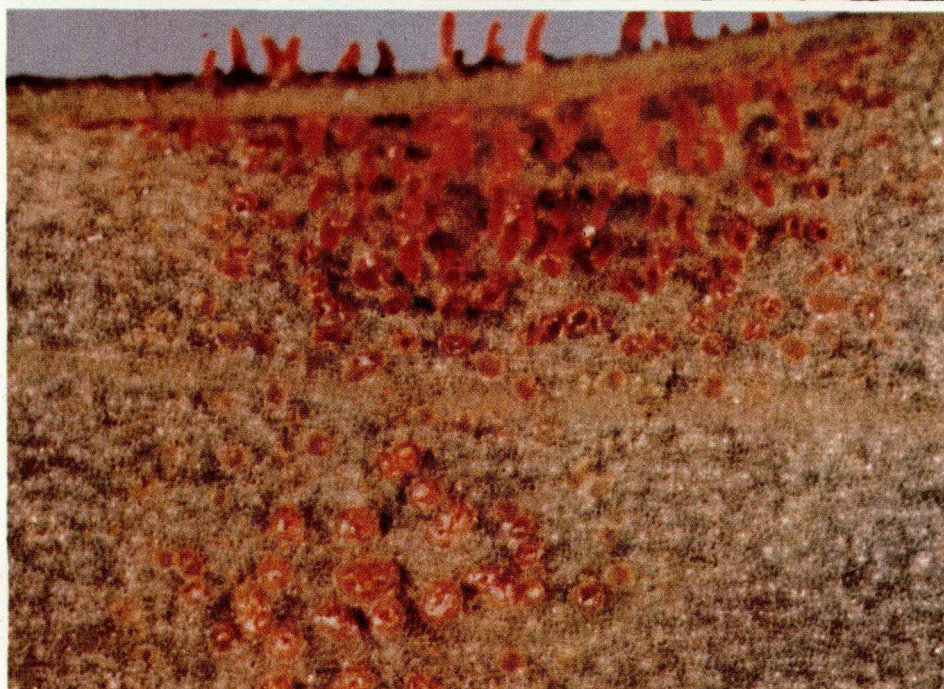
31



32



- 33 Bastard toadflax (*Comandra umbellata* ssp. *pallida*), an alternate host of comandra blister rust (*Cronartium comandrae*).
- 34 Close-up of infected leaf of bastard toadflax (*Comandra umbellata* ssp. *pallida*) with comandra blister rust (*Cronartium comandrae*). Columns of telia (upper part) and dome-shaped uredinia (lower part).



35



- 36 Sweet fern (*Comptonia peregrina*), an alternate host of sweet fern blister rust (*Cronartium comptoniae*).
- 37 Close-up of infected leaves of sweet fern (*Comptonia peregrina*) with sweet fern blister rust (*Cronartium comptoniae*).

36



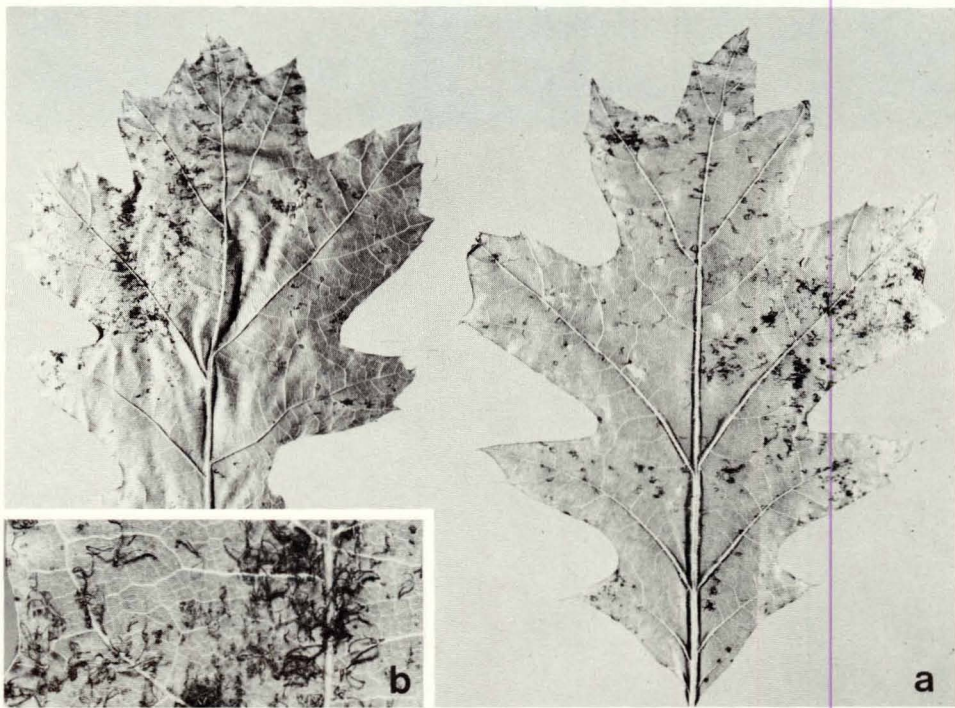
37

- 38 Sweet gale (*Myrica gale*), an alternate host of sweet fern blister rust (*Cronartium comptoniae*).
- 39 a. Leaves of red oak (*Quercus rubra*) infected with eastern gall rust (*Cronartium quercuum*), b. close-up of telial columns.

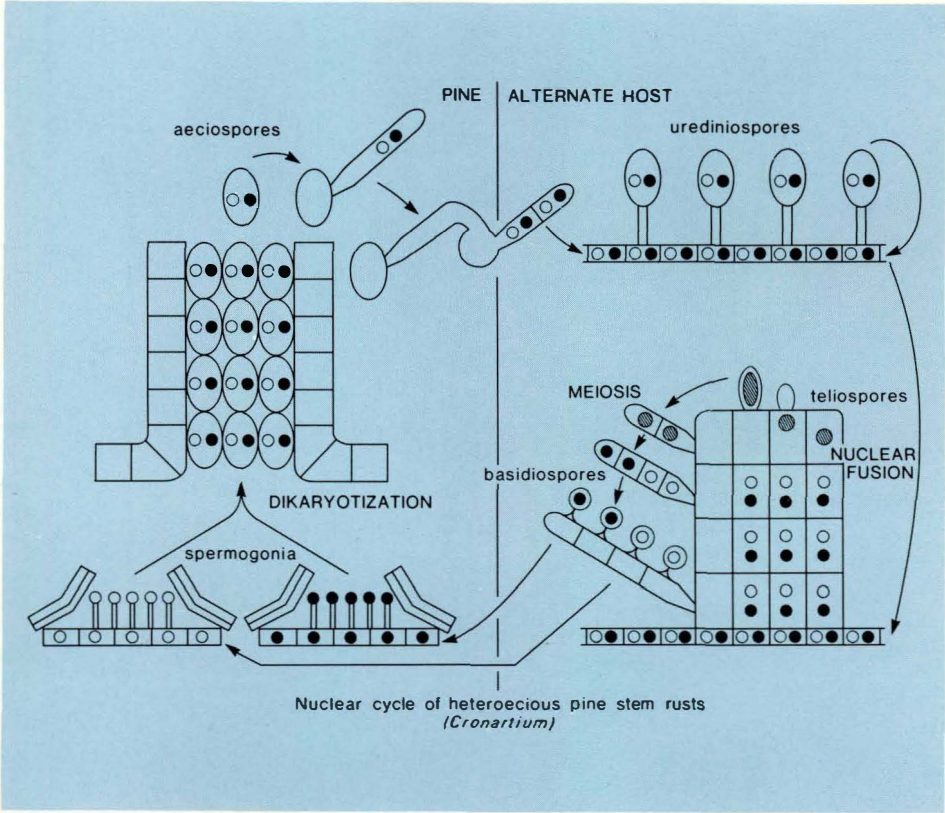
38

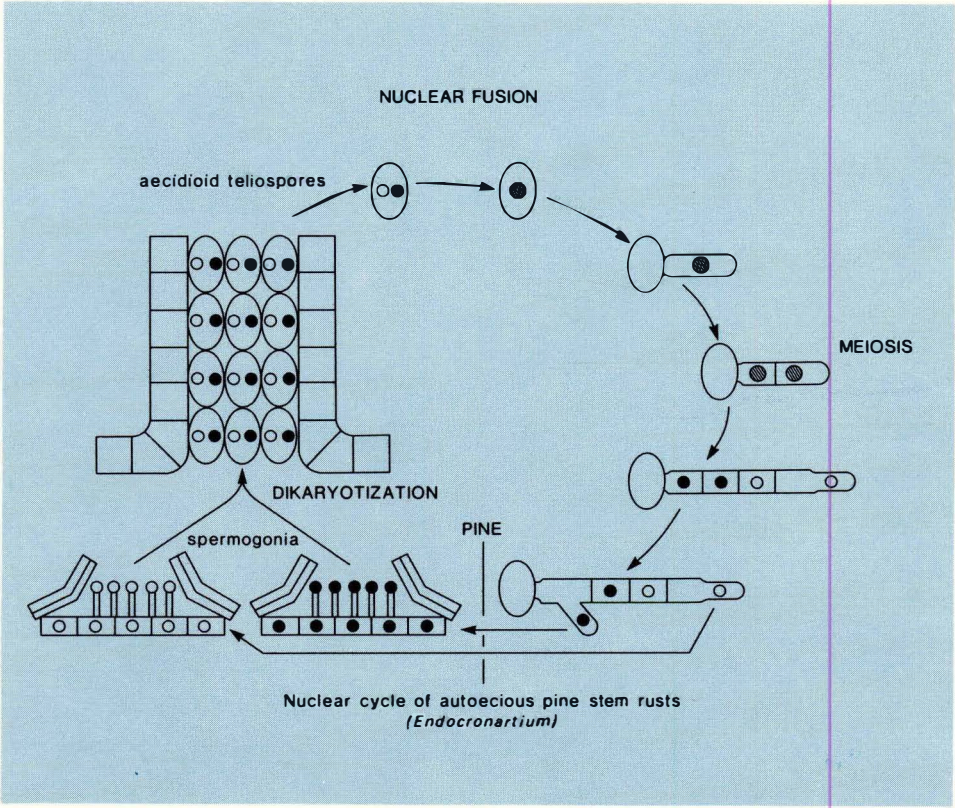


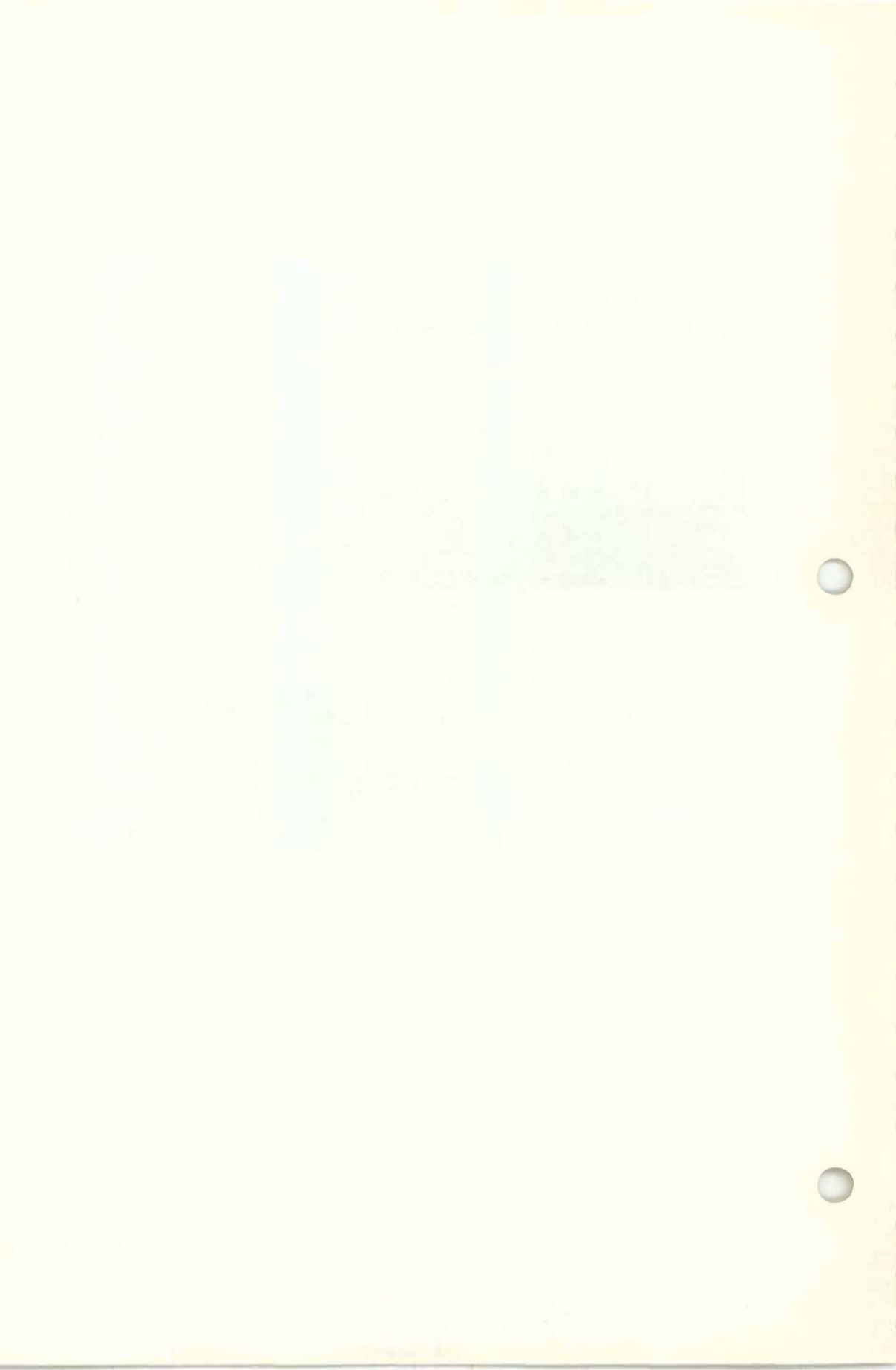
39



40 Nuclear cycle of heteroecious (host alternating) pine stem rust (*Cronartium* spp.).







Limiting and optimal conditions of the environment must be known before stem rust infection in the forest can be predicted, both on pines and on the alternate hosts. Considerable information has been gathered for *C. ribicola*, and some laboratory and field studies have been made for some spore states of *C. coleosporioides*, *C. comandrae*, *C. quercuum*, and *E. harknessii*. Little information is available for *C. comptoniae*.

Phenology of spore production:

The time that spore sporulation begins and ends varies over the range of the rust, within a local area because of differences in aspect and elevation, and between years because of climatic conditions. Other factors also play a role. Mielke (1943) noted a correlation between size of canker, age of host tissues, bark thickness and *C. ribicola* aeciospore production. Spaulding (1922) gives the duration of *C. ribicola* aeciospore production in different years for a number of areas in eastern North America. Duration in most years lasted 48 to 90 days, although he gives extremes of 12 and 140 days. Mielke and Kimmey (1935) indicated that the main *C. ribicola* aeciospore period occurs from mid-April to mid-June in western North America, but may be a month later at higher elevations. Mielke (1943) stated that during warm and dry springs the main aecial sporulation may only last 2 or 3 weeks, but during cool, wet springs may last 2 or more months. Krebill (1968b) reported a variation of 3 to 17 weeks in *C. comandrae* aeciospore production between localities in the Rocky Mountain States but aecia were only abundant through June and July. Development of aecia was earliest at the lowest elevation, and the duration of aecial production was shortest at the higher elevations. Krebill (1968b) and Powell (1969), both illustrate spor-

ulation periods for all spore states of *C. comandrae*, and Krebill includes information on the developmental phenology of the rust hosts, lodgepole pine and comandra. Powell (1969) showed the variation in sporulation at one location during 4 years. He also noted the great variation in the duration of aeciospore production from individual aecial cankers and aecial pustules. Most *C. comandrae* aecia produced aeciospores for 35 to 50 days (Powell 1969), a slightly longer period than reported for *C. ribicola* (Spaulding 1922). A second aecial sporulation production period may occur infrequently in late September and early October, if favorable conditions prevail. Such sporulations, which occur on the zone of the canker producing spermogonia earlier in the year, have been reported for *C. comandrae* (Kreibill 1968b; Powell 1969), *C. comptoniae* (Lachmund 1929) and *C. ribicola* (Lachmund 1933). During two years of observation in Nebraska, G. W. Peterson (1973) found that 88-91% of *E. harknessii* spores were dispersed in May, and dispersal was essentially completed in June.

Spore germination:

There appears to be minimal development of *Cronartium* basidiospores above 23°C. Optimal temperatures for germination of teliospores and basidiospores are generally 15 to 21°C (Bega 1960; Hirt 1942; Krebill 1968b; McGrath 1968; Nighswander and Patton 1965). Few teliospores or basidiospores germinate at temperatures below 8°C (Nighswander and Patton 1965; Krebill 1968b).

The minimum time from teliospore germination through basidiospore germination at optimal temperatures is generally 13 hrs or less (Hirt 1942; McGrath 1968; Nighswander and Patton 1965). The moist period covering teliospore

germination to basidiospore penetration ranges from less than 24 hrs (Hirt 1942; McGrath 1968; Krebill 1968b) to longer than 48 hrs especially if telia form under unfavorable conditions (Van Arsdell 1968; Van Arsdell *et al.* 1956).

The time needed for infection of pine by basidiospores is frequently complicated by the production of secondary or further generations of sporidia. These secondary or later generation sporidia can infect pine directly or they themselves may produce further sporidia rather than germ tubes (Bega 1960; Krebill 1968b, 1972). Such occurrences have been reported for *C. ribicola*, *C. comandrae*, and other stem rusts and they may occur in all heteroecious species. Bega (1960) found basidiospores germinated over a range of pH from 3 to 11, with an optimum of 3 for direct and 7-9 for indirect germination. He found very little difference in sporidial germination in the light and in the dark.

Spores of *E. harknessii* germinate over a similar range of temperatures as the teliospores or aeciospores of heteroecious species of *Cronartium* (Powell and Morf 1966; Mielke and Peterson 1967; Christianson 1968). Aeciospores of *C. comandrae* have a wider temperature range for germination (1°-33°C) than other species of *Cronartium* (Powell 1969, 1974a; Krebill 1968b).

Optimum temperatures for germination of aeciospores of the stem rusts occurring in Canada are near to 15°C (Hirt 1937; Van Arsdell *et al.* 1956; Nighswander and Patton 1965; Powell and Morf 1966; Powell 1969, 1974a). The minimum period required for germination of *C. comandrae* aeciospores and *E. harknessii* spores is 1-2 hrs (Powell 1969, 1974a; Powell and Morf 1966). This is a much shorter period than that required for *C. coleosporioides* and *C. ribicola* aeciospores (Doran 1919, 1922; Powell

and Morf 1966). Germination requirements for the white-spored form of *C. coleosporioides* are very similar to those for the orange-spored form (Powell and Morf 1966).

Aeciospores of *C. comandrae* germinate equally well in the dark and in diffused light, but there is no germination in direct sunlight (Kreibill 1968b; Powell 1969, 1974a). Free water is necessary for germination. Aeciospores of *C. coleosporioides*, *C. comandrae*, and *E. harknessii* (peridermioid teliospores) only germinate in a pH range from 4-9, with optimum between 6 and 7 (Powell and Morf 1966; Powell 1969, 1974a).

Germination of urediniospores of *C. comandrae*, *C. quercuum*, and *C. ribicola* requires free water and occurs at temperatures between 3° and 28° with an optimum between 13° and 23°C (Van Arsdell *et al.* 1956; Nighswander and Patton 1965; Krebill 1968b). Urediniospores of *C. comandrae* germinated equally well in low light and in darkness, but do not germinate in bright direct sunlight (Kreibill 1968b). Four to 6 hours were required for *C. ribicola* urediniospores to begin germination (Van Arsdell *et al.* 1956). It usually took 10 to 15 days for the uredinia to be produced, following inoculation with aeciospores, and telia generally emerged 20 to 30 days after inoculation, although the uredinial stage may be bypassed and then only telia formed (Kreibill 1968b). Nighswander and Patton (1965) reported that *C. quercuum* produced uredinia and telia after 6 days and from 9 to 14 days respectively.

Spore viability:

Viability of spores is an important factor to consider in epidemiological studies. Generally the percentage of viable spores is lower during the second half of the aeciospore production period (Doran 1922; Spauling 1922; Krebill

1968b; Powell 1971f). Viability was similarly reduced for urediniospores and teliospores (Spaulding 1922; Krebill 1968b; McGrath 1968), but evidence of this was not clear for basidiospores (Kreibill 1968b). Spore viability generally increases as temperatures decrease from the optimum germination temperature. Spores do not survive for long above the maximum temperature for germ tube formation (above 25°C) (Van Arsdel *et al.* 1956; Powell 1974a). Spores soon die if they become wet (Powell 1971f), or exposed to direct sunlight (Spaulding; 1922; Van Arsdel *et al.* 1956; Powell 1969, 1974a). Spores of *E. harknessii* retain their viability better than those of *C. coleosporioides* and *C. comandrae* when stored in cool temperatures (Powell 1971f). Lightle (1955) was able to store spores of *E. harknessii* for over a year at 4 to 5°C. Natural spore color retention is associated with viability; faded spores never germinate (Spaulding 1922; Walkinshaw 1968; Powell 1969, 1971f, 1974a).

Release and dispersal of spores:

Daily periodicity of spore release is known for some stem rusts. Basidiospores of *C. comandrae* and *C. ribicola* are generally released at night or during periods of high humidity (Van Arsdel 1967; Krebill 1968b). Aeciospores and urediniospores of *C. comandrae* are generally released during dry, warm turbulent days between 0800 and 1900 hours with a peak close to mid-day when atmospheric turbulence is at its maximum (Powell 1971e, 1972a). The onset of heavy rains also initiates aeciospore release, but light rains apparently do not have the same effect (Powell 1971e, 1972a). *E. harknessii* spores show a diurnal periodicity of release on rainless days with a maximum about 1100 hours (G. W. Peterson 1973). Rainfall inter-

rupted the diurnal periodicity, spores seldom being trapped during rain.

Spaulding (1922) reports *C. ribicola* aeciospores trapped up to a distance of 550 feet, and on another occasion 1200 feet, from pines. *C. comandrae* aeciospores were not collected at distances greater than 400 feet during two seasons (Powell 1969). G. W. Peterson (1973) seldom collected *E. harknessii* spores in a nursery 300 feet from infected stands. Powell (1971e) indicated that the chances of aeciospores of *C. comandrae* landing on a susceptible host more than a few hundred feet from a canker are small. However, aeciospores may undergo long-distance dissemination under certain conditions especially during unstable warm turbulent conditions when they are carried up and out of the forest, but they may be rapidly killed by the consequent exposure to heat and light. Davidson (cited in Mielke 1943) reported collecting *C. ribicola* aeciospores up to 5,000 feet above a heavily infected area in British Columbia, but no information on the atmospheric conditions are given. Snell (cited in Spaulding 1922) provided evidence that aeciospores of *C. ribicola* were carried at least 7 miles from pines on the mainland to infect *Ribes* on islands off the New Hampshire coast. For only a few short intervals in any one sporulation period are conditions favorable for aeciospore release, dispersal, retention of viability and germination (Powell 1974a).

Urediniospores can also be dispersed by wind over great distances during any one season through their repetition of generations. Uredinial infections have often been found more than 100 miles from the nearest known pine source (Powell 1970).

Infection spread by basidiospores is more limited and is generally restricted to a few miles (Kreibill 1968b; Kimmey

and Wagener 1961). Van Arsdel (1967) reported a particular set of atmospheric conditions relating to air movement over land and water which allowed for dispersal of *C. ribicola* basidiospores and infection of pine at distances of 10 to 17 miles from the source. Gregory (1945) concluded that spore cloud depletion rather than loss of viability was more important in determining the effective limits of spread of *C. ribicola* basidiospores. Kimmey and Wagener (1961) showed that infection patterns for a single season are usually the consequence of dissemination of *C. ribicola* basidiospores during only one or two favorably moist periods. Similarly, Krebill (1968b) showed that *C. comandrae* basidiospore production occurred rarely and that conditions seldom remain favorable long enough for infection of pines.

Conditions affecting infection:

Outbreaks of the rusts have been prominent in some years and have given rise to the term "wave years" of infection (Peterson and Jewell 1968). Outbreaks are due, in part, to the time needed to build up inoculum following initial infection, but the frequency of suitable atmospheric conditions for spore production, dispersal, and infection is more important. The conditions necessary for *C. ribicola* spread and infection in the Lake States have been well documented (Van Arsdel *et al.* 1956, 1961; Van Arsdel 1961; Anderson 1973). Anderson (1973) summarized the microclimatic relations research undertaken by Van Arsdel and colleagues. They found that topography and vegetational cover are important features accounting for variations in blister rust prevalence. The effect of topography is most pronounced in depressions and on north-facing slopes, especially during the clear, cool, windless nights that also favor dew forma-

tion. Vegetation has a similar effect to that of topography but its influence is more complex. The probability of favorable temperature and moisture conditions persisting long enough for infection to occur is greatest in small forest openings and least in an understory.

The infection of pine by *Cronartium* species is usually limited by the absence of the necessary, long, moist period after teliospores germinate. Temperatures too high for normal production of basidiospores are also cited as a frequent cause of failure (Peterson and Jewell 1968). Krebill (1971) suggested that low temperatures found at high elevations might reduce the inoculum potential of *C. ribicola* teliospores.

The pine-to-pine infecting *E. harknessii* also shows long intervals between major years of infection (Peterson 1971). Outbreaks of the rusts may be local or extend over large forest regions (Peterson and Jewell 1968; Peterson 1971). Powell and Hiratsuka (1973a) reported a sudden intensification of infection on a plantation in Alberta and found a further substantial increase the following year (Powell and Hiratsuka 1973b).

Epidemics of *C. comandrae* and *C. comptoniae* generally occur in nurseries or plantations rather than in natural stands (Spaulding and Hansborough 1932; Mielke *et al.* 1968), indicating the adverse effect of intensive culture. Various climatic indices have been developed to establish hazard zones or areas for *C. ribicola* infection (Charlton 1963; Kimmey and Wagener 1961; Paine and Slipp 1947; Van Arsdel 1961, 1964; Van Arsdel *et al.* 1961), but are lacking for other species that occur in Canada.

Pine stem rust damage in natural stands is not usually spectacular, although the effect of the introduced *C. ribicola* on the white pine stands of North America has often been drastic. Accuracy of damage estimates for the individual native rusts has sometimes been hampered by mis-identifications (Peterson and Jewell 1968), especially in eastern North America. Rust damage has often been attributed to rodent gnawing, because squirrels and other small mammals have removed infected bark (Mielke 1963; Mielke *et al.* 1968; Powell 1969). Damage in natural stands is limited by the distribution of the alternate hosts for some species and by the density of the stand. In dense stands infected branches tend to die early, due to natural suppression, which reduces the possibility of the more damaging stem cankers developing.

Canker-forming species:

The canker-forming species attack trees of all ages and sizes, often the most vigorous; mortality is caused by girdling. The period between initial infection and death of the tree may be more than 30 years. Krebill (1965) found that some *C. comandrae* cankers were 100 years old. Seedlings and saplings are usually killed within a few years of infection, because the rusts enter through needles on the small main stem and soon girdle it. The rusts characteristically enter the main stem of older trees via branch infections. They only grow 1 to 3 inches downward on a branch each year so may not reach the main stem for many years. Branch cankers more than 18 inches from the stem tend to die out, since the rust generally kills the branch before the hyphae can reach the stem.

On the main stem, vertical growth of the canker is more rapid than lateral growth (Kreibill 1965; Lachmund 1934). Mielke (1956) reported it to average

almost 7 inches per year for *C. coleosporioides*, with a greater average annual growth downward than upward. This form of growth is also true for cankers of *C. ribicola* and *C. comandrae*, although the actual growth rate may be slower (Lachmund 1934; Rhoads 1920; Buchanan 1938). The lateral rate of growth for *C. ribicola* and *C. comandrae* is much greater than for *C. coleosporioides*; thus girdling and death of the stem is more rapid. Cankers of *C. coleosporioides* up to 30 feet long have been reported (Mielke 1956). Dead tops or spike-tops are evident in mature stands where *C. comandrae* or *C. ribicola* have girdled the upper stem. Childs (1968) showed that downward growth on the stem by *C. comandrae* is less than 6 inches a year, so the lower portion of the tree may live for many years if vigorous lower branches remain. Most stem cankers occur in the bottom 10 feet of a tree (Anderson and French 1964b; Phelps and Weber 1969b; Calfley 1958), but Krebill (1965), in a study of *C. comandrae* cankers on lodgepole pine in the Rocky Mountain States, found the average height to be 26 feet above ground.

Cronartium ribicola

C. ribicola is the most damaging disease of white pines (Hepting 1971), and probably the most damaging of all the forest tree rusts (Arthur 1929). It causes damage wherever susceptible species of the alternate host genus *Ribes* occur, and microclimatic conditions favor basidiospore formation, dissemination, and germination. It has not yet spread to the range limits of white pines in western North America (Peterson and Jewell 1968) although reports of new range extensions are still appearing (Kreibill 1964; Brown 1967, 1970; Brown and Graham 1969; Smith 1971). Seedlings and saplings are quickly killed so that

there is no regeneration to perpetuate a stand when the mature trees are cut or finally killed. Powers and Stegall (1971) reported only 2% mortality among seedlings in an unprotected stand in North Carolina in 1948, but 41% mortality in 1966. Another 45% had been killed by suppression and other causes but many of these were also infected with the rust. At the same time, 41% of the older trees were dead or dying from blister rust infections.

Similar increasing mortality figures have been reported in Canada. In a western white pine stand, averaging over 20 feet in height near Garibaldi, British Columbia, practically 100% of the trees were killed 16 years after the introduction of the rust into the locality. In an adjacent stand, 56% of the larger trees died during the same period (Lachmund 1934). Gautreau (1963) surveyed limber pine stands infected by the rust in southwestern Alberta and found that infection ranged from 79 to 100% with less infection in the north, where there apparently had not been any mortality due to the rust. However, 83% of the trees in the southern area had been killed by the rust and all regeneration in the area was heavily infected. This rust threatens to completely destroy limber pine in southern Alberta. Whitebark pine has also been severely damaged in the same area of Alberta (Ives *et al.* 1973).

Stillwell and Davidson (1954) stated that white pines observed in Newfoundland were for the most part heavily infected, particularly in the central portion where most of the trees were dead or had dead tops or many dead branches. Clark and Singh (1971) reported moderate to heavy infection on planted and natural growing eastern white pine in various parts of Newfoundland. Kingston and McGinn (1951) found that infection by the rust averaged 10% in Nova Scotia

and 14% in New Brunswick. A later survey of the same areas in New Brunswick indicated that 11.5% of the living eastern white pine were infected by the rust, with infection ranging from 0 to 33% in any one area (Van Sickle 1966). A lower percentage of infection was recorded in the up to 2.5 inch d.b.h. class than in larger diameter classes, which suggested that the rust was not a factor seriously limiting regeneration of white pine in that area. A similar survey in Nova Scotia indicated 6% of trees infected, with 1.4% dead (Forbes *et al.* 1968).

A 1931 survey of natural stands in Quebec showed that less than 3.5% of the white pines were infected; on reforested areas the situation was more serious (Pomerleau 1961). In a 3-year study of a 15-year-old plantation, Pomerleau found that the number of trees with trunk cankers increased from 27 to 50%, those with branch cankers from 50 to 67%, and dead trees from less than 1% to almost 15%. However, infection of trees in three other plantations, some in areas subject to *Ribes* eradication, ranged from only 4 to 13% (Pomerleau and Bard 1969). Martineau and Lavallee (1973) suggested that white pine had an increased susceptibility to the rust at higher altitudes. They reported on several plantations and natural stands where 20% or more of the trees were infected.

Various surveys carried out in Ontario, mainly between 1952 and 1954 in young stands, gave infection percentages from 3 to 71% and mortality from the rust from 0 to 17%. Similar percentages for young regeneration were 1 to 19% and 0.2 to 6% (Haddow 1956). In many areas it was expected that infection and mortality would increase greatly as the trees had been exposed to rust infection for only a small portion of their normal life span. Cafley (1958) found that 8.8% of the trees examined in white

pine plantations in 24 locations in southern Ontario were infected by the rust; with incidence ranging from 0.5 to 26.7%. The variation he found was closely related to the occurrence of *Ribes* bushes in adjacent natural hardwood stands. In that study he found that all infected stems less than 4 inches in diameter had been girdled completely by the fungus during a 7-year period. Larger trees showed an ability to survive for a longer period. Infection and mortality throughout Ontario in 1967 was generally rated at less than 10% in most districts, although the incidence in some areas was as high as 42% (Sippell *et al.* 1968).

Cronartium coleosporioides

Infection from *C. coleosporioides* occurs only in stands or plantations close to areas of the alternate host. Mielke (1956) reports areas in southern Idaho where 30% of the trees have trunk cankers, and mentions reports of most of the trees being infected although cautioning that accurate appraisals are required to establish the degree of damage. There is little information in the literature of mortality caused by *C. coleosporioides*. Anderson and French (1962) reported that 82% of their inoculated jack pine trees were killed. Baranyay and Bouchier (1963) reported that 5% of the lodgepole pine had been killed in a stand on the Mackenzie Highway where 70% of the trees examined were infected. Mielke (1956) stated that girdling seldom occurs except when two or more cankers on a single trunk coalesce. Incidence is reported to be low on jack pine in Quebec although one stand had 20% infection (Martineau and Smerlis 1969). In northwestern Ontario, the incidence of the rust on jack pine was found to be high (over 25%) or moderate (5-24%) in a few locations, but was generally only a trace (Sippell

et al. 1972). In British Columbia the incidence on lodgepole pine ranged from 6 to 90% (Molnar *et al.* 1969). In Banff National Park, Alberta, 33% of the trees on a 0.1 acre plot in a 25-year-old lodgepole pine stand were infected (Baranyay, unpublished data). In one area north of Burmis, Alberta, approximately 80% of a lodgepole pine stand was infected (Tripp *et al.* 1967).

Cronartium comandrae

There are widespread reports of damage by *C. comandrae* in natural stands in the United States, especially in the west on ponderosa and lodgepole pines (Mielke *et al.* 1968). In some of these areas, mature stands covering several square miles were reported with 50 to 98% of the trees infected (Mielke 1957). Other reports indicated 21 to 35% of young or mature trees infected (Hedcock and Long 1915; Meinecke 1928; Peterson 1962a; Krebill 1965). More recently *C. comandrae* has become a problem in young plantations of ponderosa, loblolly, and shortleaf pines in southeastern United States (Powers *et al.* 1967; Cordell *et al.* 1967; Dooling 1967). Powers *et al.* (1967) reported plantations with over 90% of the less than 10-year-old trees infected on the Cumberland Plateau, and one case, with 57% of the 2-year-old loblolly pines infected. In Arkansas, Dooling (1967) found 44% of the shortleaf pines planted on three plots in 1958 were dead by 1967.

In eastern Canada, 22% of the trees in a jack pine plantation at Thunder Bay, Ontario, were infected (Dance and Lynn 1965). More than 10% of young jack pine in a small area at Saint-Urbain, Quebec, were infected (Martineau and Ouellette 1966), and at Godbout, in 1968, 90% of semi-mature jack pine were infected and 5% of the trees were dead (Martineau and Smerlis 1969).

There are several published and unpublished reports of damage in western Canada (Molnar 1960; Baranyay and Stevenson 1964; Powell 1969). A survey in a 20-year-old jack pine stand south of Rae, Northwest Territories, showed 44% of the 725 trees on a 0.1 acre plot were infected in 1965, and in 1966, 7.9% of the infected trees had died (J. A. Baranyay, unpublished data 1965, 1966). In a small lodgepole pine regeneration area in southwestern Alberta, where few trees were over 5 years old, 23% of the trees were infected in 1967 and 44% of the trees with cankers died within 1 year (Powell 1969). By 1971, only 12% of the 1967 infected trees were still alive (Powell, unpublished data). In 1966 and 1967 a total of 440 live cankers were tagged on lodgepole pine at 24 localities in southwestern Alberta, and by 1968 23% of these were dead (Powell 1969). In 1971, when 403 of the earlier tagged cankers were observed, 44% were dead, 31% were inactive, and only 25% were classified as still active. Canker mortality amounted to over 60% in several localities, with most mortality occurring in the younger stands (Powell 1971 and unpublished data).

Cronartium comptoniae

Mortality from *C. comptoniae* is common in the younger age class of trees, particularly seedlings where losses as high as 25% are common (Spaulding and Hansbrough 1932; Anderson, G. W. 1963; Van Sickle 1969). Mortality of 48 to 52% has also been reported in mature and overmature stands of jack pine in the Lake States (Anderson and French 1964a). G. W. Anderson (1963) reported that infected stands over 25 years old suffer reduced height and diameter growth. The irregular growth of the stem, with its pronounced ridges near the base, caused by the rust, makes infected stems

undesirable for pulpwood or lumber (Anderson and French 1964b; Dance and Lynn 1965).

Molnar (1961) reported three plantations of Monterey pines on Vancouver Island with over 75% of the seedlings infected by *C. comptoniae* and a plantation of Bishop pine with over 50% infection. Van Sickle (1969) found 82% infection in a 6-year-old shortleaf pine plantation in the Maritimes, and 71% of the infected trees were dead. In older lodgepole and jack pine plantations, 34 and 12% respectively of the stems were infected. However, in natural jack pine stands an average of 2% of the trees were infected. At Normandin, Quebec, 25% of the semi-mature jack pines were infected and 2% of these were dead (Martineau and Smerlis 1969). Moderate (5 to 24%) and high (over 25%) levels of infection are also reported from several areas of Ontario (Sippell *et al.* 1969, 1970, 1971). Mortality in one sample plot in the Cochrane District of Ontario increased from 0 to 18% over a 3-year period (Sippell *et al.* 1968). There are reports of light to moderate infection in the Rae and Yellowknife areas of the Northwest Territories, and in areas of northern Saskatchewan (Ives *et al.* 1971).

Gall-forming species:

The gall-forming *C. quercuum* and *E. harknessii* also invade pines of all ages through the needles or young shoot tissue and then move into the stem, where they stimulate extensive cambium activity, which causes the formation of a globose gall. Like the canker-forming stem rusts, the gall rusts gradually girdle the stem or branch, which dies above the gall. Galls that form on the main stem of seedlings usually kill the plant within a few years. On older trees the galls may weaken the stems, making them more subject to wind breakage. The primary gall may die but

secondary ridges of swollen tissue may develop on each side of it. Bark above and below the band of infected tissues usually dies so that dead tissues may extend vertically for up to 12 feet but no mycelium is present in the elongate area (Peterson 1960a, 1961). Vertical growth of the rust is usually very slow. Peterson (1961) was unable to find rust mycelium more than 0.4 inches from an *E. harknessii* gall. He also reported that active cankers 200 years old were common on lodgepole pine; he observed one canker older than 277 years (Peterson 1960b, 1961). There are also instances where hundreds of galls occur on the branches of a single tree, causing conspicuous damage (Peterson 1960a; Powell and Hiratsuka 1973a). On most pine species, *E. harknessii* produces few or no trunk galls but they are fairly common on lodgepole and ponderosa pines.

Cronartium quercuum

This rust is mainly a problem in nurseries or plantations and in the management of seedling, sapling, and pole-sized stands (Anderson, N. A. 1963; Nighswander and Patton 1965). Some nurseries report losses of over 25% of Scotch pine. Nighswander and Patton (1965) reported that in some years up to 60% of the 2-year-old jack pine seedlings had visible galls when they were lifted in the spring. Rudolf (1958) also reported 40-50% of young jack pine seedlings infected in some areas of the Lake States. Weir (1915) reported that jack pine infected by this rust produce smaller cones with more aborted sporophylls and seeds about 20% lower in viability than normal. There have been reports of damage by this rust in Canada (various entries in the Annual Report of the Forest Insect and Disease Survey) but most, if not all, of these have involved misidentifications. Surveys therefore need to be undertaken

in certain areas of Ontario to establish if any damage is caused by *C. quercuum*.

Endocronartium harknessii

Thousands of ponderosa pine seedlings per acre have been killed by this rust in the Pacific Northwest, but such severe outbreaks are limited to only a few acres (Peterson 1960a). In Canada there are numerous reports of local damage by this rust. Forbes *et al.* (1970) found that 24% of the jack pine on 35 areas in the Maritime Provinces had one to more than 50 galls. Tree mortality was not observed but trees were stunted and malformed. Most galls were no more than 4 years old and at least 75% of the infections apparently originated in current needles or shoots. In Quebec, the incidence of infected trees ranged from a trace to high, with reports of 40% to nearly all trees infected (Martineau and Ouellette 1966; Martineau and Smerlis 1969). Over a 3-year period (1968 to 1971) there was a 40 to 400% increase in the incidence of *E. harknessii* at three locations in Saguenay County, Quebec (Martineau and Lavallee 1972).

In Ontario, high levels of *E. harknessii* incidence have been reported, especially in the northern areas (Sippell *et al.* 1969, 1971). On the Prairies, 50 to 100% of the trees in some localities were infected; on some trees 25 to 70% of the branches had galls (Ives *et al.* 1968, 1969, 1971; Baranyay *et al.* 1962). Ives *et al.* (1971) suggested that infection rates are higher in manipulated stands. High percentages of infection are also recorded from some areas of British Columbia but the incidence is generally less than 10% (Molnar *et al.* 1967, 1970; Ross *et al.* 1973).

Carlson (1969) found up to 3% infection by *E. harknessii* on jack pine nursery stock which was growing by a heavily-infected natural stand in Man-

itoba. There is a similar report of damage to lodgepole pine nursery stock in British Columbia (Molnar *et al.* 1970). In New Brunswick a Scotch pine Christmas tree plantation was abandoned because of the high frequency and intensity of *E. harknessii* galls, causing branch and top mortality (Forbes *et al.* 1972). A recent survey on a tree farm in Alberta found 63% of the 6- to 12-year-old lodgepole pine stock infected, with an average of 27 galls per infected tree (Powell and Hiratsuka, 1973a).

Control of pine stem rusts has been attempted through tree improvement and resistance studies, and by silvicultural, chemical and biological means. So far none has proved to be effective in all situations although economical losses can be minimized in certain conditions.

Silvicultural

Removal of infected trees during thinning operations and in intermediate cuts is the only practical way to reduce pine stem rust damage in forests. Childs (1968) gives recommendations for thinning operations in sapling and mature ponderosa pine stands for control of *C. comandrae*.

Pruning of branch cankers and galls has been carried out in plantations or in areas where the trees are of special value. Branch cankers should be removed if they are close to the main stem. Branch galls of *E. harknessii* and *C. quercuum* will do little harm to a tree unless within a few centimeters of the trunk, although they will continue to serve as sources of inoculum. Branch stems should be cut at least 6 inches below the lower edge of the canker margin, close to the trunk (Martin and Gravatt 1954). Removal of main stem cankers is only economical on trees having a special ornamental value. Success will depend on the extent to which the stem has been girdled and the distance of the canker from the ground. The wound area must be treated to prevent attacks by other fungi and insects.

Pruning of *C. ribicola* cankers on sugar pine proved economically feasible in Oregon to provide crop trees (Hayes and Stein 1957). Stewart (1957) obtained 100% control on eastern white pine in Minnesota through branch pruning, 95% with top-pruning and 69 to 100% with trunk pruning, the latter percentage varying according to the distance of the cut

from the margin of the canker. He also showed that a combination of pathological and silvicultural treatments in a natural forest was even more effective, but economically questionable as a forest operation. Weber (1964) demonstrated that pruning substantially reduces losses in high-hazard areas. Lately, pruning has become a major control method for *C. ribicola* in the eastern United States; 1.2 million white pines were pruned to control rust in the fiscal year 1967 (Peterson and Jewell 1968).

Cafley (1958) found that there was a higher percentage of *C. ribicola* infection in pure eastern white pine plantations than in mixed stands. The wider spacing of pines in mixed stands helps to reduce the amount of infection. Krebill (1972) suggested that *Cronartium* rust damage in pines might be reduced through manipulating forest land vegetation so as to increase interception of basidiospores by non-host plants.

Up until about 1957 the eradication of *Ribes* was generally the only method of control used for *C. ribicola*. Peterson and Jewell (1968) report that some 1.4 billion *Ribes* bushes have been destroyed on 23 million acres. In many areas there has been a sharp decrease of the infection rate on pine after *Ribes* control (Martin 1944; Stewart and Ritter 1962). In other areas, where intensive eradication programs were carried out, surveys showed that infection was increasing at an average rate of 3 percent per year (Ketcham *et al.* 1968).

Van Arsdell (1967) showed that some areas are subject to regular long-distance transport of spores; in these areas, local *Ribes* eradication does not effectively reduce infection. In other areas, control by *Ribes* eradication has not been considered feasible because of the general low density of white pine per acre, a heavy population of native *Ribes*, rough

topography and favorable weather conditions for pine infection in most years (Porter 1960). Most eradication programs have involved the destruction of all *Ribes* bushes within 900 feet of pine trees. In some areas, eradication programs over varying distances have been carried out depending on the topography, direction of dominant winds, or the location of suitable *Ribes* habitats (Quick 1962; Kimmey and Wagener 1961; McIntyre 1942). Initial costs of control per acre in eastern white pine are less than half those in the west. Nearly all of the eastern areas have been worked for *Ribes* at least once (Peterson and Jewell 1968). In western United States, because of ineffective control in some areas and rising costs, the program of *Ribes* removal was re-evaluated through intensified distribution surveys (Benedict 1966; Toko and Dooling 1968; Ketcham *et al.* 1968). In the west, the *Ribes* eradication programs have been generally curtailed and direct control programs by either mechanical excision or chemical spraying are being used in areas of aesthetic value.

Ribes bushes have largely been removed by hand pulling and grubbing, but chemical and mechanical methods have also been widely employed. Various herbicides such as 2, 4-D and 2, 4, 5-T have generally been used for chemical eradication (Offord *et al.* 1952). Silvicultural methods can also be used to restrict the development of *Ribes* in managed forest areas (Moss and Wellner 1953). Cafley (1958) found that in Ontario plantations, the development of *Ribes* is suppressed by a reduction in light as the crown canopy closes. Therefore, the rate of infection normally decreases with the growth of the stand. However, the disease may be a threat to older plantations if they lack a closed crown canopy for an extended period after any thinning operations. All plantation areas should be

cleared of *Ribes* at time of establishment and checked again within a few years. Care should also be taken in selecting nursery sites for growing white pines. Any *Ribes* growing within 1 mile of nurseries should be eradicated.

Little effort has been made to control the alternate hosts of the native pine stem rusts except in the immediate vicinity of nurseries, as eradication in forested areas is impractical, and in the case of *C. quercuum* involves valuable oak trees. The two alternate hosts of *C. comandrae* and of *C. comptoniae* inhabit two different types of site, which would make eradication programs extremely difficult in or near natural stands. Also, the hosts for *C. comandrae* have extensive underground rhizomes which would make eradication by grubbing impossible. Numerous herbicides have been tested but none have yet effected a satisfactory kill of comandra (Mielke *et al.* 1968). Spring grazing by sheep reduces *Comandra* (Laycock and Krebill 1967). For nurseries and plantations, ground preparation and interplanting with competing vegetation to keep *Comandra* down in the first few years may be practical.

If nurseries must be, or already are, established near alternate hosts, the seedlings should be protected by spraying schedules during critical infection conditions. Such spraying schedules are now well established in the southern United States against *C. fusiforme* (Foster and Henry 1956; Mitchem 1967; Snow 1960).

Care must also be taken in locating pine plantations in areas away from alternate hosts, which often have quite local distributions. *C. comandrae* has become a major problem in pine plantations in the south and southeast United States where these have been planted near and among alternate hosts of the rust. In the case of the autoecious *E.*

harknessii, nurseries and plantations should not be located near infected pine stands unless it is planned to destroy or prune all diseased trees in the immediate vicinity before planting. Boyce (1961) recommended that trees with galls be removed for a distance of 300 or more yards around nurseries. Carlson (1969) drew attention to this problem at a nursery in Manitoba. Nursery stock showing a few rust infected seedlings should be destroyed and the remaining stock checked carefully for several years after being planted out, as incipient infections are probably present in a number of seedlings not showing signs of infection (Cafley 1958; Powell and Hiratsuka 1973a). There are several cases reported in the literature where new centres of infection have been established from infected stock.

Tree improvement

Another approach to control is through the selection and breeding of pines showing resistance to the rusts. Breeding programs to produce western and eastern white pine and sugar pine stock which is resistant to *C. ribicola* have been underway in North America since 1937. Most of the Canadian work has been centred at Maple, Ontario (Heimbürger 1962; Boyer 1963, 1967), and Victoria, British Columbia (Porter 1960; Hopkins 1973). There have been no programs in Canada to develop pine stock resistant to our native pine stem rusts, but some preliminary studies have been undertaken with *Endocronartium harknessii* in California (Hanover 1966) and with *Cronartium comptoniae* and *C. quercuum* in the Lake States (Rudolf and Patton 1966). Generally, all native hard pine : stem rust systems appear to possess sufficient resistance to maintain the host species relatively free of rust, providing the delicately balanced host :

pathogen system is not upset, as occurred with the fusiform rust (*Cronartium fusiforme*) in the southern United States (Bingham *et al.* 1971). Breeding programs have also been undertaken to develop rust resistant currant bushes (Hunter and Davis 1943; Hahn 1948).

Much of the work on eastern white pine has been summarized by Riker *et al.* (1943), Farrar (1947), and Hirt (1948), and on western white pine by Bingham *et al.* (1953, 1969, 1972). Inheritance of partial resistance to *C. ribicola* has been shown for eastern and western white pines (Bingham 1966; Heimbürger 1962; Hoff 1966; Patton and Riker 1966; Porter 1960). Inheritance of resistance to blister rust in most white pines appears to be controlled by several genes (Heimbürger 1962, 1966; Hoff 1966), although major or dominant genes are clearly implicated (Kinloch *et al.* 1970; Bingham *et al.* 1971, 1972). The inheritance of five resistance genes in western white pine and sugar pine have been determined and are known to occur at a high frequency level in U. S. Forest Service, Region 6, of the Pacific Northwest (C. G. Jorgensen 1971, personal communication). Resistance is manifest in the foliage and bark but genes have only been determined for the former. Bingham *et al.* (1971) lists the known resistance mechanisms found in white pines, and indicates six steps necessary to develop a resistant population based on a balanced white pine : blister rust system. They also stress that we must learn to live with disease and accept some losses in a balanced host : pathogen system.

Tree breeding programs appear to have the most practical long-term prospects of any of the control methods for *C. ribicola* and have already been incorporated in management plans in the northwestern United States (Peterson and Jewell 1968; C. G. Jorgensen 1971,

personal communication). Under the plan in U.S. Forest Service, Region 6, nineteen breeding zones have been established for the development of rust resistant white pines. By proper selection of parent trees, production of seed from trees with a high level of resistance is possible, both in the forest and in the open-pollinating seed orchards established in each breeding zone.

Chemical control

Pine nursery stock has successfully been protected with fungicide sprays during the period of teliospore production. Unless the source of inoculum is reduced or eliminated, however, repeated spraying will be necessary when favorable infection conditions exist during the annual sporulation period. Results from spraying programs, based on forecasts of high infection periods, have sometimes been disappointing, indicating that these programs need improvement.

Bordeaux mixture and lime-sulfur have long been used to protect nursery seedlings. Ferbam is the most frequently used fungicide; others, such as Zineb, Ziram, and nickel chloride, have effectively reduced the percentage of infection caused by *C. quercuum* and *C. fusiforme* (Nighswander and Patton 1965; Siggers 1955; Koenigs 1968). Quick (1967b) tested 14 conventional fungicides against *C. ribicola*; they showed varying promise of development for satisfactory control, but little promise of systemic control. Phelps and Weber (1969a, 1970) tested a large number of chemicals and a number of solvents against *C. ribicola* on eastern white pine but none proved any better than the materials used by others. Sodium arsenite has been successfully applied to *C. fusiforme* cankers (Brown and Rowan 1967), although Van Sickle (1973), using lower concentrations, found

it to be phytotoxic on *C. comptoniae* cankers. As mentioned earlier, chemicals, especially herbicides, have been used to eradicate the alternate hosts.

Since the late- 1950's a vast amount has been published on the use of antibiotic sprays to control pine stem rust cankers, applied as aerial or basal stem treatments. The antibiotics, cycloheximide derivatives and phytoactin, have largely been used in attempts to control the introduced *C. ribicola* (Benedict 1966; Cafley and Punter 1964, 1966; Glew and MacLeod 1963; Harvey 1966; Leaphart and Wicker 1968; Lemin *et al.* 1960; Moss 1957, 1958, 1961; Moss *et al.* 1960; Phelps and Weber 1966; Pomerleau and Bard 1965; Powers and Stegall 1965; Quick 1967a; Van Arsdell 1960, 1962; Viche *et al.* 1962). Some tests have been carried out on other pine stem rust species (Hinds and Peterson 1966; Koenigs 1966; Leaphart 1963; Van Sickle 1973). These tests have given widely divergent results, depending upon formulation of antibiotics, age of trees and cankers at time of treatment, method and season of treatment and of evaluation (Dimond 1966).

Since 70% of the cankers were killed in early trials (Moss 1961; Viche *et al.* 1962), the antibiotics were put into local use. However, as the promised control had not materialized, operational use of these chemicals was suspended or severely curtailed (Acti-dione) in 1965 although evaluations were continued for several years to determine if there were any delayed reactions to the treatments. Dimond (1966), in summarizing their status, indicated that certain treatments retarded expansion of cankers temporarily, but the cankers remained active and later recommenced sporulation. The effect of antibiotic treatment on eastern white pine was consistently negative. In western North America, the effect of

Tuberculina maxima (see following Biological control section) in inactivating cankers had contributed to the problem of evaluating the effect of antibiotics. Wicker (1968) later concluded that these antibiotics impeded rather than assisted the control of blister rust due to their injurious effects on *T. maxima* and other potential biological control agents of the disease.

Biological control

Biological agents reduce the damage caused by rusts and provide a possible approach to control. In Germany, a purple mold, *Tuberculina maxima* Rost. (Fig. 10) was reported to suppress *C. ribicola* cankers. Attempts were made in the early 1930's to use local cultures of *T. maxima*, collected from native rusts, against *C. ribicola* in the Pacific Northwest (Hubert 1935; Mielke 1933). These attempts were abandoned largely because of the slow development and spread of *T. maxima*. At about the same time, a *Fusarium* found on *Cronartium conigenum* Hedgc. and Hunt in Arizona was introduced in Oregon and Idaho where it appeared to control *C. ribicola* and *E. harknessii* (Wollenweber 1934). These experiments were also abandoned, mainly because of slow spreading of the hyperparasite.

During the 1960's renewed attention was given to the role of *T. maxima* in inactivating the cankers of *C. ribicola* as the mold fungus became more abundant (Benedict 1966; Dimond 1966; Kimmey 1969; Leaphart and Wicker 1968; Quick and Lamoureaux 1967; Wicker 1968; Wicker and Woo 1973). Its effect on *C. comandrae* cankers has been noted (Koenigs 1966; Powell and Morf 1965; Powell 1971b, c, and d). *T. maxima* is less commonly found on *C. coleosporioides*, *C. comptoniae* and *E. harknessii* in Canada (Powell 1971b, 1972b). In the United

States, *T. maxima* has also been reported on *C. quercuum* (Hedgcock 1935; Hubert 1935). Kimmey (1969) and Powell (1971d) found *T. maxima* on 20 to 41% of the active cankers in any one year. Leaphart and Wicker (1968) reported even higher incidences. The cankered bark dies out after invasion by *T. maxima* and the production of aeciospores is greatly reduced or entirely inhibited. Wicker and Woo (1973) conclude that the mode of action of *T. maxima* in the inactivation of rust cankers is enzymatic and is directed at the rust parasitized pine cells and not at the rust organism *per se*. *T. maxima* should therefore not be considered as a hyperparasite of the stem rusts. On *C. ribicola* and *C. comptoniae*, *T. maxima* sporulates most abundantly on the spermatogonial zone, but on *C. comandrae* it is most abundant on the aecial zone. *T. maxima* was indicated as the main cause of inactivating half the cankers (Powell 1971d).

A large number of other fungi and bacteria are regularly associated with pine stem rust cankers (Byler and Cobb 1969; Byler *et al.* 1972a, b; Powell 1971c; E. F. Wicker, unpublished data). An undescribed *Cladosporium* sp. and *Penicillium* spp. were found to affect aeciospore production of *C. comandrae* (Powell 1971c). Byler *et al.* (1972b) similarly reported that *Cladosporium aecidiicolum* and *Penicillium uredineicolum* attacked spores of *E. harknessii* terminating spore production, but that only *C. aecidiicolum* reduced the viability of the rust spores. Byler *et al.* (1972a and b) found that *Gibberella lateritium*, *Nectria fuckeliana* and *Diplodia pinea* were secondary fungi that sometimes partially or completely killed *E. harknessii* galls. *N. fuckeliana* was the most virulent of these pathogens and usually killed the entire gall. Byler and Cobb (1969) reported that 44% of the 2-year-old *E. harknessii* galls, and

97% of the 3- to 6-year-old galls were dead through the action of associated fungi. Byler *et al.* (1972a) considered that *N. fuckeliana* was largely responsible for stabilizing the native rust population of coastal California at a low equilibrium level. Some of the other organisms associated with pine stem rusts (Byler *et al.* 1972b; Powell 1971c) assist in controlling other diseases, but their potential in controlling pine stem rusts has yet to be established.

Rodents have been reported feeding on rust cankers (Mielke 1935; Anderson *et al.* 1967; Krebill 1965; Powell 1969, 1974b) thereby acting as a control (Figs. 2, 6). Most rodent feeding on cankers occurs during winter and spring and is usually restricted to the living infected tissues. On many occasions the whole infected area is removed. Powell (1971d, 1974b) indicated that 17% of canker inactivation was caused through rodent gnawing. In some areas nearly all of the cankers show evidence of rodent chewing (Kreibill 1965). Powell (1969, 1974b) estimated that rodents were responsible for gnawing about 30% of the potential aecial producing tissues in any one year.

Insects have been reported from pine stem rusts, but there is little reference to their damage to the rusts (Powell 1971a). Powell showed that at least three species, *Epuraea obliquus*, *Paracacoxenus guttatus* and a *Mycodiplosis* sp., were true mycetobionts, dependent on the pine stem rust for the development of part or all of their life cycle. Larvae or adult individuals of these insects consumed large numbers of spores as food. Incidence of insect damage ranged from 32 to 59% in any one year, and the microfaunal agents probably reduced the production of aeciospores by about 10%. The insects causing most damage to the active canker zone of *C. comandrae* were the moth *Dioryctria* spp., and the weevils

Cylindrocopturus deleoni and *Pissodes schwarzi*. Wong (1972) has recently described the development of *Dioryctria banksiana* in *E. harknessii* galls. Powell *et al.* (1972) gave a compilation of the arthropods occurring in *E. harknessii*, *C. comptoniae*, *C. comandrae* and *C. coleosporioides* cankers on jack and lodgepole pine within the Prairie Provinces. Furniss *et al.* (1972) reported twelve arthropods associated with *C. ribicola* cankers on western white pine in Idaho. Many of the insects listed in these reports are common to all the rusts and obviously play roles in reducing the amounts of inoculum available for dispersal, thereby assisting in the natural biological control of the disease.

Powell (1969, 1974b) estimated that in any one year probably 50% of all potential aecial material of *C. comandrae* had been destroyed by all these biological agents.

Potentially dangerous species not yet found in Canada

***Cronartium fusiforme* Hedgc. & Hunt ex Cummins (fusiform rust of southern pines):**

This rust is causing a major problem in the management of slash (*P. elliotii* Engelm.) and loblolly pine (*P. taeda* L.) plantations in the southeastern United States (Czabator 1971). It is known to attack 25 other species of native and exotic pines, including such species as *P. contorta* Dougl., *P. ponderosa* Laws., *P. rigida* Mill. and *P. sylvestris* L. Alternate hosts are species of *Quercus*, *Castanea*, *Castanopsis*, and *Lithocarpus*. The spore morphology is very similar to that of *C. quercuum*. This rust is potentially dangerous to hard pine plantation within the alternate host's distribution.

***Peridermium filamentosum* Pk. complex (limb rust):**

This complex contains at least three different races and is the most destructive rust attacking ponderosa (*P. ponderosa* Laws.) and Jeffrey pine (*P. jeffreyi* Grev. & Balf.) throughout most of their geographic distribution (Peterson 1966b, 1968). One race is heteroecious (host-alternating) and alternates to Indian paintbrush (*Castilleja* spp.), as does *Cronartium coleosporioides*, but their appearances on the pine hosts are considered to be different. Two races are autoecious and can infect pine directly. Krebill and Nelson (1970) found the nuclear condition of their germ tubes was similar to that of *Endocronartium harknessii* and *E. pini*. The taxonomy and nomenclature of this complex therefore needs to be clarified.

***Cronartium flaccidum* (Alb. & Schw.) Wint. (= *Peridermium cornui* Rostr. ex Kleb.) (Scotch pine blister rust):**

This rust occurs across Europe and eastwards to the far eastern parts of Asia. *Pinus sylvestris* L. is the main host but it is known to infect most hard pines, including most major North American species. The alternate hosts of this rust belong to many genera of plants including *Asclepias*, *Impatiens*, *Loasa*, *Melampyrum*, *Nemesia*, *Paeonia*, *Pedicularis*, *Ruellia*, *Schizanthus*, *Trapaecolum*, *Verbena*, and *Vincetoxicum* (Gremmen 1964). The one and only report of this species in North America, on *Impatiens balsamea* from Prince Edward Island, is in error (see page 3).

***Endocronartium pini* (Pers.) Y. Hiratsuka (= *Peridermium pini* (Pers.) Lév. emend Kleb.):**

This species has been considered as an autoecious (pine-to-pine) race of *C. flaccidum* and occurs throughout Europe mainly on *P. sylvestris* L. From the germ-tube morphology and the nuclear conditions of the spores and germ-tubes, Hiratsuka (1968) concluded that this species has an endocyclic life cycle (see Fig. 41) similar to *E. harknessii*. Since this species does not need an alternate host and many hard pines are known to be susceptible, it is potentially dangerous outside its present range of distribution.

***Cronartium kamtschaticum* Jørstad:**

In recent years, outbreaks of alleged *C. ribicola* have been reported from northern Japan (on *P. strobus* L.) and Korea (on *P. koraiensis* Sieb. & Zucc.), but alternate hosts are found to be species of *Pedicularis* rather than *Ribes* (Yokota, S and Uozumi, T., personal communication 1973; Yee, C.K., personal communication 1973). The causal organisms are tentatively identified as the poorly understood species *C. kamtschaticum*, which was known on *P. pumila* Regel and *Pedicularis* spp.

***Endocronartium* sp. (?):**

A stem rust on *Pinus pumila* Regel in northern Japan may be autoecious like other *Endocronartium* spp. (Saho, H., personal communication 1973). If confirmed, it will be an important discovery since no pine-to-pine species have been known on five needle pines.

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- Anderson, G. W. 1963. Sweetfern rust on hard pines. U.S. Dep. Agric., For. Serv., *Forest Pest Leaflet* No. 79. 7 p.
- Anderson, G. W. 1965. The distribution of eastern and western gall rusts in the Lake States. *Plant Dis. Repr.* 49:527-528.
- Anderson, G. W. and D. W. French. 1965a. Differentiation of *Cronartium quercuum* and *Cronartium coleosporioides* on the basis of aeciospore germ tubes. *Phytopath.* 55:171-173.
- Anderson, G. W. and D. W. French. 1965b. Western gall rust in the Lake States. *For. Sci.* 11:139-141.
- Anderson, N. A. 1963. Eastern gall rust. U.S. Dep. Agric., For. Serv., *Forest Pest Leaflet* No. 80. 4 p.
- Anderson, N. A. and D. W. French. 1962. Stalactiform rust on jack pine. (Abs.) *Phytopath.* 52:721-722.
- Anderson, N. A. and D. W. French. 1964a. Sweetfern rust on jack pine. *J. Forestry* 62:467-471.
- Anderson, N. A. and D. W. French. 1964b. Debarking jack pine infected with sweet fern rust. *Plant Dis. Repr.* 48:530-531.
- Anderson, N. A., D. W. French and R. L. Anderson. 1967. The stalactiform rust on jack pine. *J. Forestry* 65:398-402.
- Anderson, R. L. 1973. A summary of white pine blister rust research in the Lake States. U.S. Dep. Agric., For. Serv., North Cent. For. Exp. Stn., Gen. Tech. Rep. NC-6. 12 p.
- Applegate, H. W. and T. Seay. 1971. Two new hosts for comandra blister rust. *Plant Dis. Repr.* 55:697.
- Arthur, J. C. 1929. The plant rusts (Uredinales). N.Y., J. Wiley & Sons, Inc. 446 p.
- Arthur, J. C. 1934. Manual of the rusts in the United States and Canada. Purdue Research Foundation, Lafayette. 438 p.
- Bakshi, B. K. and Sujan Singh. 1967. Rusts on Indian forest trees. *Indian Forest Records* (New Series) *Forest Pathology* 2:139-204.
- Baranyay, J. A. and R. J. Bouchier. 1963. Province of Alberta. Forest disease conditions. p. 99-102. In: Can. Dep. Forestry, For. Entomol. and Pathol. Br., *Annual Report of the Forest Insect and Disease Survey 1962*. 134 p.
- Baranyay, J. A., R. J. Bouchier and G. R. Stevenson. 1962. Can. Dep. Forestry, For. Entomol. and Pathol. Br., *Annual Report of the Forest Insect and Disease Survey 1961*. pp 102-106.
- Baranyay, J. A. and G. R. Stevenson. 1964. Mortality caused by *Armillaria* root rot, *Peridermium* rusts and other destructive agents in lodgepole pine regeneration. *For. Chron.* 40:350-361.
- Bega, R. V. 1960. The effect of environment on germination of sporidia in *Cronartium ribicola*. *Phytopath.* 50:61-69.
- Benedict, W. V. 1966. Experience with antibiotics to control white pine blister rust. *J. Forestry* 64:382-384.
- Bingham, R. T. 1966. Breeding blister rust resistant western white pine. III. Comparative performance of clonal and seedling lines from rust-free selections. *Silvae Genetica* 15:160-164.
- Bingham, R. T., R. J. Hoff and G. I. McDonald. 1971. Disease resistance in forest trees. *Annu. Rev. Phytopath.* 9:433-452.
- Bingham, R. T., R. J. Hoff and R. J. Steinhoff. 1972. Genetics of western white pine. U.S. Dep. Agric. Forest Serv., Res. Pap. WO-12. 18 p.
- Bingham, R. T., R. J. Olson, W. A. Becker and M. A. Marsden. 1969. Breeding blister rust resistant western white pine. V. Estimates of heritability,

- combining ability, and genetic advance based on tester matings. *Silvae Genetica* 18:28-38.
- Bingham, R. T., A. W. Squillance and J. W. Duffield. 1953. Breeding blister rust resistant western white pine. *J. Forestry* 51:163-168.
- Boyce, J. S. 1957. The fungus causing western gall rust and Woodgate rust of pines. *Forest Sci.* 3:225-234.
- Boyce, J. S. 1961. Forest Pathology. New York. McGraw Hill Book Co. Inc. 572 p.
- Boyer, M. G. 1962. Studies on white pine blister rust. Can. Dep. Forest., Forest Entomol. and Pathol. Br., Forest Pathol. Lab., Maple, Ontario. Interim Rept. 38 p.
- Boyer, M. G. 1963. Studies on factors involved in resistance of white pine to blister rust. Can. Dep. For., For. Entomol. and Pathol. Br., Maple, Ontario. Interim Res. Rept. (mimeo) 29 p.
- Boyer, M. G. 1967. The relation of growth regulators to the development of symptoms and the expression of stem resistance in white pine infected with blister rust. *Can. J. Bot.* 45:501-513.
- Brown, D. H. 1967. White pine blister rust survey in Montana and Wyoming. U.S. Dep. Agric., For. Serv., Div. State & Private Forestry, Northern Region, Missoula, Montana. Unpubl. Rept. 11 p.
- Brown, D. H. 1970. Recent discoveries extend distribution range of two destructive diseases of limber pine in southeastern Montana. *Plant Dis. Repr.* 54:441.
- Brown, D. H. and D. A. Graham. 1969. White pine blister rust survey in Wyoming, Idaho, and Utah 1967. U.S. Dep. Agric., For. Serv., Div. State & Private Forestry, Northern Region, Missoula, Montana. Unpubl. Rept. 11 p.
- Brown, R. A. and S. J. Rowan. 1967. Sodium arsenite: a possible eradicant of fusiform rust infections. U.S. Dep. Agric., Forest Serv., Southeastern For. Exp. Sta., Res. Note SE-75. 3 p.
- Buchanan, T. S. 1938. Blister rust damage to merchantable western white pine. *J. Forestry* 36:321-328.
- Buller, A.H.R. 1950. Researches on fungi. Vol. 7. Univ. Toronto Press, Toronto. 458 p.
- Byler, J. W. and F. W. Cobb, Jr. 1969. Fungi associated with galls caused by *Peridermium harknessii*. (Abs.) *Phytopath.* 59:1020.
- Byler, J. W., F. W. Cobb, Jr., and J. R. Parmeter, Jr. 1972a. Effects of secondary fungi on the epidemiology of western gall rust. *Can. J. Bot.* 50:1061-1066.
- Byler, J. W., F. W. Cobb, Jr., and J. R. Parmeter, Jr. 1972b. Occurrence and significance of fungi inhabiting galls caused by *Peridermium harknessii*. *Can. J. Bot.* 50:1275-1282.
- Cafley, J. D. 1958. On white pine blister rust in plantations in Ontario. *For. Chron.* 34:57-61.
- Cafley, J. D. and D. Punter. 1964. Treatment of white pine blister rust with antibiotic fungicides: preliminary testing of Acti-dione (cycloheximide) - 1959/60. Can. Dep. For., For. Res. Lab., Maple, Ont. Interim Res. Rept. 8 p.
- Cafley, J. D. and D. Punter. 1966. Treatment of white pine blister rust by antibiotic fungicides: testing of acti-dione (cycloheximide) and phytoactin 1960-1961. Can. Dep. For. & Rural Develop., For. Res. Lab., Maple, Ont. Intern. Rept. 0-2. 18 p.
- Carlson, L. W. 1969. Western gall rust on

- jack pine nursery stock in Manitoba. *Plant Dis. Repr.* 53:100.
- Charlton, J. W. 1963. Relating climate to eastern white pine blister rust infection hazard. U.S. Dep. Agric., For. Serv., Region 7. 38 p.
- Childs, T. W. 1968. Comandra rust damage to ponderosa pine in Oregon and Washington. U.S. Dep. Agric., For. Serv., Pacific Northwest For. & Ra. Exp. Sta., Portland, Oregon. (Unnumbered) 8 p.
- Christenson, J. A. 1968. A cytological comparison of germinating aeciospores in the *Cronartium coleosporioides* complex. *Mycologia* 60:1169-1177.
- Clark, R. C. and P. Singh. 1971. Can. Dep. Fish. & For., Can. For. Serv. *Annual Report of the Forest Insect and Disease Survey 1970*. pp. 11-18.
- Colley, R. H. 1918. Parasitism, morphology, and cytology of *Cronartium ribicola*. *J. Agr. Res.* 15:619-660.
- Colley, R. H. and M. W. Taylor. 1927. *Peridermium kurilense* Diet. on *Pinus pumila* Pall. and *Peridermium indicum* n. sp. on *Pinus excelsa* Wall. *J. Agr. Res.* 34:327-330.
- Connors, I. L. 1967. An annotated index of plant diseases in Canada and fungi recorded on plants in Alaska, Canada and Greenland. Can. Dep. Agric., Res. Br., Publ. 1251. 381 p.
- Cordell, C. E., H. W. Applegate and P. J. Huffman. 1969. Pond pine — a new host for comandra blister rust in eastern Tennessee. *Plant Dis. Repr.* 53:694.
- Cordell, C. E., J. L. Knighten and R. B. Quillin. 1967. Incidence of comandra blister rust on the Cumberland Plateau in eastern Tennessee — 1967. U.S. Dep. Agric., For. Serv., Southeastern Area, State & Private Forestry, Div. Forest Pest Control, Rept. No. 68-1-4. 13 p.
- Critchfield, W. B. and E. L. Little, Jr. 1966. Geographic distribution of the pines of the world. U.S. Dep. Agric., For. Serv., Misc. Publ. 991. 97 p.
- Cummins, G. B. 1962. Supplement to Arthur's manual of the rusts in United States and Canada. Hafner Publ. Co. 24 p.
- Czabator, F. J. 1971. Fusiform rust of southern pines — a critical review. U.S. Dep. Agric., For. Serv., Southern Forest Exp. Sta., Res. Pap. SO-65. 39 p.
- Dance, B. W. and D. F. Lynn. 1965. Can. Dep. Forestry, *Annual Report of the Forest Insect and Disease Survey 1964*. pp. 68-77.
- Dimond, A. E. 1966. Effectiveness of antibiotics against forest tree rusts: a summary of present status. *J. Forestry* 64:379-382.
- Dooling, O. J. 1967. Biological evaluation of comandra blister rust on the Buffalo Ranger District, Ozark National Forest, Arkansas. U.S. Dep. Agric., For. Serv., Southeastern Area, State & Private Forestry, Div. Forest Insect and Disease Control. Rept. No. 64-3-27, Suppl. No. 3. 2 p.
- Doran, W. L. 1919. The minimum, optimum and maximum temperature of spore germination in some Uredinales. *Phytopath.* 9:391-402.
- Doran, W. L. 1922. Effect of external and internal factors on the germination of fungous spores. *Bull. Torrey Bot. Club*, 49:313-340.
- Eastham, J. W. 1922. White-pine blister rust in B.C. *Agr. Journ. (Brit. Columbia)* 7:29, 41, 57, 64.
- Farrar, J. L. 1947. Forest tree breeding in Canada. Dominion For. Serv. Unnumbered publ. Ottawa. 17 p.
- Forbes, R. S., G. R. Underwood, and G. A. Van Sickle. 1968. Can. Dep. For. & Rural Develop., For. Br., *Annual Report of the Forest Insect and*

- Disease Survey 1967*. pp 17-33.
- Forbes, R. S., G. R. Underwood, and G. A. Van Sickle. 1970. Can. Dep. Fish. & For., Can. For. Serv., *Annual Report of the Forest Insect and Disease Survey 1969*. pp 20-36.
- Forbes, R. S., G. R. Underwood, and G. A. Van Sickle. 1972. Environment Can., Can. For. Serv., *Annual Report of the Forest Insect and Disease Survey 1971*. pp 19-33.
- Foster, A. A. and B. W. Henry. 1956. Nursery control of fusiform rust demands careful spraying. U.S. For. Serv., Tree Planter's Notes 24:13-15.
- Furniss, M. M., R. D. Hungerford and E. F. Wicker. 1972. Insects and mites associated with western white pine blister rust cankers in Idaho. *Can. Ent.* 104:1713-1715.
- Gautreau, E. 1963. Effects of white pine blister rust in limber pine stands of Alberta. Can. Dep. For., For. Entomol. & Pathol. Br., Bi-Monthly Progr. Rept. 19(4):3.
- Glew, D. R. and R. T. MacLeod. 1963. The use of antibiotics in blister rust control in British Columbia. Brit. Columbia For. Serv., For. Management Notes No. 2. 15 p.
- Gregory, P. H. 1945. The dispersion of air-borne spores. *Brit. Mycol. Soc. Trans.* 28:26-72.
- Gremmen, J. 1964. Stem diseases of conifers caused by rust fungi. 15 p. *In*. FAO/IUFRO Symp. on Internationally dangerous forest Diseases and Insects. Oxford, 20-29 July, 1964. Documents — FAO/FORPEST 64. Vol. 1. FAO of the U.N.
- Haddow, W. R. 1956. Blister rust control as an element of white pine management. *For. Chron.* 32:68-73.
- Hahn, G. G. 1948. Immunity of Canadian black currant selections from blister rust. *Phytopath.* 38:453-456.
- Hanover, J. W. 1966. Tree improvement for disease resistance in Western United States and Canada. p. 53-56. *In*. Breeding pest-resistant trees. (Ed.) H. D. Gerhold, E. J. Schreiner, R. E. McDermott, and J. A. Winieski. Oxford, Pergamon Press. 505 p.
- Harvey, G. M. 1966. An evaluation of the basal stem application of acti-dione and phytoactin for control of white pine blister rust on sugar pine in Oregon and California. *Plant. Dis. Reprtr.* 50:554-556.
- Hayes, G. L. and W. I. Stein. 1957. Eliminating blister rust cankers from sugar pine by pruning. U.S. Dep. Agric., For. Serv., Pacific Northwest For. & Ra. Exp. Sta., Res. Note 151. 8 p.
- Hedgcock, G. G. 1935. Notes on the occurrence of *Tuberculina maxima* on the aecia of *Cronartium cerebrum*. *Phytopath.* 25:117-118.
- Hedgcock, G. G. 1939. Notes on North American pine-oak species of *Cronartium* on *Castanea*, *Castanopsis* and *Lithocarpus*. *Phytopath.* 29:998-1000.
- Hedgcock, G. G. and W. H. Long. 1915. A disease of pines caused by *Cronartium pyriforme*. U.S. Dep. Agric., Bull. 247. 20 p.
- Hedgcock, G. G. and P. V. Siggers. 1949. A comparison of the pine-oak rusts. U.S. Dep. Agric., Tech. Bull. No. 978. 30 p.
- Heimbürger, C. 1962. Breeding for disease resistance in forest trees. *Forestry Chron.* 38:356-362.
- Heimbürger, C. 1966. Genetic improvement for disease and insect resistance of forest trees in Canada. p. 45-48. *In*. Breeding pest-resistant trees. (Ed.) H. D. Gerhold, E. J. Schreiner, R. E. McDermott, & J. A. Winieski. Oxford, Pergamon Press. 505 p.
- Hepting, G. H. 1957. A rust on Virginia

- pine and Buckleya. *Mycologia* 49:896-899.
- Hepting, G. H. 1971. Diseases of forest and shade trees of the United States. U.S. Dep. Agric., For. Serv., Agric. Handbook No. 386. 658 p.
- Hinds, T. E. and R. S. Peterson. 1966. Antibiotic tests on western gall rust and aspen cankers. *Plant Dis. Repr.* 50:741-744.
- Hiratsuka, N. 1960. A provisional list of Uredinales of Japan proper and the Ryukyu Islands. Univ. Ryukyus, Div. Agric., Home Econ. & Engin., Sci. Bull. 7:189-314.
- Hiratsuka, Y. 1968. Morphology and cytology of aeciospores and aeciospore germ tubes of host-alternating and pine-to-pine races of *Cronartium flaccidum* in northern Europe. *Can. J. Bot.* 46:1119-1122.
- Hiratsuka, Y. 1969. *Endocronartium*, a new genus for autoecious pine stem rusts. *Can. J. Bot.* 47:1493-1495.
- Hiratsuka, Y. 1971. Spore surface morphology of pine stem rusts of Canada as observed under a scanning electron microscope. *Can. J. Bot.* 49:371-372 + 6 plates.
- Hiratsuka, Y. 1973a. The nuclear cycle and the terminology of spore states in Uredinales. *Mycologia* 65:432-443.
- Hiratsuka, Y. 1973b. Nuclear cycle, taxonomy and nomenclature of autoecious pine stem rusts in North America and Europe. Rept. Tottori Mycol. Inst. 10:243-248.
- Hiratsuka, Y. and E. J. Gautreau. 1966. Occurrence of *Cronartium comptoniae* in Alberta and the Northwest Territories. *Plant Dis. Repr.* 50:419.
- Hiratsuka, Y. and P. J. Maruyama. 1968. Identification of *Peridermium harknessii* in eastern Canada on the basis of nuclear condition of aeciospore germ tubes. *Plant Dis. Repr.* 52:650-651.
- Hiratsuka, Y., W. Morf and J. M. Powell. 1966. Cytology of the aeciospores and aeciospore germ tubes of *Peridermium harknessii* and *P. stactiforme* of the *Cronartium coleosporioides* complex. *Can. J. Bot.* 44:1639-1643.
- Hirt, R. R. 1937. The possibility of *Ribes* infection by aeciospores of *Cronartium ribicola* at temperatures above 19°C. *Phytopath.* 27:104-106.
- Hirt, R. R. 1938. Relation of stomata to infection of *Pinus strobus* by *Cronartium ribicola*. *Phytopath.* 28:180-190.
- Hirt, R. R. 1942. The relation of certain meteorological factors to the infection of eastern white pine by the blister-rust fungus, N.Y. State College Forestry, Tech. Publ. 59. 65 p.
- Hirt, R. R. 1948. Evidence of resistance to blister rust by eastern white pine growing in the northeast. *J. Forestry* 46:911-913.
- Hirt, R. R. 1964. *Cronartium ribicola*. Its growth and reproduction in the tissues of eastern white pine. State Univ. Coll. Forestry, Syracuse Univ., Tech. Publ. No. 86. 30 p + 14 plates.
- Hoff, R. J. 1966. Blister rust resistance in western white pine. p. 119-124. In: Breeding pest-resistant trees. (Ed.) H. D. Gerhold, E. J. Schreiner, R. E. McDermott, and J. A. Winieski. Oxford, Pergamon Press. 505 p.
- Hopkins, J. C. 1973. Blister rust of western white pine: research status, need and prospects for British Columbia. Can. Dep. Environment, Pacific For. Res. Centre, Victoria, B.C., Intern. Rept. BC-39, 31 p.
- Howitt, J. E. and W. A. McCubbin. 1916. An outbreak of white pine blister rust in Ontario. *Phytopath.* 6:182-185.
- Hubert, E. E. 1935. Observations on *Tuberculina maxima*, a parasite of

- Cronartium ribicola*. *Phytopath.* 25:253-261.
- Hultén, E. 1968. Flora of Alaska and neighbouring territories. A manual of the vascular plants. Stanford Univ. Press, Stanford. 1008 p.
- Hunter, A. W. S. and M. B. Davis. 1943. Breeding rust-resistant black currants. *Amer. Soc. Hort. Sci. Proc.* 42:467-468.
- Hurst, R. R. 1957. A preliminary list of parasitic fungi in Prince Edward Island. *Can. Dep. Agric., Sci. Serv., Plant Pathology Lab., Charlottetown, P.E.I.* 23 p. (mimeo).
- Ives, W. G. H., R. A. Blauel and J. K. Robins. 1971. *Can. Dep. Fish. & For., Can. For. Serv., Annual Report of the Forest Insect and Disease Survey 1970.* pp 67-76.
- Ives, W. G. H., N. R. Brandt and J. J. Lawrence. 1969. *Can. Dep. Fish. & For., For. Br., Annual Report of the Forest Insect and Disease Survey 1968.* pp 79-97.
- Ives, W. G. H., N. R. Brandt and B. C. Sutton. 1968. *Can. Dep. For. & Rural Develop., For. Br., Annual Report of the Forest Insect and Disease Survey 1967.* pp 76-96.
- Ives, W. G. H., J. J. Lawrence and J. K. Robins. 1973. *Environment Canada, For. Serv., Annual Report of the Forest Insect and Disease Survey 1972.* pp 74-81.
- Ketcham, D. E., C. A. Wellner and S. S. Evans, Jr. 1968. Western white pine management programs realigned on Northern Rocky Mountain National Forests. *J. Forestry* 66:329-332.
- Kimmey, J. W. 1969. Inactivation of lethal-type blister rust cankers on western white pine. *J. Forestry* 67:296-299.
- Kimmey, J. W. and W. W. Wagener. 1961. Spread of white pine blister rust from *Ribes* to sugar pine in California and Oregon. *U.S. Dep. Agric., For. Serv., Tech. Bull.* 1251. 71 p.
- Kingston, J. T. and W. K. McGinn. 1951. White pine blister rust in the Maritimes. *Can. Dep. Agric., Div. For. Biof., Fredericton, N.B., Unpubl. Rept.* 30 p.
- Kinloch, B. B., Jr., G. K. Parks and C. W. Fowler. 1970. White pine blister rust: simply inherited resistance in sugar pine. *Science* 167:193-195.
- Koenigs, J. W. 1966. An evaluation of antibiotics for control of comandra rust on lodgepole pine. *Plant Dis. Repr.* 50:528-531.
- Koenigs, J. W. 1968. Control of fusiform rust on southern pines in nurseries. *Plant Dis. Repr.* 52:597-599.
- Krebill, R. G. 1964. Blister rust found on limber pine in northern Wasatch Mountains. *Plant Dis. Repr.* 48:532.
- Krebill, R. G. 1965. Comandra rust outbreaks in lodgepole pine. *J. Forestry* 63:519-522.
- Krebill, R. G. 1968a. Histology of canker rusts in pines. *Phytopath.* 58:155-164.
- Krebill, R. G. 1968b. *Cronartium comandrae* in the Rocky Mountain States. *U.S. Dep. Agric., For. Serv., Intermountain Forest & Range Exp. Sta., Res. Rep.* INT-50. 28 p.
- Krebill, R. G. 1970. Autoecious gall rusts of pines in southern Michigan and New York. *Plant Dis. Repr.* 54:853-855.
- Krebill, R. G. 1971. Effect of low temperature on germination of teliospores of *Cronartium ribicola*. (Abs.) *Phytopath.* 61:899.
- Krebill, R. G. 1972. Germination of basidiospores of *Cronartium comandrae* on rocks and vegetation. *Phytopath.* 62:389-390.
- Krebill, R. G. and D. L. Nelson. 1970. Nuclei of jeffrey pine limb rust *Peridermia*. *Mycologia* 62:996-1002.
- Lachmund, H. G. 1929. *Cronartium*

- comptoniae* Arth. in western North America. *Phytopath.* 19:453-466.
- Lachmund, H. G. 1933. Mode of entrance and periods in the life cycle of *Cronartium ribicola* on *Pinus monticola*. *J. Agr. Res.* 47:791-805.
- Lachmund, H. G. 1934. Growth and injurious effects of *Cronartium ribicola* cankers on *Pinus monticola*. *J. Agr. Res.* 48:475-503.
- Laycock, W. A. and R. G. Krebill. 1967. Comandra, grazing, and comandra blister rust. U.S. Dep. Agric., For. Serv., Intermountain For. & Ra. Exp. Stn., Res. Pap. INT-36. 9 p.
- Leaphart, C. D. 1963. Summary of treatments with antibiotics for control of native rusts (*C. comandrae*, *P. filamentosum*, *P. harknessii*, and *P. stalactiforme*). U.S. Dep. Agric., For. Serv., Intermountain For. & Ra. Exp. Sta., Moscow, Idaho. Unpubl. Rept. 7 p. (mimeo).
- Leaphart, C. D. and E. F. Wicker. 1968. The ineffectiveness of cycloheximide and phytoactin as chemical controls of the blister rust disease. *Plant Dis. Repr.* 52:6-10.
- Lemin, A. J., W. Klomparens and V. D. Moss. 1960. Translocation and persistence of cycloheximide (Actidione) in white pine. *Forest Sci.* 6:306-314.
- Lightle, P. C. 1955. Longevity of *Peridermium harknessii* aeciospores stored at 40°F. *Plant Dis. Repr.* 39:983-984.
- Martin, J. F. 1944. *Ribes* eradication effectively controls white pine blister rust. *J. Forestry* 42:255-260.
- Martin, J. F. and G. F. Gravatt. 1954. Saving white pines by removing blister rust cankers. U.S. Dep. Agric., Circ. No. 948. 22 p.
- Martineau, R. and A. Lavallee. 1972. Environment Can., Can. For. Serv., *Annual Report of the Forest Insect and Disease Survey 1971*. pp 34-53.
- Martineau, R. and A. Lavallee. 1973. Environment Can., For. Serv., *Annual Report of the Forest Insect and Disease Survey 1972*. pp 33-53.
- Martineau, R. and G. B. Ouellette. 1966. Can. Dep. Forestry, *Annual Report of the Forest Insect and Disease Survey 1965*. pp 33-43.
- Martineau, R. and E. Smerlis. 1969. Can. Dep. Fish. & For., For. Br., *Annual Report of the Forest Insect and Disease Survey 1968*. pp 35-52.
- McGrath, W. T. 1968. Infection of jack pine in Wisconsin by *Cronartium quercuum* and *Peridermium harknessii*. Dissertation Abstracts B. 28 (7): 2686-2687.
- McIntyre, H. L. 1942. White pine blister rust control policies in New York State. *J. Forestry* 40:782-785.
- Meinecke, E. P. 1920. Facultative heteroecism in *Peridermium cerebrum* and *Peridermium harknessii*. *Phytopath.* 10:279-297.
- Meinecke, E. P. 1928. The evaluation of loss from killing diseases in the young forest. *J. Forestry* 26:283-298.
- Meinecke, E. P. 1929. Experiments with repeating pine rusts. *Phytopath.* 19:327-342.
- Mielke, J. L. 1933. *Tuberculina maxima* in western North America. *Phytopath.* 23:299-305.
- Mielke, J. L. 1935. Rodents as a factor in reducing aecial sporulation of *Cronartium ribicola*. *J. Forestry* 33:994-1003.
- Mielke, J. L. 1943. White pine blister rust in western North America. Yale Univ. School Forestry, Bull. 52. 155 p.
- Mielke, J. L. 1956. The rust fungus (*Cronartium stalactiforme*) in lodgepole pine. *J. Forestry* 54:518-521.
- Mielke, J. L. 1957. The comandra blister rust in lodgepole pine. U.S. Dep. Agric., Forest Serv., Intermountain

- Forest & Range Exp. Sta., Res. Note 46. 8 p.
- Mielke, J. L. 1963. Comandra blister rust. p. 92-93. *In*. Internationally dangerous forest tree diseases. U.S. Dep. Agric., Misc. Publ. 939.
- Mielke, J. L. and J. W. Kimmey. 1935. Dates of the production of the different spore stages of *Cronartium ribicola* in the Pacific Northwest. *Phytopath.* 25:1104-1108.
- Mielke, J. L., R. G. Krebill and H. R. Powers, Jr. 1968. Comandra blister rust of hard pines. U.S. Dep. Agric., Forest Serv., Forest Pest Leaflet 62. 8 p.
- Mielke, J. L. and R. S. Peterson. 1967. Albino *Peridermium harknessii* in ponderosa pine. *Plant Dis. Repr.* 51:306-309.
- Miller, D. R., J. W. Kimmey, and M. E. Fowler. 1959. White pine blister rust. U.S. Dep. Agric., Forest Serv., Forest Pest Leaflet 36. 8 p.
- Mitchem, R. A. 1967. Nursery weather forecasts for use in the control of fusiform rust. Paper presented at the Amer. Meteor. Soc. Conf. on Weather Forecasting, Fort Worth, Texas. Nov. 6-8. 7 p. (mimeo).
- Molnar, A. C. 1960. Can. Dep. Agric., For. Biol. Div., *Annual Report of the Forest Insect and Disease Survey 1959*. pp 105-110.
- Molnar, A. C. 1961. An outbreak of *Cronartium comptoniae* on Monterey and Bishop pines on Vancouver Island, British Columbia. *Plant Dis. Repr.* 45:854-855.
- Molnar, A. C., J. W. E. Harris and D. A. Ross. 1967. Can. Dep. For. & Rural Develop., For. Br., *Annual Report of the Forest Insect and Disease Survey 1966*. pp 108-123.
- Molnar, A. C., J. W. E. Harris, D. A. Ross and J. A. Baranyay. 1970. Can. Dep. Fish. & For., Can. For. Serv., *Annual Report of the Forest Insect and Disease Survey 1969*. pp 97-109.
- Molnar, A. C., J. W. E. Harris, D. A. Ross and J. H. Ginns. 1969. Can. Dep. Fish. & For., For. Br., *Annual Report of the Forest Insect and Disease Survey 1968*. pp 111-124.
- Moss, V. D. 1957. Acti-dione treatment of blister rust cankers on western white pine. *Plant Dis. Repr.* 41:709-714.
- Moss, V. D. 1958. Acti-dione stove oil treatment of blister rust trunk cankers on reproduction and pole western white pine. *Plant Dis. Repr.* 42:703-706.
- Moss, V. D. 1961. Antibiotics for control of blister rust on western white pine. *Forest Sci.* 7:380-396.
- Moss, V. D., H. J. Viche and W. Klomparsens. 1960. Antibiotic treatment of western white pine infected with blister rust. *J. Forestry* 58:691-695.
- Moss, V. D. and C. A. Wellner. 1953. Aiding blister rust control by silvicultural measures in the western white pine type. U.S. Dep. Agric., Circ. 919. 31 p.
- Nighswander, J. E. and R. F. Patton. 1965. The epidemiology of the jack pine - oak gall rust (*Cronartium quercuum*) in Wisconsin. *Can. J. Bot.* 43:1561-1581.
- Offord, H. R., V. D. Moss, W. V. Benedict, H. E. Swanson and A. London. 1952. Improvements in the control of *Ribes* by chemical and mechanical methods. U.S. Dep. Agric., Circ. No. 906. 72 p.
- Ouellette, G. B. 1965. *Cronartium stalactiforme* on *Pinus banksiana* (jack pine) in Quebec. *Plant Dis. Repr.* 49:909.
- Packer, J. G. 1971. Endemism in the flora of western Canada. *Naturaliste Can.* 98:131-144.
- Paine, L. A. and A. W. Slipp. 1947. Eval-

- uation of the role of weather in recurrent intensification of white pine blister rust in western white pine. Univ. Idaho School Forestry, 50 p. (mimeo).
- Parmeter, J. R., Jr. and F. J. Newhook. 1967. New Zealand *Pinus radiata* is susceptible to western gall rust disease. *New Zealand J. Forestry* 12:200-201.
- Patton, R. F. and D. W. Johnson. 1970. Mode of penetration of needles of eastern white pine by *Cronartium ribicola*. *Phytopath.* 60: 977-982.
- Patton, R. F. and T. H. Nicholls. 1966. Fluorescent labeling for observation of basidiospores of *Cronartium ribicola* on white pine needles. p. 153-162. *In*. Breeding pest-resistant trees. (Ed.) H. D. Gerhold, E. J. Schreiner, R. E. McDermott, and J. A. Winieski. Oxford, Pergamon Press. 505 p.
- Patton, R. F. and A. J. Riker. 1966. Lessons from nursery and field testing of eastern white pine selections and progenies for resistance to blister rust. p. 403-414. *In*. Breeding pest-resistant trees. (Ed.) H. D. Gerhold, E. J. Schreiner, R. E. McDermott, and J. A. Winieski. Oxford, Pergamon Press. 505 p.
- Peterson, G. W. 1973. Dispersal of aeciospores of *Peridermium harknessii* in central Nebraska. *Phytopath.* 63:170-172.
- Peterson, R. S. 1960a. Western gall rust on hard pines. U.S. Dep. Agric., For. Serv., Forest Pest Leaflet 50. 8 p.
- Peterson, R. S. 1960b. Development of western gall rust in lodgepole pine. *Phytopath.* 50:876-881.
- Peterson, R. S. 1961. Western gall rust cankers in lodgepole pine. *J. Forestry* 59:194-196.
- Peterson, R. S. 1962a. Comandra blister rust in the Central Rocky Mountains. U.S. Dep. Agric., For. Serv., Rocky Mt. For. & Ra. Exp. Sta., Res. Notes No. 79. 6 p.
- Peterson, R. S. 1962b. Notes on western rust fungi. III. *Cronartium*. *Mycologia* 54:678-684.
- Peterson, R. S. 1966a. On sweet fern blister rust. *Plant Dis. Repr.* 50:744-746.
- Peterson, R. S. 1966b. Limb rust damage to pine. U.S. Dep. Agric., For. Serv., Intermountain For. & Range Exp. Sta., Res. Pap. INT-31. 10 p.
- Peterson, R. S. 1967. The *Peridermium* species on pine stems. *Bull. Torrey Bot. Club* 94:511-542.
- Peterson, R. S. 1968. Limb rust of pine: the casual fungi. *Phytopath.* 58:309-315.
- Peterson, R. S. 1971. Wave years of infection by western gall rust on pine. *Plant Dis. Repr.* 55:163-167.
- Peterson, R. S. 1973. Studies of *Cronartium* (Uredinales). Rept. Tottori Mycol. Inst. 10:203-223.
- Peterson, R. S. and F. F. Jewell. 1968. Status of American stem rusts of pine. *Annu. Rev. Phytopath.* 6:23-40.
- Phelps, W. R. and R. Weber. 1966. A preliminary evaluation of antibiotics for control of white pine blister rust in the Lake States. *Plant Dis. Repr.* 50:224-228.
- Phelps, W. R. and R. Weber. 1969a. An evaluation of chemotherapeutants for control of blister rust cankers in eastern white pine. *Plant Dis. Repr.* 53:514-517.
- Phelps, W. R. and R. Weber. 1969b. Characteristics of blister rust cankers on eastern white pine. U.S. Dep. Agric., For. Serv., North Central For. Exp. Sta., Res. Note NC-80. 2 p.
- Phelps, W. R. and R. Weber. 1970. An evaluation of carriers for chemotherapeutic treatment of blister rust

- cankers in eastern white pine. *Plant Dis. Repr.* 54:1031-1034.
- Piehl, M. A. 1965. The natural history and taxonomy of *Comandra* (Santalaceae). Mem. Torrey Bot. Club 22, No. 1. 97 p.
- Pomerleau, R. 1961. On the effects of white pine blister rust in a plantation. Can. Dep. For., For. Entomol. & Pathol. Br., Bi-Mon. Progr. Rept. 17(1):1.
- Pomerleau, R. and J. Bard. 1965. Essais sur la chimiothérapie de la rouille vésiculeuse du pin blanc à l'aide de la phytoactine et du cycloheximide. *Phytoprotection* 46:24-28.
- Pomerleau, R. and J. Bard. 1969. Les plantations de pin blanc et la rouille vésiculeuse dans le Québec. *Phytoprotection* 50:32-37.
- Porter, W. A. 1960. Testing for resistance to the blister rust disease of western white pine in British Columbia. Can. Dep. Agric., For. Biol. Lab., Victoria, B.C. 19 p.
- Powell, J. M. 1966. A white spored *Peridermium stalactiforme* in Alberta. *Plant Dis. Repr.* 50:144.
- Powell, J. M. 1969. The aerobiology of the aecial state of the comandra blister rust, *Cronartium comandrae* Peck, in Alberta. Univ. British Columbia, Ph.D. thesis. 362 p.
- Powell, J. M. 1970. *Cronartium comandrae* in Canada, its distribution and hosts. Can. Plant Dis. Surv. 50:130-135.
- Powell, J. M. 1971a. The arthropod fauna collected from the comandra blister rust, *Cronartium comandrae*, on lodgepole pine in Alberta. *Can. Entomol.* 103:908-918.
- Powell, J. M. 1971b. Occurrence of *Tuberculina maxima* on pine stem rusts in Western Canada. Can. Plant Dis. Surv. 51:83-85.
- Powell, J. M. 1971c. Fungi and bacteria associated with *Cronartium comandrae* on lodgepole pine in Alberta. *Phytoprotection* 52:45-51.
- Powell, J. M. 1971d. Incidence and effect of *Tuberculina maxima* on cankers of the pine stem rust, *Cronartium comandrae*. *Phytoprotection* 52:104-111.
- Powell, J. M. 1971e. Aerobiology of the aecial state of the comandra blister rust. Proc. 19th Western Intern. Forest Dis. Work Conf., Medford, Ore. Sept. 13-17. p. 7-14.
- Powell, J. M. 1971f. Daily germination of *Cronartium comandrae* aeciospores. *Can. J. Bot.* 49:2123-2127.
- Powell, J. M. 1972a. Seasonal and diurnal periodicity in the release of *Cronartium comandrae* aeciospores from stem cankers on lodgepole pine. *Can. J. For. Res.* 2:78-88.
- Powell, J. M. 1972b. Additional collections of *Tuberculina maxima* on pine stem rusts in western Canada. Can. Plant Dis. Surv. 52:139.
- Powell, J. M. 1974a. Environmental factors affecting germination of *Cronartium comandrae* aeciospores. *Can. J. Bot.* 52:659-667.
- Powell, J. M. 1974b. The role of natural biological agents in controlling a pine stem rust (*Cronartium comandrae*). *Blue Jay* 32:75-79.
- Powell, J. M. and Y. Hiratsuka. 1969. Nuclear condition and germination characteristics of the aeciospores of *Cronartium comandrae* and *C. comptoniae*. *Can. J. Bot.* 47:1961-1963.
- Powell, J. M. and Y. Hiratsuka. 1973a. Serious damage caused by stalactiform blister rust and western gall rust to a lodgepole pine plantation in central Alberta. Can. Plant Dis. Surv. 53:67-71.
- Powell, J. M. and Y. Hiratsuka. 1973b. Rusts are causing serious damage

- in intensively managed pine plantations in Alberta. Paper presented at Annu. Meeting, Can. Phytopath. Soc. (Alberta Region), Edmonton, November 6, 1973. 9 p. (mimeo) + Figs.
- Powell, J. M. and W. Morf. 1965. The occurrence of *Tuberculina maxima* Rost. on *Cronartium* rust-infected trees in Alberta. Can. Dep. For., For. Ent. & Path. Br., Bi-Mon. Prog. Rept. 21(1):3.
- Powell, J. M. and W. Morf. 1966. Temperature and pH requirements for aeciospore germination of *Peridermium stalactiforme* and *P. harknessii* of the *Cronartium coleosporioides* complex. *Can. J. Bot.* 44:1597-1606.
- Powell, J. M. and N. W. Wilkinson. 1973. *Pinus mugo*, a new host for comandra blister rust. *Plant Dis. Repr.* 57:283.
- Powell, J. M., H. R. Wong and J. C. E. Melvin. 1972. Arthropods collected from stem rust cankers on hard pines in western Canada. Can. Dep. Environment, Can. For. Serv., Northern For. Res. Centre, Edmonton, Inform. Rept. NOR-X-42. 19 p.
- Powers, H. R., G. H. Hepting and W. A. Stegall. 1967. Comandra rust on loblolly pine in eastern Tennessee. *Plant Dis. Repr.* 51:4-8.
- Powers, H. R., Jr., and W. A. Stegall, Jr. 1965. An evaluation of cycloheximide (Acti-dione) for control of white pine blister rust in the southeast. *Plant Dis. Repr.* 49:342-346.
- Powers, H. R. Jr., and W. A. Stegall. 1971. Blister rust on unprotected white pines. *J. Forestry* 69:165-167.
- Quick, C. R. 1962. Relation of canyon physiography to the incidence of blister rust in the central Sierra Nevada. U.S. Dep. Agric., For. Serv., Pacific Southwest For. & Ra. Exp. Sta., Tech. Pap. 67. 13 p.
- Quick, C. R. 1967a. Chemical control of blister rust on sugar pine . . . two fungicides show promise in California tests. U.S. Dep. Agric., For. Serv., Pacific Southwest For. & Ra. Exp. Sta., Res. Note PSW-147. 8 p.
- Quick, C. R. 1967b. Screening conventional fungicides . . . control of blister rust on sugar pine in California. U.S. Dep. Agric., For. Serv., Pacific Southwest For. & Ra. Exp. Sta., Res. Note PSW-149. 7 p.
- Quick, C. R. and C. H. Lamoureaux. 1967. Field inoculation of white pine blister rust cankers on sugar pine with *Tuberculina maxima*. *Plant Dis. Repr.* 51:89-90.
- Rhoads, A. S. 1920. Studies on the rate of growth and behavior of the blister rust on white pine in 1918. *Phytopath.* 10:513-527.
- Riker, A. J., T. F. Kouba, W. H. Brener and L. E. Byam. 1943. White pine selections tested for resistance to blister rust. *J. Forestry* 41:753-760.
- Ross, D. A., J. A. Baranyay and R. L. Fiddick. 1973. Environment Canada, For. Serv., *Annual Report of the Forest Insect and Disease Survey* 1972. pp 83-94.
- Rudolf, P. O. 1958. Silvical characteristics of jack pine. U.S. Dep. Agric., For. Serv., Lake States For. Exp. Sta., Sta. Pap. No. 61. 31 p.
- Rudolf, P. O. and R. F. Patton. 1966. Genetic improvement of forest trees for disease and insect resistance in the Lake States. p. 63-68. In: *Breeding pest-resistant trees*. (Ed.) H. D. Gerhold, E. J. Schreiner, R. E. McDermott and J. A. Winieski. Oxford, Pergamon Press. 505 p.
- Savile, D.B.O. 1968. Some fungal parasites of Scrophulariaceae. *Can. J. Bot.* 46:461-471.
- Siggers, P. V. 1955. Control of the fusi-

- form rust of southern pines. *J. Forestry* 53:442-446.
- Sippell, W. L., H. L. Gross and A. H. Rose. 1969. Can. Dep. Fish. & For., For. Br., *Annual Report of the Forest Insect and Disease Survey 1968*. pp 53-78.
- Sippell, W. L., H. L. Gross and A. H. Rose. 1971. Can. Dep. Fish. & For., Can. For. Serv., *Annual Report of the Forest Insect and Disease Survey 1970*. pp 49-66.
- Sippell, W. L., A. H. Rose and H. L. Gross. 1970. Can. Dep. Fish. & For., Can. For. Serv., *Annual Report of the Forest Insect and Disease Survey 1969*. pp 52-71.
- Sippell, W. L., A. H. Rose and H. L. Gross. 1972. Environment Can., Can. For. Serv., *Annual Report of the Forest Insect and Disease Survey 1971*. pp 54-72.
- Sippell, W. L., A. H. Rose and M. J. Larsen. 1968. Can. Dep. For. & Rural Develop., For. Br., *Annual Report of the Forest Insect and Disease Survey 1967*. pp 50-75.
- Smith, G. J. 1971. Distribution of white pine blister rust in the Canadian Rocky Mountains. Can. Dep. Environment, Can. For. Serv., Bi-Monthly Res. Notes 27:43.
- Snow, G. A. 1960. Spraying before rains important for fusiform rust control. U.S. Dep. Agric., For. Serv., Tree Planter's Notes 43:17-18.
- Spaulding, P. 1922. Investigations of the white pine blister rust. U.S. Dep. Agric., Bull. 957. 100 p.
- Spaulding, P. and J. R. Hansbrough. 1932. *Cronartium comptoniae*, the sweetfern blister rust of pitch pines. U.S. Dep. Agric., Circ. No. 217. 21 p.
- Stewart, D. M. 1957. Factors affecting local control of white pine blister rust in Minnesota. *J. Forestry* 55:832-837.
- Stewart, D. M. and L. B. Ritter. 1962. A white pine stand 17 years after control of blister rust. Univ. Minnesota, School Forestry, Minnesota For. Notes No. 114. 2 p.
- Stillwell, M. A. and A. G. Davidson. 1954. Can. Dep. Agric., For. Biol. Div., *Annual Report of the Forest Insect and Disease Survey 1953*. pp 20-31.
- Toko, H. V. and O. J. Dooling. 1968. An evaluation of the blister rust control program of the National Park Service in the Rocky Mountain area. U.S. Dep. Agric., For. Serv., Div. State & Private Forestry, Northern Region, Missoula, Montana. Unpubl. Rept. 8 p.
- Tripp, H. A., R. E. Stevenson and J. A. Baranyay. 1967. Can. Dep. For. & Rural Develop., For. Br., *Annual Report of the Forest Insect and Disease Survey 1966*. pp 95-107.
- Van Arsdel, E. P. 1960. Cycloheximide (Acti-dione), a new tool in white pine blister rust control. Univ. Wisconsin, Forestry Res. Notes No. 54. 2 p.
- Van Arsdel, E. P. 1961. Growing white pine in the Lake States to avoid blister rust. U.S. Dep. Agric., For. Serv., Lake States For. Exp. Sta., Sta. Pap. 92. 11 p.
- Van Arsdel, E. P. 1962. Greenhouse tests using antibiotics to control blister rust on white pine. *Plant Dis. Repr.* 46:306-309.
- Van Arsdel, E. P. 1964. Growing white pines to avoid blister rust - new information for 1964. U.S. Dep. Agric., For. Serv., Lake States For. Exp. Sta., Res. Note LS-42. 4 p.
- Van Arsdel, E. P. 1967. The nocturnal diffusion and transport of spores. *Phytopath.* 57:1221-1229.
- Van Arsdel, E. P. 1968. Stem and needle inoculations of eastern white pine with the blister rust fungus. *Phytopath.* 58:512-514.

- Van Arsdel, E. P., A. J. Riker, T. F. Kouba, V. E. Suomi and R. A. Bryson. 1961. The climatic distribution of blister rust on white pine in Wisconsin. U.S. Dep. Agric., For. Serv., Lake States For. Exp. Sta., Sta. Pap. 87. 34 p.
- Van Arsdel, E. P., A. J. Riker and R. F. Patton. 1956. The effects of temperature and moisture on the spread of white pine blister rust. *Phytopath.* 46:307-318.
- Van Sickle, G. A. 1966. White pine blister rust in New Brunswick. Can. Dep. For., For. Res. Lab., Fredericton, N.B. Intern. Rept. M-14. 11 p.
- Van Sickle, G. A. 1969. Occurrence of *Cronartium comptoniae* in the Maritime Provinces. *Plant Dis. Repr.* 53:364-371.
- Van Sickle, G. A. 1973. Chemotherapy trials on sweetfern blister rust cankers. Env. Can., For. Serv., Bi-Monthly Res. Notes 29:20.
- Van Sickle, G. A. and W. R. Newell. 1968. The occurrence of *Peridermium harknessii* of the *Cronartium coleosporioides* complex confirmed in the Maritime Provinces. *Plant Dis. Repr.* 52:455-458.
- Viche, H. J., V. D. Moss and H. J. Hartman. 1962. Developments in aerial application of antibiotics to control blister rust on western white pine. *J. Forestry* 60:782-784.
- Wagener, W. W. 1964. "Facultative heteroecism." Was it demonstrated in *Peridermium harknessii* in 1919-20? *Mycologia* 56:782-785.
- Walkinshaw, C. H. 1968. Oxygen consumption and germination of *Cronartium fusiforme* aeciospores. *Phytopath.* 58:260-261.
- Weber, R. 1964. Early pruning reduces blister rust mortality in white pine plantations. U.S. Dep. Agric., For. Serv., Lake States For. Exp. Sta., Res. Note LS-38. 2 p.
- Wehmeyer, L. E. 1950. The fungi of New Brunswick, Nova Scotia, and Prince Edward Island. National Research Council of Canada, Ottawa. 150 p.
- Weir, J. R. 1915. Observations on the pathology of the jack pine. U.S. Dep. Agric., Bull. 212. 10 p.
- Weir, J. R. and E. E. Hubert. 1917. Recent cultures of forest tree rusts. *Phytopath.* 7:106-109.
- Wicker, E. F. 1968. Toxic effects of cycloheximide and phytoactin on *Tuberculina maxima*. *Phytoprotection* 49:91-98.
- Wicker, E. F. and J. Y. Woo. 1973. Histology of blister rust cankers parasitized by *Tuberculina maxima*. *Phytopath. Z.* 76:356-366.
- Wollenweber, H. W. 1934. *Fusarium bac-tridioides* sp. nov., associated with *Cronartium*. *Science* 79:572.
- Wong, H. R. 1972. *Dioryctria banksiella* (Lepidoptera: Pyralidae) in the western gall rust *Endocronartium harknessii* (Basidiomycetes: Uredinales). *Can. Ent.* 104:251-255.
- York, H. H. 1926. A *Peridermium* new to the northeastern United States. *Science* 64:500-501.
- Zalasky, H. and C. G. Riley. 1963. Infection tests with two caulicolous rusts of jack pine in Saskatchewan. *Can. J. Bot.* 41:459-465.
- Ziller, W. G. 1967. Sweetfern blister rust *Cronartium comptoniae* Arth. p. 181-183. In: A. G. Davidson and R. M. Prentice (Eds.). Important forest insects and diseases of mutual concern to Canada, the United States and Mexico. Can. Dep. For. & Rural Develop., Publ. No. 1180. 248 p.
- Ziller, W. G. 1970. Studies of western tree rusts. VII. Inoculation experiments with pine stem rusts (*Cronar-*

- tium* and *Endocronartium*). *Can. J. Bot.* 48:1313-1319.
- Ziller, W. G. 1974. The tree rusts of western Canada. *Environ. Can., Can. Forestry Service, Publ. No. 1329.* 272 p.

aecidiospore → **aeciospore**

aecidium (pl. **aecidia**) → **aecium**

aeciospore (**aecidiospore**): non-repeating binucleate vegetative spores produced in an aecium usually due to dikaryotization, which germinate to initiate a dikaryotic mycelium; yellow-orange spores of *Cronartium* spp. on pine are aeciospores.

aecium (pl. **aecia**) (**aecidium**): sorus containing aeciospores.

alternate host: one or the other of the two unlike hosts of a heteroecious (host-alternating) rust.

amphigenous: growing either side of a leaf. cf. epiphyllous, hypophyllous.

appressorium (pl. **appressoria**): a swelling on a germ-tube during an early state of infection, from which an infection peg usually develops.

autoecious: a fungus having the ability to complete its life cycle on one host. cf. heteroecious.

basidiospore (**sporidium**): monokaryotic spore produced on a basidium usually as the result of meiosis.

basidium (pl. **basidia**): organ which usually bears 4 basidiospores; meiosis usually occurs in it.

catenulate: produced on a chain.

cuspidate: with an apex somewhat abruptly constricted into an elongated, sharp-pointed tip.

dikaryon: having two nuclei in a cell.

diploid: having the double ($2n$) number of chromosomes.

echinulate: having small spines or pointed projections as in urediniospores of *Cronartium* spp. (Fig. 25).

endocyclic life cycle: one of the simplest types of life cycle composed of spermatogonia and aecoid teliospores (resembling aeciospores but

behaving like teliospores), as in genera *Endophyllum*, *Kunkelia* and *Endocronartium*.

epiphyllous: growing on the upper side of the leaves. cf. amphigenous, hypophyllous.

filament: intrasoral columns of sterile cells in aecia of *Cronartium*.

form genus: generic names given to the imperfect states of rust fungi, e.g. *Peridermium*, *Caeoma*, *Aecidium* and *Uredo*.

globose: spherical or almost so.

haploid: having the basic (n) number of chromosomes.

hard pine: pines belonging to the sub-genus *Pinus* (*Diploxylon*), including *Pinus banksiana*, *P. contorta*, *P. ponderosa*, *P. resinosa* and *P. sylvestris*; mostly having 2 to 3 needles per fascicle. cf. soft pine.

haustorium (pl. **haustoria**): a special extension of hyphae for absorption of nutrients within a living cell of the host, occurring in rust fungi, powdery mildews and some other parasitic fungi.

heteroecious: requiring two unrelated plants to complete a life cycle; host alternating. cf. autoecious.

hypha: a tubular filament of the fungi.

hyperplasia: excessive cell divisions of tissues.

hypertrophy: excessive enlargement of cells or tissues.

hypophyllous: growing on the under side of leaves. cf. epiphyllous, amphigenous.

intercalary cell: sterile cell occurring between the spores, as in aecia of pine stem rusts.

meiosis: "reduction division", when a diploid ($2n$) cell undergoes two successive divisions to produce four haploid cells. In rust fungi meiosis occurs in basidia.

mitosis: "somatic division", when a diploid or haploid cell undergoes a division to produce two daughter cells.

monokaryon: having one nucleus per cell.

mycelium (pl. mycelia): a mass of hyphae.

nuclear fusion: union of two haploid nuclei to produce a diploid nucleus; in rust fungi it occurs in teliospores before basidium formation.

obtuse: blunt, rounded.

pedicellate: having a pedicel or stalk.

peridium (pl. peridia): the outer wall of the fructification.

peridermioid: having the appearance of a *Peridermium*, as in the peridermioid telia of *Endocronartium*.

petioliculous: growing on petioles.

pycniospore → **spermatium**

pycnium (pl. pycnia) → **spermogonium**

pyriform: pear-shaped.

rust (rust fungus): a fungus which belongs to the Uredinales (Basidiomycetes), the Uredinales include about 120 genera and 5,000 species; some economically important species are *Puccinia graminis* (wheat stem rust), *Hemileia vastatrix* (coffee rust) and *Cronartium* spp. (pine stem rusts).

soft pine: pines belonging to the sub-genus *Strobus* (*Haploxylo*), including *Pinus albicaulis*, *P. flexilis*, *P. monticola* and *P. strobus*; "five needle pines". cf. hard pine.

sorus: fruiting structure of fungi containing spores.

spermogonium (pl. spermogonia) (pycnium): a small fruiting structure containing spermatia.

spermatium (pl. spermatia) (pycniospore): spore-like male gametes which are non-motile and uni-nucleate, produced in spermogonia (Fig. 15).

sporidium (pl. sporidia) → **basidiospores.**

stalactiform: a stalactite- or icicle-like pendent structure; *Cronartium coleosporioides* is called "stalactiform blister rust" because the filaments in the aecia of this species hang down from the upper wall of periderm.

subglobose: not quite spherical.

teleutosorus (pl. teleutosori) → **telium**

teleutospore → **teliospore**

teliospore (teleutospore): basidia-producing spore of a rust fungus.

telium (pl. telia) (teleutosorus): sorus-containing teliospores.

urediniospore (urediospore, uredospore): repeating binucleate vegetative spores produced usually on dikaryotic mycelium.

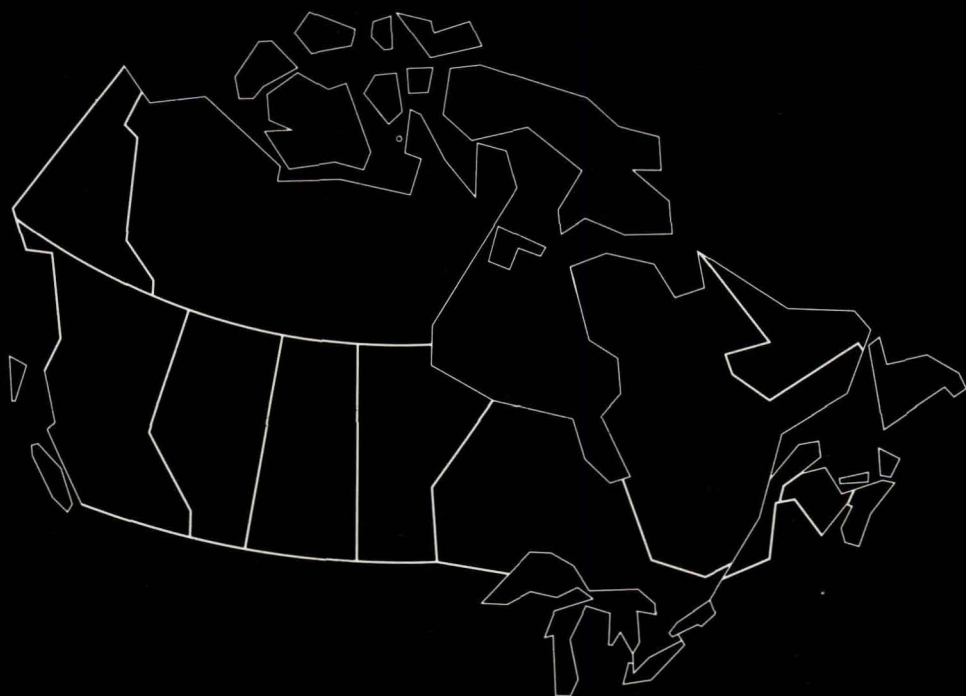
uredinium (pl. uredinia) (uredium, uredosorus): sorus-containing urediniospores.

urediospore → **urediniospore.**

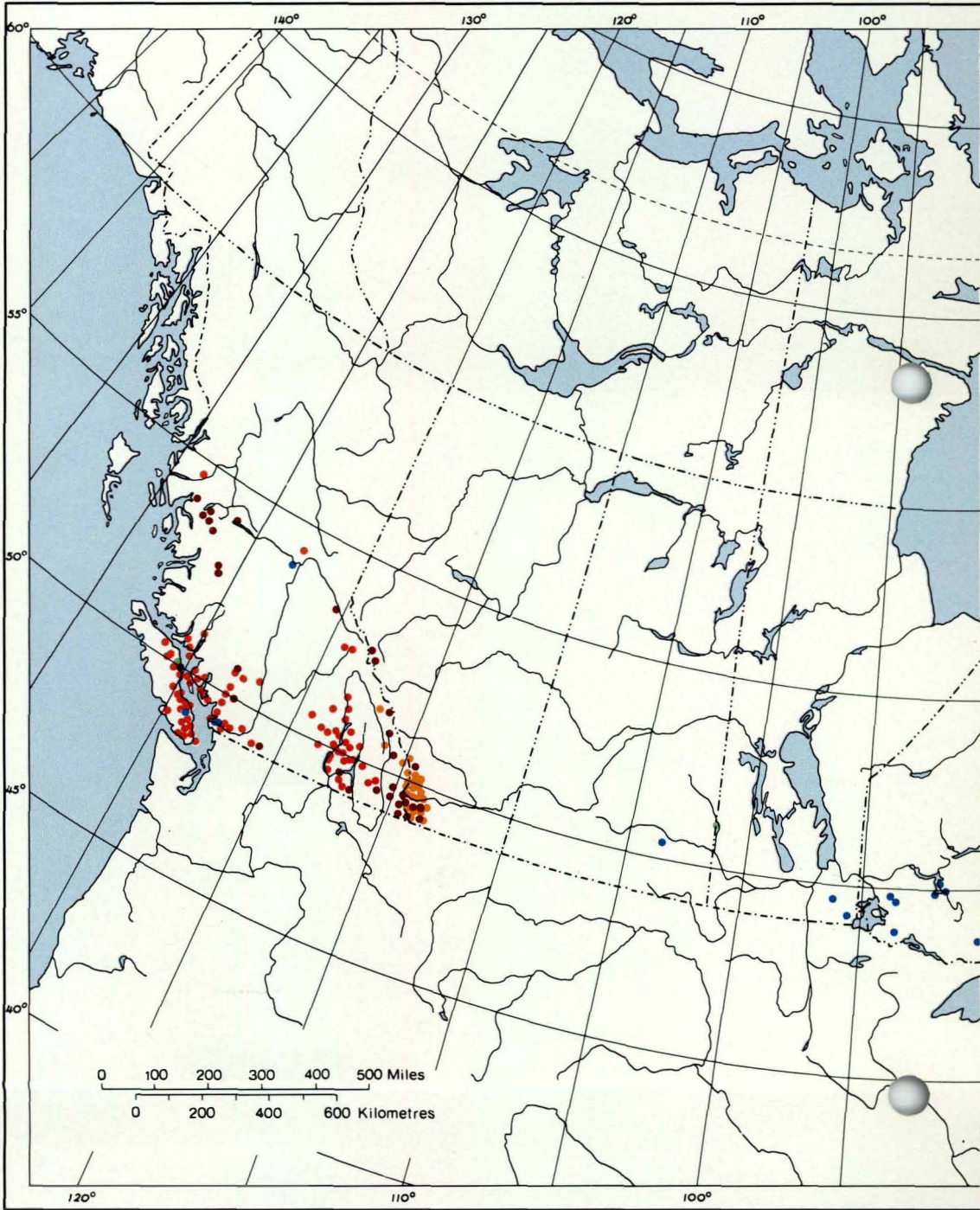
uredium (pl. uredia) → **uredinium.**

uredosorus (pl. uredosori) → **uredinium**
uredospore → **urediniospore**

verrucose: having small rounded processes or "warts", as on aeciospores of pine stem rusts.

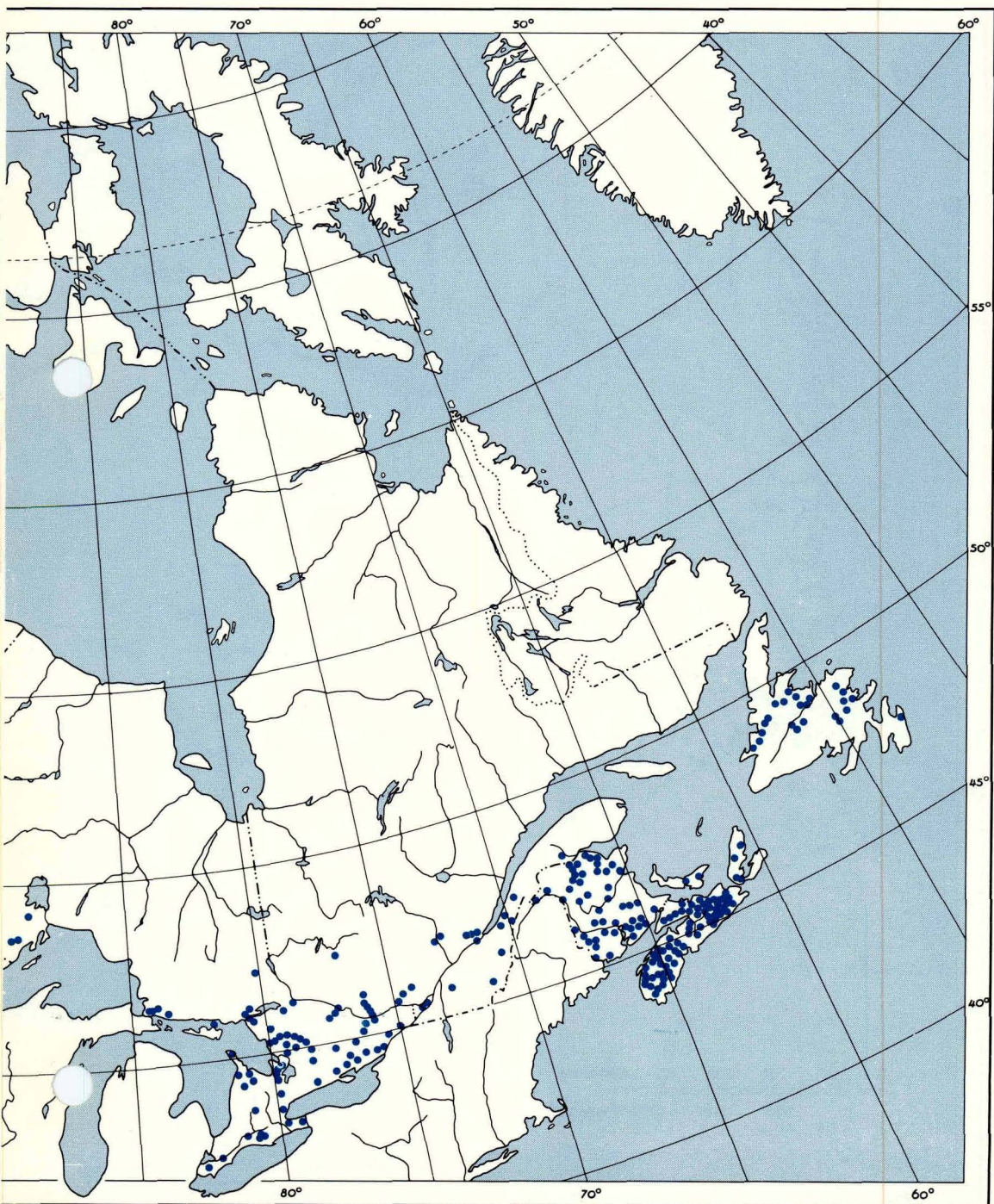


***Cronartium
ribicola* — *Pinus* spp.**

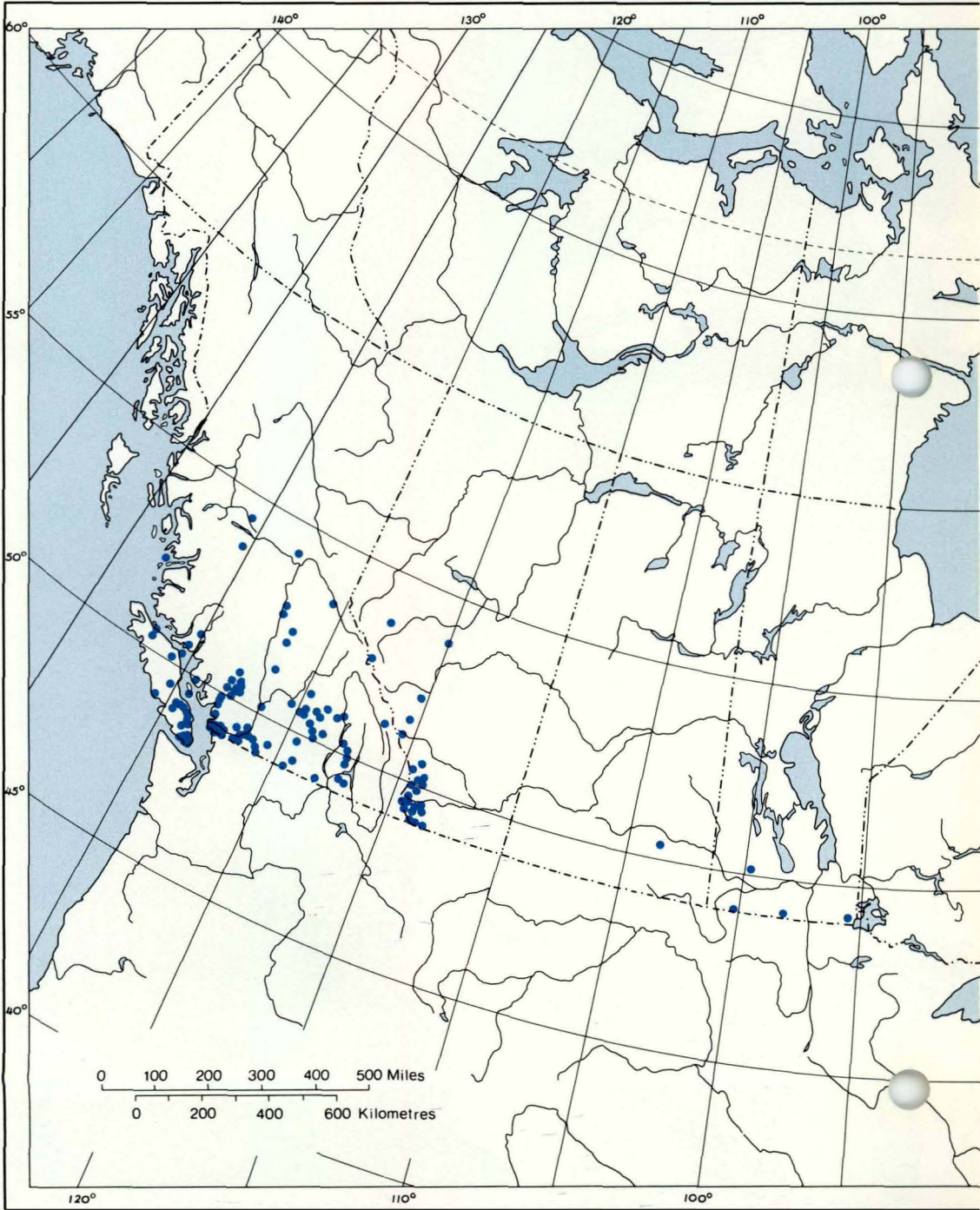


1 Collections of *Cronartium ribicola* on *Pinus albicaulis*, *P. cembra*, *P. flexilis*, *P. lambertiana*, *P. monticola* and *P. strobus* in Canada.

- *Pinus albicaulis*
- *Pinus cembra*
- *Pinus flexilis*
- *Pinus lambertiana*
- *Pinus monticola*
- *Pinus strobus*



***Cronartium*
ribicola — *Ribes* spp.**

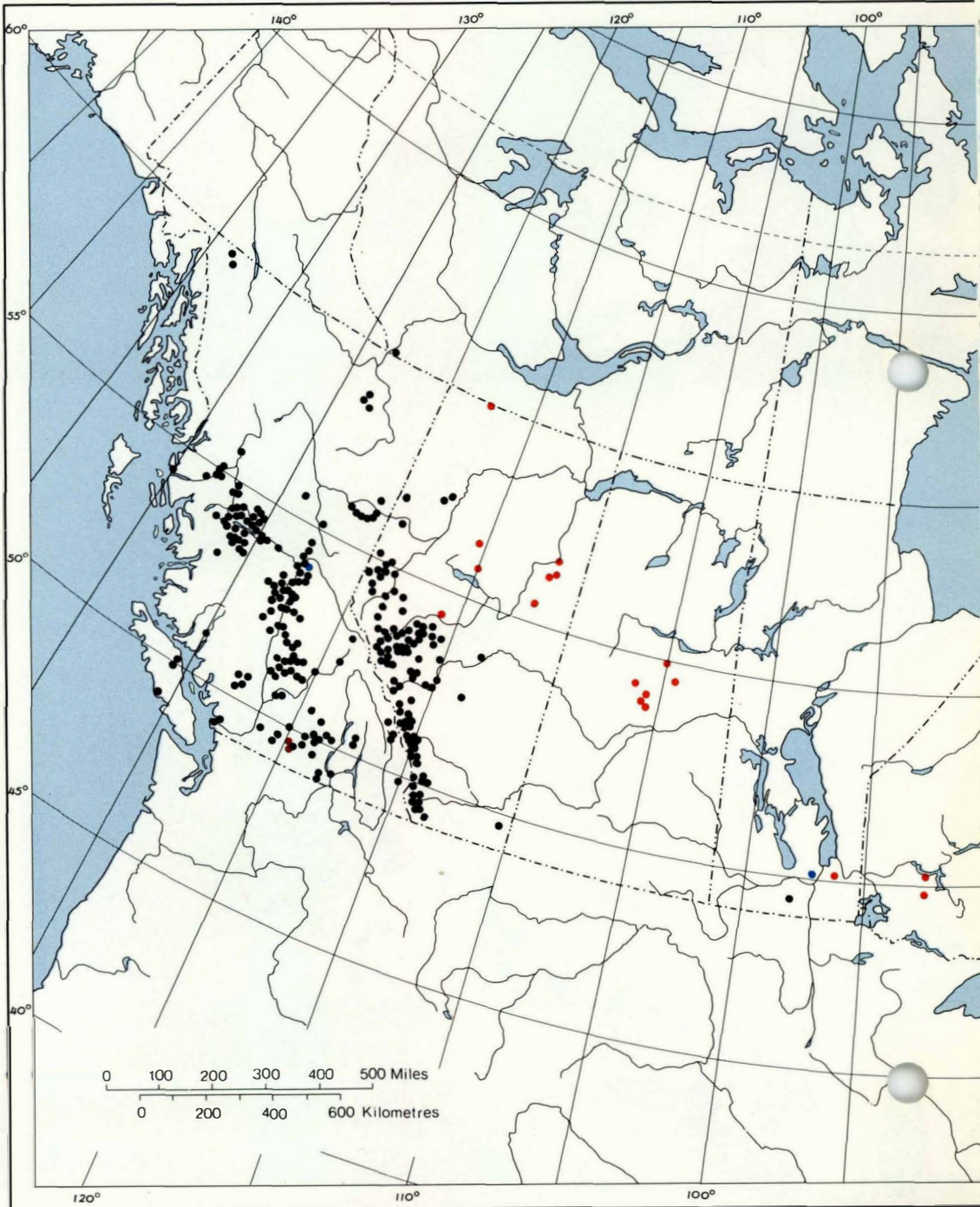


2 Collections of *Cronartium ribicola* on *Ribes*
spp. in Canada.

• *Ribes* spp.



***Cronartium
coleosporioides* —
Pinus spp.**

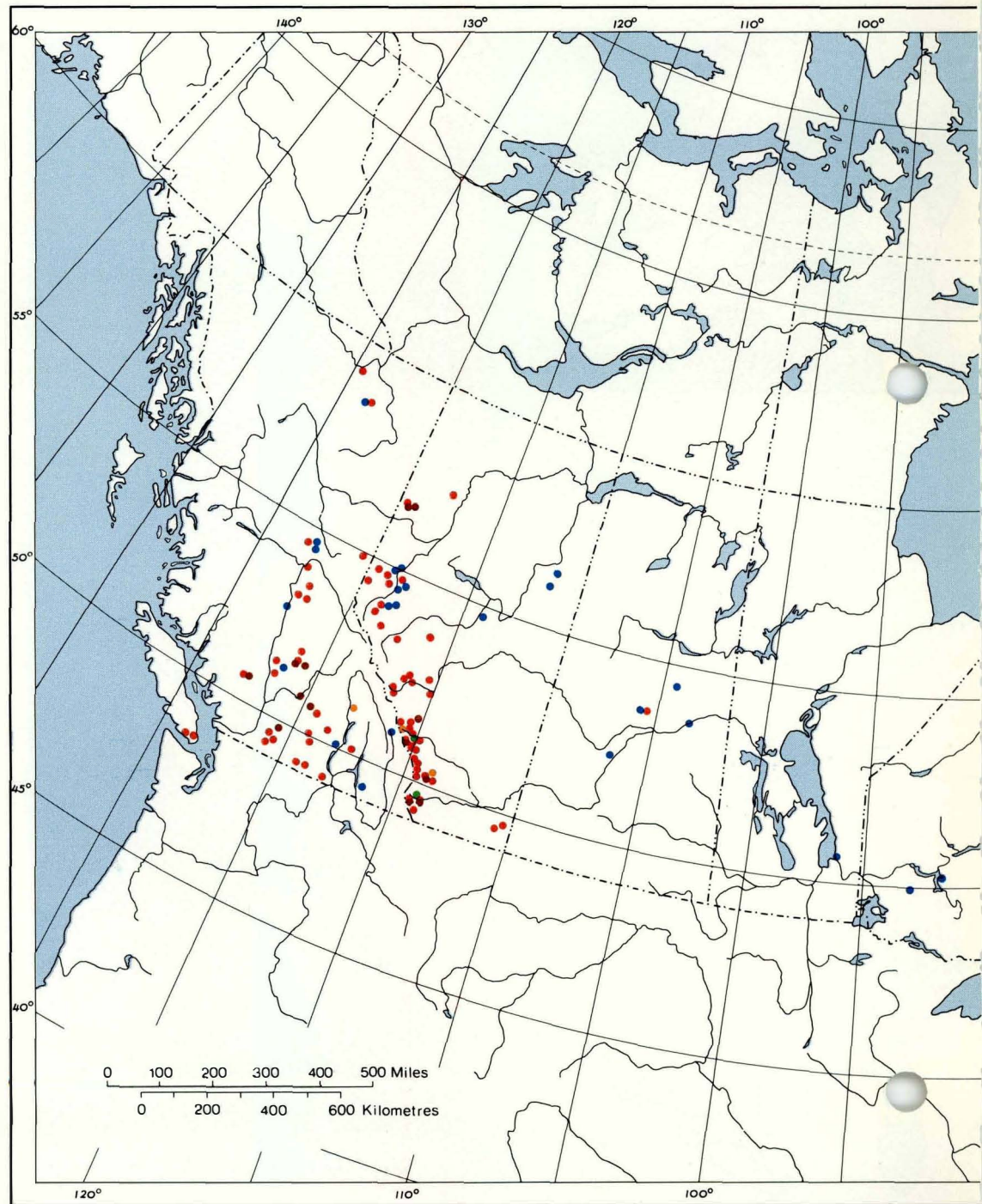


3 Collections of *Cronartium coleosporioides*
on *Pinus banksiana*, *P. contorta*, *P. echinata*,
P. ponderosa and *P. sylvestris* in Canada.

- *Pinus banksiana*
- *Pinus contorta*
- *Pinus echinata*
- *Pinus ponderosa*
- *Pinus sylvestris*



***Cronartium*
coleosporioides —
Castilleja, etc., spp.**

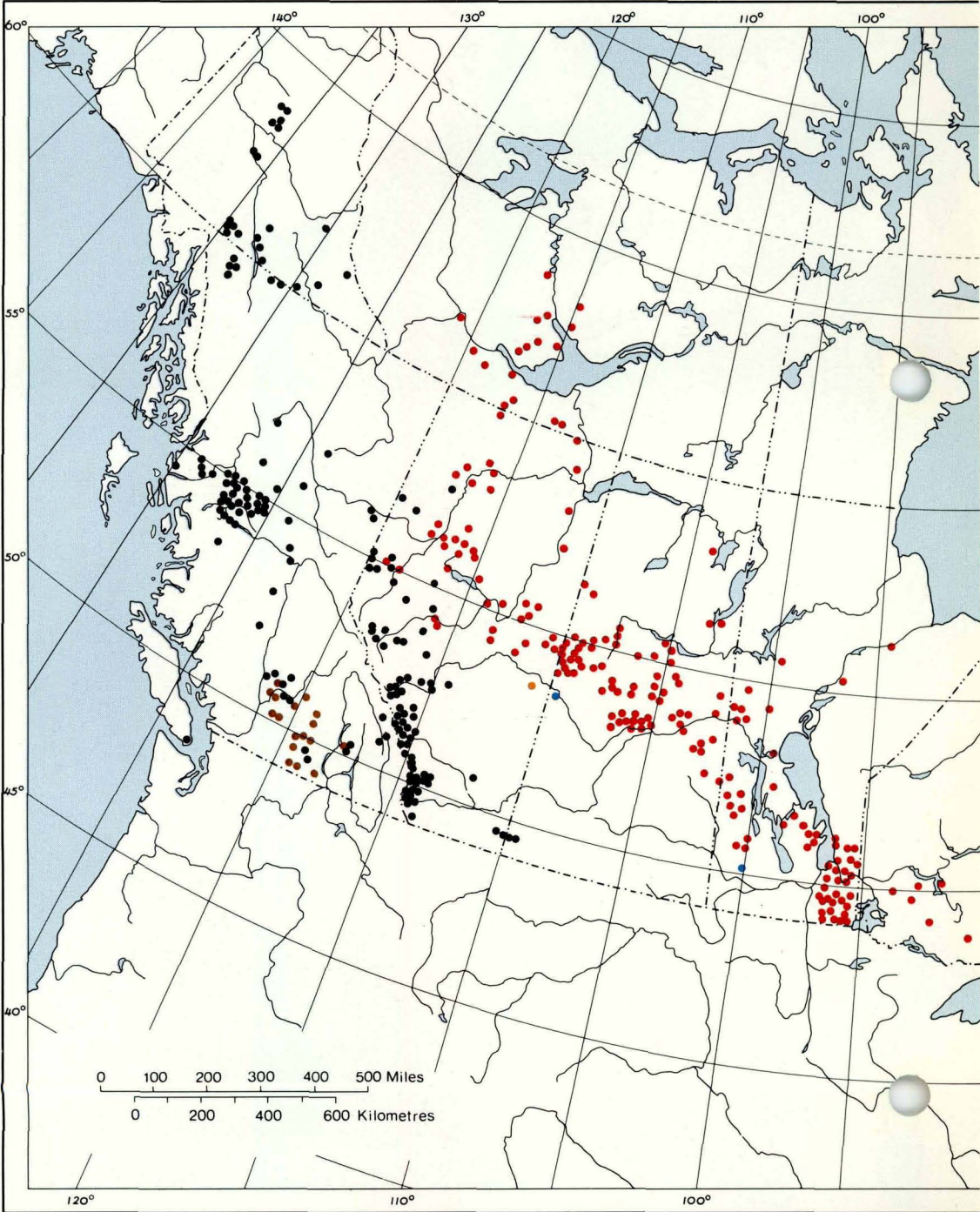


4 Collections of *Cronartium coleosporioides* on *Castilleja* spp., *Melampyrum lineare*, *Orthocarpus luteus*, *Pedicularis bracteosa* and *Rhinanthus crista-galli* in Canada.

- *Castilleja* spp.
- *Melampyrum lineare*
- *Orthocarpus luteus*
- *Pedicularis bracteosa*
- *Rhinanthus crista-galli*



***Cronartium*
comandrae — *Pinus* spp.**

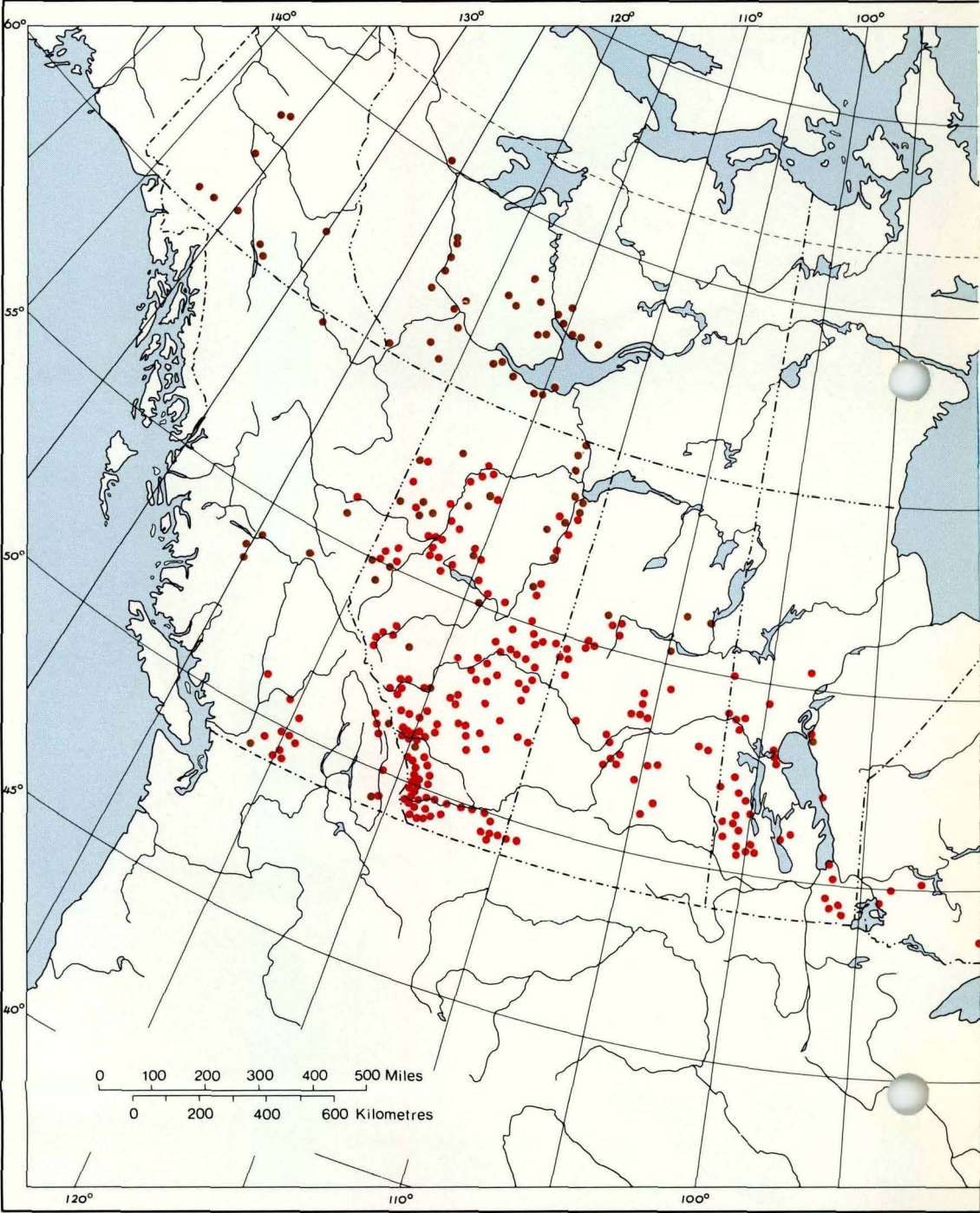


5 Collections of *Cronartium comandrae* on *Pinus banksiana*, *P. contorta*, *P. mugo*, *P. ponderosa* and *P. sylvestris* in Canada.

- *Pinus banksiana*
- *Pinus contorta*
- *Pinus mugo*
- *Pinus ponderosa*
- *Pinus sylvestris*



**Cronartium
comandrae —
Comandra/
Geocaulon spp.**

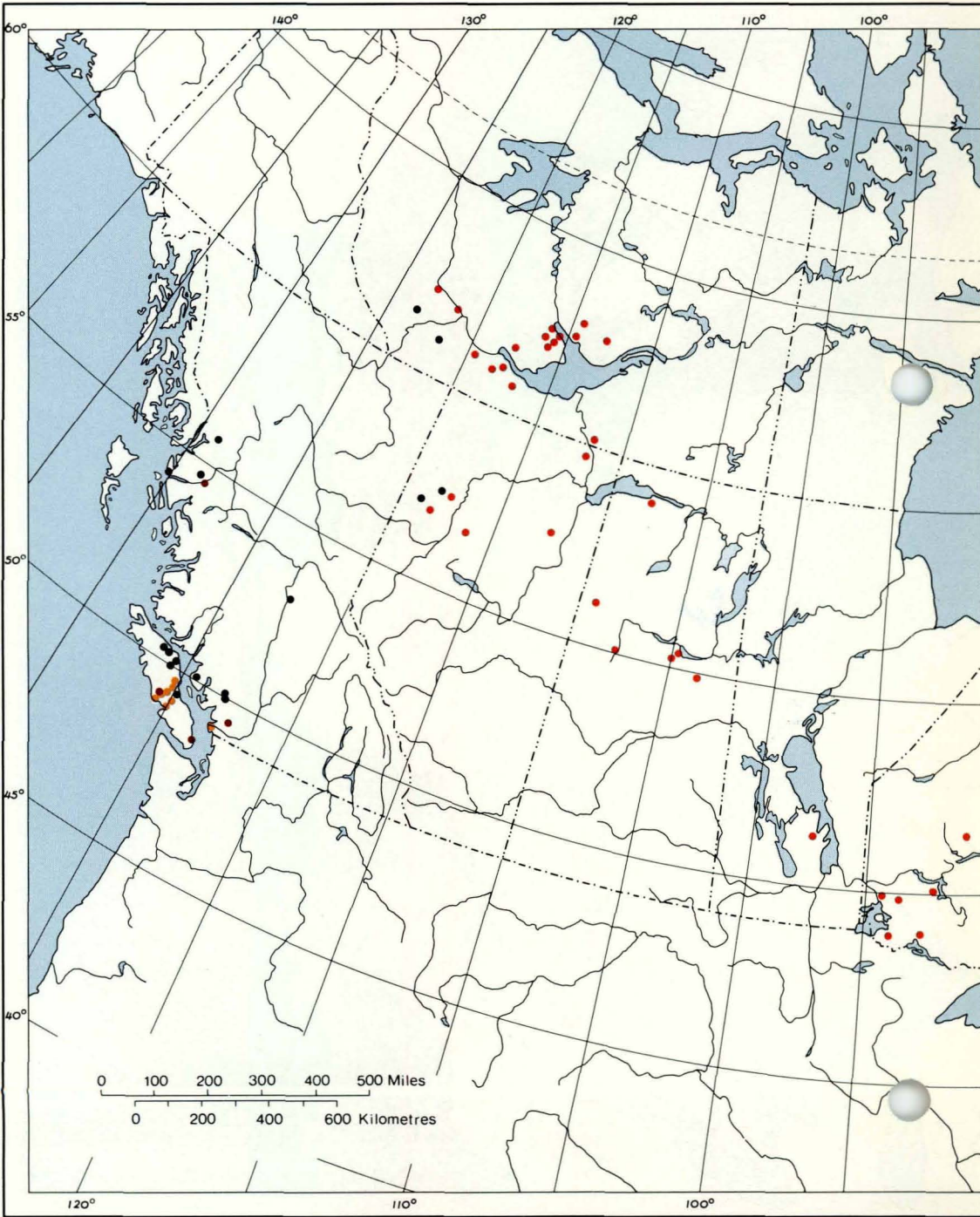


6 Collections of *Cronartium comandrae* on
Comandra umbellata and *Geocaulon*
lividum in Canada.

- *Comandra umbellata*
- *Geocaulon lividum*



**Cronartium
comptoniae — Pinus spp.**

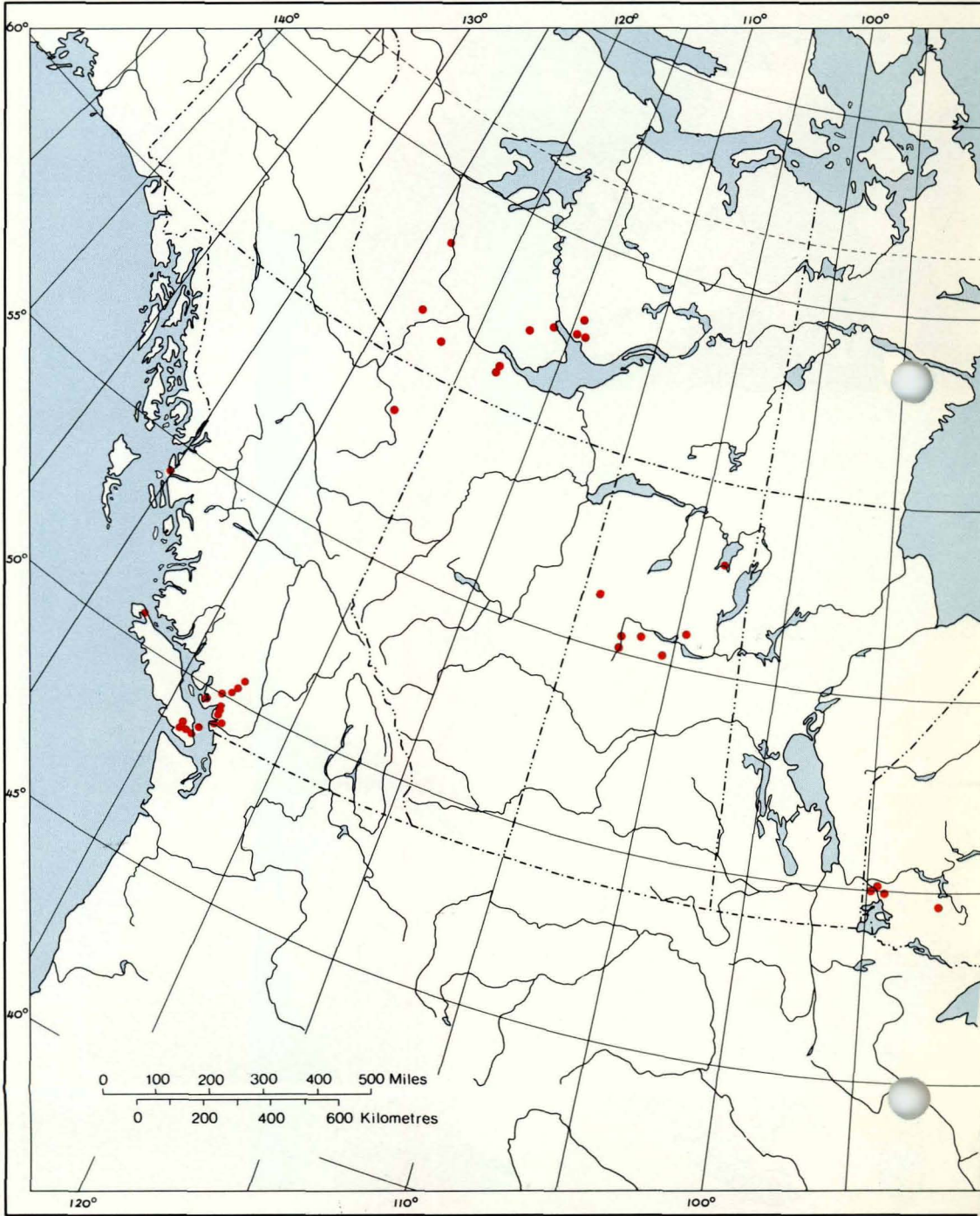


7 Collections of *Cronartium comptoniae* on *Pinus banksiana*, *P. contorta*, *P. ponderosa*, *P. sylvestris* and other *Pinus* spp. (*P. echinata*, *P. mugo*, *P. muricata*, *P. nigra*, *P. radiata* and *P. resinosa*) in Canada.

- *Pinus banksiana*
- *Pinus contorta*
- *Pinus ponderosa*
- *Pinus sylvestris*
- *Pinus echinata*
- *Pinus mugo*
- *Pinus muricata*
- *Pinus nigra*
- *Pinus radiata*
- *Pinus resinosa*



**Cronartium
comptoniae —
Comptonia/Myrica spp.**

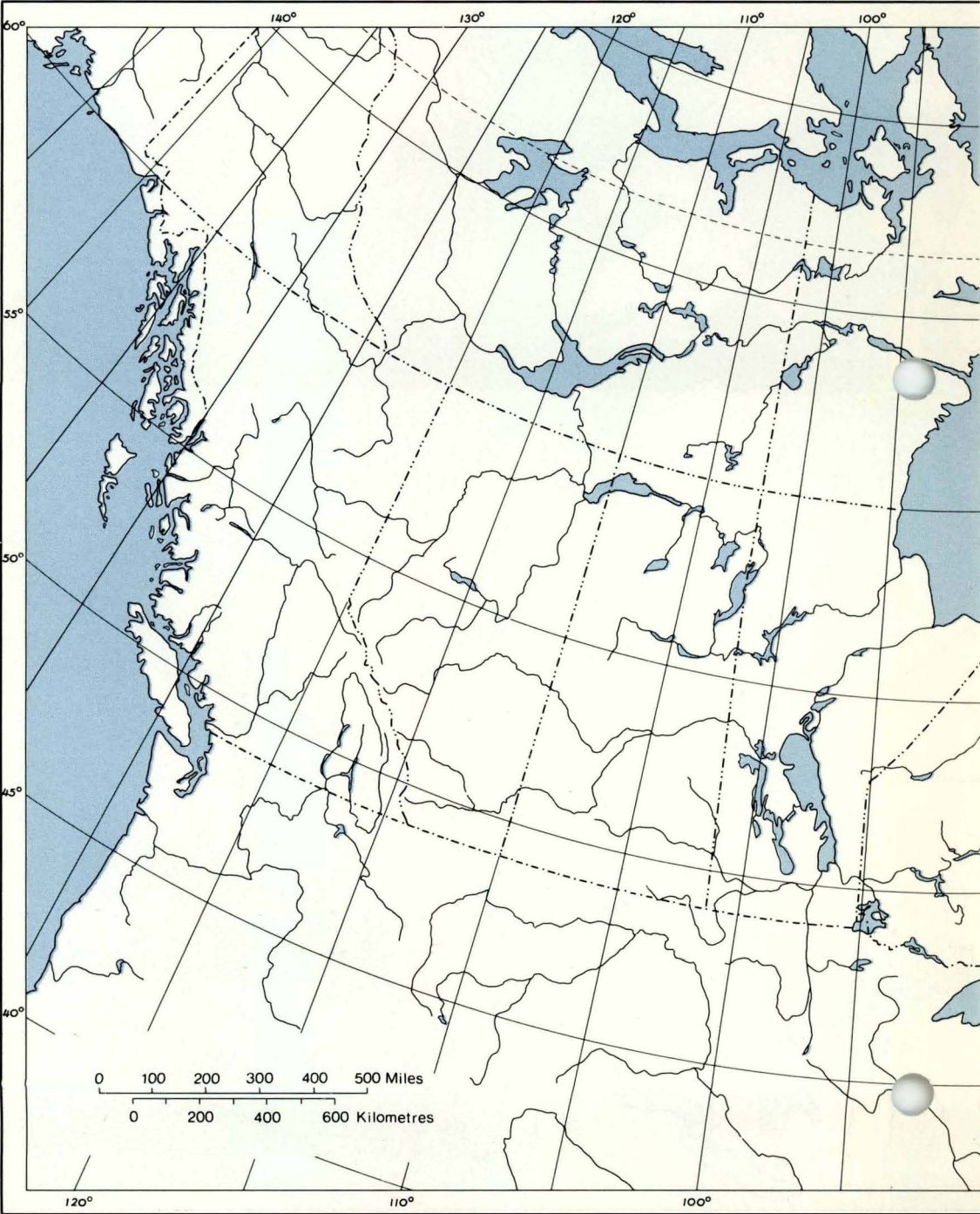


8 Collections of *Cronartium comptoniae* on
Comptonia peregrina and *Myrica gale* in
Canada.

- *Comptonia peregrina*
- *Myrica gale*

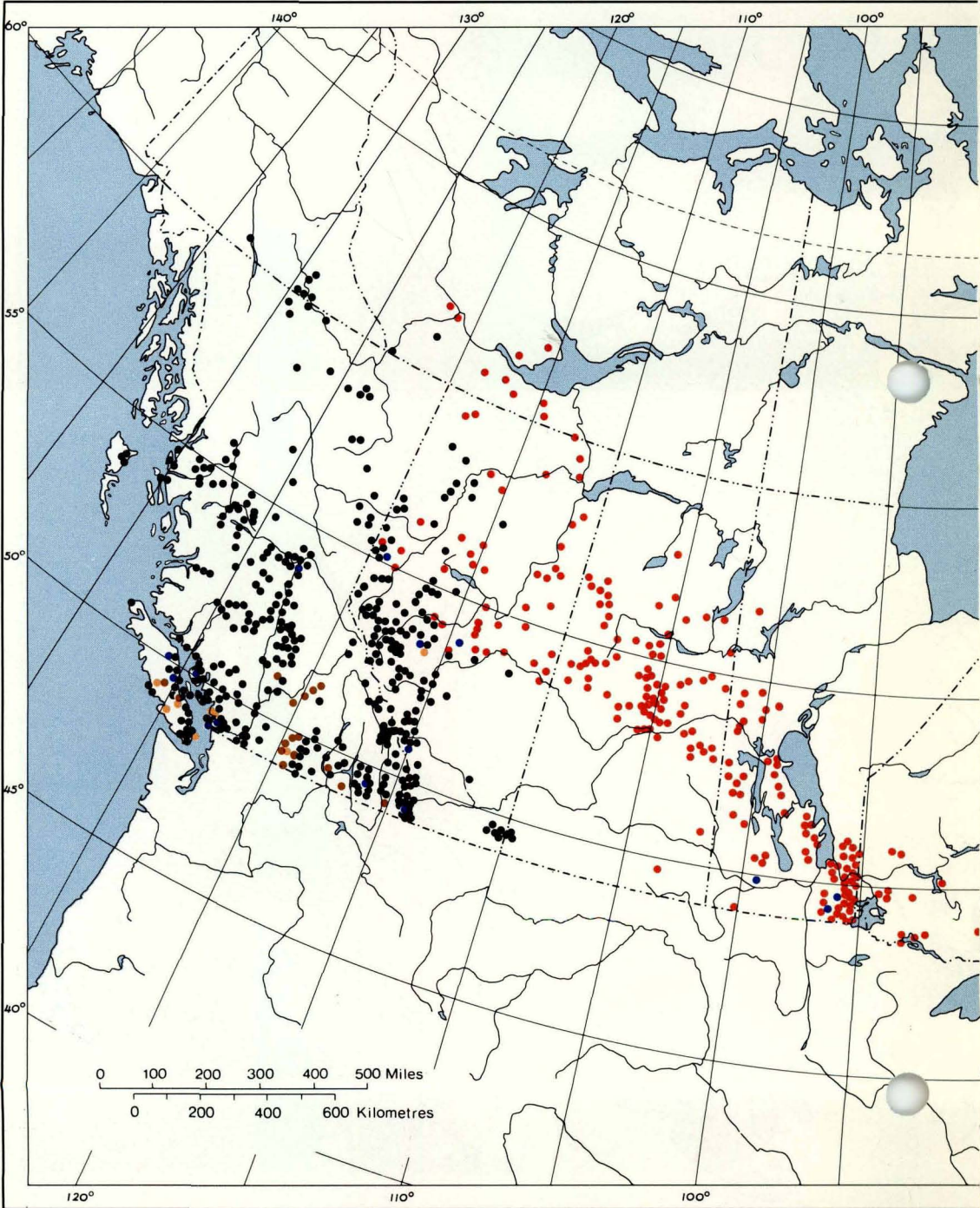


**Cronartium
quercuum —
Pinus/Quercus spp.**



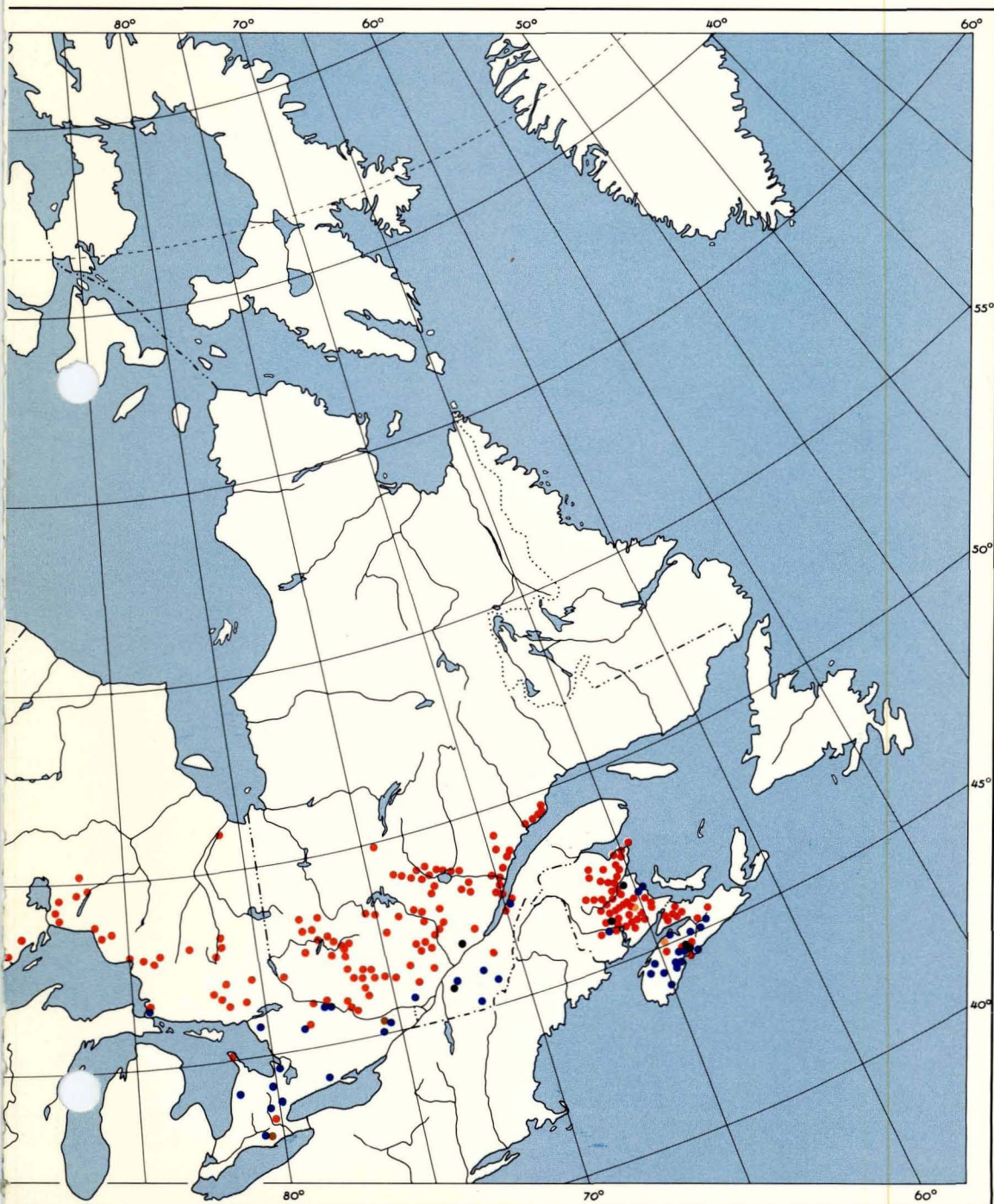


***Endocronartium
harknessii* —
Pinus spp.**



10 Collections of *Endocronartium harknessii* on *Pinus banksiana*, *P. contorta*, *P. ponderosa*, *P. sylvestris* and other *Pinus* spp. (*P. mugo*, *P. muricata*, *P. nigra*, *P. pinaster* and *P. radiata*) in Canada.

- *Pinus banksiana*
- *Pinus contorta*
- *Pinus ponderosa*
- *Pinus sylvestris*
- *Pinus mugo*
- *Pinus muricata*
- *Pinus nigra*
- *Pinus pinaster*
- *Pinus radiata*





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