

1 **Recovery Plan for Scots Pine Blister Rust Caused by *Cronartium pini***

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3 Mee-Sook Kim,<sup>1\*</sup> Jarkko Hantula,<sup>2</sup> Juha Kaitera,<sup>3</sup> Paul J. Zambino,<sup>4</sup> Stephen Woodward,<sup>5</sup>

4 Bryce A. Richardson,<sup>6</sup> Jane E. Stewart,<sup>7</sup> Pauline Spaine,<sup>8</sup> David C. Shaw,<sup>9</sup> Yu Takeuchi,<sup>10</sup> Ned

5 B. Klopfenstein<sup>6</sup>

6

7 <sup>1</sup>U.S.D.A. Forest Service, Pacific Northwest Research Station, Corvallis, OR 97331, U.S.A.

8 <sup>2</sup>Natural Resources Institute Finland, Latokartanonkaari 9, FI-00790 Helsinki, Finland

9 <sup>3</sup>Natural Resources Institute Finland, Paavo Havaksen tie 3, FI-90570 Oulu, Finland

10 <sup>4</sup>U.S.D.A. Forest Service, Forest Health Protection, Coeur d'Alene, ID 83815, U.S.A.

11 <sup>5</sup>University of Aberdeen, School of Biological Sciences, Aberdeen, Scotland, UK

12 <sup>6</sup>U.S.D.A. Forest Service, Rocky Mountain Research Station, Moscow, ID 83843, U.S.A.

13 <sup>7</sup>Colorado State University, Department of Agricultural Biology, Ft. Collins, CO 80525,  
14 U.S.A.

15 <sup>8</sup>U.S.D.A. APHIS, PPQ-PHP-IRM, Plants for Planting Policy, Riverdale, MD 20737, U.S.A.

16 <sup>9</sup>Oregon State University, Department of Forest Engineering, Resources & Management,  
17 Corvallis, OR 97331, U.S.A.

18 <sup>10</sup>North Carolina State University, Center for Integrated Pest Management, Raleigh, NC  
19 27606, U.S.A.

20 \*Corresponding author: M.-S. Kim; E-mail: [meesook.kim@usda.gov](mailto:meesook.kim@usda.gov)

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22 Keywords: invasive forest pathogen, National Plant Disease Recovery System, pine stem rust,  
23 resin-top disease

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39 This recovery plan is one of several plant disease-specific documents produced as part of the  
40 National Plant Disease Recovery System (NPDRS) requested by the Homeland Security  
41 Presidential Directive Number 9 (HSPD-9). The purpose of the NPDRS is to ensure that the tools,  
42 infrastructure, communication networks, and capacity required for mitigating impacts of high-  
43 consequence, plant-disease outbreaks are implemented so that a reasonable level of crop production  
44 is maintained.

45 Each plant disease-specific plan is intended to provide a brief summary of the disease,  
46 assess the status of critical recovery components, and identify disease management research,  
47 extension, and education needs. These documents are not intended to serve as stand-alone

48 documents that address all of the many and varied aspects of plant disease outbreaks, all of the  
49 critical decisions that must be determined, or all of the actions needed to achieve effective response  
50 and recovery. These plans are, however, documents that will help the USDA to guide further efforts  
51 directed toward plant disease recovery.

52

53

### Executive Summary

54 Scots pine blister rust caused by *Cronartium pini*, which includes the fungal rust pathogen  
55 with either a heteroecious life-cycle (previously known as *Cronartium flaccidum*) or an  
56 autoecious life-cycle (formerly known as *Peridermium pini* or *Endocronartium pini*), is capable  
57 of infecting many Eurasian pines including *Pinus sylvestris* (Scots pine), *P. pinaster* (maritime  
58 pine), *P. pinea* (Italian stone pine), *P. halepensis* (Aleppo pine), *P. mugo* (mugo pine), *P. nigra*  
59 (Austrian pine or black pine), *P. brutia* (brutia pine or Turkish pine), *P. densiflora* (Japanese red  
60 pine or Korean red pine), *P. radiata* (Monterey pine or radiata pine), *P. koraiensis* (Korean pine),  
61 *P. massoniana* (Masson pine), *P. tabuliformis* (Manchurian red pine), *P. taiwanensis*  
62 (Taiwan red pine), *P. pumila* (Siberian dwarf pine), *P. uncinata* (Swiss mountain pine), *P.*  
63 *wallichiana* (Himalayan pine or Bhutan Pine), *P. takahasii*, and *P. yunnanensis* (Yunnan pine).  
64 According to population genetic studies, the two forms of *C. pini* have not been differentiated by  
65 presently available DNA sequencing analyses, likely because gene flow occurs between the two  
66 forms. However, the aecia of the two forms of the rust pathogen differ in the heterozygotic state,  
67 which can only be observed in the heteroecious form. The heteroecious form completes its life  
68 cycle alternating between pines and various species of flowering plants (Angiospermae) (see  
69 Table 2 for a list of alternate host species); the related autoecious form spreads directly from pine  
70 to pine. Scots pine blister rust is widely distributed across Eurasia. The impact is most severe on  
71 Scots pine and several Mediterranean pines.

72           Susceptibility of native North American pine species and populations to Scots pine blister  
73 rust is mostly unknown at this time, although *P. radiata* and *P. ponderosa* (ponderosa pine) are  
74 reported to be susceptible. *Pinus resinosa* (red pine), which is closely related to known hosts,  
75 should be considered as a potential pine host. However, if the Scots pine blister rust pathogen  
76 possesses or gains the capacity to infect North American pines, the economic and ecological  
77 impacts could be quite significant, and the potential influences of climate change and other  
78 environmental factors remain unknown. The direct cost to control white pine blister rust (caused  
79 by *C. ribicola*) since its introduction into North America during the early 1900s has been  
80 estimated at over 1 billion in current US dollars, and this disease has caused much greater indirect  
81 losses through reduced forest productivity and ecological impacts.

82           Scots pine is one of the most widely distributed conifers in the world. It grows naturally  
83 from Scotland east to the Pacific Ocean, from the 69<sup>th</sup> latitude in Scandinavia to the  
84 Mediterranean Basin. In addition, Scots pine has been widely planted in colder regions of North  
85 America, and it has become naturalized in the northeastern and midwestern United States. It is  
86 planted in North America for erosion control, ornamental purposes, and pulp/timber production,  
87 but its primary economic value is as a Christmas tree crop. According to the 2019 Census of  
88 Horticultural Specialties in the United States, nearly 2,857 operations sold 11.7 million  
89 Christmas trees valued at \$357.1 million in 2019, and Scots pine is one of the most commonly  
90 used Christmas tree species in the United States.

91           Scots pine blister rust is also called resin-top disease and top-dieback of pine for  
92 affected trees in all age and size classes. Symptoms in pine include stem swelling, branch  
93 flagging, excessive pitch flow, and top-kill, and, in the alternate hosts, leaf spotting. The rust  
94 pathogen is spread in nature by wind-borne spores, which require live hosts for infection.  
95 However, the rust pathogen can also be transported on infected plant materials that can be non-

96 symptomatic. Early infections of host plant infections by *C. pini* are difficult to detect and  
97 diagnose, but molecular techniques offer a potential approach for early detection and diagnosis.

98 Scots pine blister rust is widespread across Eurasia, and it has long been a major factor in  
99 reducing forest productivity in Europe; however, this rust disease has not been found in North  
100 America. The safest plant protection policy for North America would be to prohibit the importation  
101 of pine and non-pine hosts of Scots pine blister rust. If host plants were imported, a thorough visual  
102 inspection for signs and symptoms of Scots pine blister rust should be conducted, followed by a  
103 quarantine and/or extended monitoring. Early detection of Scots pine blister rust at port facilities  
104 can provide some defense against introduction. However, non-symptomatic infections in this slow-  
105 developing disease could easily be overlooked by visual inspections, so out-plantings should be  
106 monitored for several years. Further diagnostic techniques, such as microscopy and simple DNA-  
107 based tools, can be used to confirm rust pathogen infection and identity in symptomatic plants. The  
108 following strategies may help to prevent the introduction of the Scots pine blister rust pathogen:

- 109
- 110 • Ban importation of living Scots pine trees/seedlings for nursery trade (*Pinus* spp. from all  
111 countries, except Canada, Japan, and South Korea, are currently prohibited from  
112 importation to the United States); allow importation of known angiosperm alternate hosts  
113 only as seed (or at least as dormant and leafless plants).
  - 114 • Determine potential susceptibility of North American pines to Scots pine blister rust.
  - 115 • Establish a monitoring system for Scots pine blister rust and other invasive rust pathogen  
116 species, especially in tree nursery and Christmas tree farm settings near likely points of  
117 introduction.
  - 118 • Develop time-efficient, species-specific molecular tools to detect and identify *C. pini*.
  - 119 • Develop models that predict potential spread of the Scots pine blister rust pathogen

120 from introduction points using distribution of suitable hosts and bioclimatic models

121 that identify suitable climate niches across the geographic ranges of diverse hosts.

122 • Improve educational awareness about potentially invasive rust pathogens among plant  
123 diagnosticians, extension agents, forest managers, nursery growers, Christmas tree  
124 growers, horticulturalists, and the general public.

125 • Conduct genetic analyses of the Scots pine blister rust pathogen and its known and potential  
126 hosts to predict potential invasive risks in North America.

127

128

### I. Introduction

129 The causal agent of Scots pine blister rust (resin-top disease; top-dieback of pine) is

130 *Cronartium pini* (Willd.) Jørstad [(syn. *Cronartium flaccidum* (Alb. & Schwein.) G. Winter,

131 *Peridermium pini* (Pers.) Lév., *C. asclepiadeum* (Willd.) Fr., *Endocronartium pini* (Pers.) Y.

132 Hiratsuka)] (Fig. 1). The sexually reproducing heteroecious form of the Scots pine blister rust

133 pathogen, formerly known as *C. flaccidum*, completes its life cycle by alternating between pines

134 mostly in the subgenus *Pinus* (hard pines) and flowering plants of various families. Scots pine

135 blister rust is also caused by an autoecious form of the rust pathogen, formerly known as

136 *Peridermium pini* and *Endocronartium pini*, that spreads directly from pine to pine.

137 Scots pine blister rust infects many *Pinus* species in Europe and Asia. The heteroecious

138 form causes severe damage in natural forests on *P. sylvestris* L. (Scots pine) in northern Finland;

139 whereas, the heteroecious form of *C. pini* is reported on Scots pine, *P. pinaster* Ait. (maritime

140 pine), *P. pinea* L. (Italian stone pine), *P. halepensis* Mill. (Aleppo pine), *P. mugo* Turra (mugo

141 pine), and *P. nigra* Arn. (Austrian pine or black pine) in southern Europe. Other reported *Pinus*

142 host species of *C. pini* include *P. brutia* Ten. (brutia pine or Turkish pine), *P. densiflora* Siebold

143 & Zucc. (Japanese red pine or Korean red pine), *P. radiata* D. Don (Monterey pine or radiata

144 pine), *P. koraiensis* Siebold & Zucc. (Korean pine), *P. massoniana* Lamb. (Masson pine), *P.*  
 145 *tabuliformis* Carrière (Manchurian red pine), *P. taiwanensis* Hayata (Taiwan red pine), *P. pumila*  
 146 Regel (Siberian dwarf pine), *P. uncinata* Ramond ex DC. (Swiss mountain pine), *P. wallichiana*  
 147 A.B.Jacks. (Himalayan pine or Bhutan Pine), *P. takahasii* Nakai, and *P. yunnanensis* Franch.  
 148 (Yunnan pine) (CABI 2020). North American pines reported to be susceptible to *C. pini* include  
 149 *P. radiata* (CABI 2020), and *P. ponderosa* Douglas ex C.Lawson (ponderosa pine) (Gibbs and  
 150 Kaitera 2018). The autoecious form of *C. pini* causes damage on Scots pine and mugo pine  
 151 (Kaitera and Nuorteva 2008). Of the Eurasian pine hosts, Scots pine and Austrian/black pine are  
 152 commonly planted in North America. Needle symptoms have been reported after artificial or  
 153 natural exposure to *C. pini* inoculum on other native and exotic two-needle pines that occur in the  
 154 United States (Raddi and Fagnani 1978). The alternate (telial) hosts for the heteroecious form of  
 155 *C. pini* belong to the angiosperm families: Gentianaceae, Balsaminaceae, Loasaceae, Paeoniaceae,  
 156 Tropaeolaceae, Verbenaceae, Apocynaceae, Orobanchaceae, Acanthaceae, Plantaginaceae,  
 157 Scrophulariaceae, Solanaceae, Papaveraceae, Saxifragaceae, and Myricaceae.

158 Scots pine blister rust is widely distributed across Europe and Asia. Both the heteroecious  
 159 and the autoecious forms of *C. pini* cause severe damage on pines (Fig. 2), where they produce  
 160 branch and stem lesions. Lesions caused by the heteroecious form typically kill the tree more  
 161 rapidly than those caused by the autoecious form. The rust is most severe on Scots pine and  
 162 several of the Mediterranean pine hosts. Scots pine blister rust has been reported in widely  
 163 ranging Eurasian countries including Armenia, Austria, Azerbaijan, Belgium, Bosnia and  
 164 Herzegovina, Bulgaria, Croatia, Czech Republic, Denmark, Estonia, Finland, France, Georgia,  
 165 Germany, Great Britain, Greece, Hungary, Italy, Kosovo, Latvia, Lithuania, Macedonia,  
 166 Montenegro, Netherlands, Norway, Poland, Portugal, Romania, Russia (from Europe to far  
 167 eastern Russia), Serbia, Slovenia, Spain, Sweden, Switzerland, Turkey, and Ukraine (CABI 2020,

168 Özkazanç and Maden 2013). In Asia, a rust referred to as Scots pine blister rust is also found in  
169 China, Japan, Kazakhstan, Korea, and Taiwan (CABI 2020).

170

## 171 **GEOGRAPHIC DISTRIBUTION OF SCOTS PINE**

172 Scots pine (sometimes previously referred to as ‘Scotch’ pine) is one of the most widely  
173 distributed conifers in the world. Its native range extends from Great Britain and Spain east  
174 through Siberia, south to the southern Caucasus region and north to Lapland. Scots pine has been  
175 widely planted in New Zealand and the colder regions of North America, and it has become  
176 naturalized in the northeastern, midwestern, and Pacific northwestern United States. Scots pine is  
177 the only pine native to northern Europe and once formed much of the Caledonian Forest of the  
178 Scottish Highlands. In its northern distribution, it ranges from sea level to 914 m (3000 ft) in the  
179 British Isles; whereas, in its southern distribution, Scots pine grows at higher elevations, from  
180 1219 to 2590 m (4000 to 8500 ft).

181 Scots pine trees can typically attain a height of 24 m (80 ft), a diameter in excess of 0.9  
182 m (3 ft), and an age of 200 years, or, exceptionally, a height of 46 m (150 ft), a diameter of 1.7  
183 m (5½ ft), and an age of 700 years. Scots pine requires full sun and the absence of excessive  
184 grazing to establish from seed, and it can quickly invade disturbed areas. In the United States,  
185 Scots pine has been planted for erosion control, ornamental purposes, and pulp/timber  
186 production; however, its primary economic value is currently as Christmas trees (Agricultural  
187 Marketing Resource Center 2008), although other conifers are becoming more favored,  
188 recently.

189

## 190 **NOMENCLATURE/TAXONOMY OF SCOTS PINE BLISTER RUST**

191 The rust fungi (Basidiomycota: Pucciniomycetes: Pucciniales) are a large, diverse group



192 of biotrophic fungi that reproduce only in living plant tissue, containing the family Cronartiaceae,  
193 which comprises three genera (*Cronartium*, *Endocronartium*, and *Peridermium*). Among the  
194 many important plant pathogens in this group are the pine stem rust fungi *Cronartium* and  
195 *Peridermium*. The taxonomy of the Scots pine blister rust pathogen has been particularly  
196 confusing, owing to a relationship between the host-alternating and pine-to-pine forms that were  
197 previously known as *C. flaccidum* and *P. pini* (*E. pini*), respectively. Foresters and mycologists  
198 have long recognized the similarity of the rust diseases caused by these fungi and the apparently  
199 identical morphology of their spores produced on infected pine stems and branches. The chief  
200 difference between the pine-borne spores of the two rust fungi is their infection of flowering  
201 plants and pines vs. sole infection of pines. Hiratsuka (1968) reported developmental differences  
202 in spore germination (and life cycle), which prompted him to name the pine-to-pine form  
203 *Endocronartium pini*. However, molecular evidence points to a very close evolutionary  
204 relationship between these rust pathogens (e.g., Vogler and Bruns 1998). Hantula et al. (2002)  
205 provided morphological and molecular evidence demonstrating Scots pine blister rust pathogens  
206 as a single species with alternative life cycles. Later, other population studies also confirmed  
207 that Scots pine blister rust pathogens belong to a single species (Samils et al. 2011, 2021). As a  
208 consequence, the two forms of *C. pini* have not been differentiated by presently available DNA  
209 sequence analyses or aeciospore morphology, although an analysis of  
210 homozygotic/heterozygotic loci can potentially differentiate the rust pathogen forms in the  
211 aecial stage (Kasanen 1997). Although the morphology of the Scots pine blister rust pathogen  
212 shares some similarities to other rust pathogens, DNA sequences (e.g., ITS) of the Scots pine  
213 blister rust pathogen are distinct from other known rust pathogen species. For this reason, the  
214 Scots pine blister rust pathogen could be detected by molecular means for quarantine control.

215 Recently, the Scots pine blister rust fungus has been renamed as *C. pini* (Willd.) Jørstad.

216 (Species Fungorum 2021, Wijesinghe et al. 2019). In this review, we refer to Scots pine blister  
217 rust without distinguishing between its life cycle forms. However, the Scots pine blister rust  
218 form is reported when specific studies pertain to a specific life-cycle form.

219

220

## II. Biology and Symptoms

### 221 LIFE CYCLE

222 A typical *Cronartium* species that alternates between pine and angiosperm hosts has five  
223 spore stages; nomenclature, morphology, and nuclear condition given here are from Cummins and  
224 Hiratsuka (2003) (Fig. 3).

225

226 Stage 0 – Spermata—borne in spermogonia.

227 Spermogonia are hermaphroditic structures containing female receptive hyphae and male  
228 spermata. Spermogonia occur in the outer pine stem cortex under the host periderm and  
229 produce spermata in a sugary fluid, which is attractive to insects.

230 Monokaryotic haploid (N) spermogonia produce haploid, uninucleate spermata that are  
231 small, thin-walled, and globose to flask-like in shape. Spermata are transferred by insects to  
232 other spermogonia, where, following union with a receptive hypha, a dikaryotic (N+N) mycelium  
233 is produced that eventually produces aecia.

234

235 Stage 1 – Aeciospores—borne in aecia.

236 Aecia develop in the stem cortex of a host pine and are often associated with hypertrophy of the  
237 stem tissue. The aecium is a structure that produces chains of binucleate, warty, thick-walled,  
238 pigmented aeciospores that are bordered by a prominent papery peridium. The host cortex ruptures  
239 as the aecia mature, the peridium ruptures, and aeciospores are released. Aeciospores are dispersed

240 aerially, and, following germination, produce a dikaryotic mycelium in angiosperm plant species  
241 that serve as alternate hosts.

242

243 Stage 2 – Urediniospores—borne in uredinia.

244 Urediniospores, like aeciospores, are dikaryotic. Urediniospores and aeciospores both infect the  
245 non-pine hosts through stomata and give rise to a mycelium that can form uredinia or telia.

246 However, urediniospores can cause a repeating cycle of infections on the non-pine hosts without a  
247 sexual stage. The uredinium develops from subepidermal mycelium, and urediniospores erupt

248 through the epidermis. Urediniospores are spiny, borne individually, and aerially dispersed.

249

250 Stage 3 – Teliospores—borne in telia.

251 The telium arises from subepidermal, heterokaryotic hyphae that may have previously produced  
252 urediniospores, and develops into an erumpent, hair-like column of dark, thick-walled

253 teliospores on the non-pine host. Teliospores are not dispersed, but are the site of karyogamy

254 and produce metabasidia (2N) that undergo meiosis, leading to formation of an elongate, septate  
255 basidium and basidiospores.

256

257 Stage 4 – Basidiospores—borne on basidia.

258 Basidiospores are globose, thin-walled, haploid (N) spores that develop on projections of the  
259 basidia called sterigmata, which aid forcible ejection of the basidiospores. Basidiospores are

260 discharged away from the telium and dispersed in moist air currents to a pine host needle or

261 shoot. Basidiospores germinate and infect pine needles through stomata. The haploid mycelium

262 grows down the needle and into the stem; when the mycelium reaches sufficient quantity and

263 density, spermogonia will be produced to complete the cycle.

264 Cummins and Hiratsuka (2003) describe the life cycle of *Peridermium pini* as endocyclic  
265 and justify their nomenclature of *Endocronartium pini*. In this case, spores that morphologically  
266 resemble aeciospores are produced on the pine host, dispersed, and directly infect other pines.  
267 Spermogonia may also be produced.

268 The heteroecious form of Scots pine blister rust infects a host pine through needle  
269 stomata (Ragazzi and Dellavalle Fedi 1992), but symptoms on the branch or main stem only  
270 become apparent later in development. Infection of the autoecious form can also occur through  
271 wounds (Kaitera and Nuorteva 2008). In pine, the Scots pine blister rust fungus produces several  
272 types of reproductive structures that are observed as either tiny sacs of a sugary “nectar” with  
273 spermatia (Fig. 4A) or small, white, or light orange bladders (Fig. 4B) filled with powdery,  
274 orange-colored aeciospores. Both the heteroecious and autoecious forms produce spermogonia  
275 and aecia. Spermogonia usually form within a swelling of the phloem, 1 (autoecious form) to 2  
276 (heteroecious form) years after infection (Kaitera and Nuorteva 2008). Aecia formation follows a  
277 year after the spermogonia are produced, and aecia formation can last in the same lesion for up to  
278 8 years (Kaitera 2003). Diseased branches become swollen; after release of the aeciospores, the  
279 bark cracks, darkens, and the end of the branch is killed if the branch becomes girdled. Infection  
280 in a main stem by the Scots pine blister rust pathogen can also produce spermatia and  
281 aeciospores. The disease first appears as a diamond-shaped, resinous canker, and eventually  
282 girdles the stem, which kills the distal part of the branch or acropetal portion of the stem. Insects  
283 carry spermatia among Scots pine blister rust cankers of diseased pines and aid in fertilization.  
284 After formation of aecia, aeciospores can develop in aecia several years after fertilization.  
285 Aeciospores are released in summer, and they can be wind carried for long distances to infect a  
286 suitable host. The Scots pine blister rust pathogen grows downwards in a pine stem >10 cm  
287 (several inches) per year. Small trees are killed within several years of infection; larger trees are

288 often infected in the middle of the crown, so if not killed by a girdling, resinous canker, an  
289 infected tree may persist for decades with a dead top, hence the name “resin-top disease” (Fig. 2).

290

### 291 **III. Spread and Risk Map**

#### 292 **SPREAD OF THE SCOTS PINE BLISTER RUST PATHOGEN**

293 Although natural spread of the Scots pine blister rust pathogen is principally via aerial  
294 dispersal, important differences between the two life-cycle forms of the rust pathogen determine if  
295 infection occurs pine-to-pine or through an alternate host. Infection of a pine by the heteroecious  
296 form eventually results in production of specialized structures (spermogonia) that mediate cross-  
297 fertilization (genetic exchange) by transfer of insect-vectored spermatia to the receptive hyphae of  
298 a separate infection. In late spring through summer, hyphae fertilized in the previous year form  
299 blister-like aecia with yellow-pigmented, thick-walled aeciospores that aerially disseminate the  
300 rust pathogen to the alternate host. Although most dispersal is likely limited to within ca. 10 km  
301 (ca. 6 miles) and is mostly much closer, a very small proportion of aeciospores may be carried  
302 >300 km (>200 miles) from the parental canker. The first spore stage produced on alternate hosts,  
303 uredinia with urediniospores (Fig. 4), may increase infection on the same or different alternate  
304 host plants, which can affect some further rust dispersal. More importantly, the uredinial stage can  
305 produce a large, nonsexual amplification of inoculum under some environmental conditions, such  
306 as increased temperature and/or moisture during critical periods that promote urediniospore  
307 amplification. In late summer or early autumn, another spore stage, the teliospore, is produced.  
308 The teliospores produce the final spore stage, the basidiospores, that are ejected into the air and  
309 dispersed by the wind. Since basidiospores are delicate, they are usually dispersed <10 km (ca. 6  
310 miles), but typically for much shorter distances. If a viable basidiospore lands on a pine needle,  
311 germinates, grows into the needle (usually through a stomata), and avoids a resistance response

312 by the host, the pine becomes infected. Although a description of the sexual process in the pine-  
313 to-pine form is subject to disagreement, the initial stages resemble those of the spermogonia and  
314 aecia with the difference that aeciospores infect a pine host directly without intermediate stages  
315 on alternate hosts.

316 Alternate hosts of the Scots pine blister rust pathogen reside in diverse angiosperm  
317 families and genera. Based on inoculation tests in Scandinavia, the genera *Loasa*, *Nemesia*,  
318 *Melampyrum*, *Tropaeolum*, *Vincetoxicum*, *Pedicularis*, and *Paeonia* are all reported as alternate  
319 hosts of the Scots pine blister rust pathogen (Kaitera et al. 1999). Kaitera and Nuorteva (2003a)  
320 reported that *C. pini* produces uredinia and telia on *Melampyrum nemorosum* and on Finnish  
321 *Vincetoxicum hirundinaria*. Elsewhere in Europe, evidence is growing that *C. pini* commonly  
322 spreads in nature on other alternate hosts in the cow-wheat family of herbaceous plants  
323 (*Melampyrum* spp.) (Kaitera et al. 2005). Newly described hosts within the *Melampyrum* genus  
324 are *M. pratense*, *M. nemorosum*, and *M. arvense*. Previously known alternate hosts are *V.*  
325 *hirundinaria* (Swallow-wort) (Fig. 5) and *M. sylvaticum* (small cow-wheat). Other susceptible  
326 species have been observed in the genera *Veronica* (Kaitera et al. 2015, 2018), *Hyoscyamus*  
327 (Kaitera et al. 2015), *Nicotiana* (Kaitera et al. 2015), *Bartsia* (Kaitera and Hiltunen 2012; Kaitera  
328 et al. 2012), *Rhinanthus* (Kaitera et al. 2015, 2018), *Euphrasia* (Kaitera et al. 2012, 2018),  
329 *Castilleja* (Kaitera et al. 2015), *Odontites* (Kaitera et al. 2018), *Saxifraga* (Kaitera et al. 2015,  
330 2018), *Myrica* (Kaitera et al. 2012, 2015), *Caiophora* (Kaitera et al. 2012), *Asclepias* (Kaitera and  
331 Hiltunen 2012), *Apocynum* (Kaitera et al. 2015), *Swertia* (Kaitera et al. 2015, 2018), *Impatiens*  
332 (Kaitera et al. 2012, 2015), and *Papaver* (Kaitera et al. 2018) (Fig. 5).

333

### 334 RISK MAPPING OF SCOTS PINE BLISTER RUST

335 A risk map for Scots pine blister rust pathogen was created based on the temperatures required for

336 germination of *C. pini* aeciospores. The temperature range of *C. pini* aeciospore germination was  
337 previously determined as 5 - 30°C, and telia formation was enhanced by precipitation (Ragazzi  
338 1983; Ragazzi et al 1986). The areas with suitable weather conditions were characterized using  
339 tools within the Spatial Analytic Framework for Advanced Risk Information Systems (SAFARIS)  
340 and PRISM climatic data from 2000 to 2019 (PRISM Climate Group 2021; SAFARIS 2021). In  
341 addition, the distribution of *Pinus* species was incorporated in the climate suitability map. The  
342 risk map represents a combination of pine distribution (including all *Pinus* species and assuming  
343 equal susceptibility for all *Pinus* species) and incidence of perceived weather that is considered  
344 favorable for infection (Fig. 6). However, caution is warranted in interpreting this model because  
345 it does not account for differences in different pine species' susceptibility to and host suitability  
346 for Scots pine blister rust. Furthermore, this model does not incorporate information associated  
347 with potential alternate hosts of *C. pini*. An improved prediction model based on more accurate  
348 host and climate data would more precisely predict geographic areas at risk from *C. pini*  
349 infection.

350

## 351 **VI. Monitoring, Detection, and Identification**

352 Although widespread in Eurasia, Scots pine blister rust has not been found in North  
353 America. Thus, exclusion of *C. pini* is the first line of defense to protect North America from Scots  
354 pine blister rust. Preventing the introduction of *C. pini* will require effective monitoring and  
355 detection procedures. Based on past introductions of plant pathogens, importation of infected  
356 primary or alternate host material represents the most likely pathway of introduction. Host  
357 materials, such as whole plants or leaf and stem tissue from the host plants listed above, represents  
358 the highest risk for harboring the pathogen. *Pinus thunbergii* Parl. (Japanese black pine), mugo pine  
359 or other two- or three-needled pines, commonly used for bonsai, pose a significant risk if imported

360 as whole plants.

361 Scots pines in each region of the United States should be routinely monitored to detect  
362 any outbreaks of Scots pine blister rust. The United States Departments of Agriculture (USDA),  
363 Animal and Plant Health Inspection Service (APHIS) should be requested to include Scots pine  
364 blister rust in their diseases of special interest for inspections of nurseries and Christmas trees.  
365 State, federal, and private organizations should be requested to inspect for Scots pine blister rust  
366 in Scots pine forest and resource conservation plantings. These requests should be accompanied  
367 by descriptions of the disease (symptoms, signs, biology), a sampling protocol, and a list of  
368 laboratories equipped to provide proper identification of the pathogens. The USDA APHIS -  
369 Cooperative Agricultural Pest Survey Program  
370 (<https://www.aphis.usda.gov/aphis/ourfocus/planthealth/pest-detection>) and Forest Service -  
371 Forest Health Monitoring Program ([https://www.fs.fed.us/foresthealth/protecting-forest/forest-](https://www.fs.fed.us/foresthealth/protecting-forest/forest-health-monitoring/)  
372 [health-monitoring/](https://www.fs.fed.us/foresthealth/protecting-forest/forest-health-monitoring/)) should collaborate with state Departments of Agriculture for monitoring and  
373 detecting Scots pine blister rust. USDA Extension programs (<https://nifa.usda.gov/extension>) at  
374 Land Grant Universities should also be employed to educate growers and landowners.

375 Early detection of Scots pine blister rust at port facilities represents the first and best defense  
376 against introduction. The safest policy would be to prohibit the importation of primary and alternate  
377 host plants and plant parts into North America; however, the importation of host plant seed would  
378 represent only minimal risk for carrying *C. pini*. *Pinus* spp. seed is allowed to be imported into the  
379 United States from all countries.

380 Perennial host plants that are regulated as prohibited or as Not Authorized Pending Pest  
381 Risk Analysis (NAPPRA) are imported under a USDA APHIS Controlled Import Permit  
382 (PPQ588: [https://www.aphis.usda.gov/aphis/ourfocus/planthealth/import-](https://www.aphis.usda.gov/aphis/ourfocus/planthealth/import-information/permits/plants-and-plant-products-permits/prohibited/cip)  
383 [information/permits/plants-and-plant-products-permits/prohibited/cip](https://www.aphis.usda.gov/aphis/ourfocus/planthealth/import-information/permits/plants-and-plant-products-permits/prohibited/cip)). Scots pine plants imported



384 under this permit are required to follow quarantine procedures outlined in the permit. Quarantine  
385 procedures allow time for symptoms and signs of *C. pini* infection to develop, which may not  
386 have been expressed at the time of importation; quarantined plants that manifest signs or  
387 symptoms of *C. pini* infection must be destroyed according to USDA-APHIS-PPQ regulations. A  
388 thorough visual inspection of signs and symptoms of Scots pine blister rust should be conducted  
389 under a controlled environment (i.e., a biological containment greenhouse or a type II biological  
390 safety hood). Pine host symptoms include fusiform-shaped swelling (Figs. 4 and 7), resinosis of  
391 stem or branches (Fig. 7A), and/or yellow flecking of needles. Primary host signs include sticky,  
392 yellow, malodorous spore nectar and/or yellow-orange pustules on the stem or branches, and/or  
393 powdery yellow-orange spores (Fig. 4). Symptoms on angiosperm hosts include small spots (1–4  
394 mm across) of yellow or lighter green than surrounding tissues on the underside of leaves.  
395 Angiosperm host signs include orange pustules (uredinia) or hair-like fungal structures (telia)  
396 protruding from the underside of leaves (Fig. 5). Visual diagnoses can be made with a hand lens  
397 or dissecting microscope; however, signs and symptoms may be latent for 3 to 4 years in infected  
398 pine host material, and up to a month in leafy alternate hosts. Non-symptomatic infections could  
399 be easily overlooked by visual inspections, especially upon arrival of recently infected materials.

400

#### 401 **DIAGNOSIS OF THE PATHOGEN**

402 Morphological features of aeciospores and/or urediniospores of *C. pini* are not specific  
403 enough to allow rapid identification of this rust pathogen species, but identification can be  
404 accomplished with DNA sequence-based tools (Hantula et al. 2002). Rust spores, whether  
405 collected from leaves, cankers, aecia, or uredinia (from the host/alternate host), spore traps, or  
406 washes from plants, would first be subjected to DNA extraction prior to subsequent analyses.  
407 Aeciospores have a thick outer wall, and DNA extractions can be conducted using a CTAB

408 method (Samils et al. 2021; Chen et al. 1993). Several approaches have been used and/or  
409 developed to distinguish *C. pini* from other *Cronartium/Peridermium* species, yet, species-  
410 specific identification tools have not yet been developed for *C. pini*. A common method for *C.*  
411 *pini* identification is based on Sanger sequencing of ribosomal DNA regions, including the ITS2  
412 and IGS-1. The ITS2 and IGS-1 regions can be amplified using polymerase chain region (PCR)  
413 with primers Rust3 and ITS4 (Moricca and Ragazzi 1998; White et al. 1990) for the ITS2 region  
414 and H and 5B (Moricca and Ragazzi 1998; Buchko and Klassen 1990) for the IGS-1 region.  
415 Generated sequences are then compared to sequences within databases, such as the National  
416 Center of Biotechnology Information (NCBI) database (<https://blast.ncbi.nlm.nih.gov/Blast.cgi>),  
417 using BLAST algorithms to determine similarity of sequences to reference sequences of known  
418 and verified rust species. Using currently available tools and techniques, detection of *C. pini*  
419 could require a few days or even weeks. Development of species-specific molecular tools,  
420 including quantitative PCR (qPCR), loop-mediated isothermal amplification (LAMP) detection,  
421 or antibody-based assays would help to identify *C. pini* more rapidly in newly invaded geographic  
422 regions. Microsatellite markers, Pp1 and Pp2, could be used for identification and gaining a better  
423 understanding of genetic diversity of *C. pini* across geographic regions. These microsatellite  
424 markers were first developed by Kasanen et al. (2000), and these markers were subsequently  
425 adapted by Samils et al. (2011) to allow amplification of the shorter simple sequence repeat  
426 amplicons. Using these markers and Amplified Fragment Length polymorphism (AFLP), Samils  
427 et al. (2021) identified six genetically distinct Bayesian clusters across 14 sampled locations in  
428 Finland and Sweden.

429

430

## V. Response

431 The response to all plant health emergencies in the United States is under the authority of

432 USDA-APHIS-Plant Protection and Quarantine (PPQ) delegated by the Secretary of Agriculture  
433 under the Plant Protection Act of 2000.

434 If a detection of *C. pini* were confirmed by a USDA-APHIS-PPQ recognized authority,  
435 APHIS would be in charge of the state(s) where detection has occurred. For typical first detections  
436 of an exotic pathogen, response would begin with an initial assessment. For a nursery site, a Rapid  
437 Assessment Team (RAT) consisting of state and federal experts on *Cronartium* and associated  
438 regulatory personnel may be deployed on-site to collect additional plant, soil, and water samples to  
439 conduct epidemiological investigations and initiate environmental delimiting surveys outside the  
440 nursery grounds. Possible actions include quarantines of infested or potentially infested production  
441 areas, prohibiting movement of infected or potentially infected materials in commerce, host removal  
442 and destruction, requiring adherence to sanitary practices, and application of registered fungicides  
443 and disinfectants. Trace-forward and trace-back surveys would be required for locations that have  
444 sent or received potentially infected nursery stock to/from the nursery with a confirmed pathogen  
445 detection. APHIS could impose quarantines and regulatory requirements to control and prevent the  
446 interstate movement of quarantine-significant pathogens or regulated articles (high risk host  
447 material), and APHIS works in conjunction with states that impose actions parallel to APHIS  
448 regulatory actions to restrict intrastate movement. The RAT would also attempt to ascertain if the  
449 introduction was intentional or accidental. If the organism in question is a select agent covered  
450 under the Agricultural Bioterrorism Act of 2002, federal and local law enforcement may be  
451 involved in the initial assessment to determine if a bioterrorism event or biocrime event has  
452 occurred.

453 The USDA-APHIS-PPQ response also depends on where *C. pini* is found (e.g., forest,  
454 plantation, or nursery) and how widespread it is based on the initial RAT assessment and  
455 associated delimitation surveys. For example, if *C. pini* were found in a pine plantation, attempts

456 would be made to eradicate the pathogen through several measures including plant  
457 destruction/eradication, soil/surface dis-infestation, trace-forwards, and trace-backs similar to  
458 management of *Phytophthora ramorum* in the United States (Rizzo et al., 2005). Likewise, the  
459 practicality of eradication in a forest setting would be assessed by the RAT and a technical  
460 working group of *Cronartium* experts and a recommendation will be made as to the potential for  
461 eradication of the infestation on a case-by-case basis.

462

## 463 **VI. USDA Pathogens Permits and Regulatory Issues**

464 USDA-APHIS-PPQ permits for plant pests and biological control organisms, fall under  
465 the authority of the Plant Protection Act, codified under 7 CFR 330. A PPQ 526 Permit is required  
466 for importation and interstate movement of all plant pests and infected plant materials, including  
467 diagnostic samples, regardless of their quarantine status. The receiving person must have been  
468 granted an authorized permit. Information on PPQ 526 Permits can be found at:  
469 [https://www.aphis.usda.gov/aphis/ourfocus/planthealth/import-information/permits/regulated-](https://www.aphis.usda.gov/aphis/ourfocus/planthealth/import-information/permits/regulated-organism-and-soil-permits)  
470 [organism-and-soil-permits](https://www.aphis.usda.gov/aphis/ourfocus/planthealth/import-information/permits/regulated-organism-and-soil-permits). Applicants may also call PPQ Permit Services at Telephone (301)  
471 734-0841, Toll Free (866) 524-5421 or e-mail [Pest.Permits@usda.gov](mailto:Pest.Permits@usda.gov).

472 USDA-APHIS regulates the importation of *Pinus* species. *Pinus* spp. are Not Authorized  
473 Pending a Pest Risk Analysis (NAPPRA):  
474 [https://www.aphis.usda.gov/aphis/ourfocus/planthealth/import-information/permits/plants-and-](https://www.aphis.usda.gov/aphis/ourfocus/planthealth/import-information/permits/plants-and-plant-products-permits/plants-for-planting/ct_nappra)  
475 [plant-products-permits/plants-for-planting/ct\\_nappra](https://www.aphis.usda.gov/aphis/ourfocus/planthealth/import-information/permits/plants-and-plant-products-permits/plants-for-planting/ct_nappra)), and are prohibited from importation into the  
476 United States from all countries except Canada, Japan, and South Korea (effective on May 20,  
477 2013). Importation of two- and three-needled pines are prohibited from Japan and Korea with *C.*  
478 *pini* (listed as *C. flaccidum*) listed as one of the USDA pests of concern  
479 (<https://www.aphis.usda.gov/aphis/resources/farmbill/fb-pests/farmbill-pest-list>).

480 **VII. Economic Impact and Compensation**

481 Economic impacts are difficult to estimate and are dependent on the nature of the  
482 introduction and introduction pathways and the pathogenicity/virulence of the introduced *C. pini*  
483 on native and exotic plant species. If Eurasian pine species remain the only hosts of Scots pine  
484 blister rust in North America, the greatest economic impacts will be largely limited to nurseries  
485 and Christmas tree plantations that grow Scots pine and to cities and homeowners that will bear  
486 the cost of removal of dead or hazardous landscape and urban trees.

487 Restrictions on moving potentially infected hosts and eradication of infected materials in  
488 nurseries and Christmas tree farms could cause enormous economic losses amounting to millions  
489 of dollars (U.S.). According to the National Christmas Tree Association, Scots pine is one of the  
490 most planted commercial Christmas trees in North America. Currently, Oregon, North Carolina,  
491 Michigan, Pennsylvania, Wisconsin, Washington, New York, and Virginia are the top Christmas  
492 tree-producing states in the United States. Most Scots pine is grown primarily in the Lake States,  
493 with Michigan and Wisconsin as the top producers of Christmas trees. Scots pine is one of the  
494 top five species of Christmas trees sold in the United States though it is difficult to obtain an  
495 exact value for the Scots pine market. According to the Census of Horticultural Specialties in the  
496 United States, nearly 2,857 operations sold 11.7 million Christmas trees valued at \$357.1 million  
497 in 2019.

498 Impacts will depend on how widespread the introduction is, how fast spread might occur  
499 among areas where Scots pine has been planted, and whether or not measures to control spread  
500 are implemented. Because Christmas trees have a much shorter production cycle (compared with  
501 the life cycle of pine trees in forests), some areas that are slow to be affected by the introduced  
502 rust pathogen could transition to other, more resistant or immune conifer species or genotypes  
503 before losses from Scots pine blister rust or restrictions in tree movement impact the local

504 Christmas tree production operations.

505         A worse-case scenario would be if *C. pini* already possesses or gains the capacity to infect  
506 native North American pines, which is not completely unexpected, given the large known host  
507 range of the pathogen on pine and non-pine hosts. *Cronartium pini* is known to infect several  
508 aecial hosts. Based on previous inoculation tests, aecial hosts appear to be primarily restricted to  
509 select Eurasian two-needled pine species in the section *Pinus* (Mittempergher and Raddi 1977;  
510 Raddi and Fagnani 1978; Kaitera and Nuorteva 2008). Largely unsuccessful inoculations of North  
511 American pine species, section *Trifoliae* (ponderosa pine and *P. contorta* Douglas ex Loudon  
512 (lodgepole pine)) and section *Pinus* (red pine) have been reported (Raddi and Fagnani 1978;  
513 Kaitera and Nuorteva 2008); however, *C. pini* was able to cause needle spotting on some North  
514 American species. Needle spotting was found on lodgepole pine, *P. echinata* Mill. (shortleaf  
515 pine), *P. elliotii* Engelm. (slash pine), and red pine. In addition, mycelium was detected in needle  
516 tissue of ponderosa pine, but none of these North American pines supported the generation of  
517 pycnia (spermogonia) or aecia under the test conditions (Raddi and Fagnani 1978). Among native  
518 North American section *Pinus* species, resistance to Scots pine blister rust is apparently relatively  
519 high. Subsequent inoculation tests by Kaitera and Neorteva (2008) also showed no symptoms on  
520 seedlings of Scot pine blister rust on lodgepole pine and red pine.

521         A likely route of potential *C. pini* invasion in North America could come from the  
522 widespread use of Scots pine, mugo pine, and Austrian/black pine in urban landscapes and  
523 Christmas tree plantations. These species are also naturalized in northern regions of the United  
524 States increasing the risk that an introduction could spread beyond urban landscapes, and providing  
525 the Scots pine blister rust pathogen with more opportunities to find novel alternate hosts or to cycle  
526 directly back to *Pinus* (autoecious lifecycle). The presence of *C. pini* in North America could also  
527 conceivably provide more opportunities for this rust to jump to *Pinus* species in the section

528 Trifoliae. Although previous inoculation tests show that native North American pine species appear  
529 to be at low risk for infection from *C. pini*, such inoculation tests cannot be conducted in the  
530 environment of North America, and environment will likely influence the pathogenicity of *C. pini*.

531 Another substantial threat is that *C. pini* could potentially hybridize with native pine rust  
532 pathogens that also have broad and overlapping alternate host range [similar to the detected rust  
533 hybrid in North America between introduced *C. ribicola* J.C. Fisch., agent of white pine blister rust,  
534 and native *C. comandrae* Peck, a blister rust of lodgepole pine (Joly et al., 2006)], a scenario of *C.*  
535 *pini* or hybrids acquiring pine hosts that are currently resistant may also be possible. If such a  
536 scenario occurred, the economic and ecological impacts would be unpredictable, but potentially far  
537 greater than that posed by non-adapted or non-hybridized *C. pini*.

538

### 539 VIII. Mitigation and Disease Management

540 If Scots pine blister rust becomes sufficiently established and eradication is precluded,  
541 infested and threatened sites can be managed to mitigate impacts. Consistent restriction of *C. pini*  
542 dispersal and colonization would reduce further losses and restrict the ability of *C. pini* to adapt to  
543 its new environment and potentially new hosts. An understanding of Scots pine blister rust  
544 impacts on trees, populations, communities, and ecosystems is also useful for rehabilitation. The  
545 immediate objective of mitigation and management is efficient and effective minimization of  
546 damage to natural systems and loss of resource value. Activities range from disease control  
547 tactics, such as pruning, thinning, and removal of infected seed trees (trees grown for seed  
548 production), to program strategies, such as adaptive environmental assessment and management.  
549 Successful mitigation and management must confront with five principal issues: 1) long-distance,  
550 aerial dispersal of the Scots pine blister rust pathogen, 2) multiple hosts of which many are  
551 (probably) unknown, 3) differing objectives of various managers, 4) a Scots pine blister rust

552 pathogen that capable of both sexual and clonal reproduction, and 5) a rapidly changing  
553 environment due to climatic, ecological, and socioeconomic factors.

554

## 555 **DISEASE CONTROL**

556 The life cycle of the Scots pine blister rust pathogen, *C. pini*, has vulnerabilities that can  
557 be exploited to prevent infection (by enhancing host escape) or minimize disease damage  
558 (influencing pathogen–host compatibility). General methods to control pine stem rusts include the  
559 use of chemicals to prevent infection, eradication or separation of alternate hosts from pine hosts,  
560 natural biological agents that reduce reproduction of the rust pathogen, and cultural management  
561 of host populations (silviculture) or individuals (arboriculture). Genetic manipulation can focus  
562 on selection, breeding, and deployment of hosts with greater resistance or tolerance to Scots pine  
563 blister rust disease.

564 Chemical controls might prevent host infection by the Scots pine blister rust pathogen  
565 and reduce pathogen vigor, viability, and inoculum production; however, few specific studies  
566 are reported for Scots pine blister rust. Control trials have included prophylactic chemicals to  
567 protect pines, salts and herbicides to kill alternate hosts, antibiotics to clear infections, and  
568 insecticides to control insect vectors. Triadimefon has been demonstrated to be a useful  
569 prophylactic for white pine blister rust (Pitt et al. 2006). Yao and Peixin (1991) report that  
570 application of Topsin® and triadimefon to a canker surface was effective in eliminating aecial  
571 sporulation of Scots pine blister rust pathogen in China. Salt spray can kill alternate hosts, but  
572 eradication was only practical in proximity to a pine plantation and likely would require  
573 intensive applications. Maloy (1997) reviewed the history of control of *C. ribicola* in the United  
574 States, including abandoned efforts with antibiotics and herbicides. Pappinen and von  
575 Weissenburg (1996) describe how pine-top weevil wounding pine twigs increased Scots pine



576 blister rust infection, which suggests that this disease could perhaps be managed in part by  
577 reducing pine-feeding insects. Studies on the effective use of insecticides to reduce insect  
578 vectors (that carry either spermatia or aeciospores) are apparently unavailable.

579 Control of pine stem rusts with biological agents has focused on rust canker-associated  
580 fungi that interfere with rust sporulation. Early work investigated *Tuberculina maxima*, which is  
581 a secondary fungus on cankers of many pine stem rusts caused by different pathogens, including  
582 Scots pine blister rust, but it has not been shown to be effective. Previous attention also focused  
583 on *Cladosporium tenuissimum*, which acts as an antagonistic hyperparasite. When suspensions of  
584 the mycoparasite *Trichoderma atroviride* were applied to *C. ribicola* aecia on *P. armandii*  
585 Franch. (Chinese white pine) in China, aeciospores were destroyed (Li et al. 2013).

586 Cultural activities provide numerous opportunities to mitigate damage by Scots pine  
587 blister rust. Although management for stem rusts must consider details of each specific  
588 pathosystem, general approaches developed for other *Cronartium* rusts and invasive tree  
589 pathogens have potential relevance (for general review see Waring and O'Hara 2005). Potential  
590 disease problems can often be avoided with careful matching of site and tree selection.  
591 Because some microclimates are more favorable for development of Scots pine blister rust and  
592 some sites have close proximity between uninfected trees and inoculum, hazard at some sites  
593 may be sufficiently high that alternative management, such as the use of non-host species, or  
594 host pines with adaptive traits (i.e., greater resistance should be considered; Pei and Brodie  
595 1995). In Finland, Kaitera and Nuorteva (2008) observed that susceptibility to *C. pini* infection  
596 varied among host provenances, with interactions with rust source and weather. In their study,  
597 lodgepole pine (native to North America) was not infected. Raddi and Fagnani (1978) also  
598 noted differences in susceptibility of Italian pines and some resistance in ponderosa pine  
599 (native to North America). The potential existence of different *C. pini* races with varying

600 virulence among hosts must also be considered, although this feature has not yet been  
601 established.

602         Whether thinning to improve stand growth or removing diseased trees (sanitation or  
603 salvage), management practices can mitigate disease loss, depending on numerous interacting  
604 factors. Kaitera (2002) observed that thinning Scots pine did reduce *C. pini* infection compared  
605 to unthinned plots, but year-to-year variation was high in both thinned and unthinned treatments.  
606 Such results are not unexpected because thinning affects microclimate to increase foliage drying,  
607 which would likely decrease *C. pini* spore germination. Thinning can also increase dispersal of  
608 *C. pini* spores within a stand, enhance alternate host persistence, and result in wounding (a  
609 potential infection pathway). Generally, thinning, fertilization, and augmentation with  
610 mycorrhiza are considered beneficial to stand growth; however, these activities could also  
611 potentially increase Scots pine blister rust by increasing susceptible tissue. As with species  
612 preference, thinning effects on Scots pine blister rust are not simple to predict.

613         Pruning can remove infected branches before the rust pathogen enters the trunk,  
614 eliminate branches that may become infected later and lead to lethal trunk cankers, and improve  
615 wood quality as knot-free timber. In some situations, trunk cankers can be excised, rendered  
616 inactive by chemical or biological agents, and/or contained over time through host resistance  
617 reactions. Because pruning and individual canker treatments are labor-intensive and time-  
618 sensitive activities, the economics of treatment are important in determining whether this type  
619 of control is practical for saving individual trees, especially since significant reduction in  
620 inoculum should not be expected.

621         Although eradication of the alternate host has been effective for mitigating impacts of  
622 other rust diseases in certain regions, host eradication is generally not practical for Scots pine  
623 blister rust. The range of hosts that contribute to pine infection is large, diverse, and includes the

624 pine itself in northern regions where the autoecious form prevails. Nonetheless, reducing the  
625 proximity of pine to alternate hosts can reduce but not eliminate *C. pini* infections especially in  
626 sites where only heteroecious rust occurs. Genetic control tactics can be effective for future  
627 generations and can be implemented by favoring natural reproduction from less-diseased trees or  
628 outplanting seedlings from resistant parents. Variation in blister rust incidence among Scots pine  
629 provenances has been reported by Kaitera (2003) and some cultivars of some alternate host  
630 species are immune. Selection in natural stands or breeding programs can increase the frequency  
631 of resistance in the host, but the potential for *C. pini* evolution must also be considered.  
632 Designing and monitoring a genetic control tactic should therefore consider the several host-  
633 pathogen interactions of resistance, virulence, tolerance, and aggressiveness. Hybridization or  
634 genetic exchange among different rust pathogens or hosts could also affect the ability to  
635 reproduce or sustain disease (Brasier 2001). Although resistance-breeding programs (e.g., Murray  
636 1964) are expensive due to management and associated research costs, they can provide not only  
637 improved seed but also valuable genetic information (Kinloch 1972). Federal cooperative genetic  
638 tree-improvement programs at several locations are currently addressing several pine stem rusts  
639 other than Scots pine blister rust.

640         Disease control tactics should be employed in a strategic context. Given the complexity  
641 and uncertainty of mitigating Scots pine blister rust and managing infested ecosystems for a  
642 novel disturbance, adaptive management is especially appropriate (Williams et al. 2009).

643 Decisions over control (and monitoring) of pine stem rusts are frequently made with use of rust  
644 hazard models that typically provide landscape or stand projections of infection likelihood,  
645 incidence, or damage severity (e.g., Van Arsdel et al. 1961).

646

647

648 **RISK MANAGEMENT**

649 Even during the phase of mitigation and management, it is important to identify risk  
650 factors and consider alternative outcomes of treatment. The epidemiology and damage from  
651 Scots pine blister rust varies in space and time due to differences in climate, soil type, stand age,  
652 host species, growth, genetics, and other unknown factors (Murray et al. 1969; Greig 1987;  
653 Kaitera et al. 1994).

654 Risk management techniques (see U.S. EPA 2003; Lovett et al. 2006) provide procedures  
655 to incorporate complexity and uncertainty into hazard maps and simulation models. For example,  
656 a regional map of predicted severity of white pine blister rust based on synoptic climate, a lake  
657 effect, and alternate host distribution was developed by Van Arsdel et al. (1961). McDonald et al.  
658 (1981) developed an epidemiological simulation model for white pine blister rust that projects  
659 growth and mortality of *P. monticola* Douglas ex D. Don (western white pine) within infested  
660 stands that considered the abundance of hosts, climate, and site productivity. The potential  
661 influence of climate change on white pine blister rust has also been examined (Dudney et al.  
662 2021). Such approaches, maps, and models can be useful where many complex factors must be  
663 considered in selecting a disease management regime.

664 Typically, rust-hazard assessments have been based on environmental and demographic  
665 processes without regard for evolutionary (e.g., genetic and environmental) interactions. The  
666 outcome of these interactions, however, can have profound effects on the naturalization of an  
667 introduced pathogen and the resulting condition of the affected ecosystem (see Parker and Gilbert  
668 2004). An uncertain risk that increases the difficulty in planning mitigation is the potential for a  
669 pathogen to shift to a new host. *Pedicularis* and *Castilleja* are among several genera of flowering  
670 plants that are included as potential alternate host species of Scots pine blister rust. Although the  
671 susceptibility to Scots pine blister rust has not been determined for many species of *Pedicularis*

672 and *Castilleja* endemic to North America, they are known hosts of other pine stem rusts and  
673 should be considered as potential hosts of Scots pine blister rust as well. The risk is not that North  
674 American populations of *Pedicularis* and *Castilleja* (or other alternate hosts such as *Euphrasia*  
675 and *Rhinanthus*) would be jeopardized, but that these alternate hosts could act as a *C. pini*  
676 inoculum source to infect pines or even serve as an alternate host for a hybrid rust pathogen. The  
677 North American pines, which are potential hosts of Scots pine blister rust, are also hosts of other,  
678 native pine stem rusts.

679 As mentioned, hybrids between a different Eurasian pine stem rust (*C. ribicola*) and a  
680 North American stem rust (*C. comandrae*) has been observed as sporulating aecia on pine at a  
681 few locations (Joly et al. 2006), but no alternate host has been reported for this rust hybrid. If  
682 Scots pine blister rust were established in North America, opportunities could occur that could  
683 facilitate hybridization of rust pathogens. Because of the pine and angiosperm host ranges and  
684 the conditions favoring *C. pini* infection, the likelihood and consequences of *C. pini* hybrid  
685 pathogens arising is difficult to predict (see Brasier 2001 for hybrids in non-rust pathogens).

686

## 687 **XI. Research, Extension, and Education Priorities**

### 688 **RESEARCH PRIORITIES**

689 Many questions remain about the ecological behavior of the heteroecious and autoecious  
690 forms of *C. pini* even within its native range. Predicting actual impacts of Scots pine blister rust  
691 on potential hosts is a formidable task because of potential influences of host/pathogen genetic  
692 structure and the interaction of environment on virulence/resistance reactions. Although the  
693 Scots pine blister rust pathogen has been reported in eastern Asia, much less is known about the  
694 pathogen in eastern Asia than in Europe. Because great genetic variation could occur across the  
695 native ranges of *C. pini* and its hosts, research is needed to develop effective diagnostic

696 techniques to characterize *C. pini* at the species, subspecies, and population levels, while also  
697 furthering our understanding the geographic distribution of the heteroecious and autoecious  
698 forms. Pathogen characterization is the initial step needed to assess variation in life cycle, host  
699 ranges, variation in virulence, and environmental optima for infection. Information gathered  
700 from such studies will allow improved predictions of geographic areas and host species at risk  
701 from *C. pini*.

702 Management of rust diseases often relies on resistance breeding programs, and this  
703 approach offers promise for Scots pine blister rust. Biological control also offers promise  
704 toward managing different forms of *C. pini*; therefore, continued research efforts are needed to  
705 identify biological control agents and associated techniques for enhancing biological control of  
706 Scots pine blister rust.

707

### 708 **Most Important**

- 709 • Determine if historical reports or herbarium records exist of rust disease on North  
710 American pines in historical European arboreta and other plantings, where Scots pine  
711 blister rust occurs. A search for these records/reports can initially focus on rust diseases  
712 on pine clades with a close phylogenetic relationship with Scots pine.
- 713 • Use inoculation tests in infested countries to determine potential aecial and telial hosts  
714 of Scots pine blister rust in plants that occur naturally or are planted in North America.
- 715 • Conduct phylogenetic analyses of known and potential non-pine hosts of Scots pine  
716 blister rust.
- 717 • Develop prediction models of potential spread of Scots pine blister rust based on  
718 distribution of aecial and telial hosts combined with present and future climate models.
- 719 • Conduct phylogenetic analysis of the Scots pine blister rust pathogen (*C. pini*) and other

720 pine stem rust pathogens present in North America (e.g., *C. arizonicum* Cummins, *C.*  
721 *coleosporioides* f. *album* Ziller, *C. comandrae*, *C. ribicola*, and *P. harknessii*  
722 J.P.Moore).

723 • Conduct population genetic analysis to determine the genetic diversity of *C. pini* across  
724 its native range.

725 • Determine the range of pine hosts and non-pine, alternate hosts, and environmental  
726 requirements for each genetic group of *C. pini*.

727

### 728 **Highly Important**

729 • Assess potential sources of Scots pine blister rust resistance in aecial host (pine) populations  
730 of North America.

731 • Begin assessments of potential biological control agents for Scots pine blister rust.

732

### 733 **Needs Evaluation**

734 • Evaluate potential genetic information and assess status of germplasm collections for diverse  
735 geographic sources of potential pine hosts of Scots pine blister rust in North America.

736 • Establish sentinel tree and alternate host plantings, preferably using known susceptible  
737 seed sources, in areas with Scots pine blister rust to help in early detection and establish a  
738 baseline of susceptibility against which the results from genetic screening can be compared.

739

### 740 **EXTENSION PRIORITIES**

741 Rust pathogens are difficult to identify reliably based solely on morphology and symptoms.

742 Periodic surveys of rust on aecial and telial hosts should include sensitive (e.g., DNA-based)

743 diagnostic protocols to identify rust pathogens, their hosts, and distribution.

744 The following action items must be developed:

745 • Cooperate with National Plant Diagnostic Network (NPDN) to develop tree-rust diagnostic  
746 tools that accurately identify tree-rust pathogens.

747 • Conduct surveys of potential aecial and telial hosts using DNA-based diagnostic tests to  
748 identify rust pathogens.

749 • Develop means to prevent the introduction/spread of *C. pini* via movement of aecial  
750 and telial hosts.

751 • Develop and circulate educational materials describing Scots pine blister rust  
752 (symptoms, signs, biology) and comparing with rust diseases currently present, and  
753 describing the threats associated with introduction of the Scots pine blister rust  
754 pathogen.

755

#### 756 **EDUCATION PRIORITIES**

757 • Educate plant pathologists, plant health professionals, extension agents, forest managers,  
758 nursery growers, Christmas tree growers, horticulturalists, general public, etc. about potentially  
759 invasive rust pathogens, including *C. pini*.

760 • Develop targeted education programs directed toward areas that may be at high risk for Scots  
761 pine blister rust, such as Christmas tree growers or horticultural nurseries.

762 • Engage Master Gardener and Master Naturalist programs and other relevant existing outreach  
763 programs to educate stakeholders about Scots pine blister rust and other potentially invasive tree  
764 rust pathogens.

765 • Integrate Scots pine blister rust into state and regional “pest detector” educational programs  
766 that focus on non-native invasive pests.

767



768 **ACKNOWLEDGEMENTS**

769 We would like to acknowledge the funding and support from the National Plant Disease  
770 Recovery System (NPDRS) of the USDA-Office of Pest Management Policy. In addition, this  
771 work was partially funded by the USDA Forest Service, Forest Health Protection, Special  
772 Technology Development Program (R1-FY2020-01). We also thank the contributors (Drs.  
773 Brian W. Geils, Charles G. Shaw III, James Walla, Russ Bulluck, Laura Redmond, and Kent  
774 Smith) who provided inputs on the original version of this plan and Melissa Morley for  
775 graphic drawing (Fig. 3).

776

777

**X. References**

778 Agricultural Marketing Resource Center. 2008. Christmas trees. Ag Marketing Resource  
779 Center, Ames, IA. Retrieved 21 May 2021 from [https://www.agmrc.org/commodities-](https://www.agmrc.org/commodities-products/forestry/christmas-trees)  
780 [products/forestry/christmas-trees](https://www.agmrc.org/commodities-products/forestry/christmas-trees)

781

782 Brasier, C. M. 2001. Rapid evolution of introduced plant pathogens via  
783 interspecific hybridization. *BioScience* 51:123-133.

784

785 Buchko, B., and Klassen, G. R. 1990. Detection of length heterogeneity in the ribosomal DNA  
786 of *Pythium ultimum* by PCR amplification of the intergenic region. *Current Genetics* 18:203-  
787 205.

788

789 CABI. 2020. *Cronartium flaccidum* (Scots pine blister rust) in: Invasive Species Compendium.  
790 Wallingford, UK: CAB International. Retrieved 21 May 2021 from  
791 <https://www.cabi.org/isc/datasheet/16148>

- 792 Chen, X. M., Line, R. F., and Leung, H. 1993. Relationship between virulence variation and  
793 DNA polymorphism in *Puccinia striiformis*. *Phytopathology* 83:1489-1497.  
794
- 795 Cummins, G. B., and Hiratsuka, Y. 2003. Illustrated genera of rust fungi. American  
796 Phytopathological Society Press. St. Paul, MN.  
797
- 798 Dudney, J., Willing, C. E., Das, A. J., Latimer, A. M., Nesmith, J. c. B., and Battles, J. J. 2021.  
799 Nonlinear shifts in infectious rust disease due to climate change. *Nature Communications* 12:5102.  
800
- 801 Gibbs, J., and Kaitera, J. 2018. Resin Top Disease. In; Hansen, E.M., K.J. Lewis, and G.A.  
802 Chastagner (Editors). *Compendium of Conifer Diseases*. APS Press, St. Paul, Minnesota,  
803 USA.  
804
- 805 Greig, B. J. W. 1987. History of *Peridermium* stem rust of Scots pine (*Pinus sylvestris* L.) in  
806 Thetford Forest, East Anglia. *Forestry* 60:193-202.  
807
- 808 Hantula, J., Kasanen, R., Kaitera, J., and Moricca, S. 2002. Analyses of genetic variation suggest  
809 that pine stem rust *Cronartium flaccidum* and *Peridermium pinibelong* to the same species.  
810 *Mycological Research* 106:203-209.  
811
- 812 Hiratsuka, Y. 1968. Morphology and cytology of aeciospores and aeciospore germtubes of host-  
813 alternating and pine-to-pine races of *Cronartium flaccidum* in northern Europe. *Canadian Journal*  
814 *of Botany* 46:1119-1122.  
815

- 816 Joly, D. L., Langor, D. W., and Hamelin, R. C. 2006. Molecular and morphological evidence for  
817 interspecific hybridization between *Cronartium ribicola* and *C. comandrae* on *Pinus flexilis* in  
818 Southwestern Alberta. *Plant Disease* 90:1552.
- 819
- 820 Kaitera, J. 1999. *Cronartium flaccidum* fruitbody production on *Melampyrum* spp.  
821 and some important alternate hosts to pine. *European Journal of Forest Pathology* 29:391-398.
- 822
- 823 Kaitera, J. 2002. Short-term effect of thinning on *Pinus sylvestris* damage and sporulation  
824 caused by *Cronartium flaccidum*. *Scandinavian Journal of Forest Research* 17:158-165.
- 825
- 826 Kaitera, J. 2003. Susceptibility and lesion development in Scots pine saplings infected with  
827 *Peridermium pini* in northern Finland. *Forest Pathology* 33:353-362.
- 828
- 829 Kaitera, J., Aalto, T., and Jalkanen, R. 1994. Effect of resin-top disease caused by *Peridermium pini*  
830 on the volume and value of *Pinus sylvestris* saw timber and pulp wood. *Scandinavian Journal of*  
831 *Forest Research* 9:376-381.
- 832
- 833 Kaitera, J., and Hantula, J. 1998. *Melampyrum sylvaticum*, a new alternate host for pine stem rust  
834 *Cronartium flaccidum*. *Mycologia* 90:1028-1030.
- 835
- 836 Kaitera, J., and Hiltunen, R. 2011. Susceptibility of *Pedicularis* spp. to *Cronartium ribicola* and *C.*  
837 *flaccidum* in Finland. *Forest Pathology* 41:237-242.
- 838

- 839 Kaitera, J., and Hiltunen, R. 2012. New alternate hosts for the rusts *Cronartium ribicola* and  
840 *Cronartium flaccidum* in Finland. Canadian Journal of Forest Research 42:1661-1668.  
841
- 842 Kaitera, J., Hiltunen, R., and Samils, B. 2012. Alternate host ranges of *Cronartium flaccidum* and  
843 *Cronartium ribicola* in northern Europe. Botany 90: 694-703.  
844
- 845 Kaitera, J., Hiltunen, R., and Hantula, J. 2015. *Cronartium* rust sporulation on hemiparasitic plants.  
846 Plant Pathology 64:738-747.  
847
- 848 Kaitera, J., Hiltunen, R., Kauppila, T., and Hantula, J. 2017a. Five plant families support natural  
849 sporulation of *Cronartium ribicola* and *C. flaccidum* in Finland. European Journal of Plant  
850 Pathology 149:367-383.  
851
- 852 Kaitera, J., Hiltunen, R., and Hantula, J. 2017b. *Nasa*, *Nemesia* and *Euphrasia*:  
853 New alternate hosts of *Cronartium* spp. Forest Pathology 47:6  
854
- 855 Kaitera, J., Kauppila, T., and Hantula, J. 2018. New alternate hosts for *Cronartium* spp.: *Odontites*,  
856 *Euphrasia*, *Rhinanthus* and *Papaver*. Forest Pathology 48:1-8.  
857
- 858 Kaitera, J., Kalleinen, L., Mikkilä, J., and Hantula, J. 2017c. *Cronartium flaccidum* sporulates on  
859 new *Euphrasia* species in natural habitats in Finland. Forest Pathology 47:6.  
860
- 861 Kaitera, J., and Nuorteva, H. 2003a. *Cronartium flaccidum* produces uredinia and telia on  
862 *Melampyrum nemorosum* and on Finnish *Vincetoxicum hirundinaria*. Forest Pathology 33:205-

863 213.

864

865 Kaitera, J., and Nuorteva, H. 2003b. Relative susceptibility of four *Melampyrum* species  
866 to *Cronartium flaccidum*. Scandinavian Journal of Forest Research 18:499-504.

867

868 Kaitera, J., and Nuorteva, H. 2008. Inoculations of eight *Pinus* species with *Cronartium* and  
869 *Peridermium* stem rusts. Forest Ecology and Management 255:973-981.

870

871 Kaitera, J., Nuorteva, H., and Hantula, J. 2005. Distribution and frequency of *Cronartium*  
872 *flaccidum* on *Melampyrum* spp. in Finland. Canadian Journal of Forest Research 35:229-

873 234.

874

875 Kaitera, J., Seitamäki, L., Hantula, J., Jalkanen, R., and Kurkela, T. 1999. Inoculation of known  
876 and potential alternate hosts with *Peridermium pini* and *Cronartium flaccidum* aeciospores.

877 Mycological Research 103:235-241.

878

879 Kasanen, R. 1997. Aeciospores of *Cronartium flaccidum*, *C. ribicola* and *Endocronartium*  
880 *pini* show no differences in morphology. European Journal of Forest Pathology 27:251-260.

881

882 Kasanen, R., Kaitera, J., and Hantula, J. 2000. The genetic composition of *Peridermium pini*  
883 and *Cronartium flaccidum* cankers on Scots pine as revealed by two multi-allelic loci. Forest  
884 Pathology 30:221-230.

885

886 Kinloch, B. B., Jr. 1972. Genetic variation in resistance to *Cronartium* and *Peridermium* rusts

887 in hard pines. Pages 445-463 in: Biology of rust resistance in forest trees: Proceedings NATO-  
888 IUFRO Advanced Study Institute August 17–24 1969. Bingham, R. T., Hoff, R. J., and  
889 McDonald, G. I. U.S. Department of Agriculture, Forest Service, Washington, DC.

890  
891 Li, J., Yang, Y. H., Zhou, L., and Cheng, L. J. 2013. Destructive effects of a mycoparasite  
892 *Trichoderma atroviride* SS003 on aeciospores of *Cronartium ribicola*. Journal of  
893 Phytopathology 162:396-401.

894  
895 Lovett, G. M., Canham, C. D., Arthur, M. A., Weathers, K. C., and Fitzhugh, R. D. 2006.  
896 Forest ecosystem responses to exotic pests and pathogens in eastern North America.  
897 BioScience 56:395-403.

898  
899 Maloy, O. C. 1997. White pine blister rust control in North America: a case history. Annual  
900 Review of Phytopathology 35: 87-109.

901  
902 McDonald, G. I., Hoff, R. J., and Wykoff, W. R. 1981. Computer simulation of white pine  
903 blister rust epidemics. I. Model formulation. Research Paper INT-258. U.S. Department of  
904 Agriculture, Forest Service, Intermountain Forest and Range Experiment Station, Ogden, UT.

905  
906 Mittempergher L., and Raddi P. 1977. Variation of diverse sources of *Cronartium flaccidum*. Eur J  
907 Forest Pathology 7:93-98.

908  
909 Moricca, S., and Ragazzi A. 1996. Culture characteristics and variation of *Cronartium*  
910 *flaccidum* isolates. Canadian Journal of Botany 74:924-933.

- 911 Moricca, S., and Ragazzi A. 1998. Use of RFLP and SSCP analysis to differentiate the  
912 pine rust *Cronartium flaccidum* and *Peridermium pini*. Mycological Research 102:666-  
913 670.
- 914
- 915 Murray, J. S. 1964. Establishment of disease susceptibility plantations. Page 4 in:  
916 FAO/IUFRO Symposium on Internationally Dangerous Forest Diseases and Insects. 1964  
917 July 20–30. Oxford, UK.
- 918
- 919 Murray, J. S., Millar, C. S., and van der Kamp, B. J. 1969. Incidence and importance of  
920 *Peridermium pini* (Pers.) Lev. in north-east Scotland. Forestry 42:164-184.
- 921
- 922 Özkazanç, N. and Maden, S. 2013. Some important shoot and stem fungi in pine (*Pinus* spp.)  
923 and firs (*Abies* sp.) in western blacksea region, Turkey. Bartın Orman Fakültesi Dergisi 15:32-  
924 38. <https://dergipark.org.tr/en/download/article-file/39940>
- 925
- 926 Pappinen, A., and von Weissenburg, K. 1996. Weevil feeding on Scots pine affects  
927 germination of *Endocronartium pini*. European Journal of Forest Pathology 26:225-234.
- 928
- 929 Parker, I. M., and Gilbert, G. S. 2004. The evolutionary ecology of novel plant–pathogen  
930 interactions. Annual Review of Ecology, Evolution and Systematics 35:675-700.
- 931
- 932 Pei, M. H., and Brodie, J. 1995. Inoculation of young pine seedlings with *Peridermium pini* from  
933 north-east Scotland. European Journal of Forest Pathology 25:24-30.
- 934

- 935 Pitt, D. G., Meyer, T., Park, M., MacDonald, L., Buscarini, T., and Thompson, D. G. 2006.  
936 Application of slow-release tablets to enhance white pine regeneration: Growth response and  
937 efficacy against white pine blister rust. *Canadian Journal of Forest Research* 36:684-698.  
938
- 939 Price, R. A., Liston, A., and Strauss, H. 1998. Phylogeny and Systematics of *Pinus*. Pages 49-  
940 63 in: *Ecology and Biogeography of Pinus*. Richardson, D. M. ed. Cambridge University Press,  
941 Cambridge, UK.  
942
- 943 PRISM. 2021. PRISM Gridded Climate Data. Oregon State University, PRISM Climate Group,  
944 Corvallis, OR. <http://prism.oregonstate.edu>  
945
- 946 Raddi, P., and Fagnani, A. 1978. Relative susceptibility to blister rust caused by  
947 *Cronartium flaccidum* of several species of pine. *European Journal of Forest Pathology*  
948 8:58-61.  
949
- 950 Ragazzi, A. 1983. Development of *Cronartium flaccidum* (Alb. et Schw.) Wint. on *Vincetoxicum*  
951 *officinale* Moench in connection with some environmental factors. *Phytopathologische Zeitschrift*  
952 108:160-171.  
953
- 954 Ragazzi, A., and Dellavalle Fedi, I. 1992. Penetration of *Cronartium flaccidum* into pine needles.  
955 *European Journal of Forest Pathology* 22:78-283.  
956
- 957 Ragazzi, A., Fedi, I. D., and Mesturino, L. 1986. *Cronartium flaccidum* on *Pinus* spp.: relation of  
958 inoculum concentration to symptom development. *European Journal of Forest Pathology* 16:16-21.



- 959 Rizzo, D. M., Garbelotto, M., and Hansen, E. M. 2005. *Phytophthora ramorum*: Integrative  
960 research and management of an emerging pathogen in California and Oregon forests. Annual  
961 Review of Phytopathology 43: 309-335.
- 962
- 963 Ruefenacht, B., Finco, M. V., Nelson, M. D., Czaplewski, R., Helmer, E. H., Blackard, J. A.,  
964 Holden, G. R., Lister, A. J., Salajanu, D., Weyermann, D., and Winterberger, K. 2008.  
965 Conterminous U.S. and Alaska forest type mapping using forest inventory and analysis data. USDA  
966 Forest Service - Forest Inventory and Analysis (FIA) Program & Geospatial Technology and  
967 Applications Center (GTAC), Salt Lake City, UT.
- 968
- 969 SAFARIS. 2021. Spatial Analytic Framework for Advanced Risk Information Systems (SAFARIS).  
970 United States Department of Agriculture and North Carolina State University, Raleigh, NC.
- 971
- 972 Samils, B., Ihrmark, K., Kaitera, J., Stenlid, J., and Barklund, P. 2011. New genetic markers for  
973 identifying *Cronartium flaccidum* and *Peridermium pini* and examining genetic variation within  
974 and between lesions of Scots pine blister rust in Sweden. Fungal Biology 115:1303-1311.
- 975
- 976 Samils, B., Kaitera, J., Persson, T., Stenlid, J., and Barklund, P. 2021. Relationship and genetic  
977 structure among autoecious and heteroecious populations of *Cronartium pini* in northern  
978 Fennoscandia. Fungal Ecology 50:101032
- 979
- 980 Species Fungorum. 2021. <http://www.speciesfungorum.org/names/Names.asp>  
981 (Accessed: June 2020).
- 982

- 983 U.S. EPA. 2003. Generic ecological assessment endpoints (GEAEs) for ecological risk  
984 assessment. EPA/630/P02/004F. Risk Assessment Forum. U.S. Environmental Protection  
985 Agency, Washington, DC. Retrieved 21 May 2021 from  
986 [https://www.epa.gov/sites/production/files/2014-11/documents/generic\\_endpoints\\_2004.pdf](https://www.epa.gov/sites/production/files/2014-11/documents/generic_endpoints_2004.pdf)  
987  
988 2019 Census of Horticultural Specialties. Census of Agriculture. National Agricultural  
989 Statistics Service. U.S. Department of Agriculture. Retrieved 21 May 2021 from  
990 [https://www.nass.usda.gov/Publications/AgCensus/2017/Online\\_Resources/Census\\_of\\_H](https://www.nass.usda.gov/Publications/AgCensus/2017/Online_Resources/Census_of_Horticulture_Specialties/index.php)  
991 [orticulture\\_Specialties/index.php](https://www.nass.usda.gov/Publications/AgCensus/2017/Online_Resources/Census_of_Horticulture_Specialties/index.php)  
992  
993 Van Arsdel, E. P., Riker, A. J., Kouba, T. F., Suomi, V. E., and Bryson, R. A. 1961. The  
994 climatic distribution of blister rust on white pine in Wisconsin. Station Paper No. 87. U.S.  
995 Department of Agriculture, Forest Service, Lake States Forest Experiment Station, St. Paul,  
996 MN.  
997  
998 Vogler, D. R., and Bruns, T. D. 1998. Phylogenetic relationships among the pine stem rust fungi  
999 (*Cronartium* and *Peridermium* spp.). *Mycologia* 90:244-257.  
1000  
1001 Waring, K. M., and O'Hara, K. L. 2005. Silvicultural strategies in forest ecosystem affected by  
1002 introduced pests. *Forest Ecology and Management* 209:27-41.  
1003  
1004 White, T. J., Bruns, T., Lee, S., and Taylor, J. 1990. Amplification and direct sequencing of  
1005 fungal ribosomal RNA genes for phylogenetics. Pages 315-322 in: *PCR Protocols: A Guide to*  
1006 *Methods and Applications*. Innis, M. A., Gelfand, D. H., Sninsky J. J., and White T. J., editors.

1007 Academic Press, San Diego, CA.

1008

1009 Wijesinghe, S. N., McKenzie, E., Wanasinghe, D. N., Boonmee, S., and Jayawardena,

1010 R. S. 2019. The genus *Cronartium* revisited. *Plant Pathology & Quarantine* 9: 219–238.

1011

1012 Williams, B. K., Szaro, R. C., and Shapiro, C. D. 2009. *Adaptive Management: The U.S.*

1013 Department of the Interior Technical Guide. Adaptive Management Working Group, U.S.

1014 Department of the Interior, Washington, DC.

1015 <https://www.doi.gov/sites/doi.gov/files/uploads/TechGuide-WebOptimized-2.pdf>

1016

1017

1018 Yao, J., and Peixin, W. 1991. A study on the blister rust of *Pinus massoniana* of China. Pages

1019 302-312 in: 3rd IUFRO Rusts of Pine Working Party Conference 1989 September. Banff, AB.

1020 Info. Rep. NOR-X-317. Hiratsuka, Y., Samoil, J. K., Blenis, P. V., Crane, P. E., and Laishley, B.

1021 L. Canadian Forest Service, Northern Forestry Centre, Edmonton, AB, Canada.

1022

## 1023 **XI. Infrastructure and Experts**

1024 The following individuals have in-depth knowledge and/or experience with Scots pine blister

1025 rust:

1026

### 1027 **United States**

1028 **Paul Zambino**

1029 U.S.D.A. Forest Service, Forest Health Protection

1030 Coeur d'Alene, ID 83815

1031 208-765-7493, [paul.zambino@usda.gov](mailto:paul.zambino@usda.gov)

- 1032            **Bryce A. Richardson**
- 1033            U.S.D.A. Forest Service, Rocky Mountain Research Station
- 1034            Moscow, ID 83843
- 1035            208-883-2322, [bryce.richardson2@usda.gov](mailto:bryce.richardson2@usda.gov)
- 1036
- 1037            **Ned B. Klopfenstein**
- 1038            U.S.D.A. Forest Service, Rocky Mountain Research Station
- 1039            Moscow, ID 83843
- 1040            208-883-2310, [ned.klopfenstein@usda.gov](mailto:ned.klopfenstein@usda.gov)
- 1041
- 1042            **Jane E. Stewart**
- 1043            Colorado State University, Department of Agricultural Biology
- 1044            Ft. Collins, CO 80525
- 1045            970-491-8770
- 1046            [Jane.Stewart@colostate.edu](mailto:Jane.Stewart@colostate.edu)
- 1047
- 1048            **Mee-Sook Kim**
- 1049            U.S.D.A. Forest Service, Pacific Northwest Research Station
- 1050            Corvallis, OR 97331
- 1051            541-750-7150
- 1052            [meesook.kim@usda.gov](mailto:meesook.kim@usda.gov)
- 1053
- 1054            **Canada**
- 1055            **Richard Hamelin**

1056 University of British Columbia  
1057 Vancouver, BC, Canada  
1058 604-827-4441, [Richard.hamelin@ubc.ca](mailto:Richard.hamelin@ubc.ca)

1059

1060 **Finland**

1061 **Jarkko Hantula**  
1062 Natural Resources Institute Finland  
1063 Helsinki, Finland  
1064 358-29-532-5419, [jarkko.hantula@luke.fi](mailto:jarkko.hantula@luke.fi)

1065

1066 **Juha Kaitera**  
1067 Natural Resources Institute Finland  
1068 Oulu, Finland  
1069 358- 29-532-5553, [juha.kaitera@luke.fi](mailto:juha.kaitera@luke.fi)

1070

1071 **Heikki Nuorteva**  
1072 Natural Resources Institute Finland  
1073 Helsinki, Finland  
1074 358-29-532-5459, [heikki.nuorteva@luke.fi](mailto:heikki.nuorteva@luke.fi)

1075

1076 **Sweden**

1077 **Berit Samils**  
1078 Sveriges lantbruksuniversitet  
1079 Uppsala, Sweden

1080 [berit.samils@slu.se](mailto:berit.samils@slu.se)

1081

1082 **Austria**

1083 **Thomas Kirisits**

1084 University of Natural Resources and Applied Life Sciences, Institute of Forest

1085 Entomology, Forest Pathology and Forest Protection

1086 Vienna, Austria

1087 43-1-47654-91601, [thomas.kirisits@boku.ac.at](mailto:thomas.kirisits@boku.ac.at)

1088

1089 **Italy**

1090 **Salvatore Moricca**

1091 Università degli Studi di Firenze, Scienze e Tecnologie Agrarie, Alimentari,

1092 Ambientali e Forestali

1093 Firenze, Italy

1094 [salvatore.moricca@unifi.it](mailto:salvatore.moricca@unifi.it)

1095

1096 **United Kingdom**

1097 **Stephen Woodward**

1098 University of Aberdeen, School of Biological Sciences

1099 Aberdeen, Scotland, UK

1100 44-1224-272669, [s.woodward@abdn.ac.uk](mailto:s.woodward@abdn.ac.uk)

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1102 **XII. Web Resources**

1103 CABI – *Cronartium flaccidum* (Scots pine blister rust)

- 1104 <https://www.cabi.org/isc/datasheet/16148>
- 1105
- 1106 Purdue University - The Center for Environmental and Regulatory Information Systems
- 1107 *Cronartium flaccidum* (Alb. & Schwein) Winter
- 1108 <http://download.ceris.purdue.edu/file/3540>
- 1109
- 1110 British Columbia Ministry of Forests, Forest Practices Code, Pine Stem Rust Management
- 1111 Guidebook
- 1112 [https://www.for.gov.bc.ca/ftp/HFP/external!/publish/FPC%20archive/old%20web%20site%20conten](https://www.for.gov.bc.ca/ftp/HFP/external!/publish/FPC%20archive/old%20web%20site%20contents/fpc/fpcguide/PINESTEM/pine-toc.htm)
- 1113 [ts/fpc/fpcguide/PINESTEM/pine-toc.htm](https://www.for.gov.bc.ca/ftp/HFP/external!/publish/FPC%20archive/old%20web%20site%20contents/fpc/fpcguide/PINESTEM/pine-toc.htm)
- 1114
- 1115 EPPO Global Database - *Cronartium flaccidum*
- 1116 <https://gd.eppo.int/taxon/CRONFL>
- 1117
- 1118 Plant Parasites of Europe - *Cronartium flaccidum*(Albertini & Schweinitz) Winter, 1880
- 1119 [https://bladmineerders.nl/parasites/fungi/basidiomycota/pucciniomycotina/pucciniales/cronartiaceae](https://bladmineerders.nl/parasites/fungi/basidiomycota/pucciniomycotina/pucciniales/cronartiaceae/cronartium/cronartium-flaccidum/)
- 1120 [/cronartium/cronartium-flaccidum/](https://bladmineerders.nl/parasites/fungi/basidiomycota/pucciniomycotina/pucciniales/cronartiaceae/cronartium/cronartium-flaccidum/)
- 1121
- 1122 Luke - *Cronartium flaccidum*, *Peridermium pini*
- 1123 [http://www.metla.fi/metinfo/metsienterveys/lajit\\_kansi/crflac-n.htm](http://www.metla.fi/metinfo/metsienterveys/lajit_kansi/crflac-n.htm) (Finnish)
- 1124
- 1125 USDA APHIS – Plant Import Information
- 1126 <https://www.aphis.usda.gov/aphis/ourfocus/planthealth/import-information>
- 1127

- 1128 USDA NIFA - Extension
- 1129 <https://nifa.usda.gov/extension>



**TABLE 1**  
**Pine aecial hosts of *Cronartium pini*.**

| Host  | Geographic Region                  | Reference                 |
|---|------------------------------------|---------------------------|
| <i>Pinus sylvestris</i> (Scots pine)  | temperate and other regions        | Kaitera and Hantula 1998  |
| <i>P. pinea</i> (Italian stone pine)  | Mediterranean region               | CABI 2020                 |
| <i>P. mugo</i> (Mountain pine)  | Alps and to south and east         | Kaitera and Nuorteva 2008 |
| <i>P. nigra</i> (Austrian pine)   | Mediterranean region               | CABI 2020                 |
| <i>P. nigra</i> subsp. <i>laricio</i><br>(Laricio pine) (syn. <i>P.</i><br><i>nigricans</i> ; <i>P. austriaca</i> ) | Mediterranean region               |                           |
| <i>P. pinaster</i> (Maritime pine)  | Mediterranean and other<br>regions | CABI 2020                 |
| <i>P. halepensis</i> (Aleppo pine)  | Mediterranean region               | Moricca and Ragazzi 1996  |
| <i>P. densiflora</i>  | Japan                              | CABI 2020                 |
| <i>P. brutia</i>  | Turkey                             | CABI 2020                 |
| <i>P. koraiensis</i>  |                                    | CABI 2020                 |
| <i>P. massoniana</i>  | China                              | Yao and Peixin 1991       |
| <i>P. pumila</i>  |                                    | CABI 2020                 |
| <i>P. radiata</i>   |                                    | CABI 2020                 |
| <i>P. ponderosa</i>   |                                    | Gibbs and Kaitera 2018    |
| <i>P. tabuliformis</i>  | China                              | Yao and Peixin 1991       |
| <i>P. taiwanensis</i>   |                                    | CABI 2020                 |
| <i>P. takahasii</i>   |                                    | CABI 2020                 |
| <i>P. uncinata</i>  |                                    | CABI 2020                 |
| <i>P. wallichiana</i>   |                                    | CABI 2020                 |
| <i>P. yunnanensis</i>   |                                    | CABI 2020                 |

1130 Pine taxonomy follows Price et al. (1998)

1131

**TABLE 2**  
**Angiosperm telial (alternate) hosts of *Cronartium pini*.**

| Host   | Reference  |
|--|--|
| <i>Melampyrum sylvaticum</i>                       | Kaitera and Hantula 1998; Kaitera et al. 1999, 2012; Kaitera 1999; Kaitera and Hiltunen 2011 |
| <i>Melampyrum pratense</i>                         | Kaitera 1999; Kaitera et al. 2012  |
| <i>Melampyrum nemorosum</i>                        | Kaitera and Nuorteva 2003a   |
| <i>Melampyrum arvense</i>                          | Kaitera and Nuorteva 2003b   |
| <i>Pedicularis palustris</i> ssp. <i>palustris</i> | Kaitera et al. 1999, 2012; Kaitera and Hiltunen 2011   |
| <i>Pedicularis sceptrum-carolinum</i>              | Kaitera and Hiltunen 2012; Kaitera et al. 2012, 2015   |
| <i>Pedicularis dolichorrhiza</i>                   | Kaitera et al. 2012  |
| <i>Pedicularis lapponica</i>                       | Kaitera and Hiltunen 2011  |
| <i>Pedicularis groenlandica</i>                    | Kaitera et al. 2015  |
| <i>Verbena x hybrida</i>                           | Kaitera and Hiltunen 2012  |
| <i>Verbena canadensis</i>                          | Kaitera et al. 2012  |
| <i>Verbena officinalis</i>                         | Kaitera and Hiltunen 2012  |
| <i>Vincetoxicum hirundinaria</i>                   | Kaitera et al. 1999, 2012, 2015, 2017b; Kaitera and Hiltunen 2011, 2012                      |
| <i>Vincetoxicum mongolicum</i>                     | Kaitera et al. 1999  |
| <i>Vincetoxicum fuscum</i>                         | Kaitera et al. 1999  |
| <i>Vincetoxicum nigrum</i>                         | Kaitera et al. 1999  |
| <i>Paeonia lactiflora</i>                          | Kaitera et al. 2012, 2018  |
| <i>Paeonia anomala</i>                             | Kaitera et al. 1999, 2012; Kaitera and Hiltunen 2012   |
| <i>Paeonia obovata</i>                             | Kaitera et al. 2012  |
| <i>Paeonia officinalis</i>                         | Kaitera et al. 1999, 2015  |
| <i>Paeonia tenuifolia</i>                          | Kaitera et al. 2015  |
| <i>Paeonia mlokosewitchii</i>                      | Kaitera et al. 2017a   |
| <i>Paeonia oreogeton</i>                           | Kaitera et al. 2017a   |
| <i>Grammatocarpus volubilis</i>                    |  |
| <i>Impatiens glandulifera</i>                      | Kaitera and Hiltunen 2012; Kaitera et al. 2015   |
| <i>Impatiens balsamina</i>                         | Kaitera et al. 2012, 2015  |
| <i>Impatiens parviflora</i>                        | Kaitera et al. 2018  |
| <i>Loasa (Nasa) tricolor</i>                       | Kaitera et al. 2012, 2015  |
| <i>Loasa (Nasa) triphylla</i>                      | Kaitera and Hiltunen 2012; Kaitera et al. 2012, 2017b  |
| <i>Loasa (Nasa) urens</i>                          | Kaitera et al. 2017b   |
| <i>Nemesia versicolor</i>                          | Kaitera and Hiltunen 2012  |
| <i>Nemesia strumosa</i>                            | Kaitera and Hiltunen 2012  |
| <i>Nemesia floribunda</i>                          | Kaitera et al. 2017b   |
| <i>Tropaeolum majus</i>                            | Kaitera and Hiltunen 2012; Kaitera et al. 2012, 2015, 2017b                                  |
| <i>Veronica longifolia</i>                         | Kaitera and Hiltunen 2012; Kaitera et al. 2012, 2015   |
| <i>Veronica incana</i>                             | Kaitera et al. 2015  |
| <i>Veronica daurica</i>                            | Kaitera et al. 2012, 2015, 2017b   |
| <i>Veronica grandis</i>                            | Kaitera et al. 2015  |
| <i>Veronica krylovii</i>                           | Kaitera et al. 2015  |
| <i>Apocynum cannabinum</i>                         | Kaitera et al. 2015  |
| <i>Asclepias incarnata</i>                         | Kaitera and Hiltunen 2012  |
| <i>Bartsia alpina</i>                              | Kaitera and Hiltunen 2012; Kaitera et al. 2012, 2017b  |
| <i>Caiophora lateritia</i>                         | Kaitera et al. 2012  |

|                                |   |
|--------------------------------|---|
| <i>Castilleja miniata</i>      | Kaitera et al. 2015   |
| <i>Delphinium elatum</i>       |   |
| <i>Euphrasia stricta</i>       | Kaitera and Hiltunen 2012; Kaitera et al. 2012, 2015, 2017b, 2018 |
| <i>Euphrasia breivipila</i>    | Kaitera et al. 2015   |
| <i>Euphrasia officinalis</i>   | Kaitera et al. 2015   |
| <i>Euphrasia minima</i>        | Kaitera et al. 2015   |
| <i>Euphrasia nemorosa</i>      | Kaitera et al. 2017c  |
| <i>Euphrasia frigida</i>       | Kaitera et al. 2017c  |
| <i>Gentiana verna</i>          |   |
| <i>Hyoscyamus niger</i>        | Kaitera et al 2015  |
| <i>Myrica gale</i>             | Kaitera et al. 2012, 2015   |
| <i>Nicotiana rustica</i>       | Kaitera et al. 2015   |
| <i>Odontites verna</i>         | Kaitera et al. 2018   |
| <i>Papaver rhoeas</i>          | Kaitera et al. 2018   |
| <i>Rhinanthus minor</i>        | Kaitera et al. 2015   |
| <i>Rhinanthus aestivalis</i>   | Kaitera et al. 2015   |
| <i>Rhinanthus serotinus</i>    | Kaitera et al. 2018   |
| <i>Ruellia elegans</i>         |   |
| <i>Saxifraga hostii</i>        | Kaitera et al. 2012, 2015   |
| <i>Saxifraga cespitosa</i>     | Kaitera et al. 2012   |
| <i>Saxifraga exarata</i>       | Kaitera et al. 2012   |
| <i>Schizanthus grahamii</i>    |   |
| <i>Siphonostegia chinensis</i> | Yao and Peixin 1991   |
| <i>Swertia fedtchenkoana</i>   | Kaitera et al. 2012, 2015   |

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1132

1133

1134 **Figure Legends**

1135

1136 **FIGURE 1**

1137 Scots pine blister rust (resin-top disease) caused by *Cronartium pini* on Scots pine (*Pinus*  
1138 *sylvestris*). Photos by Juha Kaitera.

1139 **FIGURE 2**

1140 Damage caused by *Cronartium pini* on Scots pine (*Pinus sylvestris*). (A) Branch mortality caused  
1141 by the heteroecious form, where the branch tip has died distal to a branch lesion. (B) Tree mortality  
1142 caused by the heteroecious form, where the tree has been killed above a stem lesion. (C) Rust  
1143 damage caused by the autoecious form. In the center, the stem leader of the tree has been killed  
1144 above a stem lesion, while the lower canopy is still alive. On the right, a whole tree has been killed  
1145 by Scots pine blister rust. An old stem lesion where sporulation occurred, which that is blackened  
1146 and resinous, is located on the lower stem. (Photos by Juha Kaitera).

1147 **FIGURE 3**

1148 Scots pine blister rust (*Cronartium pini*) disease cycle.

1149 **FIGURE 4**

1150 (A) Spermatial droplets of the heteroecious form of *Cronartium pini* on Scots pine (*Pinus*  
1151 *sylvestris*). (B) Aecia of the autoecious form of *C. pini* on Scots pine. (Photos by Juha Kaitera).

1152 **FIGURE 5**

1153 Uredinia and telia of the heteroecious form of *Cronartium pini* on *Vincetoxicum hirundinaria*  
1154 (Swallow-wort) (A) and *Euphrasia officinalis* (B). (Photos by Juha Kaitera).

1155 **FIGURE 6**

1156 Scots pine blister rust (*Cronartium pini*) infection risk levels in the contiguous United States.

1157 **FIGURE 7**

- 1158 (A) Old sporulated lesion with new aecia of the autoecious form of *Cronartium pini* on Scots pine
- 1159 (*Pinus sylvestris*), (B) Swelling with spermogonia of *C. pini* on Scots pine. (Photos by Juha
- 1160 Kaitera).



Figure 1. Scots pine blister rust (resin-top disease) caused by *Cronartium pini* on Scots pine (*Pinus sylvestris*). Photos by Juha Kaitera.

67x96mm (900 x 900 DPI)

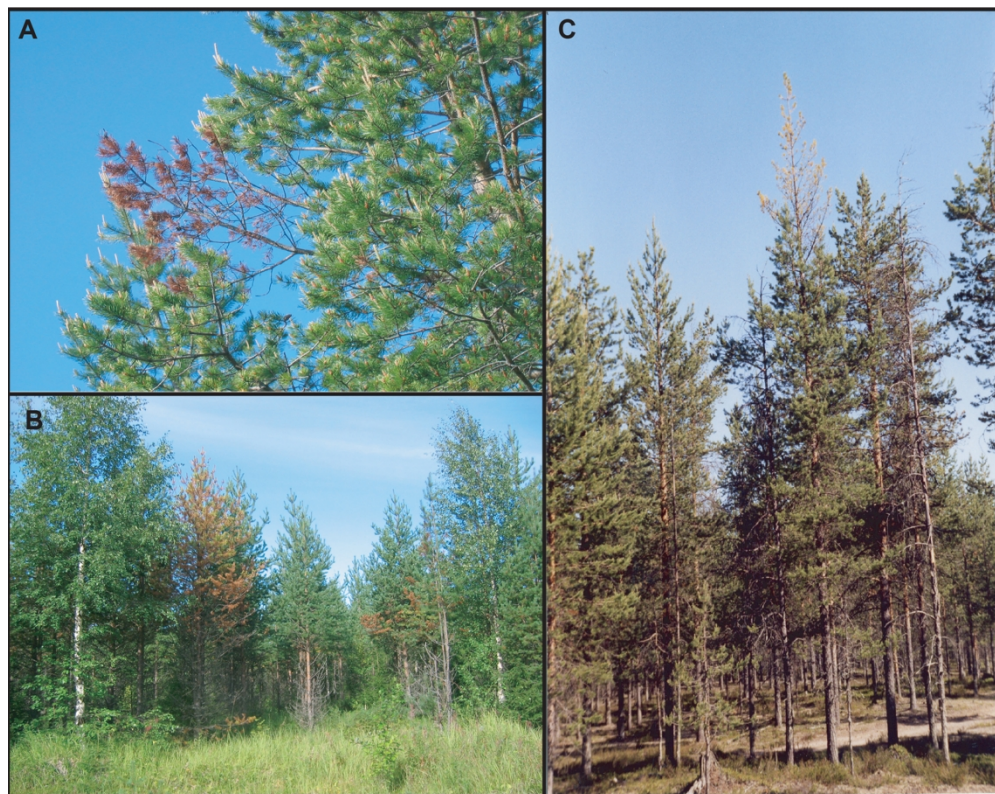


Figure 2. Damage caused by *Cronartium pini* on Scots pine (*Pinus sylvestris*). (A) Branch mortality caused by the heteroecious form, where the branch tip has died distal to a branch lesion. (B) Tree mortality caused by the heteroecious form, where the tree has been killed above a stem lesion. (C) Rust damage caused by the autoecious form. In the center, the stem leader of the tree has been killed above a stem lesion, while the lower canopy is still alive. On the right, a whole tree has been killed by Scots pine blister rust. An old stem lesion where sporulation occurred, which that is blackened and resinous, is located on the lower stem. (Photos by Juha Kaitera).

177x140mm (300 x 300 DPI)



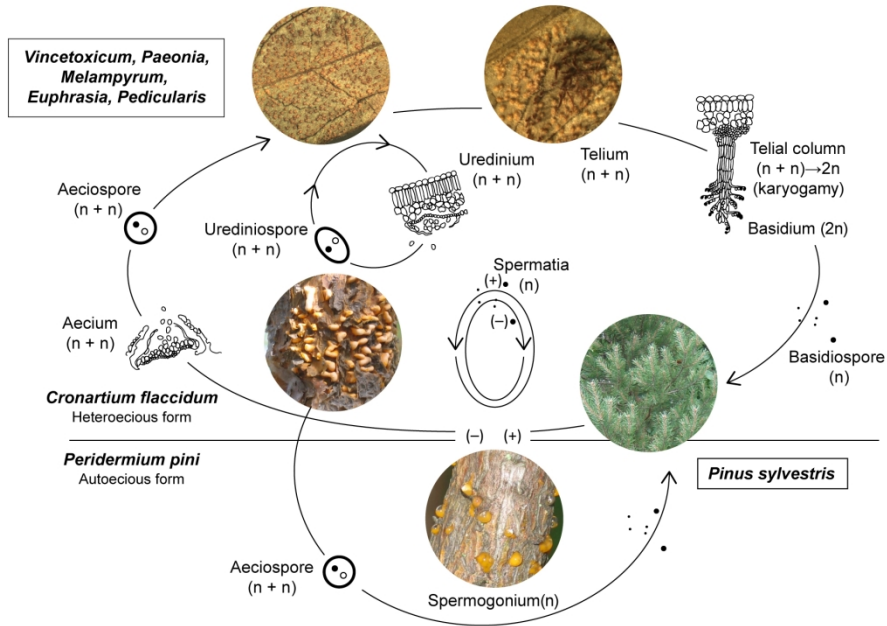


Figure 3. Scots pine blister rust (*Cronartium pini*) disease cycle.

533x387mm (100 x 100 DPI)



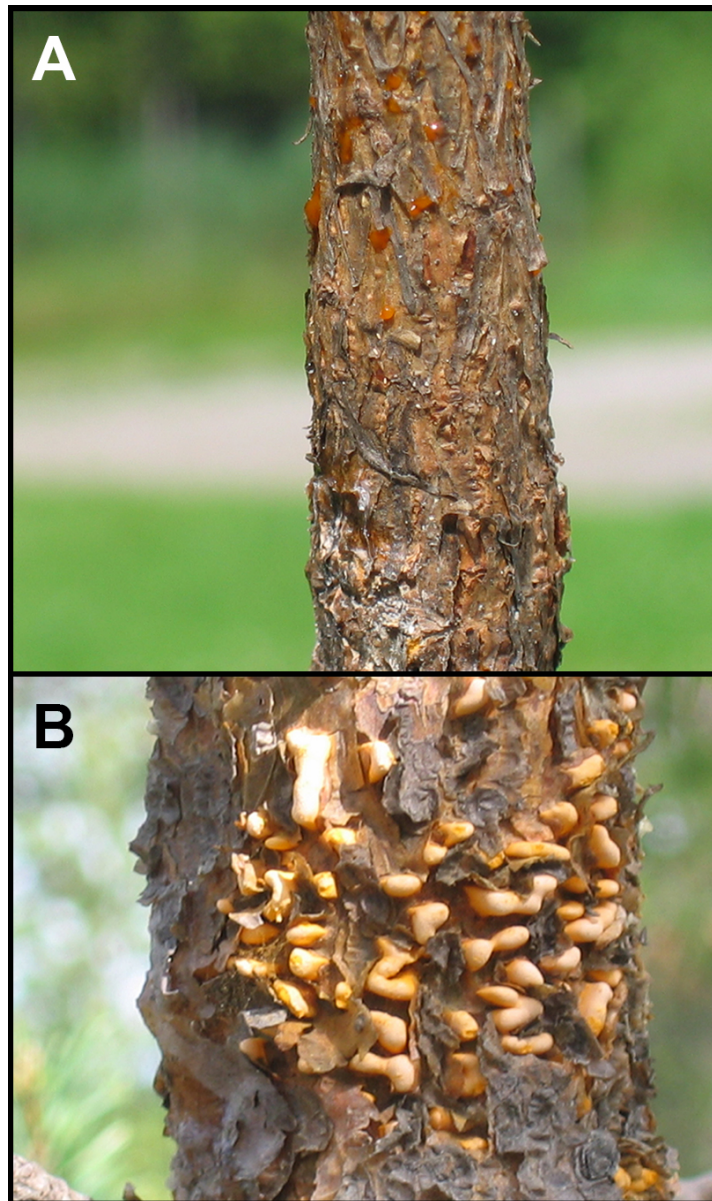


Figure 4. (A) Spermatal droplets of the heteroecious form of *Cronartium pini* on Scots pine (*Pinus sylvestris*). (B) Aecia of the autoecious form of *C. pini* on Scots pine. (Photos by Juha Kaitera).

68x115mm (300 x 300 DPI)

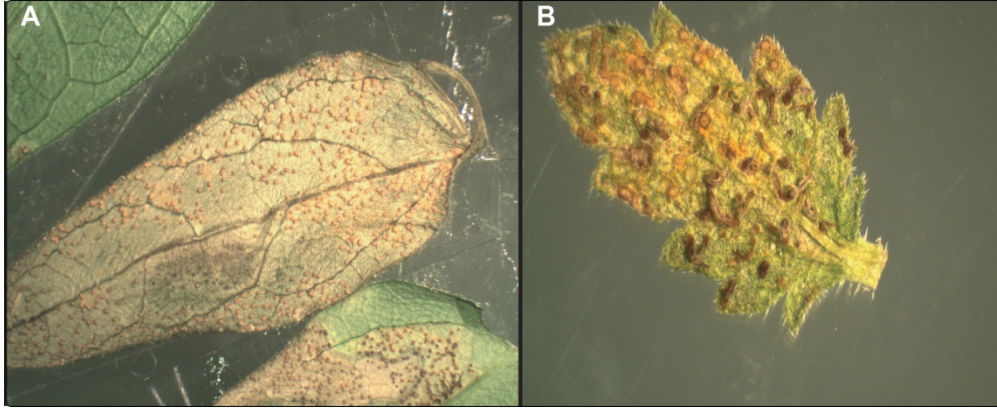


Figure 5. Uredinia and telia of the heteroecious form of *Cronartium pini* on *Vincetoxicum hirundinaria* (Swallow-wort) (A) and *Euphrasia officinalis* (B). (Photos by Juha Kaitera).

177x72mm (300 x 300 DPI)

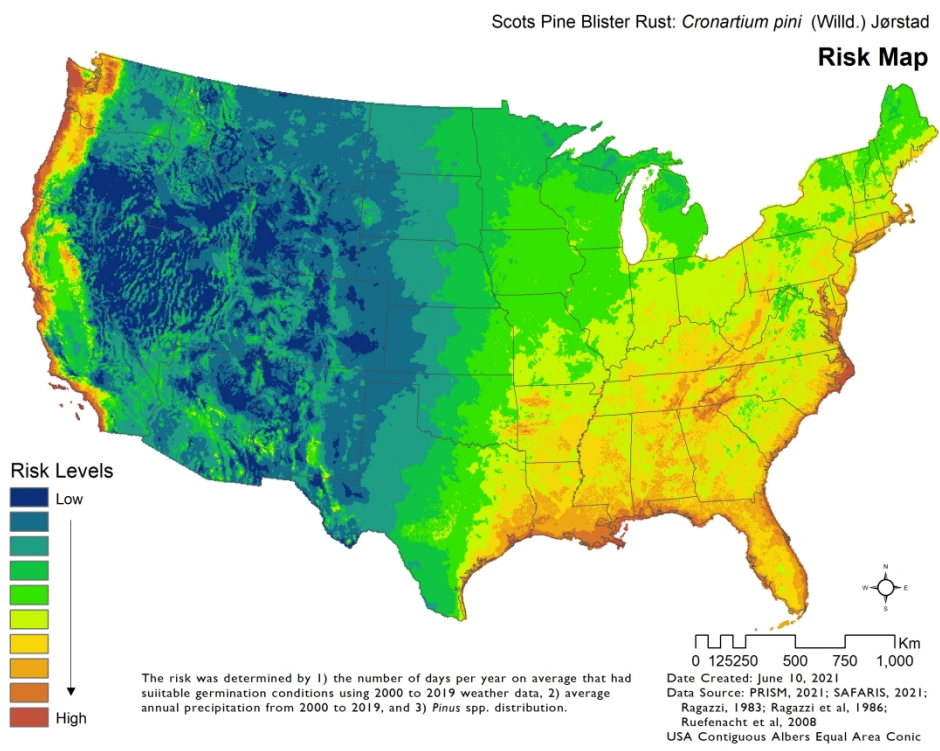


Figure 6. Scots pine blister rust (*Cronartium pini*) infection risk levels in the contiguous United States.

279x215mm (300 x 300 DPI)

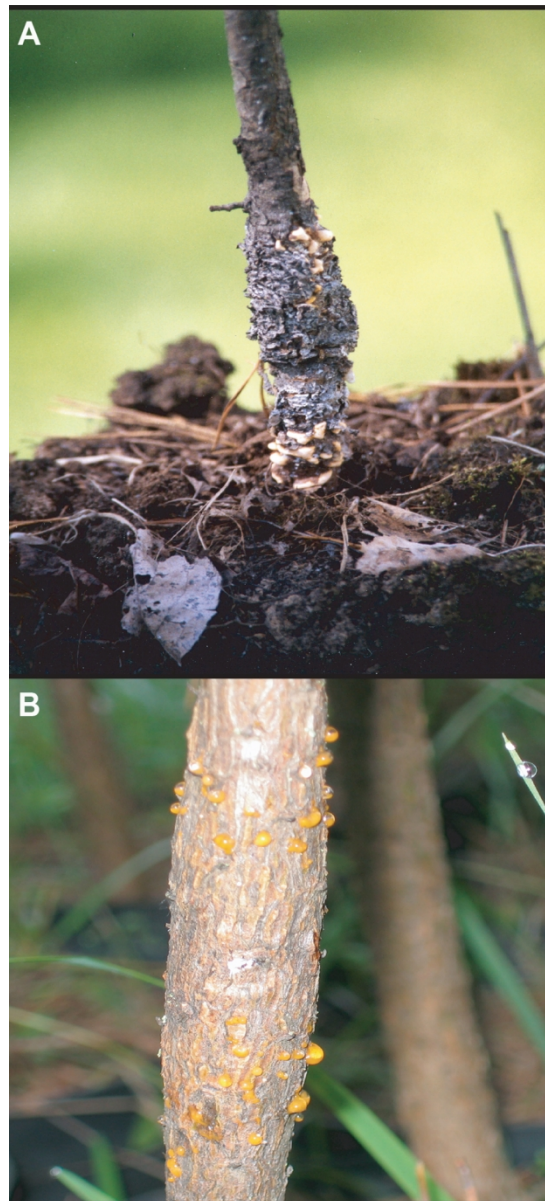


Figure 7. (A) Old sporulated lesion with new aecia of the autoecious form of *Cronartium pini* on Scots pine (*Pinus sylvestris*), (B) Swelling with spermogonia of *C. pini* on Scots pine. (Photos by Juha Kaitera).

82x180mm (300 x 300 DPI)