



Lack of induced chemical changes in leaves of susceptible alternate hosts of *Cronartium* spp. after inoculation by *Cronartium pini* and *C. ribicola*

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Abstract Phenolic compounds, known for their antioxidant and antifungal properties may be connected to infection processes of *Cronartium* rusts in alternate host plants. We studied changes in leaf chemistry after *Cronartium* inoculation on susceptible alternate hosts of *C. pini* and *C. ribicola*. *Impatiens balsamina* and *Paeonia lactiflora* were inoculated with *C. pini*, and *R. nigrum* with *C. ribicola* in the greenhouse. Leaves of the inoculated plants were harvested 3 and 6 days after inoculation for chemical analysis, which was done using LC–MS (liquid chromatography mass spectrometry). Species-specific differences were found in dominant phenolics ferulic

acid, hyperoside, quercitrin, and rutin. Rust inoculation produced limited changes in phenolic concentrations, with significant increases only in *p*-coumaric acid in *I. balsamina* and rutin in *R. nigrum*. Significant post-inoculation decrease was found in several cases. While phenolic fluctuations varied by species and incubation time, there was no significant interaction between inoculation and incubation time, suggesting the absence of induced phenolic accumulation during early infection stages. The results support the hypothesis that susceptible alternate hosts exhibit weak, delayed phenolic defenses, possibly due to rust virulence factors suppressing these responses. Indirectly, they provide support for the defensive role of phenolics in resistant congeneric hosts, emphasizing also the importance of further molecular studies to explore plant defense mechanisms against rust pathogens.

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Introduction

Cronartium rusts are common pathogens of *Pinus* spp. In the northern hemisphere (Gäumann, 1959; Ziller, 1974). Among *Cronartium*, *Cronartium pini* (Willd.) Jørst. causes severe damage especially on *Pinus sylvestris* L. in northern Fennoscandia (Kaitera,

2000; Wulff et al., 2012). Another rust, *Cronartium ribicola* Fisch., is a serious pathogen of five-needle pines especially in North America (Zambino, 2010). The aeciospores of the heteroecious life-cycle form of *C. pini* infect over 50 species belonging to 14 plant families, forming urediniospores and later teliospores on the leaves of these alternate hosts (CABI, 2020; Kaitera et al., 2015; Kim et al., 2022). Re-infection of pines occurs via basidiospores that develop from basidia after germination of teliospores. The presence and susceptibility of alternate hosts is thus a significant determinant of the rust infection risk in pine forests. Important host plants for *C. pini* belong to families Orobanchaceae, Paeoniaceae and Balsaminaceae (Kaitera, 1999; Kaitera & Nuorteva, 2003a, 2003b; Kaitera et al., 1999, 2012, 2015, 2017, 2018). *C. ribicola* spreads mainly via *Ribes* in the family Grossulariaceae (Kaitera & Nuorteva, 2006b; Zambino, 2010). Alternate host genera contain both susceptible and resistant species to *Cronartium*, but the specific reasons for these differences have not been studied.

The chemical constituents of leaves, including phenolic metabolites, may at least partly explain the resistance patterns of plants. Phenolics are characterized by the presence of one or more hydroxyl groups (-OH) attached to an aromatic ring and include simple molecules (e.g., salicylic acid), complex polymers (e.g., condensed tannins), and intermediate structures such as flavonoids and stilbenes. They have multiple functions in plants, and contribute to structural support (e.g., lignin in cell walls), pigmentation (e.g., flavonoids), and defense against biotic (pathogens, herbivores) and abiotic (UV radiation, oxidative stress) stress (Witzell & Martín, 2008). These compounds are known to accumulate at infection sites, inhibiting spore germination and hyphal growth. Ullah et al. (2017) reported that poplar genotypes with higher flavan-3-ol levels or overexpressing the MYB134 transcription factor showed enhanced resistance to rust fungi, while silencing PnMYB134 reduced flavan-3-ol production and increased susceptibility, underscoring their importance in poplar antifungal defense. Earlier results have also found that in interactions between willows (*Salix* spp.) and their leaf rusts (*Melampsora* spp.), both the constitutive phenolics and induced phenolic responses may contribute to the expression of rust resistance, but in a highly genotype and compound specific manner (Hakulinen & Julkunen-Tiitto, 2000; Hakulinen et al., 1999).

In previous studies, phenolic compounds, such as chlorogenic acid and quercitrin, have been connected to *C. pini*-resistance in alternate hosts and these compounds are, therefore, potential antifungal or fungistatic compounds (Kaitera & Witzell, 2016; Piispanen et al., 2023). In addition, leaf extracts from rust-resistant alternate hosts inhibited more strongly germination of *Cronartium* spores than extracts from rust-susceptible species (Piispanen et al., unpublished). Chemical variation between rust-resistant and rust-susceptible species is, however, high (Piispanen et al., 2023) and little is known about the possible chemical responses in susceptible alternate hosts. Induced defensive responses, especially in the early phase of the infection can suppress the development of disease (Hönig et al., 2023).

We hypothesized that chemical responses in susceptible alternate hosts are weak or delayed, which could explain their susceptibility to rust infections. To investigate this, we studied the changes in phenolic acids and flavonoids taking place in infected leaves of rust-susceptible plants during the early stage of infection (3 and 6 days after inoculation), before fruiting of *Cronartium*.

Material and methods

Plant material

Forty plants of *Ribes nigrum* L. (cultivar Melalahti) and *Paeonia lactiflora* Pall. were first grown in a nursery (Särkän taimitarha), and *Impatiens balsamina* L. were grown from seeds in the Botanical Gardens of Oulu in May 2021. Plants were further grown in plastic pots in the greenhouse and irrigated by hose irrigation: once a day ca. 100–300 ml per seedling, and for 2 s every 15 min, on a greenhouse table for a month.

Inoculum

Aeciospores from four lesions of *C. ribicola* carrying unopened aecia on *P. cembra* L. in Oulunsalo (64°56,50N, 25°22,60E), northern Ostrobothnia, were dusted from fresh aecia using a sterilized scalpel straight to Petri dishes in the field in late May (21st) 2021. Five lesions of *C. pini* carrying unopened aecia were cut from *P. sylvestris* L. from Kolari (67°9,64N,

23°40,06E), northern Finland, in mid-June (14th) 2021, and transported directly to Lynet laboratory in Oulu (Luke). Aeciospores of *C. pini* were dusted aseptically on Petri dishes using a sterilized scalpel in the laboratory. The aecial remnants and other impurities were removed from the dishes using sterile forceps.

Germination rate of the aeciospores was measured by dusting a sub-sample of spores on 1.5% water agar followed by incubation at 21.5°C for 24 h and counting spore germination on 10 microscopic fields on the agar plates using a light microscope (Meiji). The germination rate ranged between 81%–91% (mean 85%) for *C. pini* and between 87%–98% (mean 94.4%) for *C. ribicola* aeciospores.

Inoculation of the plants

As *C. ribicola* does not infect alternate hosts of *C. pini* including *Paeonia* and *Impatiens* (Kaitera & Nuorteva, 2006b; Kaitera et al., 2012) and *C. pini* does not infect alternate hosts of *C. ribicola*, *Ribes* (Kaitera & Nuorteva, 2006a), only susceptible alternate hosts of either of the rusts were inoculated. Circa 30000 aeciospores of *C. ribicola* per cm² (Kaitera & Nuorteva, 2006a) were dusted on the lower surface of the leaves of one branch per plant of 20 *R. nigrum* plants using an artist's pencil in the greenhouse in early June 2021. The inoculated branches were moistened prior to inoculation and covered after inoculation with a moistened polyethylene plastic bag (LAMU PE) for 24 h to enhance spore germination. Twenty uninoculated

plants of *R. nigrum* were incubated similarly as controls. In addition, all leaves of 20 plants each of *P. lactiflora* and *I. balsamina* were inoculated with aeciospores of *C. pini*, 20 plants of each species were left uninoculated as controls, and the leaves were incubated similarly as *Ribes* in the greenhouse in mid-June 2021 (Figs. 1a–d). Ten leaves per inoculated plant (=sample) and control were harvested 3 and 6 days after the inoculation before uredinia formation. *C. pini* uredinia are known to appear 8 days after infection (Ragazzi et al., 1989). During the experiment the average relative humidity inside the greenhouse was 64.8%, temperature was 21.3°C and solar radiation was less than 250 W per m².

Treatment and extraction of the leaves

In the laboratory, healthy green leaves of the 120 plants without any sign of fungal or insect damage, were separated from the rest of the plant material in a laminar cabin with sterile tweezers. The leaves were air-dried for ca. one week in a laminar cabin in open paper bags at 21.5 °C under natural light and stored at –20 °C. For the analysis, the leaf samples were crushed manually inside a paper bag until a powdery consistency was achieved. About 15 mg of each sample was weighed into an Eppendorf vial. Methanol (1 mL), containing 5 mg/l of internal standard (ampicillin) cooled to +4 °C was added to vials which were kept at +4 °C for one hour. Using Eppendorf Mix-Mate, the samples were shaken (5 min, 1400 rpm) and centrifuged at +4 °C (5 min, 12,000 rpm, Hettich



Fig. 1 Test plants **a.** *I. balsamina*, **b.** *P. lactiflora* and **c.** *R. nigrum*, and **d.** incubation of a test plant with a plastic bag

Mikro 200). The supernatant was transferred to a new vial and the residue was extracted with 0.5 ml of pure methanol. After combining the supernatants, the extracts were filtered through a disposable syringe filter (pore size 0.2 μm , Pall Corporation) and stored at $-20\text{ }^{\circ}\text{C}$ until analysed.

Chemical analysis

A total of 240 samples, i.e., the harvested leaves from 20 plant individuals from each of the three species, collected at two incubation times (3 and 6 days), as well as the corresponding controls, were analyzed in the quantitative LC–MS analysis that was carried out following the method described by Piispanen et al. (2023). Briefly, 15 mg of freeze dried healthy green leaf material was extracted with methanol into a final volume of 1.5 ml. 5 μL sample aliquots were subjected to LC–MS analysis using a Waters Acquity Premier HSS T3 column ($2.1 \times 100\text{ mm}$, 1.8 μm) with a gradient of 0.1% formic acid in water and acetonitrile (8–70% over 13 min) at $40\text{ }^{\circ}\text{C}$ column temperature. Detection was performed on a Q-Exactive Plus Orbitrap mass spectrometer (Thermo Fisher Scientific) in negative polarity, with a resolution of 70,000 A and an m/z range of 115–1200. The AGC target was set to 3e6 with 200 ms maximum injection time. Target compounds were identified with their accurate mass and chromatographic retention time by comparing to the pure standards (chlorogenic acid (Acros Organics, 109,240,010), caffeic acid, syringic acid, *p*-coumaric acid, rutin, hyperoside, ferulic acid, and quercitrin (Cayman Chemical Company, CAYM19866), myricetin, apigenin and kaempferol).

For quantitation, calibration curves with eight levels (1 $\mu\text{g}/\text{mL}$ to 1 ng/mL) were established using extracted ion chromatograms with 5 mmu windows. Data were analyzed with Xcalibur's QuanBrowser option (Thermo).

Statistical analysis

Concentrations of the selected compounds were compared after 3 and 6-days of incubations between inoculated and control leaves separately for each test plant and *Cronartium* species using ANOVA with Tukey's HSD test. Statistical analyses were conducted using SPSS (IBM Corp. Released 2023. IBM SPSS

Statistics for Windows, Version 29.0.0.0 Armonk, NY: IBM Corp) software.

Results

Impatiens balsamina

In *I. balsamina* leaves, inoculation with *C. pini* decreased significantly the concentration of chlorogenic acid and ferulic acid but increased the concentration of *p*-coumaric acid ($p < 0.001$) but had no significant effect on caffeic acid and syringic acid (Table 1, Table S1). The concentration of chlorogenic acid, ferulic acid and caffeic acid increased significantly ($p < 0.001$) from 3 to 6 days post inoculation, whereas no significant changes were found for syringic acid and *p*-coumaric acid (Table 1). Interaction between inoculation and time was non-significant for all phenolic acids.

Inoculation did not significantly affect concentration of any of the analyzed flavonoid compounds (Table 1). However, there was significant increase between 3 to 6 days incubation time in concentration of rutin ($p < 0.001$), quercitrin ($p < 0.005$) and kaempferol ($p < 0.01$) (Table 1). Interaction between inoculation and time was non-significant for all flavonoid compounds.

Paeonia lactiflora

In *P. lactiflora* leaves, *C. pini* inoculation had no effect on the concentration of chlorogenic acid, caffeic acid, *p*-coumaric acid or ferulic acid (Table 1, Table S1). However, it increased the concentration of syringic acid ($p = 0.039$) (Table 1). There were no significant changes in concentration of any of the quantified phenolic acids during the period from 3 to 6 days post inoculation (Table 1) and the interaction between inoculation and time was also non-significant for all the phenolic acids.

Inoculation with *C. pini* decreased rutin concentration ($p = 0.032$) but did not affect the concentration of other flavonoids in *P. lactiflora* leaves (Table 1). The incubation time from 3 to 6 days did not cause significant changes in concentration of any of the quantified flavonoids (Table 1) and also the interaction between inoculation and time was non-significant for all flavonoid compounds.

Table 1 Summary of the impacts of rust inoculation (R) and incubation time from 3 to 6 days post inoculation (T) and their interaction (R x T) on five phenolic acids and six flavonoids in three alternate host species, *I. balsamina*, *P. lactiflora* and *R. nigrum*

		<i>I. balsamina</i>			<i>P. lactiflora</i>			<i>R. nigrum</i>		
		R	T	RxT	R	T	RxT	R	T	RxT
Ph. acids	CHL	↓	↑	o	o	o	o	↓	↓	o
	CAF	o	↑	o	o	o	o	↓	o	o
	SYR	↓	↑	o	o	o	o	↓	o	o
	PCA	↑	o	o	o	o	o	↓	↓	o
	FER	o	o	o	↑	o	o	o	o	o
Flavonoids	RUT	o	↑	o	↓	o	o	↑	↓	o
	HYP	o	o	o	o	o	o	o	↓	o
	QUE	o	↑	o	o	o	o	o	o	o
	MYR	o	o	o	o	o	o	o	o	o
	API	o	o	o	o	o	o	o	↓	o
	KAE	o	↑	o	o	o	o	o	o	o

Arrows and colors show significant ($\alpha=0.05$) effect (upwards arrow in red=increase; downwards arrow in blue=decrease), “o” indicates non-significant effects. CHL=chlorogenic acid, CAF=caffeic acid, SYR=syringic acid, PCA=p-coumaric acid, FER=ferulic acid, RUT=rutin, HYP=hyperoside, QUE=quercitrin, MYR=myricetin, API=apigenin, KAE=kaempferol

Ribes nigrum

Inoculation with *C. ribicola* decreased significantly the concentration of chlorogenic acid ($p<0.01$), caffeic acid ($p<0.001$), *p*-coumaric acid ($p<0.001$) and ferulic acid ($p=0.014$) in leaves of *R. nigrum* (Table 1, Table S1). The concentration of chlorogenic acid and *p*-coumaric acid decreased from 3 to 6 days post inoculation incubation ($p=0.011$) but incubation time did not change the concentrations of other phenolic acids (Table 1). Interaction between inoculation and time was non-significant for all phenolic acids.

Inoculation with *C. ribicola* increased rutin concentrations in leaves of *R. nigrum* ($p=0.013$) but did not affect the concentration of other flavonoids in *R. rubrum* leaves (Table 1). The concentration of rutin ($p<0.001$), hyperoside ($p=0.005$) and apigenin ($p<0.01$) decreased significantly from 3 to 6 days' incubation (Table 1). Interaction between inoculation and time of incubation was non-significant for all the quantified flavonoid compounds in *R. nigrum* leaves.

Discussion

Phenolic metabolites are widespread in plants, where they act as antioxidants and potentially antifungal agents (Witzell & Martín, 2008), possibly contributing to the resistance of alternate host plants against rust infections (Hakulinen & Julkunen-Tiitto, 2000; Hakulinen et al., 1999; Ullah et al., 2017). Present as both constitutive and induced constituents in plants, phenolics can have multiple roles in the interactions between pathogenic fungi and the host plants (Witzell & Martín, 2008). Previous studies have suggested that certain phenolic compounds may function as resistance factors in alternate hosts of *Cronartium* rusts (Kaitera & Witzell, 2016). For example, chlorogenic acid and quercitrin have been associated with resistance to *C. pini* in species belonging to genera of *Melampyrum* (Kaitera & Witzell, 2016; Piispanen et al., 2023), *Veronica*, and *Impatiens* (Piispanen et al., 2023).

In the current study, we examined three alternate host species known to be susceptible to rust infections and observed distinct differences in their phenolic acid and flavonoid profiles. In *I. balsamina*, the

profile was dominated by ferulic acid along with the flavonoids (glycosides of quercetin) hyperoside and quercitrin, whereas in *P. lactiflora* the dominant compounds were only hyperoside and quercitrin (Suppl. Table 1). The leaves of *R. nigrum*, a susceptible host for *C. ribicola*, were characterized by a phenolic profile with three prominent flavonoids: rutin, hyperoside, and quercitrin (Suppl. Table 1). Similar profiles have been described in literature, e.g., quercetin glycosides have been described in the leaves of *Impatiens* species (Szewczyk, 2018) and *Paeonia* (Xin et al., 2023).

In our experiment, rust inoculation had only minor effects on the concentrations of phenolic acids and flavonoids. In most cases where differences were observed, phenolic levels were lower in inoculated plants compared to controls. Only *p*-coumaric acid in *I. balsamina* and rutin in *R. nigrum* showed a significant increase following inoculation. The lower concentration after inoculation may result from inhibition of biosynthesis or increased metabolic turn-over in plants, but it could also be a result of dilution effect in case allocation to other cell constituents, e.g. carbohydrates, increases (Lu et al., 2017). The cell level mechanisms behind the observed effects were outside the scope of the current study but should be elucidated in future studies using transcriptomics approaches.

While six individual compounds in *I. balsamina* increased over the incubation period (up to six days post-inoculation), four phenolic acids decreased in *R. nigrum* during the same period, suggesting plant and pathogen species specific fluctuations in the phenolic pool. Moreover, the interaction between inoculation and incubation time was consistently non-significant across all three plant species. Therefore, we did not find evidence for an induced accumulation of phenolics in response to inoculation during the early stages of rust infection. Based on our study that only covered the early stages of the rust infection, we cannot exclude that induction by phenolic accumulation may occur later in the infection process. However, the susceptibility of the studied alternate hosts to rusts suggests that *Cronartium* rusts have virulence mechanisms and effector molecules (Petre et al., 2014) to suppress or re-program any induced defense responses in these plant species.

Taken together, the results from this study support our initial hypothesis that defensive responses, as indicated by the concentrations of potentially protective

phenolics are weak, and possibly delayed, in the susceptible alternate hosts of *Cronartium* rusts. The lack of activation in phenolic metabolism following rust inoculation in the susceptible hosts provides indirect evidence for the defensive role of phenolics in the resistant, congeneric alternate hosts of *Cronartium* rusts (Kaitera & Witzell, 2016; Piispanen et al., 2023). Future studies should explore the molecular mechanisms activated by rusts in the alternate hosts, considering particularly the role of *Cronartium* effectors (Ma et al., 2019).

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

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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