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Juha Kaitera[1], Leena Aarnio[2], Tiina Ylioja[2] and Jouni Karhu[1]

Naohidemyces vaccinii sporulates on wild species of ground flora in Finnish Norway spruce seed orchards but *Thekopsora areolata* does not on other species than *Prunus*

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Highlights

- Cherry-spruce rust, *Thekopsora areolata,* was not found on any of the common species of ground vegetation in Finnish Norway spruce seed orchards.
- Blueberry rust, *Naohidemyces vaccinii*, was common on *Vaccinium myrtillus* and occasional on *V. vitis-idaea* in all seed orchards.
- *Thekopsora areolata* occurs only on *Prunus* in Finnish Norway spruce seed orchards.

Abstract

Thekopsora areolata (Fr.) Magnus is a serious cone pathogen that reduces seed crop of *Picea abies* (L.) Karst. and other *Picea* spp. Natural sporulation of *T. areolata* was investigated in nine Norway spruce seed orchards suffering from severe successive *T. areolata* epidemics in Finland. Habitats occupied by *Vaccinium myrtillus* L., *V. vitis-idaea* L., *Empetrum nigrum* L. and *Calluna vulgaris* (L.) Hull, and a number of other wild species belonging to ground flora were investigated for *Thekopsora areolata* uredinia 9–10 times in May–September 2018–2019. Occurrence of *Thekopsora* uredinia was estimated in current-year leaves of the plants in ca. 25 sample plots of 1 m^2 in each seed orchard. A sample of plant leaves with rust uredinia or necrotic pustules were collected from each plot. No rust fruiting stages of *T. areolata* were found on any of the test species of ground flora. However, rust uredinia were observed regularly on leaves of *V. myrtillus* and *V. vitis-idaea* in all seed orchards between mid-July and the end of September. Rust sporulation started on *V. myrtillus* in July and on *V. vitis-idaea* in August. Based on symptoms, uredinia and spore morphology, the rust on both *V. myrtillus* and *V. vitis-idaea* was identified as blueberry rust, *Naohidemyces vaccinii* (Jørst.) S. Sato, Katsuya & Y. Hirats. ex Vanderwegen & Fraiture. The uredinial stage of the rust on *Vaccinium* spp. were described. No evidence of natural sporulation of *T. areolata* on wild plant species other than *Prunus* was observed in Finnish Norway spruce seed orchards.

Keywords *Picea abies*; *Prunus*; blueberry rust; cherry-spruce rust; epidemics; *Naohidemyces vaccinii*
Addresses [1]Natural Resources Institute Finland (Luke), Natural Resources and Bioproduction, FI-90570 Oulu, Finland; [2]Natural Resources Institute Finland (Luke), Natural Resources and Bioproduction, FI-00790 Helsinki, Finland
E-mail juha.kaitera@luke.fi
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1 Introduction

Thekopsora areolata (Fr.) Magnus is a pathogen that causes cherry-spruce rust in Norway spruce [*Picea abies* (L.) Karst.] cones. The rust highly reduces Norway spruce seed crop in seed orchards in southern Finland (Savonen 2001; Kaitera 2013) and in seed tree stands in northern Finland (Nikula and Jalkanen 1990; Kaitera 2013). The rust reduces the number of seeds in infected cones and seed viability (Kaitera and Tillman-Sutela 2014). Recently, the heteroecious nature of the rust was confirmed by molecular (Capador et al. 2020) and inoculation studies (Kaitera et al. 2019). In addition to the cones of *P. abies*, the rust sporulates also on other spruce species, such as *P. engelmannii* Parry ex Engelm., *P. glauca* (Moench) Voss and *P. omorika* (Panĉić) Purk. that are non-native in Finland (Kaitera et al. 2009, 2014, 2017) as well as in shoots of *P. abies* and *P. engelmannii* (Roll-Hansen 1947; Hietala et al. 2008).

The alternate hosts of *T. areolata* are known to belong to the genus *Prunus* (Gäumann 1959; Kaitera et al. 2014, 2017, 2019). Seed orchard managers try to control and remove *Prunus padus* L. populations from within and the vicinity of orchards. However, the infection rate can be high even in seed orchards where *P. padus* appears non-existing (Kaitera et al. 2009, 2021b). This can be either due to efficient long-distance spore dispersal or there exist other alternate hosts than *Prunus* within the seed orchards.

Rust genera *Thekopsora* and *Pucciniastrum* have been considered to belong to the same genus, *Pucciniastrum* sensu lato, although teliospores of *Thekopsora* are produced in plant epidermis and those of *Pucciniastrum* in mesophyll (Cummins and Hiratsuka 1983). Yet, the phylogeny of these two genera is still unclear (Maier et al. 2003). Recently, however, their phylogenetic relationship was reviewed (Aime and McTaggert 2021). In general, the rusts in these genera spread via species of Rosaceae, Ericaceae, Rubinaceae, Asteraceae, Hydrangeaceae and Boraginaceae (Gäumann 1959). Other *Thekopsora* and *Pucciniastrum* rusts have been described on e.g. *Vaccinium* spp., *Arctostaphylos* spp., *Erica* spp., *Calluna* spp. and *Galium* spp. (Gäumann 1959; CABI 2019).

Epidemics of *T. areolata* have been reported in remote locations (Nikula and Jalkanen 1990) and seed orchards (Kaitera et al. 2009), where *Prunus* species have either low prevalence or are missing, suggesting that other species than *Prunus* might serve as alternate hosts for the rust. The aim of the study was to clarify, if other plant species than *Prunus* can spread *T. areolata* under natural conditions in Finnish seed orchards, and therefore, to investigate and describe the natural sporulation of *T. areolata* on species of Ericaceae and some other species belonging commonly to the ground flora in Norway spruce seed orchards in Finland. Recently, we tested by artificial inoculation the susceptibility of a number of species to *T. areolata* (Kaitera et al. 2019, 2021a), the current monitoring of natural sporulation of rusts on various plant species providing supplementary evidence. It was also aimed to describe another rust found commonly on *Vaccinium* in seed orchards.

2 Materials and methods

2.1 Rust estimation and sampling of plants

Plant communities of *Vaccinium myrtillus* L., *V. vitis-idaea* L., *Empetrum nigrum* L. and *Calluna vulgaris* (L.) Hull growing within seed orchards, were investigated for rust uredinia in nine Norway spruce seed orchards in southern Finland (Fig. 1; Nikkanen et al. 1999) in May–September 2018 (nine times) and 2019 (eight times). The sampling dates are presented in Table 1. Young leaves

Fig. 1. Locations of investigated Norway spruce seed orchards in Finland. 1 = Heinämäki 170 (62°13´N, 25°24´E), 2 = Metsä-Ihala 176 (62°12´N, 24°07´E), 3 = Riihimäki 169 (61°53´N, 24°52´E), 4 = Paronen 1 365 (61°39´N, 26°17´E), 5 = Sillanpää 235 (60°55´N, 26°13´E), 6 = Taavetti 428 (60°56´N, 27°35´E), 7 = Imatra 374 (61°09´N, 28°47´E), 8 = Paronen 2 366 (61°39´N, 26°17´E), 9 = Palvaanjärvi 172 (60°48´N, 27°29´E).

Table 1. Plant species investigated for uredinia of *Thekopsora areolata* and *Naohidemyces vaccinii* in nine Finnish seed orchards in 2018–2019. Numbers refer to sampling dates of the plants in each seed orchard. The sampling dates were: 1 = May 21–24, 2 = June 11–13, 3 = July 2–5, 4 = July 16–18, 5 = July 30 – Aug 1, 6 = Aug 13–15, 7 = Aug 27–29, 8 = Sept 10–12 and 9 = Sept 24–27 in 2018, and 1 = May 20–22, 2 = June 11–13, 3 = June 24–27, 4 = July 8–10, 5 = July 22–25, 6 = Aug 5–7, 7 = Aug 19–21 and 8 = Sept 2–5 in 2019. For the locations of the seed orchards, see Fig. 1.

Test species	Seed Orchard								
	1	2	3	4	5	6	7	8	9
	Sampling dates								
2018									
Vaccinium myrtillus L.	2–9	1–9	1–9	1–9	2–9	1–9	1–9	1–9	2–9
Vaccinium vitis-idaea L.	2–9	2–9	9	1–9	2–9	1–9	1–9	1–9	2–9
Calluna vulgaris (L.) Hull	0	1–9	9	1–9	0	2–9	1–9	1–9	2–9
Empetrum nigrum L.	0	1–9	9	1–9	0	0	0	0	0
Salix sp.	-	2	-	-	-	-	-	-	-
Lysimachia europaea (L.) U.Manns & Anderb.	-	2,4,6	-	-	-	-	-	-	-
Maianthemum bifolium (L.) F.W. Schmidt	-	2,4	-	-	-	-	-	-	-
Chamaenerion angustifolium (L.) Scop.	2,4	6	-	4	4	6	4,6,7	-	-
Lupinus polyphyllus Lindl.	2,4	-	-	-	-	-	-	-	-
Tanacetum vulgare L.	4	-	-	-	-	-	-	-	-
Rubus idaeus L.	4	-	-	-	-	-	-	-	-
Anthriscus sylvestris (L.) Hoffmann	4	-	-	4	4	-	-	-	-
Sorbus aucuparia L.	-	-	4	-	4	-	-	-	4
Filipendula ulmaria (L.) Maxim.	4	-	-	-	-	-	-	-	-
Populus tremula L.	-	-	-	-	-	-	4	-	-
Betula pubescens Ehrh.	-	-	-	-	-	-	6	-	-

Table 1. continued.

Test species	Seed Orchard								
	1	2	3	4	5	6	7	8	9
	Sampling dates								
2019									
Vaccinum myrtillus L.	1–8	1–8	1–8	1–8	1–8	1–8	1–8	1–8	1–8
Vaccinum vitis-idaea L.	1–8	1–8	1–8	1–8	1–8	1–8	1–8	1–8	1–8
Calluna vulgaris (L.) Hull	1–8	1–8	1–8	1–8	1–8	1–8	1–8	1–8	1–8
Empetrum nigrum L.	1–8	1–8	1–8	1–8	1–8	1–8	1–8	1–8	1–8
Salix sp.	1,2,4	-	2	-	-	2	2	-	-
Lysimachia europaea (L.) U.Manns & Anderb.	-	2,4	-	3	-	-	-	-	-
Maianthemum bifolium (L.) F.W. Schmidt	-	-	-	-	-	-	-	4	-
Chamaenerion angustifolium (L.) Scop.	2,4	-	2	2,4	2	2	2	-	-
Lupinus polyphyllus Lindl.	1,2,4	-	-	4	-	-	2	-	-
Rubus idaeus L.	2	-	-	-	2	2	2	-	-
Anthriscus sylvestris (L.) Hoffmann	2	-	-	2	2	-	2	-	-
Sorbus aucuparia L.	1,2,4	-	-	-	-	-	2	-	2
Filipendula ulmaria (L.) Maxim.	-	-	-	3	1	-	-	-	-
Populus tremula L.	-	2	-	-	-	-	2	-	-
Betula pubescens Ehrh.	-	2	-	-	-	-	-	-	2
Fragaria vesca L.	1,2	-	-	-	-	-	-	-	-
Viola tricolor L.	-	-	-	-	1	-	-	-	-
Convallaria majalis L.	2	-	2	2	2	-	-	-	2
Geranium sylvaticum L.	2,4	-	2	-	2	-	2	-	-
Melampyrum sylvaticum L.	2	-	-	-	2	-	-	-	2
Rubus saxatilis L.	-	2	2	-	-	-	-	-	2
Betula pendula Roth	4	-	-	-	-	2	2	-	2
Salix caprea L.	-	-	-	-	-	-	-	-	2
Alnus incana (L.) Moench	-	-	-	-	-	-	2	-	-
Quercus robur L.	-	-	-	-	-	-	2	-	-
Melampyrum pratense L.	-	2	2	-	-	-	-	-	-
Veronica chamaedrys L.	2	-	-	-	-	-	-	-	-
Ranunculus sp.	2	-	-	-	-	-	-	-	-
Pteridium aquilinum (L.) Kuhn	2,4	-	-	4	-	-	2	-	-
Cirsium helenioides (L.) Hill.	2	-	-	-	-	-	2	-	-
Ribes rubrum L.	2,4	-	-	-	-	-	-	-	-
Malus sylvestris (L.) Mill.	2,4,5	-	-	-	-	-	-	-	-
Silene dioica (L.) Clairv.	2,4	-	-	2	-	-	-	-	-
Paris quadrifolia L.	2	-	-	-	-	-	-	-	-

0 = No leaves observed.
- = Not sampled.

of the plants growing in homogenous habitats of ca. 1 m^2 were checked visually in the field. The plant communities covered various areas within the seed orchards, and some plants were either missing or with very low frequency in some orchards. In each seed orchard ca. 25 habitats per species were randomly selected for the investigation. In addition, other common plant species of the ground flora were also checked visually for rust fruiting stages during some of the sampling dates (Table 1) at the same time, when *T. areolata* sporulated on *Prunus padus* L. in the seed orchards (Kaitera et al. 2021b). When leaves with rust symptoms including violet pustules with whitish to yellowish uredinia (Kaitera et al. 2019) were observed, a sample of ca. 25 leaves per sampling time were collected to paper bags and transported into laboratory for rust checking.

2.2 Morphological identification of the rust fungi

The morphology of rust pustules on the sampled plant leaves was described. The size (length and width) of ca. 150 rust pustules carrying uredinia were measured. The diameters (length and width) of ca. 450 uredinia were measured. In addition, the diameters (length and width) of 100 urediniospores on both *Vaccinium myrtillus* and *V. vitis-idaea* were measured. The diameters were compared to species descriptions in the literature (Gäumann 1959; Sato et al. 1993). Typical rust pustules, uredinia and urediniospores were photographed. In case uredinia of *T. areolata* were found, their morphology was compared to reference material from inoculations with *T. areolata* on *Prunus* (Kaitera et al. 2019). The measurements were done using stereo (Meiji Techno RZ, Meiji Techno Co., ltd, Japan) and light microscopy (Meiji MX, Meiji Techno Co., ltd, Japan) with magnification up to 600 x.

2.3 Statistical analysis

The average diameters of rust pustules, uredinia and urediniospores were counted and compared with t-test using SAS software (SAS Institute Inc., version 9.4) between *V. myrtillus* and *V. vitis-idaea*. The diameters of uredinia and pustules of the rust on *V. myrtillus* were compared between the collection times (2018 and 2019), and between seed orchards (observations from different sampling times pooled together) with Tukey's test of one-way ANOVA.

3 Results

3.1 Sporulation of *Thekopsora areolata* and an unspecified rust on wild plants in the sample plots in seed orchards

No uredinia of *T. areolata* were observed on *V. myrtillus*, *V. vitis-idaea*, *E. nigrum* or *C. vulgaris* in the sample plots in any of the seed orchards either in 2018 or 2019. Neither were *T. areolata* uredinia observed on species of ground vegetation other than *Prunus* in any of the seed orchards during the investigation.

Unspecified rust pustules were not observed on other species of ground vegetation except on *Vaccinium* in any of the seed orchards regardless of the sampling date and year of investigation. However, orange-yellowish uredinia of an unspecified rust were observed on *V. myrtillus* and orange-yellowish-brownish uredinia on *V. vitis-idaea*. Uredinia of the rust occurred commonly on *V. myrtillus* in nine seed orchards in 2018 and in four seed orchards in 2019 (Table 2). Urediniospores were formed from mid-July to the end of September in 2018. In 2019, sporulation was observed in the second week of July, which continued until early September. On *V. vitis-idaea*, uredinia were detected in three seed orchards both in 2018 and 2019. Sporulation occurred in early September in 2018 and late August in 2019 (Table 2).

3.2 Morphology of an unspecified rust on sample leaves

Violet to brownish pustules were typical for unspecified rust infection on leaves of *V. myrtillus* (Fig. 2A). Such patches were missing on *V. vitis-idaea*. The average length and width of these pustules was 1367 µm (N = 142, std = 741 µm, min-max = 375-4750 µm) and 828 µm (N = 142, std = 492 µm, min-max = 125-3750 µm), respectively, on *V. myrtillus*, while on *V. vitis-idaea* the average length and width was 2406 µm (N = 4, std = 1891 µm, min-max = 625-5000 µm) and

Table 2. Number of sample leaves of *Vaccinium myrtillus* and *V. vitis-idaea* bearing uredinia of *Naohidemyces vaccinii* during the growing seasons in 2018–2019 in nine Norway spruce seed orchards in Finland. For the names of the seed orchards, see Fig. 1.

Time/Plant species	Seed orchard								
	1	2	3	4	5	6	7	8	9
2018									
Vaccinium myrtillus									
21.–23.5.	-	0	0	0	-	0	0	0	0
11.–13.6.	0	0	0	0	0	0	0	0	0
2.–5.7.	0	0	0	0	0	0	0	0	0
16.–18.7.	0	0	10	0	0	0	0	0	0
30.7.–2.8.	0	2	3	1	7	1	0	1	2
13.–15.8.	0	0	4	0	1	0	1	0	2
27.–29.8.	0	0	1	4	3	0	5	0	0
10.–11.9.	0	0	1	1	8	0	0	0	0
24.–27.9.	0	1	1	0	0	0	1	0	2
Vaccinium vitis-idaea									
21.–23.5.	-	-	0	0	-	0	0	0	0
11.–13.6.	0	0	0	0	0	0	0	0	0
2.–5.7.	0	0	0	0	0	0	0	0	0
16.–18.7.	0	0	0	0	0	0	0	0	0
30.7.–2.8.	0	0	0	0	0	0	0	0	0
13.–15.8.	0	0	0	0	0	0	0	0	0
27.–29.8.	0	0	0	0	0	0	0	0	0
10.–11.9.	0	2	2	1	0	0	0	0	0
24.–27.9.	0	0	0	0	0	0	0	0	0
2019									
Vaccinum myrtillus									
20.–23.5.	-	-	-	-	-	-	-	-	-
11.–14.6.	-	-	-	-	-	-	-	-	-
24.–26.6.	0	-	0	0	-	0	0	0	-
8.–10.7.	0	0	0	0	0	0	0	0	2
22.–24.7.	0	2	0	0	0	0	0	1	0
5.–8.8.	0	0	0	3	0	0	0	4	4
19.–21.8.	0	4	0	0	0	0	0	5	0
2.–4.9.	0	1	0	0	0	0	0	1	0
Vaccinum vitis-idaea									
20.–23.5.	-	-	-	-	-	-	-	-	-
11.–14.6.	-	-	-	-	-	-	-	-	-
24.–26.6.	0	-	0	0	-	0	0	0	-
8.–10.7.	-	-	-	-	0	0	0	0	0
22.–24.7.	0	0	0	0	0	0	0	0	0
5.–8.8.	0	0	0	0	0	0	0	0	0
19.–21.8.	0	3	1	0	0	0	0	1	0
2.–4.9.	0	0	0	0	0	0	0	0	0

- = No leaves were observed.

1562 µm (N=4, std=1048 µm, min-max=500-3000 µm), respectively. Uredinia were orange-yellowish on *V. myrtillus* (Fig. 2B) and orange-yellowish-brownish on *V. vitis-idaea* (Fig. 3A), and they occurred on lower leaf surface of the leaves. There was a central pore at the top of the uredinium. On *V. myrtillus* their average length and width was 170 µm (N=407, std=38 µm, min-max=75-300 µm) and 143 µm (N=407, std=31 µm, min-max=50-250 µm), respectively. On *V. vitis-idaea* the average length and width of uredinia was 243 µm (N=44, std=59 µm, min-

Fig. 2. A. Violet pustules (black arrows), B. uredinia (black arrows) and C. urediniospores (black arrows) of blueberry rust (*Naohidemyces vaccinii*) with sharp edges on leaf of *Vaccinium myrtillus*.

max = 125-375 µm) and 207 µm (N = 44, std = 59 µm, min-max = 100-325 µm), respectively. The urediniospores were orange-yellowish, subglobose and echinulate, with an average length of 21.11 µm (N = 100, std = 2.77 µm, min-max = 16.13-29.03 µm) and average width of 16.52 µm (N = 100, std = 2.06 µm, min-max = 11.29-22.58 µm) on *V. myrtillus* (Fig. 2C), while on *V. vitis-idaea* their average length and width was 24.39 µm (N = 100, std = 2.89 µm, min-max = 16.13-32.26 µm) and 16.81 µm (N = 100, std = 1.81 µm, min-max = 12.90-20.97 µm; Fig. 3B), respectively. The average length (t = 2.62, DF = 144, p < 0.01) and width (t = –2.84, DF = 144, p < 0.01) of pustules, length (t = –11.24, DF = 449, p < 0.001) and width (t = –11.51, DF = 449, p < 0.001) of uredinia and length of urediniospores (t = –8.17, DF = 198, p < 0.001) were significantly larger on *V. vitis-idaea* than on *V. myrtillus*. The width of urediniospores was similar (t = –1.06, DF = 198, p = 0.291) between *V. myrtillus* and *V. vitis-idaea*. Based on rust symptoms, and the size of pustules, uredinia and urediniospores on *V. myrtillus* and *V. vitis-idaea* leaves, the rust was identified as *Naohidemyces vaccinii* (Jørst.) S. Sato, Katsuya & Y. Hirats. ex Vanderwegen & Fraiture.

The average length (F = 11.93, p < 0.001) and width (F = 7.05, p < 0.001) of uredinia, collected in the third (July 16–18), fourth (July 30.7.–2.8.) and seventh (Aug 27–29) time were significantly lower than when collected in the eighth (Sept 10–12) time in 2018. In 2019, neither length (F = 0.03, p = 0.995) nor width (F = 2.22, p = 0.088) of uredinia differed significantly between the sampling times. Neither did the length (F = 1.31, p = 0.274) nor width (F = 1.54, p = 0.196) of pustules differ significantly between sampling times in 2018 or 2019 (F = 0.18, p = 0.833 and F = 0.49, p = 0.616).

The average length (F = 4.63, p < 0.001) and width (F = 4.25, p < 0.001) of uredinia from seed orchards 2 and 3 were significantly higher than those from seed orchard 7. The length (F = 1.70, p = 0.126) and width (F = 2.29, p = 0.039) of pustules did not differ significantly between seed orchards.

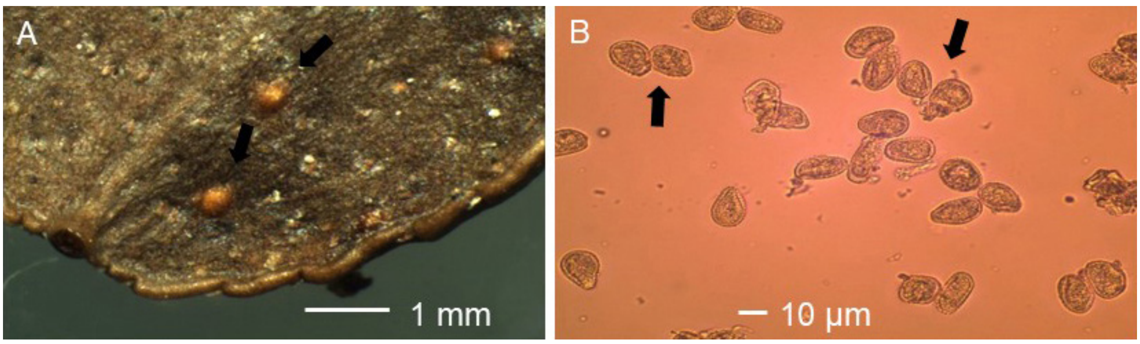

Fig. 3. A. Uredinia (black arrows) and B. urediospores (black arrows) of blueberry rust *Naohidemyces vaccinii* on leaf of *Vaccinium vitis-idaea*.

4 Discussion

In this study, no uredinia of *T. areolata* were observed on any of the species of Ericaceae or other species of ground flora in the Finnish Norway spruce seed orchards. This was evident regardless of the time of investigation within growing seasons among years. At the same time *T. areolata* sporulated regularly in May–September on *P. padus* in the investigated seed orchards (Kaitera et al. 2021b). This suggests that the only wild species that acts as alternate host for *T. areolata* in the seed orchards is *P. padus*. This is also supported by recent pathogenicity tests of *T. areolata* on *Prunus* and *Picea* (Kaitera et al. 2019). In addition, common ground flora species at the seed orchards, other than *Prunus,* were also inoculated recently using *T. areolata,* with negative results (Kaitera et al. 2021a). Therefore, no wild plant species other than *Prunus* were found to be susceptible to *T. areolata* either under artificial or natural conditions in Finnish Norway spruce seed orchards.

Other rust species were observed on *Vaccinium* species in the seed orchards. The rust on both *V. myrtillus* and *V. vitis-idaea* was identified as *Naohidemyces vaccinii*. This species is common on *Vaccinium* spp. in Norway (Aamlid 2001). Based on our results, the rust was also common on *V. myrtillus* but less frequent on *V. vitis-idaea* in the seed orchards in southern Finland, where the rust sporulated from mid-July to September. The sporulation occurred earlier on *V. myrtillus* in the seed orchards, which is probably due to overwintering of the rust as mycelium on *V. myrtillus* (Gäumann 1959) that allows the rust to form uredinia rapidly on blueberry leaves in early summer. Symptoms and spore morphology of the rust agrees with descriptions in the literature (Gäumann 1959; Sato et al. 1993; Aamlid 2001). The rust had bigger uredinia and longer urediniospores and it sporulated later on *V. vitis-idaea* than on *V. myrtillus*. However, this variation in spore morphology agrees with morphological comparison between *T. myrtillina* P. Karst. on *V. myrtillus* and *T. vaccinii* (Jørst.) Hirats on *V. vitis-idaea* (Gäumann 1959). In a recent review, *Naohidemyces* was grouped to Milesinaceae, *Thekopsora* to Coleosporaceae and *Pucciniastrum* to Pucciniastraceae (Aime and McTaggert 2021). Longer and wider uredinia on *V. myrtillus* at the latest time of collection in September compared to collections earlier in July and August is explained by the development of uredinia to their full size during the growing season.

In conclusion, *Thekopsora areolata* did not fruit and sporulate on wild species of Ericaceae or any other common species of ground vegetation in Finnish Norway spruce seed orchards. As neither the inoculation studies nor inventories on wild plants species during rust epidemics in 2018–2019 revealed any other species that were susceptible to the rust and able to spread it besides *P. padus*, we conclude that *Prunus* spp. are the only susceptible species capable of spreading the rust in Finnish Norway spruce seed orchards. Therefore, control of *T. areolata* should be concentrated only on *Prunus* species in Norway spruce seed orchards. Blueberry rust is common on *Vaccinium myrtillus* and occasional on *V. vitis-idaea* in southern Finland, where it may cause early withering of leaves of *Vaccinium* spp.

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Declaration of openness of research materials and data

The research materials and data are available on request from the authors.

Authors' contribution

Kaitera: Planning of the study, writing of the manuscript, field inventory and data collection, laboratory work, microscopy and photographing of the samples.
Aarnio: Field inventory and data collection.
Ylioja: Organising the field work and reviewing the manuscript.
Karhu: Statistical analysis of the data.

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