RESEARCH ARTICLE

A Comparative Study of the Aecial Stages of Rusts Caused by *Gymnosporangium asiaticum* and *Gymnosporangium yamadae* in Diverse Plant Species of Malinae (Rosaceae) at the Korea National Arboretum

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ABSTRACT

The Korea National Arboretum (KNA) in Pocheon, Korea has diverse plant species including Rosaceae species of high ecological and landscape significance; however, no fungal disease surveys have been conducted. Thus, we investigated rust occurrence and identification across diverse plant species of the subtribe Malinae (Rosaceae) and examined host diversity (or specificity) of rusts in this study, as well as in the literature and databases. We collected rust (aecial stages) samples from the leaves of nine Malinae species on June 20, July 7, July 21, or August 8, 2025. We also identified rust samples by analyzing the sequences of internal transcribed spacer and large subunit rDNA regions, as well as aeciospore characteristics. We revealed that *Gymnosporangium asiaticum* occurred in six host species of five genera (*Aria*, *Chaenomeles*, *Crataegus*, *Pseudocydonia*, and *Pyrus*) in subtribe Malinae; *Gymnosporangium yamadae* occurred in three species of the genus *Malus* in the subtribe. Literature and databases further revealed that *G. asiaticum* occurred in plant species of nine genera (*Aria*, *Chaenomeles*, *Crataegus*, *Cydonia*, *Malus*, *Photinia*, *Pourthiaea*, *Pseudocydonia*, and *Pyrus*); *G. yamadae* occurred in plant species of only the genus *Malus* in Malinae. This is the first comparative study of rusts caused by *G. asiaticum* and *G. yamadae* at KNA; it provides basic information on the occurrence of two different rusts and may facilitate the development of appropriate rust management strategies.

Keywords: Aeciospore, *Gymnosporangium asiaticum*, *Gymnosporangium yamadae*, Host diversity, Korea National Arboretum

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INTRODUCTION

Rusts (Pucciniales) are obligate parasites that can survive only in living organisms [1,2]; more than 8,000 species are known [1,3,4]. They are among the most severe threats to a wide range of hosts, including agricultural crops and woody plants [4]. In addition, climate change may influence the emergence and spread of new, unexpected rusts. For example, Lee et al. [5] reported that climate changes might promote a

rust spread caused by *Neophysopella kraunhiae* in *Wisteria floribunda* (primary host) and *Corydalis incisa* (alternative host).

Most *Gymnosporangium* species as causal agents of rusts are widely distributed in Asia, Europe, and North America [6]. These rust fungi generally produce four different spores (*i.e.*, demicyclic rust), such as aeciospores, basidiospores, spermatia, and teliospores, and require two unrelated host species (*i.e.*, heteroecious rust) to complete their life cycles [7–9]. Therefore, rusts produce spermatia and aeciospores in their aecial hosts and teliospores and basidiospores in their telial hosts. However, a few *Gymnosporangium* species, such as *G. gaeumannii*, *G. nootkatense*, *G. paraphysatum*, and *G. tianschanicum*, are macrocyclic rusts that can produce urediospores, including four different spores [10]. In general, aecial stages of *Gymnosporangium* species are characterized by distinct symptoms on infected leaves, which serve as primary indicators of rust infections [11]. However, morphological characteristics (*i.e.*, leaf symptoms) of rust aecial stages are somewhat different between diverse host species; consequently, molecular phylogenetic analyses were needed for their precise identification [12,13].

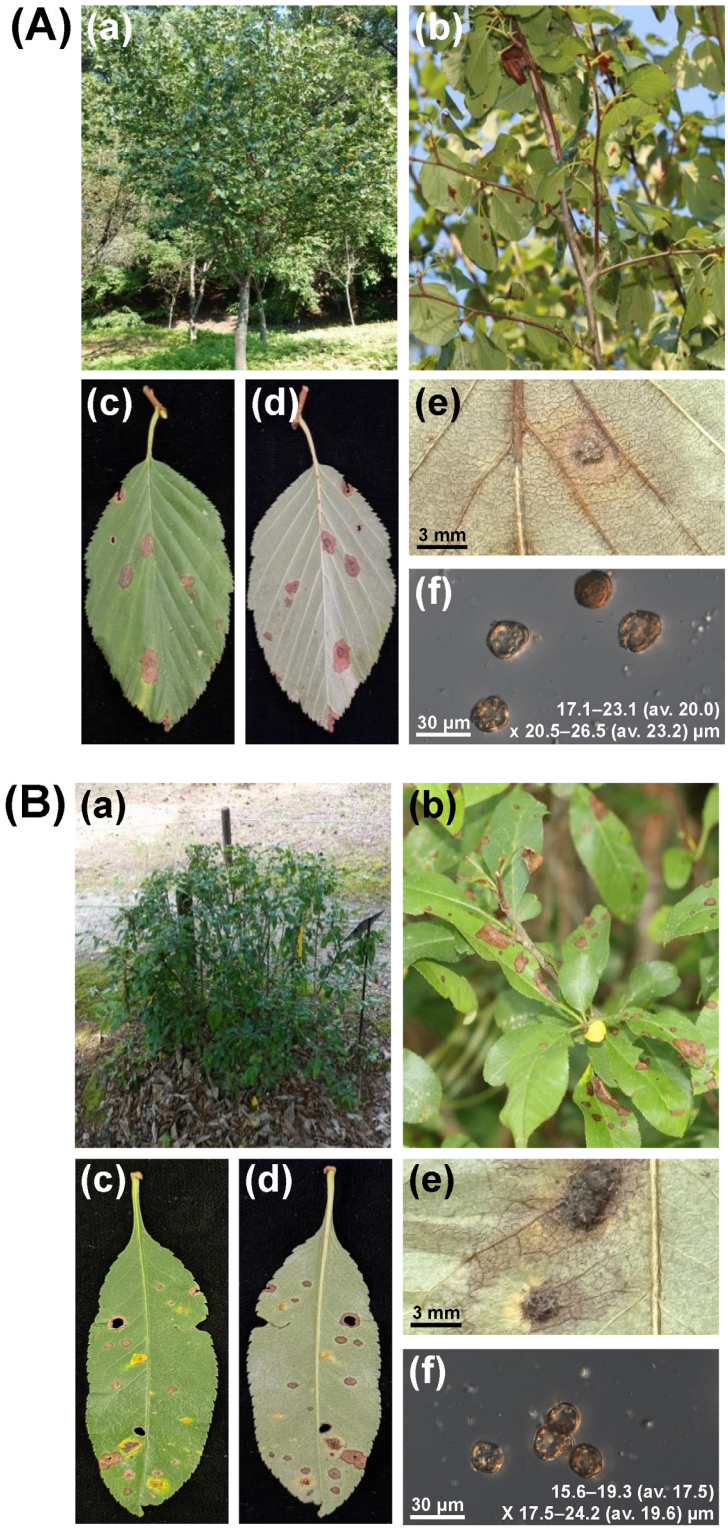
The Korea National Arboretum (KNA) in Pocheon, Korea, originated from 'Gwangneung Forest', which was initially designated as the Royal Tomb Forest of King Sejo in 1468 [14]. Since then, the forest has been strictly preserved for more than 550 years. The KNA was established during 1984–1987, with various gardens; it was officially reopened as the National Arboretum on 24 May 1999. The KNA comprises 25 thematic gardens and 4,854 plant species across 102 ha [14]. The KNA has diverse plant species, including members of the family Rosaceae, which have not only economic but also aesthetic value; however, disease surveys to develop plant disease management systems have not been conducted except for a recent virus study of our co-workers [15]. Therefore, the objectives of this study were (i) to investigate rust occurrence and identification in diverse host plant species of subtribe Malinae (Rosaceae) at the KNA, and (ii) to examine host diversity (or specificity) of rusts in this study as well as in the literature and databases.

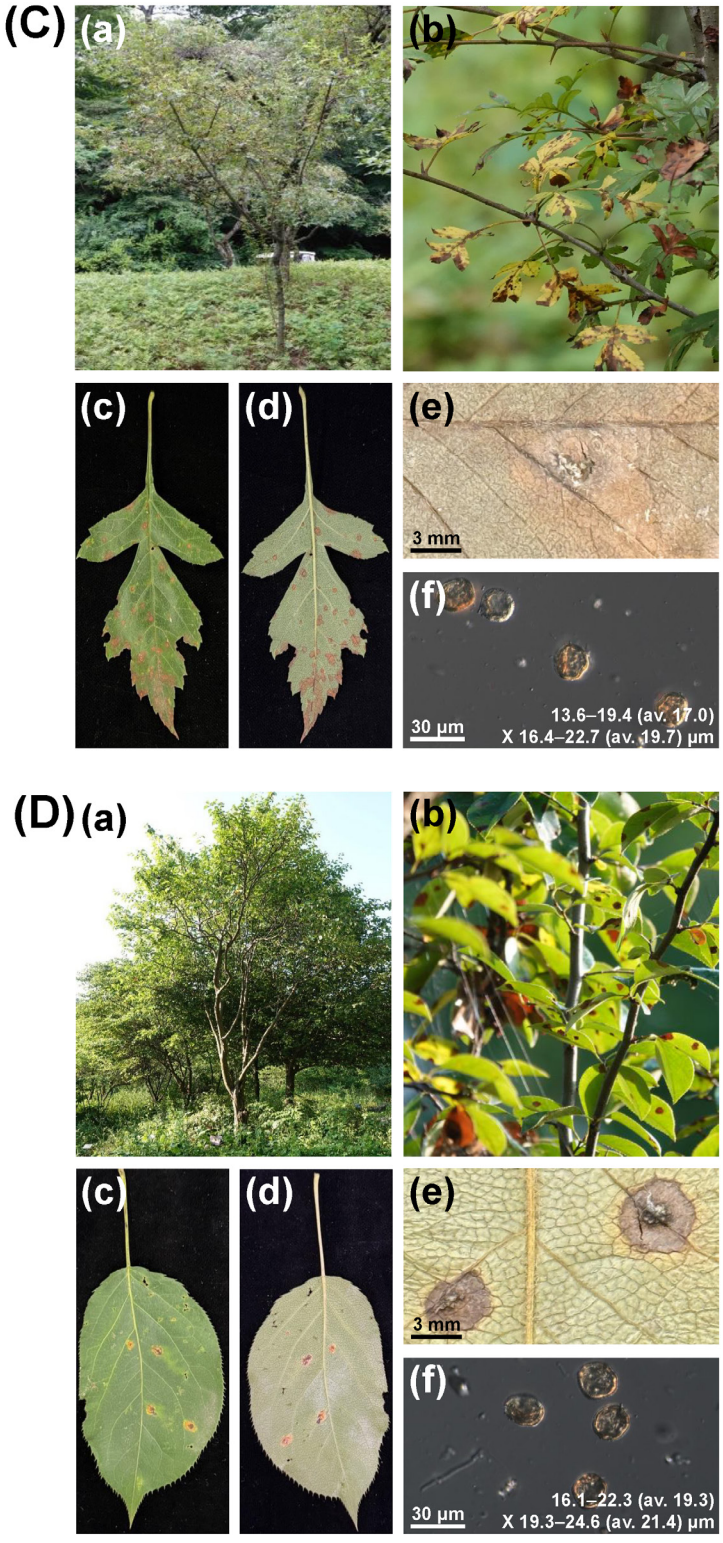
MATERIALS AND METHODS

Rust samples

During plant disease surveys at the KNA (37°45'18.0"N, 127°09'54.0"E) in Pocheon, Korea, from June to August 2025, yellow, brownish, and/or orange to reddish symptoms were observed on upper (adaxial) and/or lower (abaxial) leaf surfaces of different host plant species. In particular, aecial structures were observed on the lower leaf surfaces of the samples from various host species (Fig. 1 and 2). Three rust samples per host species were collected from leaves of nine host species on June 20, July 7, July 21, and August 8, 2025 (Table 1). Aeciospores from aecial structures on the lower leaf surfaces of the samples were obtained by scraping the aecia with sterilized needles, followed by harvesting spores with moistened cotton swabs. The cotton swabs with aeciospores were vigorously vortexed for about 10 seconds in 2-mL microtubes (Axygen, Corning, Glendale, AZ, USA) containing 1 mL sterile distilled water. Aeciospores (pellets) were obtained by centrifuging the tubes for 5 min at 13,000 rpm at 28°C using a Mikro 200/200R

centrifuge (Hettich, Tuttlingen, Germany), then discarding the supernatant. The aeciospores of rust samples from the host species were further used for morphological and molecular phylogenetic analyses. The rust-infected leaf specimens were dried and deposited at the KNA Herbarium in Pocheon, Korea (Table 1).

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X 16.4–22.7 (av. 19.7) µm
(D)
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16.1–22.3 (av. 19.3)
X 19.3–24.6 (av. 21.4) µm

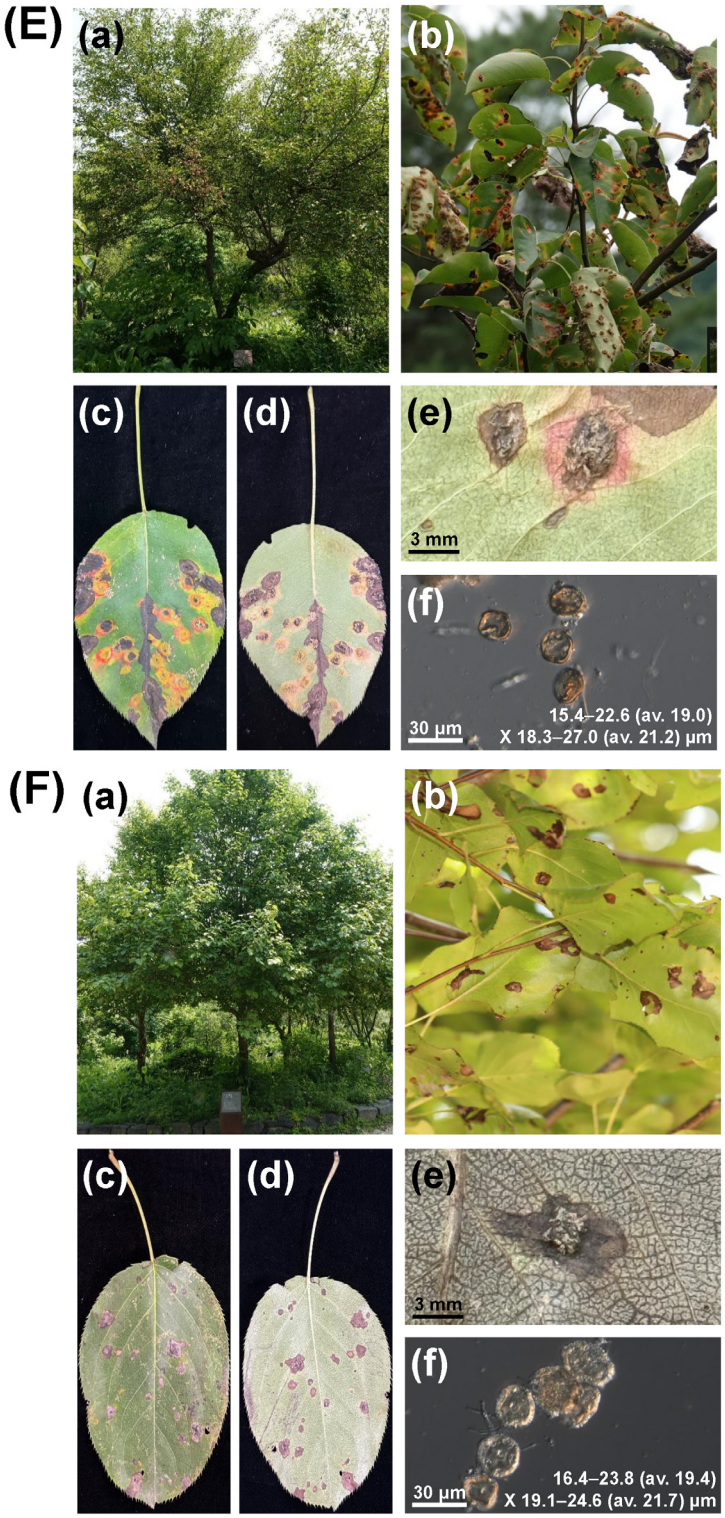
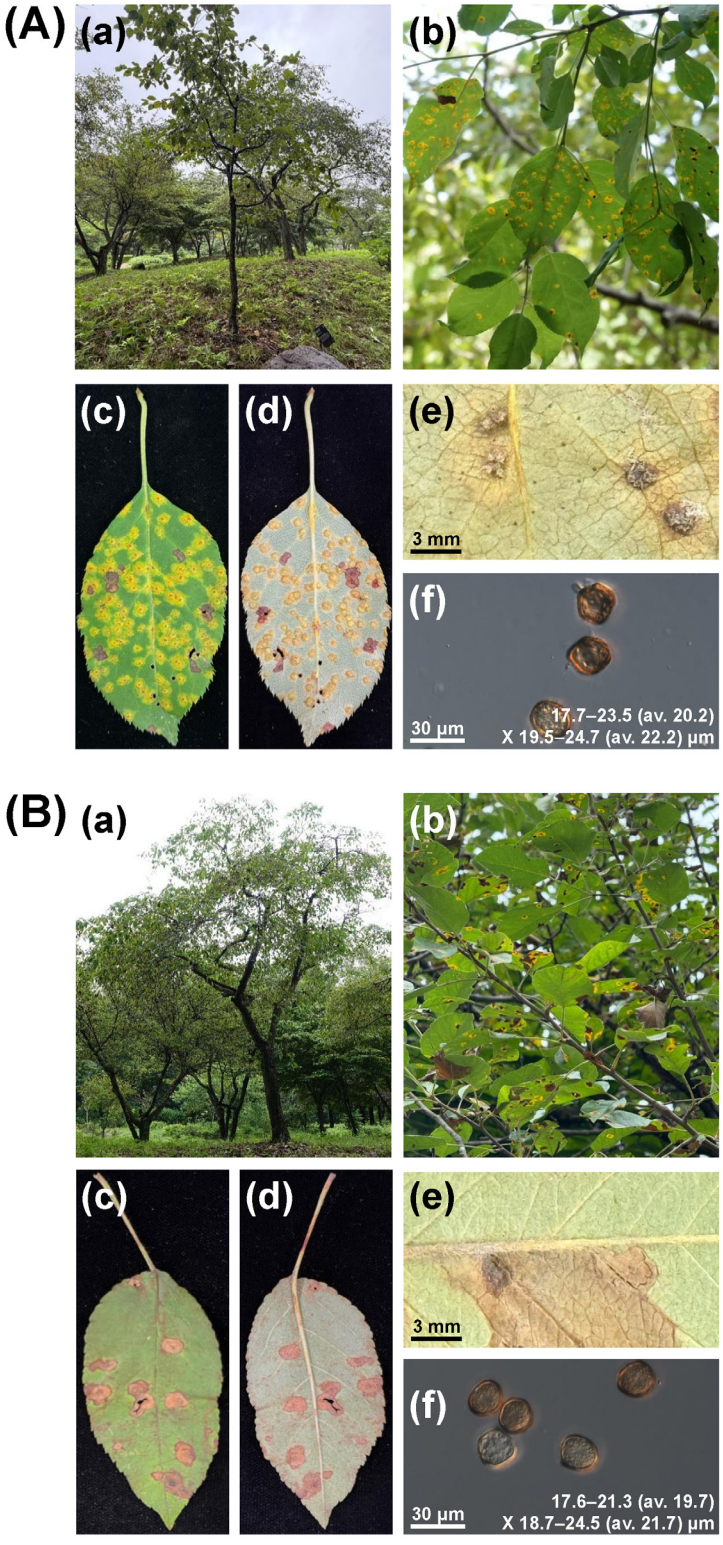


Fig. 1. Aecial stages of rusts caused by *Gymnosporangium asiaticum* in the six host plant species (A) *Aria alnifolia*, (B) *Chaenomeles speciosa*, (C) *Crataegus pinnatifida*, (D) *Pseudocydonia sinensis*, (E) *Pyrus calleryana*, and (F) *Pyrus pyrifolia*. (a) Host plant, (b) symptoms of infected leaves of the host plant, (c) necrotic lesions on the upper leaf surface, (d) aecia on the lower leaf surface, and (e) an aecium (or aecia) with (f) aeciospores on the lower leaf surface. The numbers in picture-f indicate aeciospore diameters (µm) (n = 40), expressed as width ranges from minimum to maximum (average) × length ranges from minimum to maximum (average).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(a)
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17.7–23.5 (av. 20.2)
X 19.5–24.7 (av. 22.2) μm
(B)
(a)
(b)
(c)
(d)
(e)
3 mm
(f)
30 μm
17.6–21.3 (av. 19.7)
X 18.7–24.5 (av. 21.7) μm

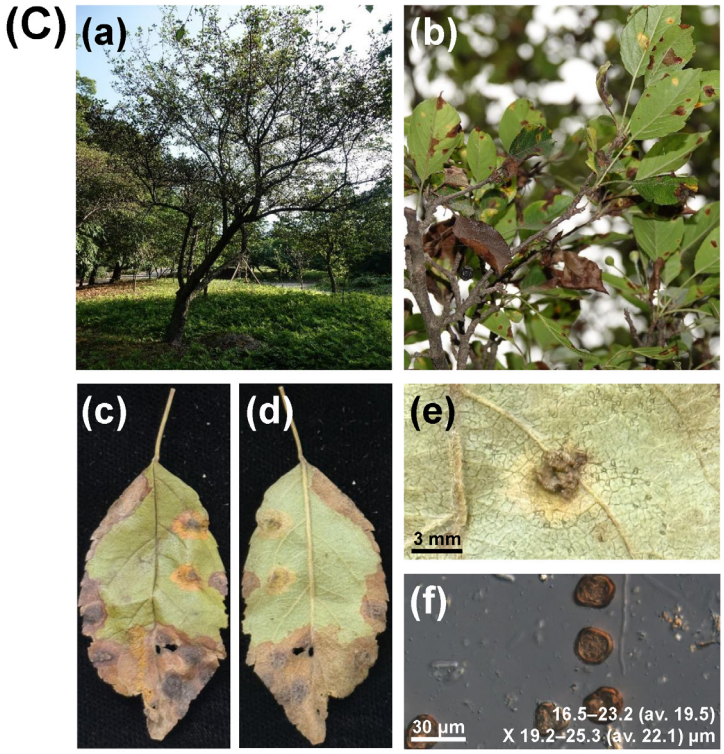

Fig. 2. Aecial stages of rusts caused by *Gymnosporangium yamadae* in the three host plant species (A) *Malus baccata*, (B) *Malus floribunda*, and (C) *Malus toringo*. (a) Host plant, (b) symptoms of infected leaves of the host plant, (c) necrotic lesions on the upper leaf surface, (d) aecia on the lower leaf surface, and (e) an aecium (or aecia) with (f) aeciospores on the lower leaf surface. The numbers in picture-f indicate aeciospore diameters (μm) (n = 40), expressed as width ranges from minimum to maximum (average) × length ranges from minimum to maximum (average).

Morphological characterization

The morphological characteristics of previously prepared aeciospores from host species samples were examined under a differential interference-contrast light microscope (Zeiss AX10, Carl Zeiss, Oberkochen, Germany). Microphotographs were captured with the AxioCam MRc5 (Carl Zeiss), which was operated *via* AxioVision Rel. 4.8 software (Carl Zeiss). The shapes and sizes (lengths and widths) of aeciospores (n = 40) were determined as described by Kim et al. [16]. Spore sizes (μm) are expressed as width ranges from minimum to maximum (average) × length ranges from minimum to maximum (average).

Molecular phylogenetic analysis

For molecular phylogenetic analysis of the rust samples, genomic DNA was extracted from aeciospores prepared as described previously, using an i-genomic BYF DNA Extraction Mini Kit (iNtRON Biotechnology, Seongnam, Korea) according to the manufacturer's instructions. Polymerase chain reaction (PCR) was performed to amplify the internal transcribed spacer (ITS) rDNA region with the primers Rust2inv (5′-GATGAAGAACACAGTGAAA-3′) [17] and ITS4rust

Table 1. Rust specimens collected from various host plant species at the Korea National Arboretum (KNA) in Pocheon, Korea

Host species		Specimen no. (KNA[a])	Specimen no. (GenBank[b])	Collection date	GenBank accession no.[c]	
Scientific name	English name				ITS	LSU
Aria alnifolia	Korean mountain ash	KA25 -1474	Aa2507-1	7 July 2025	PX3 52013	PX3 62945
		KA25 -1475	Aa2507-2	21 July 2025	PX4 53359	PX4 53398
		KA25 -1476	Aa2508	8 August 2025	PX4 53397	PX4 53401
Chaenomeles speciosa	Chinese-quince	KA25 -1477	Cs2506	20 June 2025	PX3 52014	PX3 62946
		KA25 -1478	Cs2507-1	7 July 2025	PX3 52015	PX3 62947
		KA25 -1479	Cs2507-2	21 July 2025	PX4 53645	PX4 53646
Crataegus pinnatifida	Mountain hawthorn	KA25 -1480	Cp2507-1	7 July 2025	PX3 52016	PX3 62948
		KA25 -1481	Cp2507-2	21 July 2025	PX3 52017	PX3 62949
		KA25 -1482	Cp2508	8 August 2025	PX4 53711	PX4 53771
Malus baccata	Siberian crabapple	KA25 -1492	Mb2506	20 June 2025	PX3 17706	PX3 62931
		KA25 -1493	Mb2507-1	7 July 2025	PX3 62928	PX3 62932
		KA25 -1494	Mb2507-2	21 July 2025	PX4 53872	PX4 53882
Malus floribunda	Japanese flowering crabapple	KA25 -1495	Mf2507-1	7 July 2025	PX3 62929	PX3 62933
		KA25 -1496	Mf2507-2	21 July 2025	PX4 53885	PX4 68897
		KA25 -1497	Mf2508	8 August 2025	PX5 69139	PX4 53897
Malus toringo	Three-lobe crabapple	KA25 -1498	Mt2507-1	7 July 2025	PX3 62930	PX3 62934
		KA25 -1499	Mt2507-2	21 July 2025	PX4 68772	PX4 68775
		KA25 -1500	Mt2508	8 August 2025	PX4 68778	PX4 65779
Pseudocydonia sinensis	Chinese flowering-quince	KA25 -1483	Ps2506	20 June 2025	PX3 52020	PX3 52950
		KA25 -1484	Ps2507-1	7 July 2025	PX3 52021	PX3 62951
		KA25 -1485	Ps2507-2	21 July 2025	PX4 53774	PX4 53775
Pyrus calleryana	Korean sun pear	KA25 -1486	Pc2506	20 June 2025	PX3 52022	PX3 62952
		KA25 -1487	Pc2507-1	7 July 2025	PX3 52023	PX3 62953
		KA25 -1488	Pc2507-2	21 July 2025	PX4 53777	PX4 53792
Pyrus pyrifolia	Sand pear	KA25 -1489	Pp2507-1	7 July 2025	PX3 52024	PX3 62954
		KA25 -1490	Pp2507-2	21 July 2025	PX3 52025	PX3 62955
		KA25 -1491	Pp2508	8 August 2025	PX4 53778	PX4 53793

[a]The specimens were deposited at the KNA Herbarium in Pocheon, Korea.

[b]The specimen numbers (no.) were used in depositing their sequences in GenBank.

[c]GenBank accession numbers (no.) for internal transcribed spacer (ITS) and large subunit (LSU) sequences of rust specimens.

(5′-CAGATTACAAATTTGGGCT-3′) [18]. In addition, the large subunit (LSU) region was amplified with the primers LRust1R (5′-TAAGACCTCAAATCAGGT-3′) and LRust3 (5′-GGGTCATTTAAAG CTAT-3′) [18]. The PCR amplification of the ITS and LSU regions and DNA sequencing were conducted by the Cosmogenetech sequencing service (Cosmogenetech, Seoul, Korea). Phylogenetic analyses were conducted according to the procedure described by Sang et al. [19]. Briefly, the gene sequence was edited using BioEdit 7.2 (https://bioedit.software.informer.com/7.2/) and analyzed with BLAST sequence analysis software (https://blast.ncbi.nlm.nih.gov/Blast.cgi) using the National Center for Biotechnology Information server. The ITS and LSU sequence data were then combined and aligned using ClustalW [20]. Phylogenetic trees using the maximum-likelihood (ML) and neighbor-joining (NJ) methods based on the Tamura–Nei model in MEGA 11 [21] were constructed with these concatenated gene sequences. The stability of the phylogenetic trees was assessed using the bootstrap method with 1,000 replicates. The reference sequences from GenBank used in the phylogenetic analysis are listed in Table 2 [10,12,13,22–26].

Literature and database reviews on host diversity

Plant species infected by aecial stages of either *Gymnosporangium asiaticum* or *Gymnosporangium yamadae* were investigated to examine their host species [*i.e.*, host diversity (or specificity)] in the literature [13,27–30]. This investigation was further conducted using databases such as the United States Department of Agriculture (USDA) Fungal Database [6] and the European and Mediterranean Plant Protection Organization (EPPO) Global Database [31]. Additionally, the information obtained from the literature and databases was compared with aecial rusts of nine host species caused by *G. asiaticum* and *G. yamadae* examined in this study.

RESULTS

Morphological characterization of rust aeciospores

All collected samples of nine host plant species exhibited rust symptoms, with aecial structures on diseased leaves of the plant species (Fig. 1a–e, 2a–e), similar to typical rust symptoms in plants [9]. In the early stages of infection, the symptoms on the upper (adaxial) surfaces of infected leaves appeared as chlorotic, brownish, or orange spots, with aecial structures clearly visible on the lower (abaxial) surfaces. When infections developed, the symptoms appeared as severe chlorotic, brownish, or reddish lesions with well-developed, enlarged, and darkened aecia (Fig. 1a–e, 2a–e).

In contrast, aeciospores of aecial structures of *G. asiaticum* obtained from six host plant species (*Aria alnifolia*, *Chaenomeles speciosa*, *Crataegus pinnatifida*, *Pseudocydonia sinensis*, *Pyrus calleryana*, and *Pyrus pyrifolia*) were yellow to pale yellow, globose to subglobose, and verrucose with germ pores (Fig. 1f). The size of aeciospores from *A. alnifolia* was 17.1–23.1 (average 20.0) × 20.5–26.5 (average 23.2) μm, whereas those of aeciospores from *C. speciosa* and *C. pinnatifida* were smaller than that of *A. alnifolia* and were 15.6–19.3 (17.5) × 17.5–24.2 (19.6) μm and 13.6–19.4 (17.0) × 16.4–22.7 (19.7) μm, respectively

Table 2. Reference sequences [internal transcribed spacer (ITS) and large subunit (LSU) sequences] of *Gymnosporangium* species and an outgroup *Endoraecium tropicum* used for phylogenetic analyses

Rust fungi	Host species	Specimens	GenBank accession numbers		References
			ITS	LSU	
Gymnosporangium amelanchieris	*Amelanchier ovalis*	20141009	KP261040	KP261041	[22]
Gymnosporangium annulatum	*Cotoneaster* sp.	BJFC-R01502	MH178663	MH184511	[10]
Gymnosporangium asiaticum	*Malus pumila*	HMAS38650	MN605764	MN605686	[13]
Gymnosporangium asiaticum	*Juniperus excelsa*	HMAS45640	MN605747	MN605669	[13]
Gymnosporangium clavariiforme	*Malus communis*	HMAS24626	KU288672	KU342766	[12]
Gymnosporangium confusum	*Crataegus altaica*	BJFC-R03203	MH178623	MH184471	[10]
Gymnosporangium corniculans	*Amelanchier canadensis*	CUP-3087	MN605771	MN605693	[13]
Gymnosporangium cornutum	*Juniperus communis*	10	OL656940	OL656838	[23]
Gymnosporangium distortum	*Cotoneaster* sp.	BJFC-R02544	MH178629	MH184477	[10]
Gymnosporangium fusisporum	*Cotoneaster* sp.	BJFC-R02037	MH178634	MH184482	[10]
Gymnosporangium gansuense	*Sorbus* sp.	BJFC-R03829	MW901249	MW911439	[24]
Gymnosporangium globosum	*Malus* sp.	CUP-1553	MN605776	MN605698	[13]
Gymnosporangium gracile	*Cydonia oblonga*	20140529-1a	KM486543	KM486545	[22]
Gymnosporangium granulatosporum	*Cotoneaster multiflorus*	BJFC-R03827	MW907970	MW911441	[24]
Gymnosporangium juniperi-virginianae	*Malus baccata*	HMAS74424	MN642597	MN642621	[13]
Gymnosporangium lianhuaense	*Crataegus* sp.	BJFC-R03115	MH178643	MH184491	[10]
Gymnosporangium miyabei	*Malus sylvestris*	HMAS:70746	KU288645	KU342747	[12]
Gymnosporangium przewalskii	*Sorbus koehneana*	BJFC-R02084	KX528447	KX528445	[25]
Gymnosporangium sabinae	*Pyrus communis*	PyC	OL657026	OL656921	[23]
Gymnosporangium sikangense	*Cotoneaster* sp.	BJFC-R02455	MH178650	MH184498	[10]
Gymnosporangium turkestanicum	*Sorbus tianschanica*	BJFC-R02051	MH178654	MH184502	[10]
Gymnosporangium yamadae	*Malus prunifolia*	HMAS30992	MN605817	MN605739	[13]
Endoraecium tropicum	*Acacia tropica*	BRIP:56557	KJ862392	KJ862337	[26]

(Fig. 1A–C-f). The aeciospore size of *P. sinensis* was 16.1–22.3 (19.3) × 19.3–24.6 (21.4) μm; those of *P. calleryana* and *P. pyrifolia* ranged in 15.4–22.6 (19.0) × 18.3–27.0 (21.2) μm and 16.4–23.8 (19.4) × 19.1–24.6 (21.7) μm, respectively (Fig. 1D–F-f).

The aeciospores of *G. yamadae* obtained from three host species (*Malus baccata*, *Malus floribunda*, and *Malus toringo*) were yellow to golden yellow, globose to subglobose or ovoid, and verrucose with or without germ pores (Fig. 2f). The sizes of aeciospores from *M. baccata* were 17.7–23.5 (20.2) × 19.5–24.7 (22.2) μm; those of *M. floribunda* were 17.6–21.3 (19.7) × 18.7–24.5 (21.7) μm (Fig. 2A-f, B-f). The aeciospore size [16.5–23.2 (19.5) × 19.2–25.3 (22.1) μm] of *M. toringo* was smaller than that of *M. baccata* but was similar to that of *M. floribunda* (Fig. 2C-f). These morphological characteristics of the aeciospores of rust samples from six host species and three *Malus* species were similar to those reported for *G. asiaticum,* and *G. yamadae* [10,13,32].

Molecular phylogenetic analysis of rust aeciospores

Partial ITS and LSU sequences of the rust (aeciospores) samples collected from nine host species were obtained (Table 1), and phylogenetic analyses using ML and NJ methods were conducted with the concatenated ITS and LSU gene sequences (alignment length = 778 bases).

ML analysis revealed that the aeciospores of each rust samples from *A. alnifolia*, *C. speciosa*, *C. pinnatifida*, *P. sinensis*, *P. calleryana*, and *P. pyrifolia* clustered with the reference sequences of *G. asiaticum* HMAS38650 (accession no. for ITS = MN605764, LSU = MN605686) or *G. asiaticum* HMAS45640 (accession no. for ITS = MN605747, LSU = MN605669) (Fig. 3). However, those of each rust samples from *M. baccata*, *M. floribunda*, and *M. toringo* clustered with *G. yamadae* HMAS30992 (accession no. for ITS = MN605817, LSU = MN605739). Similarly, application of the NJ method to concatenated gene sequences revealed that test aeciospores from the six and three plant species also clustered with *G. asiaticum* HMAS38650 and HMAS45640, as well as *G. yamadae* HMAS30992. Therefore, based on these results, rust samples were clearly divided into two *Gymnosporangium* species: those from six host species, as mentioned previously, were identified as *G. asiaticum*, and those from three *Malus* species were identified as *G. yamadae* (Fig. 3).

Literature and database reviews on host diversity of *G. asiaticum* and *G. yamadae*

According to the literature and databases, aecial stages of all *Gymnosporangium* species have been recorded in eight families: Eucommiaceae, Euphorbiaceae, Grossulariaceae, Hydrangeaceae, Juglandaceae, Myricaceae, Rosaceae, and Theaceae. Among these eight families, both *G. asiaticum* and *G. yamadae* examined in this study could occur only in the family Rosaceae. Rosaceae consists of three subfamilies: Amygdaloideae, Dryadoideae, and Rosoideae. Subfamily Amygdaloideae can be divided into nine tribes, including Maleae, which contains four subtribes (Gilleniinae, Lindleyinae, Malinae, and Vauqueliniinae). Among these subtribes, Malinae contains approximately 28 genera (*Amelanchier*, *Aria*, *Aronia*, *Chaenomeles*, *Chamaemeles*, *Cotoneaster*, *Crataegus*, *Cydonia*, *Dichotomanthes*, *Docynia*, *Eriobotrya*, *Hesperomeles*, *Heteromeles*, *Macromeles*, *Malacomeles, Malus*, *Mespilus*, *Osteomeles*, *Peraphyllum*, *Phippsiomeles*, *Photinia*, *Pourthiaea*, *Pseudocydonia*, *Pyracantha*, *Pyrus*, *Rhaphiolepis*, *Stranvaesia*, and *Weniomeles*). Among these 28 genera, aecial host species of the rust fungi comprise nine different genera (*Aria*, *Chaenomeles*, *Crataegus*, *Cydonia*, *Malus, Photinia*, *Pourthiaea*, *Pseudocydonia*, and *Pyrus*) in the subtribe Malinae (Rosaceae). As a result, the literature and databases revealed that 37 plant species served as hosts for either *G. asiaticum* or *G. yamadae* (Table 3).

In general, *G. asiaticum* causes rusts in 17 species of eight different genera (*Aria*, *Chaenomeles*, *Crataegus*, *Cydonia*, *Photinia*, *Pourthiaea*, *Pseudocydonia*, and *Pyrus*), and six species of the genus *Malus* in the subtribe Malinae (Rosaceae). However, *G. yamadae* induced rusts in 20 species (except *M. ioensis*) of the genus *Malus* only, but not in other genera of the subtribe (Table 3).

DISCUSSION

This study presents the first field survey results on rusts caused by *G. asiaticum* and *G. yamadae* in diverse host plant species of the family Rosaceae at the KNA in Pocheon, Korea. Morphological and

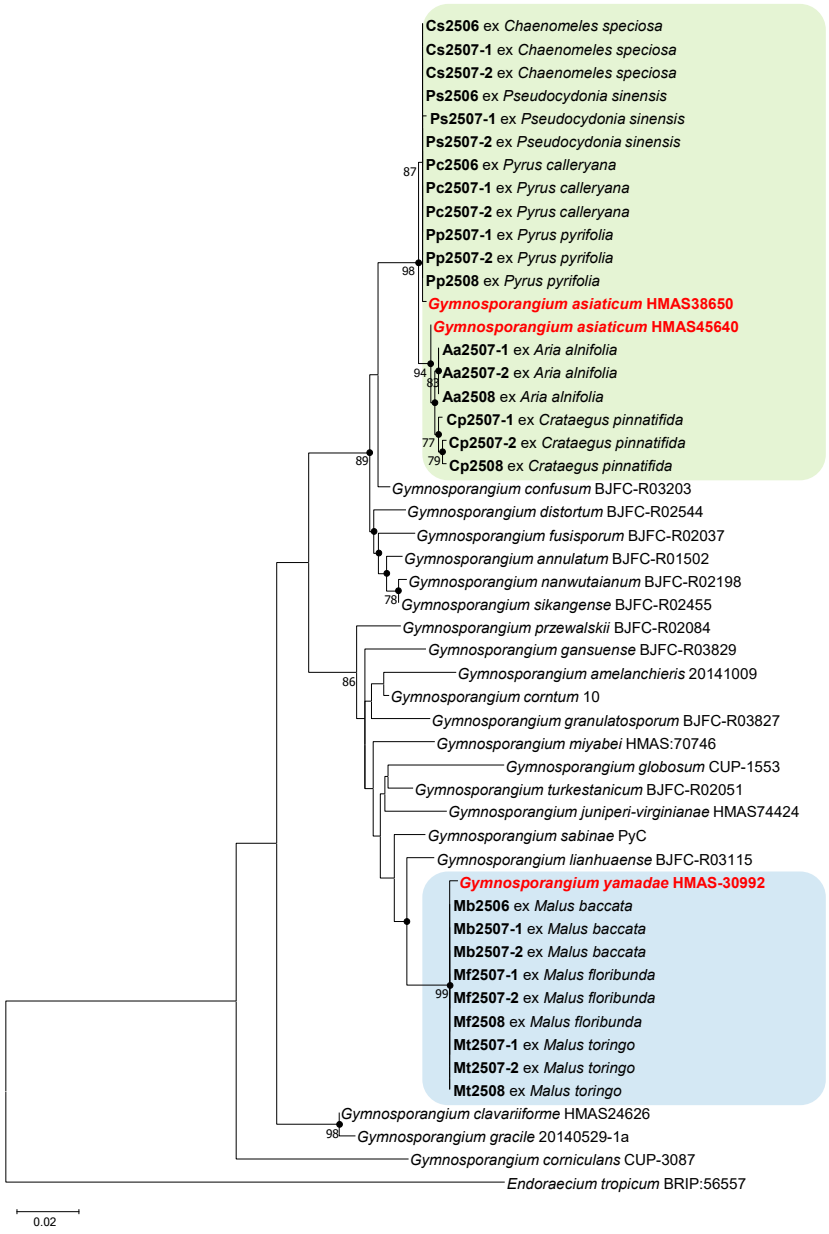

Fig. 3. Phylogenetic tree constructed with the maximum-likelihood method, showing the relationships among test rust species, other members of the genus *Gymnosporangium*, and *Endoraecium tropicum* (the outgroup) based on the concatenated alignments of the internal transcribed spacer (ITS) and large subunit (LSU) sequences. The numbers at the branching points are bootstrap values (>70%) for 1,000 replicates. Black dots indicate that the corresponding nodes were also recovered with bootstrap values (>70%) in the tree constructed using the neighbor-joining method. Scale bar = number of nucleotide (nt) substitutions per 100 nt of the sequences.

molecular phylogenetic analyses of the collected rust samples from different host plant species revealed that *G. asiaticum* occurred in six host species of five genera (*Aria*, *Chaenomeles*, *Crataegus*, *Pseudocydonia*, and *Pyrus*) in the subtribe Malinae (Rosaceae); *G. yamadae* occurred in three species of the genus *Malus* in the subtribe. Furthermore, the literature and databases indicate that *G. asiaticum* caused rusts in many

Table 3. Host plant species of *Gymnosporangium asiaticum* and *Gymnosporangium yamadae* in the nine genera of the subtribe Malinae[a] (Rosaceae)

Host species	Rust fungi		Host species	Rust fungi	
	G. asiaticum	*G. yamadae*		*G. asiaticum*	*G. yamadae*
Aria alnifolia[b]	+[b]/+[c]	−	*Malus platycarpa*	−	+
Chaenomeles cathayensis	+	−	*Malus prunifolia*	−	+
Chaenomeles japonica	+	−	*Malus pumila*	+	+
Chaenomeles speciosa	+/+	−	*Malus spectabilis*	+	+
Crataegus cuneata	+	−	*Malus spontanea*	−	+
Crataegus pinnatifida	+/+	−	*Malus toringo*	−	+/+
Crataegus wilsonii	+	−	*Malus transitoria*	−	+
Cydonia oblonga	+	−	*Malus yunnanensis*	−	+
Malus asiatica	+	+	*Malus ×scheideckeri*	−	+
Malus baccata	−	+/+	*Photinia villosa*	+	−
Malus domestica	+	+	*Pourthiaea villosa*	+	−
Malus floribunda	−	+/+	*Pseudocydonia sinensis*	+/+	−
Malus halliana	−	+	*Pyrus betulifolia*	+	−
Malus honanensis	−	+	*Pyrus bretschneideri*	+	−
Malus hupehensis	−	+	*Pyrus calleryana*	+/+	−
Malus ioensis	+	−	*Pyrus pashia*	+	−
Malus kansuensis	+	+	*Pyrus pyrifolia*	+/+	−
Malus manshurica	−	+	*Pyrus ussuriensis*	+	−
Malus micromalus	−	+			

[a]Subtribe Malinae contains approximately 28 genera such as *Amelanchier, Aronia, Chamaemeles, Cotoneaster, Dichotomanthes, Docynia, Eriobotrya, Hesperomeles, Heteromeles, Macromeles, Malacomeles, Mespilus, Osteomeles, Peraphyllum, Phippsiomeles, Pyracantha, Rhaphiolepis, Stranvaesia*, and *Weniomeles*, including nine genera in this table.

[b]+/−, rust reported/no rust reported in the literature and databases.

[c]Red + indicates that the plant species examined in this study also showed rust symptoms caused by *G. asiaticum* and *G. yamadae*.

host species across nine genera (*Aria*, *Chaenomeles*, *Crataegus*, *Cydonia*, *Malus*, *Photinia*, *Pourthiaea*, *Pseudocydonia*, and *Pyrus*) of the subtribe Malinae; *G. yamadae* was recorded only in the genus *Malus*.

Nine species of *Gymnosporangium*, such as *G. asiaticum*, *G. clavariiforme*, *G. globosum*, *G. japonicum*, *G. monticola*, *G. nidus-avis*, *G. sabinae*, *G. unicorne*, and *G. yamadae*, were reported in Korea [32–34]; among them, only two *Gymnosporangium* spp. such as *G. asiaticum* and *G. yamadae* were observed at the KNA. In the present study, *G. asiaticum* was found in six species across five genera in subtribe Malinae, whereas *G. yamadae* was found in three species within the genus *Malus* in the subtribe. Literature and databases [6,13,27–31] also showed similar results that *G. asiaticum* caused rusts in 23 species across nine genera, including *Malus*, in Malinae, whereas *G. yamadae* caused diseases in 20 species of only *Malus* (except *M. ioensis*). In this regard, these two *Gymnosporangium* species may exhibit different host diversity (or specificity): *G. asiaticum* can cause rusts in various plant species of subtribe Malinae, whereas *G. yamadae* can induce diseases only in the genus *Malus* within the subtribe. Previously, Tao et al. [9] conducted comparative transcriptome analysis with *G. asiaticum* and *G. yamadae*. Consequently, they found that *G. asiaticum* had a larger transcriptome than *G. yamadae*; they further observed that numbers

and families of the candidate effectors (*i.e.*, virulence factors) of the two species were markedly different. These results may present clues to the different host diversity (or specificity) of the two *Gymnosporangium* species. In another plant-microbe interaction, Wang et al. [35] recently found that host specificity (or diversity) of plant-associated bacteria was negatively (or positively) affected by host abundance and bacterial genome size; they concluded that host specialization played a crucial role in ecology and evolution of plant-microbe interactions.

In this study, aecial stages (average 120 days [36]) of the heteroecious and demicyclic rust fungi (*G. asiaticum* and *G. yamadae*) were observed in various alternative host species of the subtribe Malinae (Rosaceae) (Fig. 4) [7,9]. Because the field rust surveys at the KNA were conducted from June to August, only aecial stages (spermatia and aeciospores) were observed. However, telial stages (teliospores and basidiospores) of the rusts would be detectable in the primary hosts (*Juniperus* spp.) from April to May [36]. Basidiospores developed from teliospores could be released at temperatures of 10–15°C, with relative humidity >80% and dispersed over 3–5 km [36]. Therefore, further studies are needed to examine the rust telial stages in the primary hosts at the KNA area. Once the telial stages are identified in the primary hosts, cross-inoculation experiments between *Juniperus* and Malinae hosts could be conducted as researched by others [37–39]. Such experiments provide evidence confirming the disease cycles of *G. asiaticum* and *G. yamadae* within the KNA area and will help develop disease management strategies.

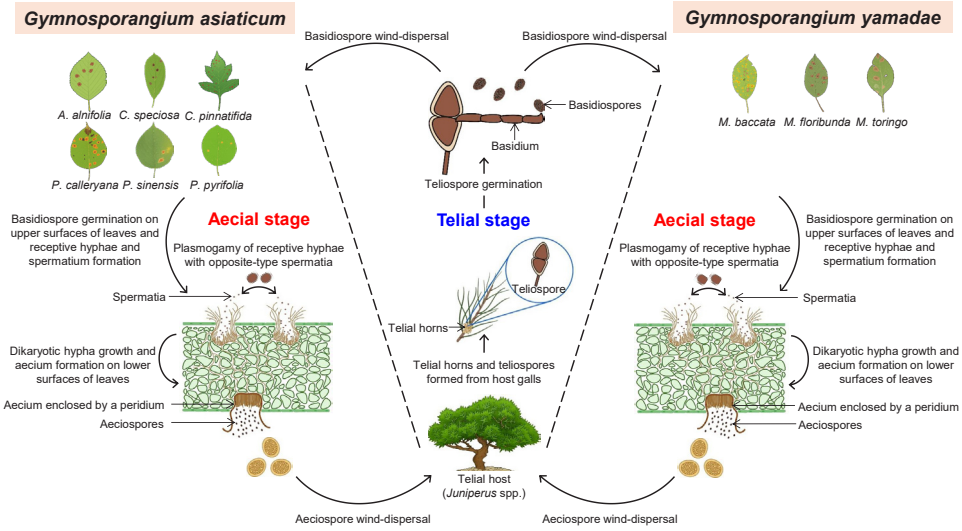

Fig. 4. Disease cycles of *Gymnosporangium asiaticum* and *Gymnosporangium yamadae* causing rusts in various host plant species of Malinae (Rosaceae), modified from Tao et al. [9]. The rust fungus *G. asiaticum* occurs in the six plant species *Aria alnifolia, Chaenomeles speciosa, Crataegus pinnatifida, Pseudocydonia sinensis, Pyrus calleryana*, and *Pyrus pyrifolia; G. yamadae* occurs in the three plant species *Malus baccata, Malus floribunda*, and *Malus toringo* as aecial stages (indicated by red letters). However, both rust fungi occur in *Juniperus* spp. as telial stages (indicated by blue letters). Both diseases are demicyclic rusts, which produce four different spores, such as teliospores, basidiospores, spermatia, and aeciospores, in disease cycles.

When managing demicyclic, heteroecious rusts in crop systems, farmers generally focus on economically important host plants, which leads to removal of alternative (or less valuable) host plants [8,40]. In contrast, management of the demicyclic rusts in arboretum systems is somewhat different because the importance of two different host plants cannot depend on the economic importance alone. The disease management may depend on not only economic value but also landscape and ecological significance. In this regard, the two different host plants such as Malinae species for aecial stages of rusts and *Juniperus* species for telial stages are essential components of the KNA. Thus, disease management in this arboretum system should be different from that in crop systems; consequently, it should manage rusts of both host species by applying the standard foliar disease control measures (*i.e.*, fungicide applications). Rust management in the system using fungicide applications may also effectively limit basidiospore production and infection on both host species in the disease cycles of *G. asiaticum* and *G. yamadae* (Fig. 4). In addition, the two rust pathogens investigated in the present study are listed as quarantine pests in the EPPO A1 list of the European Union, whereas *G. yamadae* is listed in the USA and Canada [6,31]. Accurate identification of the two rust fungi is essential because misidentification can disrupt regular plant quarantine.

Taken together, all rust samples from nine plant species at KNA in Pocheon, Korea, were identified as *G. asiaticum* or *G. yamadae* based on morphological identification and molecular analyses of ITS and LSU gene sequences. The two species also exhibited different host diversity (or specificity): *G. asiaticum* caused rusts in various host plant species across many genera of subtribe Malinae (Rosaceae), whereas *G. yamadae* induced diseases only in the genus *Malus* within the subtribe. This is the first comparative study of rust occurrence caused by *G. asiaticum* and *G. yamadae* at KNA; it provides basic information on the occurrence of two different rusts and may facilitate the development of appropriate rust management strategies.

CONFLICT OF INTEREST

The authors declare that they have no potential conflict of interest.

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