Effect of leaf extracts on fruiting and sporulation of Cronartium pini and C. ribicola on susceptible alternate hosts

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Abstract

Resistance of plants to rust fungi may depend on the chemical quality of plants, suggesting that leaf extracts from resistant plant species could be useful in development of bio-based solutions against rust diseases. Pine trees (*Pinus* spp.) are affected by *Cronartium*rusts (*C. pini*, *C. ribicola*). In their life cycle, these rusts infect alternate host plants, some of which are more rust resistant than others. We sprayed leaf extracts from resistant alternate host (*Melampyrum pratense*, *Impatiens glandulifera*, *Veronica chamaedrys*,*Ribes rubrum*) and tested—both in the laboratory and on live plants—whether those extracts reduce rust spore production on plants that are normally easy to infect (*Melampyrum sylvaticum*, *Impatiens balsamina*, *Paeonia lactiflora*, *Ribes nigrum*). Two commercial compounds, previously linked to rust resistance of alternate hosts to *Cronartium* rusts, a methanol control and an untreated control were also included to the experiment. Formation of rust uredinia and telia were estimated on the leaves after 6 weeks of incubation. In the laboratory, uredinia and telia of *C. pini*developed most abundantly on *Paeonia lactiflora*. Coverage of uredinia and telia did not differ between extracts on the leaves, but coverages of uredinia were significantly higher compared to dry control in the laboratory. In the greenhouse, infection percentage of leaves with uredinia and telia differed significantly among plant species but the treatments with extracts did not result in significant differences in infection percentage of the test plants. The results indicated that none of the tested extracts from rust-resistant alternate hosts and commercial compounds significantly inhibited fruiting and sporulation of *Cronartium* spp. on susceptible alternate hosts at medium (100 ppm) concentration.

Introduction

Cronartium pini (Willd.) Jørst. is a pathogen that kills pine (*Pinus* spp.) trees in Europe and Asia (Gäumann, 1959; CABI, 2020). The rust is also a quarantine species in North America (Kim et al., 2022). In the 2000s, *C. pini* caused severe losses on young *Pinus sylvestris* L. plantations in northern Europe, especially in nutrient-rich soils (Kaitera, 2000; Wulff et al., 2012), although the rust was previously known especially as a disease of mature pines on poor sites (Kaitera et al., 1994). Another *Cronartium, C. ribicola* Fisch., is a serious pathogen of five-needle pines especially in North America (Zambino, 2010).

Cronartium pini spreads via alternate hosts of over 50 susceptible species in 14 plant families (Kaitera et al., 2015; Kim et al., 2022). The most important alternate host species belong to hemiparasites in Orobanchaceae (Kaitera, 1999; Kaitera et al., 1999, 2012, 2015, 2017, 2018; Kaitera & Nuorteva, 2003a,b). In genus *Melampyrum*, *M. sylvaticum* L., *M. nemorosum* L., *M. arvense* L. and *M. cristatum* L. are highly susceptible, while *M. pratense* shows resistance against *C. pini* (Kaitera, 1999; Kaitera et al., 2015). *Cronartium ribicola* spreads via plants in genus *Ribes* (Grossulariaceae). In Finland, most *R. nigrum* cultivars are susceptible, while *R. rubrum* cultivars show resistance against *C. ribicola* (Kaitera & Nuorteva, 2006).

Recent studies have shown that chemical composition of *P. sylvestris* wood changes after *C. pini* infection (Kaitera et al., 2021), suggesting that terpenes and resin acids are produced by the host as defensive chemicals against *Cronartium*. Terpenes have been linked to *C. ribicola* resistance in *Pinus* also earlier (Michelozzi et al., 1991; Bullington et al., 2018) and also phenolic compounds have been assigned defensive roles in pine resistance against *Cronartium* rusts (Boyer, 1964; Hanover & Hoff, 1966; Hudgins et al., 2005; Sniezko et al., 2014). The possible role of phenolics in alternate host resistance against *Cronartium* has also

been studied, in both the susceptible and resistant species (e.g., Piispanen et al., 2023). It has been suggested that variation in rust resistance between the closely related species such as *M. sylvaticum* and *M. pratense* may be due to variation in leaf phenolic chemistry (Kaitera & Witzell, 2016). Polyphenolics, such as luteolin and apigenin flavonoids with documented antimicrobial impact on bacterial, viral and fungal pathogens (Cushnie & Lamb, 2005) occur at high concentrations in some *Melampyrum* species (Naumov et al., 1998). Recently, chlorogenic acid (Kaitera & Witzell, 2016; Piispanen et al., 2023) and quercitrin (Piispanen et al., 2023) were found to be enriched in *C. pini*-resistant *M. pratense*.

With tightening regulations on environmentally harmful synthetic fungicides, there is an urgent demand for bio-based, sustainable methods to manage tree diseases both in nurseries and in the field. The aim of this study was to explore whether extracts from alternate hosts could be useful as bio-based suppressants against *Cronartium*. Therefore, we conducted *in vivo* and *in vitro* studies to investigate the effect of leaf extracts from selected resistant alternate hosts of *C. pini* and *C. ribicola* on the fruiting and sporulation of *Cronartium* species. We hypothesized that the externally added extracts from resistant alternative host species could suppress the fruiting and sporulation of *Cronartium* rusts on the susceptible hosts.

Material and methods

Plant material for extracts

Plant species resistant to *C. pini*, i.e., *M. pratense* (65°2,69N, 25°28,04E), *Impatiens glandulifera* Royle (65°3,86N, 25°27,79E) and *Veronica chamaedrys* L. (65°1,30N, 25°25,96E), were from natural habitats in the city area of Oulu in northern Finland, while species resistant to *C. ribicola* were commercial seedlings of *Ribes rubrum* L. from a commercial nursery (Särkän taimitarha). Plants were collected and transported to the laboratory, where their healthy leaves were detached, air-dried and used for preparation of leaf extracts.

Plant material for inoculations

For the laboratory experiment, healthy leaves of susceptible *M. sylvaticum* were collected from the city area of Oulu in early July 2021. In addition, leaves of commercial plants of susceptible *R. nigrum* and *Paeonia lactiflora* Pall from the nursery (Särkän taimitarha), and *Impatiens balsamina* L. grown from seeds in the Botanical Gardens of Oulu University in May 2021, were used in the laboratory experiments. Whole plants of the above mentioned *R. nigrum*, *P. lactiflora* and *I. balsamina* were also used in the greenhouse experiment.

Preparation of plant extracts

In the laboratory, healthy green leaves of the rust-resistant plants were separated from the rest of the plant material aseptically with sterile tweezers. The leaves were air-dried for about a week in the laminar cabin in open paper bags and stored at -20°C prior to extraction. The leaf samples were crushed manually inside a paper bag until a powdery consistency was achieved. Of each sample,1 g was extracted in 40 mL methanol (HPLC grade, Merck, 1.06007.2500)(for the extraction, see Piispanen et al., 2023). The extracts were kept at + 4 ºC for 24 hours and diluted to 100 mL by sterile water. In addition, solutions of commercial compounds, potentially linked to resistance of *Cronartium* rusts based on the results of earlier studies (Kaitera & Witzell, 2016; Piispanen et al., 2023), were also tested: chlorogenic acid (Acros Organics, 109.240.010) and quercitrin

(Cayman Chemical Company, CAYM19866), 5 g each, were dissolved to 100 ml of sterile water: methanol (40:60 v/v). The further diluted solutions for the experiments were made daily from these base solutions (100 ppm for plant extracts and 0,5 ppm for chlorogenic acid and quercitrin). The methanol-water control solutions contained same amount of methanol than the plant extracts used in the experiments.

Inoculum and inoculation treatments

Aeciospores of *C. pini* were collected from Kolari (67º9,64N, 23º40,06E), northern Finland, in mid-June (June 13) 2021. The collection site was a *P. sylvestris* stand where the presence and pathogenicity of the rust had been confirmed (Kaitera et al., 2015). Five branches bearing *C. pini* lesions were cut and transported to the Lynet laboratory of the Natural Resources Institute Finland in Oulu. Aeciospores were released into sterile Petri dishes by cutting the surface of aecia aseptically in a laminar cabin using a scalpel. Aeciospores of *C. ribicola* were then dusted from *Pinus cembra* L. directly to Petri dishes in the field by cutting the surface of aecia from four lesions in Oulunsalo (64º56,50N, 25º22,60E) in late May (May 28) 2021. The aeciospores of both species were stored at 5°C before usage. Germination of the spores was measured by dusting spores on 1.5% water agar, incubating the plates at 21.5°C in the daylight for 24 h, and counting germination from 10 microscopic areas on agar using a light microscope (Mx4300H, Meiji Techno Co., LTD). Mean germination of *C. pini* was 94% (87–98%) and of *C. ribicola* 85% (81–91%).

Laboratory (*in vitro*) experiment

Five Petri dishes were prepared with two leaves of each susceptible alternate host (*R. nigrum, M. sylvaticum*, *P. lactiflora*, and *I. balsamina* and) per plate floating on sterilized water in the laboratory experiment. Prior to inoculation, leaves were treated with extracts (one extract per plate). Four extracts were from *M. pratense*, *I. glandulifera*, *V. chamaedrys* and *R. rubrum*, and chlorogenic acid and quercitrin were used as additional commercial compounds. Two controls were included: methanol-water (40:60, v/v) and dry leaves without methanol or water. The plant extracts were used at 100 ppm and commercial compounds at concentration of 0.5 ppm. The leaves were soaked in extracts, solutions or pure water:methanol for 5 sec, except for the dry control. After treatments, aeciospores of *C. pini* were dusted using an artist's pencil on leaves of *M. sylvaticum*, *P. lactiflora* and *I. balsamina*, while *C. ribicola* was dusted on *R. nigrum*. Plates without inoculation were included to control for natural infections on the leaves. The plates were incubated for 6 weeks at 18°C in the dark in a growth chamber (KB240, Binder GmbH, Tuttlingen, Germany). After the incubations, the leaves were checked using a stereomicroscope (M5A, Wild Heerbrugg, Switzerland) to determine the coverage of uredinia and telia per leaf using classes '0%', '1–20%', '21–40%', '41–60%', '61–80%', '81–99%' and '100%'. Later, the mean percentages of these classes were used in the calculations.

Greenhouse (*in vivo*) experiment

In the greenhouse, eight plants per species were prepared for the experiment. All leaves of *P. lactiflora* and *I. balsamina*, and leaves from one branch of *R. nigrum* per plant, were sprayed with six extracts and two controls. One extract or control was sprayed per plant. The extracts were the same as in the laboratory experiment. As controls, a methanol:water (40:60, v/v) treatment and a water treatment were used. The sprayed leaves of *P. lactiflora* and *I. balsamina* plants were thereafter dusted with *C. pini* and those of *R. nigrum* with *C. ribicola* aeciospores with an artist's pencil. After inoculation, the plants were covered with a

plastic bag for 48 h to promote spore germination. After 6 weeks of incubation, the leaves were collected and the numbers of leaves carrying uredinia or telia were counted using a stereomicroscope in the laboratory (see above). The infection percentage was used to indicate the success of infection.

Statistical analysis

The effect of extract treatment, plant species and their interaction on coverage of uredinia and telia was modelled using ANOVA of SAS (SAS Institute Inc., version 9.4). The data from the laboratory experiment (6 week's inoculation) was subjected to one-way analysis of variance with the GLM procedure and the Tukey's Studentized Range (HSD) post hoc test to test. For the data from the greenhouse experiment, infection percentage of leaves (%) was compared separately between plant species and treatments using also one-way analysis of variance and Tukey's (HSD) test.

Results

Cronartium fruiting and sporulation *in vitro*

In vitro inoculations were successful, resulting in mean uredinia coverage values ranging from 5% (*C. pini* on *M. sylvaticum*) to ca. 70% (*C. ribicola* on *R. nigrum*), and mean telia coverage values ranging from ca. 6% (*C. pini* on *M. sylvaticum*) to 35% (*C. pini* on *P. lactiflora*) (Table 1). Natural infections were not found on the uninoculated leaves.

Table 1
Mean coverage (x) and standard deviation (std) of uredinia and telia on detached leaf after inoculation with *Cronartium pini* on *Melampyrum sylvaticum*, *Paeonia lactiflora* and *Impatiens balsamina*, and *C. ribicola* on *Ribes nigrum* in the laboratory after 6-weeks of incubation (n = 90 per plant species). Different letters after mean values indicate significant difference (Tukey's HSD) at $p < 0.001$.

Plant species	**Fruiting stages**							
	Uredinia				**Telia**			
	x	std	min	max	x	std	min	max
Ribes nigrum	69.60[a]	33.91	0	100.0	9.08[a]	11.69	0	70.5
Melampyrum sylvaticum	5.42[c]	11.50	0	50.5	5.65[a]	13.29	0	50.5
Paeonia lactiflora	36.05[b]	35.96	0	100.0	34.51[b]	36.35	0	100.0
Impatiens balsamina	6.63[c]	13.45	0	70.5	6.12[a]	13.47	0	70.5

Significant differences occurred between plant species in the mean coverage of uredinia (ANOVA, $F_{3,356}=205.53$, $p < 0.001$) and telia ($F_{3,356}=48.14$, $p < 0.001$) after six weeks of incubation time (Table 2). In pairwise comparisons, significant differences in coverage of uredinia were found between all species except between *M. sylvaticum* and *I. balsamina* (Tukey's HSD, Table 1). The coverage of telia differed significantly only between *P. lactiflora* and the other three species (Table 1).

Table 2

ANOVA table on the effect of plant extract treatments on uredinia and telia formation after inoculation of leaves of four test plants (*R. nigrum*, *M. sylvaticum*, *P. laciflora* and *I. balsamina*) with *Cronartium pini* or *C. ribicola* after incubation of six weeks in the laboratory.

	Uredinia					Telia				
Source	**Type III SS**	**DF**	**MS**	**F**	**P**	**Type III SS**	**DF**	**MS**	**F**	**P**
Corrected	361619	35	10332	25.46	$p < 0.001$	97147	35	2776	7.73	$p < 0.001$
Intercept	311729	1	311729	768.07	$p < 0.01$	68959	1	68959	192.00	$p < 0.001$
Species	247816	3	82605	203.53	$p < 0.001$	51869	3	17290	48.14	$p < 0.001$
Treatment	48896	8	6112	15.06	$p < 0.001$	16553	8	2069	5.76	$p < 0.001$
Species x Treatment	64906	24	2704	6.66	$p < 0.001$	28725	24	1197	3.33	$p < 0.001$
Error	131499	324	406			116369	324	359		
Total	804846	360				282475	360			
Corrected total	493118	359				213516	359			

Significant differences occurred between extract treatments both in coverage of uredinia (ANOVA, $F_{8,351}=15.06$, $p < 0.001$) and telia ($F_{8,351}=5.76$, $p < 0.001$). Coverage of uredinia was significantly higher in all the other extract treatments and methanol compared to dry control and uninoculated treatment (Tukey's HSD, Table 3). Dry control did not differ significantly from uninoculated treatment, and the extract treatments and methanol control did neither differ from one another (Table 3). The coverage of telia was significantly higher after treatment with extracts from *M. pratense*, *V. chamaedrys*, chlorogenic acid and methanol control compared with uninoculated treatment (Table 3). The extract treatments including methanol and dry controls did not differ in telia coverages from one another (Table 3).

Table 3

Percentage of uredinia and telia of *Cronartium pini* and *C. ribicola* on detached leaves of test plants, pretreated with four plant extracts, two commercial chemicals, water-methanol control, dry control, and on uninoculated leaves after 6-weeks of *in vitro* incubation. Shown are the mean values of 40 replicate leaves of all the test plants per treatment, standard deviation, and minimum and maximum values. Significant differences between treatments (Tukey's HSD) are indicated with different letters at $p < 0.001$.

Treatments	Uredinia				Telia			
	x	std	min	max	x	std	min	max
Melampyrum pratense	35.41^{a}	38.49	0	100.0	16.55^{a}	22.72	0	70.5
Impatiens glandulifera	28.90^{a}	39.82	0	100.0	7.95^{ab}	19.92	0	90.0
Veronica chamaedrys	38.10^{a}	39.14	0	100.0	16.68^{a}	24.97	0	90.0
Ribes rubrum	30.85^{a}	38.45	0	100.0	16.08^{ab}	24.40	0	90.0
Chlorogenic acid	36.63^{a}	38.64	0	100.0	21.66^{a}	31.20	0	100.0
Quercitrin	32.53^{a}	38.82	0	90.0	12.25^{ab}	25.02	0	90.0
Water + methanol control	40.58^{a}	41.49	0	100.0	23.30^{a}	33.30	0	100.0
Dry control	21.85^{b}	24.29	0	90.0	10.10^{ab}	14.51	0	50.5
Control without inoculum	0^{b}	0	0	0	0^{b}	0	0	0

None of the plant extracts or commercial compounds showed significant inhibition against *C. pini* infection on the test leaves (Table 3). Among extracts, the lowest coverages of *C. pini* uredinia and telia occurred on the leaves treated with *I. glandulifera* (Table 3). The highest coverages of uredinia and telia occurred after methanol treatment on the plates (Table 3).

Effect of leaf extracts on Cronartium fruiting and sporulation in the greenhouse

The mean percentage of infected leaves per plant among plant species was highest on *P. lactiflora* in which all leaves of all plants became infected (Table 4). The mean percentage of infected leaves was ca. 50% on *R. nigrum* and ca. 18% on *I. balsamina*. The disease incidences differed statistically significantly between plant species (one-way ANOVA, $F_{2,21}=163.22$, $p < 0.001$). All plant species differed significantly from one another according to Tukey's test ($p < 0.001$, Table 4). The mean percentage of infected leaves per plant did not differ significantly between extract treatments (one-way ANOVA, $F_{7,16}=0.058$, $p = 1.0$, Table 5). The highest mean disease incidence occurred after treatment with *R. rubrum* extract and the lowest with chlorogenic acid (Table 5). None of the treatments prohibited significantly rust fruiting and sporulation on leaves of test plants in the greenhouse (Table 5).

Table 4

Mean percentage and variation of *Ribes nigrum*, Paeonia lactiflora and Impatiens balsamina leaves per plant bearing either uredinia or telia of Cronartium pini or C. ribicola after treatment with four plant extracts, two commercial chemicals and two controls and inoculation with either Cronartium pini or C. ribicola after 6-weeks of incubation in the greenhouse. N = Number of plants. Significant differences between plant species (Tukey's HSD) are indicated with different letters at p < 0.001.

Plant species	Leaves with uredinia or telia per plant				
	N	x	std	min	max
Ribes nigrum	8	50.21[a]	10.11	41.9	72.2
Paeonia lactiflora	8	100.00[b]	0	100.0	100.0
Impatiens balsamina	8	18.11[c]	12.17	0	70.5

Table 5

Mean percentage and variation of *Ribes nigrum*, Paeonia lactiflora and Impatiens balsamina leaves per plant bearing either uredinia or telia of Cronartium pini or C. ribicola after treatment with four plant extracts, two commercial chemicals and two controls and inoculation with either Cronartium pini or C. ribicola after 6-weeks of incubation in the greenhouse. N = Number of plants. Significant differences between treatments (Tukey's HSD) are indicated with different letters at p < 0.001.

Treatment with extracts	Leaves with uredinia or telia per plant				
	N	x	std	min	max
Melampyrum pratense extract	3	51.07[a]	46.90	6.5	100.0
Impatiens glandulifera extract	3	58.77[a]	39.36	21.6	100.0
Veronica chamaedrys extract	3	55.37[a]	39.74	23.8	100.0
Ribes rubrum extract	3	65.10[a]	38.94	23.1	100.0
Chlorogenic acid	3	50.00[a]	50.00	0	100.0
Quercitrin	3	53.77[a]	41.59	19.4	100.0
Water + methanol control	3	51.97[a]	45.12	11.1	100.0
Dry control	3	63.73[a]	32.01	39.4	100.0

Discussion

Creating eco-friendly plant-protection solutions is especially vital for commercially valuable forest species such as pines. Plants that naturally resist pathogens are a potential source of low-risk compounds that fit well into integrated pest-management programs for forest production systems (Lankinen et al., 2024). An

earlier study addressed the possible role of alternate host extracts on the aeciospore germination of *Cronartium* rusts (Piispanen et al*.,* 2025). The results indicated that the effect of extracts and pure compounds on the pre-haustorial phase of rust infection was not straightforward (Piispanen et al., 2025). Here, we tested the effect of extracts and individual pure compounds on the post-haustorial, sporulation phase of *Cronartium* rusts on susceptible alternate hosts.

Our experiments confirmed that rust sporulation differed markedly among the test plants, i.e., rust fruiting is strongly host-dependent. Among the tested species, *P. lactiflora* was heavily infected by *C. pini* and *R. nigrum* by *C. ribicola*. On the other hand, *I. balsamina* was the least infected in both *in vivo* and in *in vitro* tests, in accordance with earlier studies that rated it less susceptible (Kaitera et al. 2012, 2015). In Finnish gardens, paeonies (e.g., *P. lactiflora*) are appreciated ornamentals, and *R. nigrum* is commonly planted by households due to its berries. Given that susceptible plant species are common both in forests (*Melampyrum* species) and in urban areas, *Cronartium* rusts will continue to be a threat to pine forestry throughout the country.

Opposed to our expectation, none of the plant extracts from rust-resistant species and commercial chemicals significantly reduced fruiting and sporulation of either *C. pini* or *C. ribicola* in the *in vitro* tests. In contrast, all treatments, including methanol, promoted sporulation. This could indicate that the rusts were able to use the extracts or chemicals as a source of nutrients (carbon) (Blumenstein et al., 2015) or as positive signaling molecules (Mandal et al., 2010). In addition, while most extracts and pure chemicals tended to result in lower mean sporulation on intact (*in vivo*) plants, none of the treatments showed a clear and strong inhibitory effect. These inconsistent trends across the *in vitro* and *in vivo* tests further suggest that the tested plant extracts and chemicals, administered as spray treatment, are not promising protectants against *Cronartium* rusts. However, we cannot exclude that different concentration of extracts or pure compounds might have influenced rust fruiting differently. In our recent study, plant extracts with 50 and 100 ppm had stimulative effect on germination of *C. pini* and *C. ribicola* aeciospores on agar, while 500 ppm inhibited strongly spore germination (Piispanen et al., 2025). Thus, testing of plant extracts should be continued with higher concentrations and different solvents.

Declarations

Ethics declarations

The authors bear all the ethical responsibilities of this manuscript. They declare that the research was conducted in the absence of any commercial or financial relationship that could be construed as a potential conflict of interest and that it does not include any animal and/or human trials.

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Data availability The data that support the findings of this study are available from the corresponding author upon reasonable request.

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