Clarification of the life-cycle of *Chrysomyxa woroninii* on *Ledum* and *Picea*

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The rust fungus *Chrysomyxa woroninii* causes perennial witches' brooms on several species of *Ledum* in northern and subalpine regions of Europe, North America and Asia. Spruce bud rust has been assumed to be the aecial state of *C. woroninii* because of the close proximity of infected *Ledum* plants and systemically infected buds on *Picea*. The lack of experimental evidence for this connection, however, and the presence of other species of *Chrysomyxa* on the same hosts has led to confusion about the life-cycle of *C. woroninii*. In this study, infections on both spruce and *Ledum* were studied in the field and in a greenhouse. The link between the two states was proven by inoculating spruce with basidiospores from *Ledum groenlandicum*. After infection of spruce in spring, probably through the needles, the fungus overwinters in the unopened buds until the next spring, when the infected shoots are distinguished by stunting and yellow or red discolouration. Microscopic examination of dormant *Ledum* shoots showed that *C. woroninii* overwinters in this host in the bracts and outer leaves of the vegetative buds, and in the pith and cortex of the stem. The telia of *C. woroninii*, on systemically infected *Ledum* leaves of the current season, are easily distinguished from the telia of other *Chrysomyxa* species on the same hosts. The latter produce localized telia and uredinia only on overwintered leaves, produce aecia on spruce needles in the same year as infection occurs, and are not systemic in spruce. The restricted habitat distribution of *C. woroninii* and the need for overwintering outdoors suggest that this rust fungus has specific environmental requirements for survival.

INTRODUCTION

Chrysomyxa woroninii (*Uredinales*) systemically infects *Ledum* species in far northern or subalpine regions of Canada and Alaska, Europe, Siberia, Kamchatka, Japan, and China (Savile, 1950; Kuprevich & Tranzschel, 1957; Gäumann, 1959; Spaulding, 1961; Wood, 1986; He *et al*., 1995). On *Ledum* spp., *C. woroninii* causes witches' brooms, and in early spring new leaves on the brooms bear hypophyllous telia. Bud rust of spruce (*Picea*), caused by *Peridermium coruscans*, is the presumed aecial state of *C. woroninii*. In early spring, newly opened spruce buds, which are systemically infected, produce spermogonia and later aecia on the stunted needles. This disease may retard growth of heavily infected seedlings in spruce regeneration areas. In Alaska, it has also been found on female spruce cones. Because infected cones do not produce viable seeds, the disease may reduce spruce regeneration near treeline (McBeath, 1981, 1984).

Chrysomyxa woroninii is assumed to be heteroecious because of the close proximity in the field of systemic bud infections on spruce and witches' brooms on *Ledum palustre* in Europe (Kuprevich & Tranzschel, 1957) and on *L. palustre* var. *decumbens* and *L. groenlandicum* in northern Canada (Savile, 1950, 1955). The consistent proximity of spruce bud rust to infected *Ledum* spp. was also observed by the authors in the Northwest Territories, northern Finland, and western Alberta. In 1996, infections were common on both hosts in a subalpine zone 67 km north of Hinton, Alberta, near the Little Berland River (53° 40′ N, 118° 15′ W). These collections are the first record of this rust on *L. groenlandicum* in central Alberta, although bud rust was occasionally collected on spruce in central and northern Alberta (Robins *et al*., 1964, 1972, 1974). Elsewhere in western Canada it has been found on *Ledum* spp. in northern British Columbia (Wood, 1986) and in the Yukon and Northwest Territories (collection records, Mycological Herbarium (CFB), Northern Forestry Centre, Canadian Forest Service, Natural Resources Canada).

In spite of several detailed morphological studies of the spruce bud rust fungus (Kuprevich & Tranzschel, 1957; McBeath, 1984; He *et al*., 1995), several aspects of its biology are unconfirmed, including its connection with the telia on *Ledum* spp. Previous inoculation attempts to demonstrate the life-cycle were unsuccessful (Klebahn, 1914) or the results were inconclusive (Liro, 1907) because aecia of both *C. ledi* and *Peridermium coruscans* were produced on spruce. Liro (1907), whose experiments were conducted in the natural habitat of both rusts, concluded that *C. woroninii* is an overwintering form of *C. ledi*.

McBeath (1984) suggested that the bud rust fungus is autoecious and that aeciospores from infected spruce buds

cause secondary infections on adjacent shoots later in the season. As further evidence of an autoecious life-cycle, she asserted that aeciospore germ-tube cytology of the bud rust fungus is similar to that of some autoecious pine stem rusts. He *et al*. (1995) claimed to have obtained infection of spruce 2 yr after inoculation with *C. woroninii* aeciospores from spruce, but no details of their experiments were given.

Other aspects of the life cycle of *C. woroninii* that are in question are the timing and mode of infection in spruce (Ziller, 1974; McBeath, 1984) and the occurrence of uredinia. Some researchers claim that uredinia do occur (Gäumann, 1959; Mäkinen, 1964; Gjaerum, 1974), whereas others believe that the observed uredinia belong to *C. ledi*, which occurs on the same hosts, but is not systemic (Savile, 1950, 1955).

The purpose of this study was to clarify aspects of the life-cycle of *C. woroninii*, including the connection between systemic spruce bud infections and systemic shoot infections in *Ledum* spp., the timing and mode of infection in spruce, and the means of overwintering of the rust fungus.

MATERIALS AND METHODS

Observations of disease cycle

At the Little Berland River site, near Hinton, Alberta, infected black spruce (*Picea mariana*) and *Ledum groenlandicum* were tagged and observed on 25 June, 5 July, 8 Aug. and 4 Oct. 1996, and again on 19 June 1997. Disease symptoms and the presence, time of appearance, and development of all spore states of *C. woroninii* were recorded. Infected plant samples were also collected for morphological and microscopic examination of all stages of the fungus. Dormant buds of *L. groenlandicum* (plus 1 cm of stem) were collected from witches' brooms in October, sectioned, and examined with a light microscope to determine the presence of hyphae. Fresh material was sectioned by hand and mounted in lactophenol/cotton blue or preserved in formalin/acetic acid/ethanol for later processing. The latter were dehydrated through a *t*-butanol series under vacuum, embedded in Paraplast X-TRA (Monoject Scientific) under vacuum at 57 °C, and sectioned (12 μm thick) with a rotary microtome (Jensen, 1962). Sections were mounted on microscope slides with Haupt's adhesive (Gurr, 1965). Before staining, slides were dewaxed in two changes of xylene. To stain host cells, slides were briefly dipped in aqueous safranin (1%). To stain hyphae, a mixture of aqueous aniline blue in saturated aqueous picric acid (1:5, v/v) was placed on sections with a dropper, warmed gently over a flame until simmering, and washed with distilled water (Cartwright, 1929). Slides were dehydrated in an ethanol series to absolute ethanol, then dipped in xylene before mounting in Permount (Fisher Scientific Co.).

A 4 yr old spruce tree and two small *L. groenlandicum* plants infected with the rust were collected in early summer, potted, and kept in a greenhouse in Edmonton, Alberta, for observation of disease development during summer 1997. In the autumn of 1997, one *L. groenlandicum* plant was moved outdoors to overwinter, but snow cover was not ensured. During the second winter (1998–9), the plant was kept covered with snow.

Inoculation

During June and July, 1996 and 1997, several inoculation experiments (Table 1) were conducted in an attempt to elucidate the life cycle of *C. woroninii*. Trees were either grown from seed in a greenhouse or collected from a field location with no known occurrence of *C. woroninii*, and inoculated after buds had opened and were determined to be disease-free. Inoculum consisted of germinating telia on young systemically infected leaves found on brooms of *L. groenlandicum* or of pooled aeciospores obtained from several infected spruce buds collected at the Little Berland River site. Leaves with telia were kept in a moist chamber in a refrigerator at 4° to induce basidiospore production. Teliospore germination was confirmed by suspending leaves over glass slides in a moist chamber and observing deposited basidiospores with a light microscope. Two black spruce and 16 white spruce (*P. glauca*) were inoculated by laying the *Ledum* shoots, telia side down, onto immature needles of newly opened buds. Trees were misted with distilled water and covered with plastic bags for 48 to 72 h to maintain high humidity. The white spruce were inoculated and kept in a greenhouse at Edmonton, at least 250 km from any known natural occurrence of *C. woroninii*; the two black spruce were inoculated and kept outdoors at the same location. All trees were observed for infection until after needle flush the next spring. Before inoculation of plants with aeciospores, spore viability was tested on 0.3% water agar on glass slides; 1% germination was obtained. Nevertheless, aeciospores were placed onto young shoots of five white spruce and three *L.*

Table 1. Details of inoculation experiments with *Chrysomyxa woroninii*

Inoculation date	Source of inoculum[a]	Host, (no. of trees), age	Symptoms[b]
25 vi 1996	IV, *L. groenlandicum* (CFB 22187)	*P. glauca* (1), 4 yr	−
9 vii 1996	IV, *L. groenlandicum* (CFB 22188)	*P. glauca* (2), 3 yr	−
		P. glauca (13), 7 wk	Some needle discolouration
	I, *P. mariana*	*P. glauca* (5), 7 wk	−
		L. groenlandicum (3), age unknown	−
24 vi 1997	IV, *L. groenlandicum* (CFB 22138)	*P. mariana* (2), 3 or 4 yr	−, + (CFB 22172)

Note: Most experiments were done in a greenhouse at Edmonton, Alberta; the last (with *P. mariana*) was done outdoors.

[a] IV = basidiospores, I = aeciospores. CFB numbers refer to the mycological herbarium of the Northern Forestry Centre, Canadian Forest Service, Edmonton, Alberta, Canada.

[b] −, no infection; +, infection.

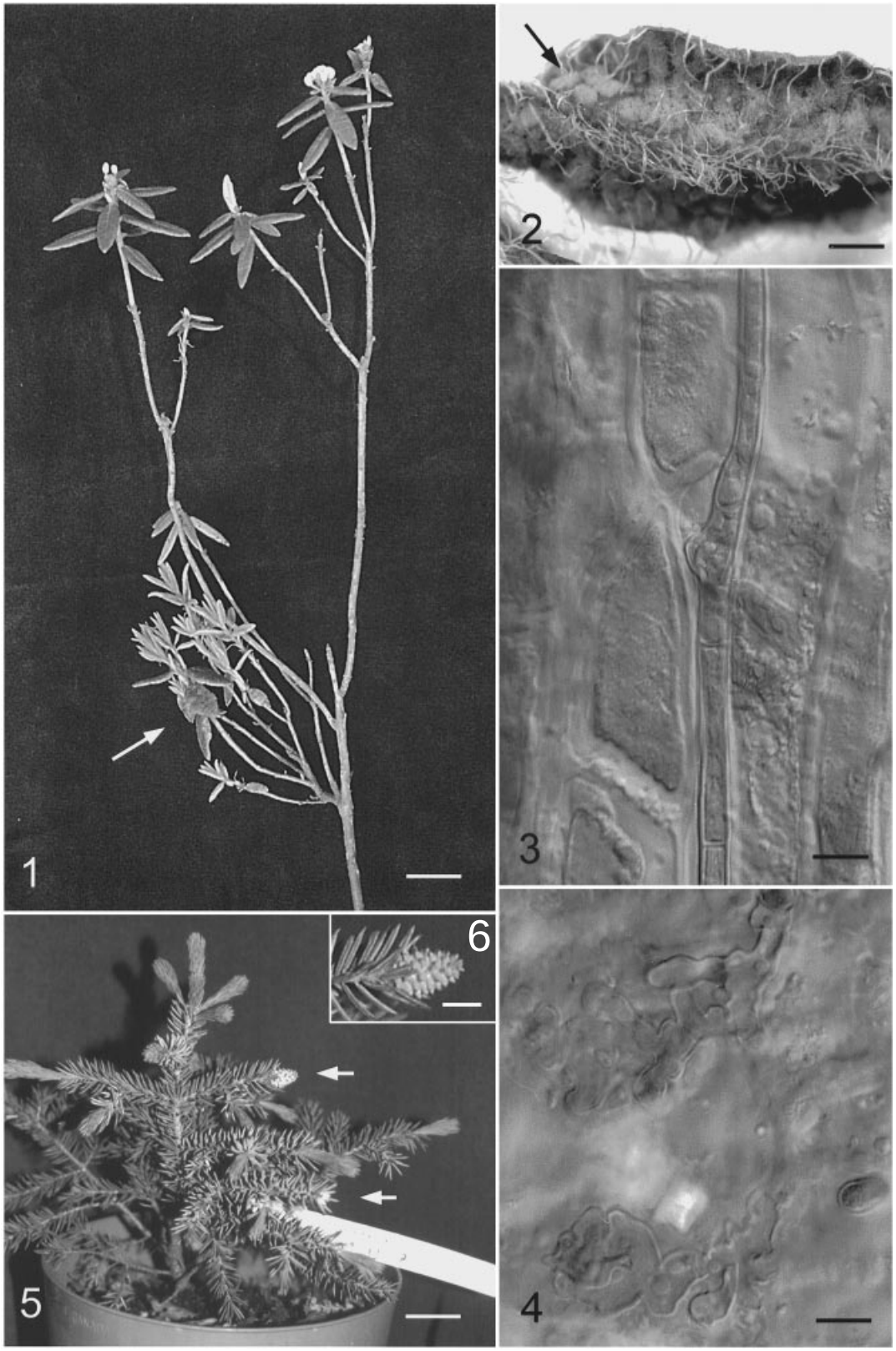

Fig. 1. Witches' broom (arrow) caused by systemic infection of *Ledum groenlandicum* with *Chrysomyxa woroninii*. The other shoots are normal in size. Bar = 2 cm. **Fig. 2.** Telia among the hairs on the underside of a newly opened leaf. Arrow points to one cushion-like telium. Bar = 1 mm. **Fig. 3.** Longitudinal section of a shoot collected in Oct. 1996 from a witches' broom on *L. groenlandicum*. Note intercellular rust hypha in the cortex of the stem below the bud. Bar = 10 μm. **Fig. 4.** Irregularly shaped hyphae in the dense stem tissue immediately below the dormant bud. Bar = 10 μm. **Fig. 5.** *Picea mariana* inoculated the previous year with basidiospores of *C. woroninii* from *L. groenlandicum*. Arrows indicate two systemically infected buds. Bar = 16 mm. **Fig. 6.** Closer view of an infected bud showing stunted needles bearing aecia. Bar = 4 mm.

groenlandicum with a small paintbrush, then plants were misted, covered as described above, and kept in a greenhouse. In all inoculations, several adjacent non-inoculated plants of the same species and age served as controls.

RESULTS

Yearly disease cycle

A naturally infected spruce kept in the greenhouse had three infected terminal buds producing aecia when it was brought from the field on 5 July. Two subtending buds appeared uninfected, although one was slightly discoloured and the needles were somewhat shrivelled. By 19 July, young aecia had begun forming at the base of these needles, but spermogonia were not observed. One of the field-infected *L. groenlandicum* plants kept in the greenhouse died. The second plant survived overwintering outdoors in spite of the lack of snow cover. The next spring, newly opened leaves on the broom were reddish at the edges, but they did not form mature telia. After the second winter, in which snow cover was provided, the broom produced new leaves covered with hypophyllous telia.

Observations of *C. woroninii* on *L. groenlandicum* and *P. mariana* at the Little Berland River site on five different dates were as follows.

25 June 1996. Small red infected buds were visible on spruce; spermogonia were present only at the ends of needles. Most spruce buds had not opened. Stunted witches' brooms were found on nearby *L. groenlandicum* (Fig. 1). Newly opened leaves on brooms were covered with immature telia on the undersides.

5 July 1996. Many infected spruce buds had turned orange; most aecia were open and shedding spores. On *Ledum* brooms, orange telia (Fig. 2) were more obvious on the underside of new leaves than on June 25. Telia and uredinia of both *C. ledi* and *C. ledicola* were present on previous year's leaves of both broomed and healthy shoots.

8 Aug. 1996. Infected spruce buds were drying up and turning black; adjacent buds had discoloured and twisted needles. Apart from the brooms there was no sign of *C. woroninii* on *Ledum*. All leaves previously infected with telia had fallen off.

4 Oct. 1996. On spruce, infected buds were black and needles had fallen off below deformed buds for 2–3 cm. *Ledum* plants had 'droopy' leaves, indicating dormancy (Harmaja, 1991). Dissection of shoots from brooms showed rust hyphae in the bracts and outer leaves of the bud, but none in the shoot apex or youngest leaves; hyphae were also seen below the bud in the pith and cortex of the stem (Fig. 3). Hyphae were intercellular, contained deep yellow vacuoles, and were 6–9 μm wide. Hyphae in the dense tissue near the bud and in the young undeveloped leaves were convoluted and irregular in shape (Fig. 4). Haustoria were simple (unbranched) and vesicular.

19 June 1997. Tagged *Ledum* plants were again producing new leaves with young telia on brooms. Spruce buds that were infected in 1996 were blackened and had no needles for some distance below the old bud. There was no new growth on these shoots, and the rust fungus did not sporulate on the same shoots.

Inoculation results

Except for needle discolouration on several seedlings during the first summer, no disease was produced on white spruce or *L. groenlandicum* inoculated with either aeciospores from rusted buds or basidiospores from *C. woroninii* on *Ledum*. Control plants for the experiments also did not show signs of disease. Two systemically infected buds were, however, produced on one black spruce tree in 1998 from inoculation with basidiospores from *L. groenlandicum* in 1997 (Table 1; Fig. 5). Unlike other inoculation attempts, which were done in a greenhouse, this successful experiment was conducted out of doors and the tree was overwintered outside. The first disease symptoms appeared 3 wk after inoculation (July 1997) as yellow to orange bands on several current-year needles that were exposed to telia on *Ledum* leaves. By late summer, infected needles had fallen from the tree. On 24 Apr. 1998, two yellow, systemically infected buds were visible on the tree. Infected buds opened before the healthy buds on the same tree. By 25 Apr., spermogonia were producing fragrant nectar at the ends of the needles. By 30 Apr., spermogonia were drying up, and needles were becoming swollen and reddish; soon after, aecia began to form along the length of the needles of both buds (Fig. 6). One bud remained much smaller than the other, and the centre needles died. Typical aecia of *C. woroninii*, however, formed on the rest of the needles of the bud. Morphological characteristics of the spermogonia, aecia, and aeciospores were consistent with published descriptions of *C. woroninii* (Savile, 1950; Kuprevich & Tranzschel, 1957; Gäumann, 1959; Ziller, 1974; McBeath, 1984; He *et al.*, 1995).

DISCUSSION

This study confirms that spruce is the alternate host of *C. woroninii*. This is supported by the successful inoculation of spruce with basidiospores produced on brooms of *L. groenlandicum* and by the constant field association of infections on both hosts. Although the successful infection was produced outdoors, the chance of two buds on one tree being infected by exogenous inoculum originating from distant natural infections is remote. In addition to the control trees kept outdoors with the infected one, there were many mature ornamental spruce of various species in the vicinity. None of these developed spruce bud rust.

This study also clarified several other aspects of the life-cycle of *C. woroninii*, most notably, the length of time required (nearly 1 yr) for systemically infected spruce buds to appear after infection. In nature, infected spruce buds open at the same time as sporulating telia are present on stunted *Ledum* shoots. Infection must, therefore, have occurred during the

previous year, as suggested earlier by Savile (1950). Such an extended life-cycle is different from non-systemic needle infecting *Chrysomyxa* species, in which infection and the production of spermogonia and aecia occur in the same growing season.

Young needles are the most likely infection site on spruce, as evidenced by the orange banding of needles during the growing season when infection takes place. Another possibility is that penetration occurs directly into the shoot axis of the newly opened bud, but infection occurs when overwintered buds have just opened, and very little expansion of this axis has occurred between the needles. In either case, hyphae could grow into or proliferate within the succulent tissue of the expanding shoot tips during the current growing season and then into the winter buds. In spruce, bud scales for the following year are already forming at shoot apices or in the needle axils when shoot elongation occurs during spring and summer. Needle primordia begin to form in these buds as soon as shoot elongation ceases in midsummer, and this continues until buds become dormant in autumn (Heide, 1974; Owens, Molder & Langer, 1977), affording ample opportunity for the rust fungus to become established in these buds.

Chrysomyxa woroninii appears to have specific environmental requirements for survival. Its patchy distribution and restriction to subalpine and far northern regions implies a high degree of ecophysiological specialization. In several greenhouse inoculations, the needle discolouration suggested that infection had succeeded. Lack of further symptom development implied, however, that requirements for dormancy, moisture, or snow cover, were possibly not met in the greenhouse. The fungus was unable to sporulate normally on the field-collected *Ledum* plant that was overwintered outdoors at Edmonton without snow cover, but it produced telia the second spring, after winter snow cover was provided. These specific environmental requirements might also explain unsuccessful attempts to produce artificial infections with this rust (Klebahn, 1914).

Production of aecia on buds adjacent to primary infected buds, as observed by McBeath (1984), was also seen in this study, both in trees at the Little Berland River site and in a naturally infected tree kept in the greenhouse for one summer. Rather than secondary infections by aeciospores, however, we believe these to be caused by systemic growth of the rust fungus within the spruce shoot as the season progresses. If these 'secondary infections' were caused by aeciospores, one would expect to find newly infected buds on other parts of the tree as well, but this was not observed. The death of needles for several centimetres below infected buds at the end of the growing season also suggests that mycelium extends for some distance below the infected bud. The rust does not recur on these buds the following year, and growth does not resume at these bud tips.

Observations of perennial brooms produced by *C. woroninii* or *L. groenlandicum* have further clarified its relationship with this host. Once telia have sporulated in the spring, the new leaves that bore them shrivel and fall off. Apart from the stunted shoots, there are no further signs of the rust for the rest of the growing season. The brooms are easily overlooked, especially in areas with a dense shrub layer. Microscopic studies of dormant shoots collected in October confirmed that *C. woroninii* overwinters within the twigs and the young leaves already formed in the dormant buds of brooms.

The relationship of *C. woroninii* to other *Ledum*-infecting rust fungi needs clarification. In addition to *C. woroninii*, there are at least three other species of *Chrysomyxa* that sporulate on the abaxial surface of leaves of *L. palustre*, *L. palustre* var. *decumbens*, or *L. groenlandicum* (members of the *C. ledi* complex, as defined by Savile, 1950, 1955, and an undescribed species (Crane *et al.*, 1998)). In addition, *C. ledicola* sporulates on the adaxial surface of leaves. All these species produce localized spruce needle infections, but not systemic bud infections, during the same growing season as inoculation (de Bary, 1879; Fraser, 1911, 1912; Crane *et al.*, 1998; Crane, unpublished). Although Liro (1907) and Jørstad (1934) maintained that aeciospores of *C. ledi sensu stricto* and *C. woroninii* are morphologically similar, our studies (unpublished) show that they are distinct. For instance, aeciospores of *C. woroninii* are extremely variable in length (up to 62 µm long), they do not have a groove (oriented parallel to the long axis of the spore), and warts are broad and flat-topped. In contrast, aeciospores of *C. ledi* (the European variety) reach a maximum length of 36 µm, they have a vertical groove, and surface warts are narrow and tapering. The North American hypophyllous *Ledum* rusts also have distinct spore morphology (Crane *et al.*, 1998). In addition, most of these fungi have a much more widespread habitat distribution than does *C. woroninii* (Jørstad, 1934; Ziller, 1974). Their presence on the same hosts probably explains the confusion over whether uredinia occur in *C. woroninii*. Uredinia that appear on leaves of the previous season, of both broomed and healthy *Ledum* shoots, were confirmed by microscopic examination to belong to one of the members of the *C. ledi* complex or to *C. ledicola*. Their telia form in small localized groups. Telia of *C. woroninii*, on the other hand, completely cover the underside of systemically infected leaves of the current year.

Confusion among these rust fungi also occurs where a severe outbreak of *C. ledi* on spruce needles is followed the next year by frequent bud rust infections (Liro, 1907; R. Jalkanen, Finnish Forest Research Institute, pers. comm.). It is likely that the conditions that are conducive to heavy infections of *C. ledi* in a given year also produce heavy *C. woroninii* infections. The outbreak of *C. ledi* would occur in the first year, however, whereas *C. woroninii* would not appear until the second. This could lead to the conclusion that they are different states of the same rust.

This study has confirmed that *C. woroninii* is a heteroecious rust, with the telia produced on current-year leaves of systemically infected shoots of *Ledum* spp. and the spermogonia and aecia on buds of *Picea* spp.; that it is perennial and systemic in the broadleaved host and systemic and annual in the conifer host; that the bud rust symptom on *Picea* spp. is visible the growing season after the one in which infection occurs; that *C. woroninii* is distinct from other *Chrysomyxa* species that inhabit the same hosts and produce localized infections; and that it has a delicately balanced relationship with both of its hosts. Its ability to coexist with but not seriously damage its host plants, and its requirement for specific environmental conditions to support these relation-

ships, suggest a long history of coevolution among the organisms in this pathosystem.

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