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RESEARCH ARTICLE

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Identification, Phylogeny, and Fungicide Sensitivity of Oomycota Species Causing Stem and Root Rots on Chrysanthemums in Korea

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ABSTRACT

Root and stem rot, caused by Pythiales (Oomycota), poses a significant threat to chrysanthemum (*Chrysanthemum* spp.) cultivation worldwide. In Korea, previously undocumented rot and blight symptoms were observed on stems, roots, and leaves of *Chrysanthemum morifolium* (=*Dendranthema morifolium*), a chrysanthemum species with high global production. This study identified the causal agents as *Globisporangium ultimum* and *Phytopythium helicoides* based on morphological features and molecular phylogenetic analysis of the internal transcribed spacer rDNA (ITS) region and the cytochrome c oxidase subunit mtDNA (*cox*1 and *cox*2) genes. Pathogenicity assay demonstrated the high aggressiveness of both species toward chrysanthemums. Fungicide sensitivity testing revealed high sensitivity to picarbutrazox, highlighting its potential as an effective control measure. These findings enhance our knowledge of identifying and managing *G. ultimum* and *P. helicoides* in chrysanthemum cultivation.

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Oomycetes; plant pathogen; fungicides; resistance

1. Introduction

Oomycota, often known as water mold, is a fungal-like group of the kingdom Chromista. It includes two agriculturally important orders, Peronosporales and Pythiales [1], which cause devastating diseases such as downy mildew, blights, and rots, leading to significant yield losses. The Pythiales consist of many plant pathogenic genera and species, which can infect roots, stems, leaves, flowers, and fruits of agricultural and ornamental crops and forest trees [2]. The genus *Pythium* sensu lato has undergone several taxonomic divisions by advancing molecular phylogenetic techniques, resulting in its split into five genera [3]. Among them, *Globisporangium* and *Phytopythium* include many plant pathogens causing root and stem rot on diverse crops worldwide, including *G. spinosum* (Sawada) Uzuhashi, Tojo & Kakish. on kiwifruit [4], *P. vexans* (de Bary) Abad, de Cock, Bala, Robideau, Lodhi & Lévesque on oak trees [5], and *P. helicoides* (Drechsler) Abad, de Cock, Bala, Robideau, Lodhi & Lévesque on pistachio [6]. In Korea, many studies have focused on their substantial influence on agricultural and ecological systems. As a result, two *Globisporangium* species (*G. irregulare* (Buisman) Uzuhashi, Tojo & Kakish., *G. ultimum* (Trow) Uzuhashi, Tojo & Kakish.), two *Phytopythium* (*P. helicoides, P. vexans*), and fourteen *Pythium* species have been reported as pathogens in various plant species [7].

Chrysanthemum (*Chrysanthemum morifolium* Ramat., synonym: *Dendranthema morifolium* (Ramat.) Tzvelev) is one of the most popular ornamental plants worldwide. This plant has the highest production volume in Korea among the cultivated flowering plants because it is widely used in ceremonies and as a seasonal flower during autumn festivals.

In the spring of 2006, previously unknown stem and root rot symptoms and leaf blight were first found on chrysanthemums cultivated in Korea. The symptoms and microscopic observation revealed that the causal agents are members of Oomycota. To date, only an oomycete species, *Phytophthora cactorum*, has been recorded on chrysanthemums in Korea [7], although a dozen species of *Pythium* sensu lato have been recorded on chrysanthemums worldwide [8]. The emergence of this new disease underscores the urgent need for detailed studies to identify and characterize the causal pathogens, directly addressing the present study's primary objective of filling critical knowledge gaps. In addition, the efficacy of the pathogens against five widely used

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anti-oomycete fungicides [9–18] needs to be evaluated to effectively control them in chrysanthemum cultivation because the Korean government implemented the Positive List System (PLS) in 2019 to regulate pesticide use.

2. Materials and methods

2.1. Oomycete isolates

Two oomycete isolates (KACC 42224 and 42226) associated with root and stem rots of chrysanthemums were obtained from the Korean Agricultural Culture Collection (KACC) in Jeonju, Korea. Both isolates were collected in April 2006 from two regions: KACC 42224 from Changwon, Gyeongsangnam-do and KACC 42226 from Hwaseong, Gyeonggi-do, Korea.

2.2. Cultural and morphological analyses

To investigate cultural features, 4 mm agar plugs were placed on three solid media: potato dextrose agar (PDA; Difco, Detroit, MI, USA), 20% V8A (200 mL of clarified V8 juice, 10 g of CaCO3, 15 g of agar, rifampicin 15 µg/mL, and 800 mL of deionized water), and cornmeal agar (CMA; Difco, Detroit, MI, USA), and incubated at 25 °C for three days. The formation of sporangia and sexual organs of two isolates was induced using the soil extract [19]. Ten grams of horticultural soil (NH Nonghyup, Sejong, Korea) were added to 1 L of sterile water, set aside overnight, and filtered through Whatman No. 1 filter paper. Mycelial plugs of five-day-old isolates grown on V8A were rinsed with sterile deionized water and placed in Petri dishes containing 10 mL of soil extract. The plates were kept at room temperature (25 °C) and examined on days 2 and 5. All microscopic structures were examined using a Zeiss Axio Imager A2 microscope (Carl Zeiss, Oberkochen, Germany) and captured using an Axiocam 512 color camera (Carl Zeiss).

2.3. Molecular phylogenetic analysis

The mycelia of *Globisporangium* and *Phytopythium* isolates were harvested after cultivating V8A in darkness at 25 °C for five days. DNA was extracted using the MagListo 5 M Plant Genomic DNA Extraction Kit (Bioneer, Daejeon, Korea). The internal transcribed spacer (ITS) region, the cytochrome c oxidase subunit I (*cox*1), and cytochrome c oxidase subunit II (*cox*2) mtDNA genes were amplified with ITS1/ITS4 primers for ITS [20], OomCox1-levup/OomCox1-levlo for *cox*1 [21] and cox2-F [22]/cox2-RC4 for *cox*2 [23], respectively. The PCR amplicons were purified using an AccuPrep PCR Purification Kit (Bioneer, Daejeon, Korea) and then sequenced by Macrogen Inc. (Seoul, Korea). Sequences were edited with DNAStar software package 5.05 (DNAStar, Inc., Madison, WI), followed by NCBI BLASTn search against the National Center for Biotechnology Information (NCBI) GenBank database. Phylogenetic analysis was performed based on a concatenated dataset of ITS, *cox*1, and *cox*2 sequences, incorporating reference sequences retrieved from NCBI GenBank and aligning by the G-INS-i algorithm [24] in MAFFT 7 [25]. MEGA 11 [26] was employed to construct phylogenetic trees, utilizing maximum likelihood (ML) and minimum evolution (ME) methods with the Tamura-Nei model and bootstrapping (BS) of 1000 replicates.

2.4. Pathogenicity tests

Cuttings of *Chrysanthemum morifolium* (Central Botanical Garden, Jeonju, Korea) were planted into pots filled with fertilized granulated soil (NH Nonghyup, Sejong, Korea) and incubated for six weeks in a greenhouse at 25 °C. Pathogenicity tests were performed thrice by inoculating six healthy chrysanthemum plants with two oomycete isolates (KACC 42224 and 42226). The isolates were incubated for a week under a dark condition on a 20% V8A at 25 °C before inoculation. Fifty mL of a sporangial suspension (10^4 sporangia/mL) was inoculated at the base of the cultivated plants [27]. Six control plants were prepared without inoculum. The inoculated and control plants were kept at 90% relative humidity and 25 °C in an incubator for the first three days to promote their infections. They were then transferred to a greenhouse at 25 °C with 70% relative humidity.

2.5. Fungicide sensitivity

Sensitivity of KACC 42224 and 42226 against five different anti-oomycete fungicides, including metalaxyl (25% WP), ethaboxam (15% WP), dimethomorph (50% WP), fluazinam (25% WP), and picarbutrazox (10% WP), was assessed using *in vitro* assays. Fungicide efficacy was determined based on mycelial growth inhibition, referring to previous fungicidal tests for *Phytopythium* species [28]. The reactivity of mycelial growth was tested using the agar dilution method with fungicide incorporation [14,29,30]. Each fungicide was diluted in sterilized distilled water and then added to 20% V8A to prepare the antibiotic media, with concentrations set from 0.01 µg/mL and increasing in

10-fold increments up to 1000 µg/mL. After culturing the pathogen on V8A at 25 °C for one week, 4 mm x 4 mm agar plugs were taken from the edge of the media and inoculated onto V8A containing the fungicide. The media inoculated with agar plugs were incubated in the dark at 25 °C with three replicates, and the growth was measured daily until the diameter of the control group, growing on fungicide-free media, reached 60 mm. The mycelial growth inhibition rate of each isolate was calculated compared to the control and expressed as the EC50, which is the concentration required to inhibit half of mycelial growth [31]. EC50 values measure the fungicide effect, with lower values indicating higher efficacy.

3. Results

3.1. Symptoms

Disease symptoms were found on the stem, root, and leaf of chrysanthemums (Figures 1B,C, 2B,C). Brown blight lesions appeared on the stem near the ground, then enlarging and rotting (Figures 1B,C, 2B). The leaves turned light green to yellow, developing brown blights (Figures 1C, 2C), which began on the lower leaves and progressed upward through the plant. The roots exhibited distinct symptoms, with their surface and internal tissues turning dark brown to black. The entire plant begins to wilt in severe infections, leading to plant death.

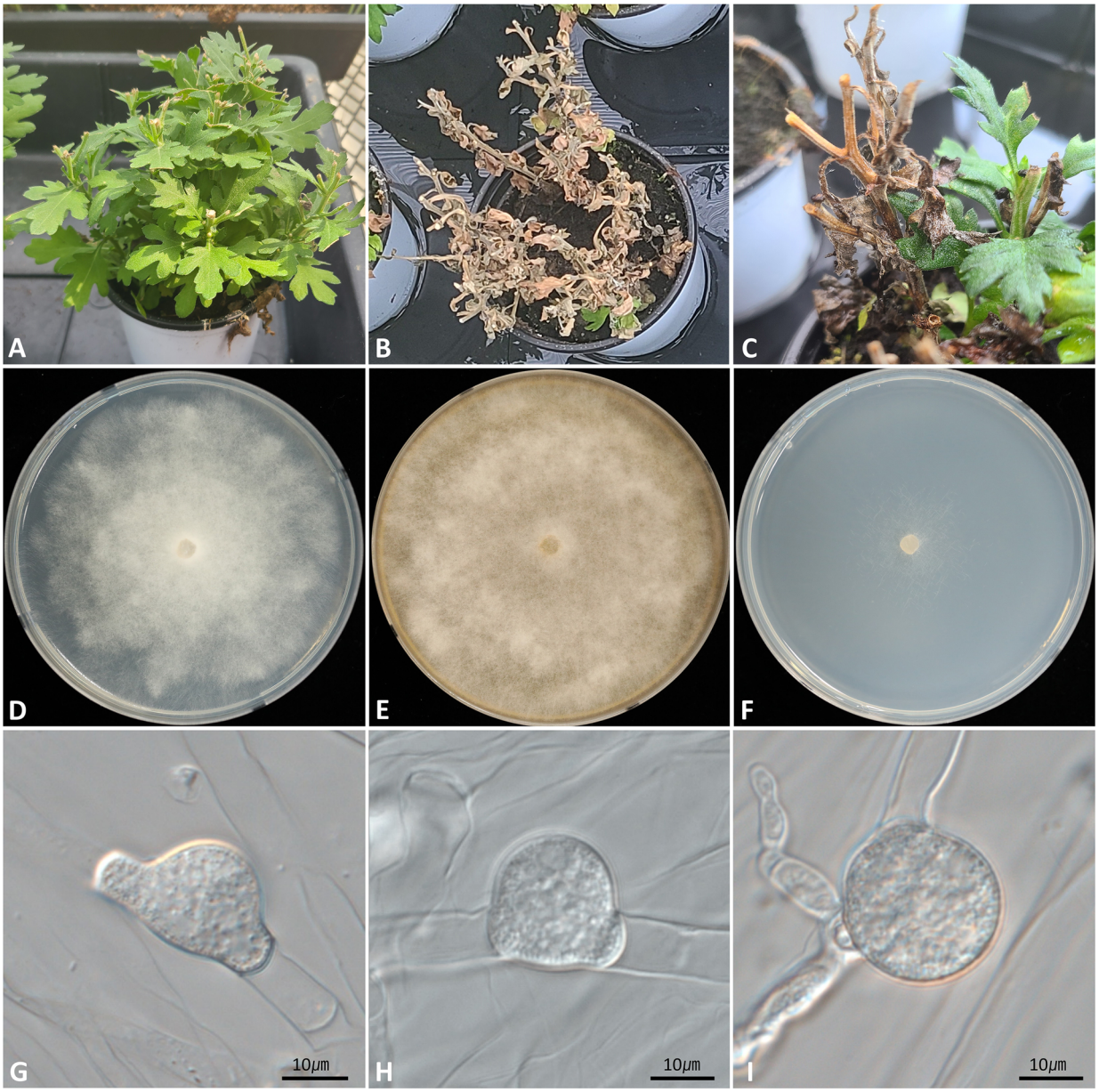

Figure 1. Disease symptoms and morphological characteristics of *Globisporangium ultimum* KACC 42224 on chrysanthemum (*chrysanthemum morifolium*). (A) Healthy chrysanthemum. (B) Stem and root rot symptoms. (C) Close-up view of affected stems and leaves. (D–F) Cultural characteristics on potato dextrose agar (D), V8 agar (E), and cornmeal agar (F) after 72 h at 25 °C. (G & H) Hyphal swelling. (I) Globose oospore.

3.2. Morphology

The present study described the cultural and morphological characteristics of two Korean isolates, KACC 42224 (Figure 1D–I) and 42226 (Figure 2D–I). These oomycetes exhibit filamentous, highly branched hyphae that are generally non-segmented and contain multiple nuclei. The shape and size of sporangia are variable (Figures 1G,H, 2G), producing mobile zoospores. Thick-walled oospores were produced on V8A media containing the soil extract (Figure 1H,I).

The colonies of KACC 42224 grew colorlessly in a radiate pattern on all three media, PDA (Figure 1D), V8A (Figure 1E), and CMA (Figure 1F). On PDA and V8A, aerial mycelia were present, covering the surface of the media with multiple layers of mycelia. On CMA, the growth was much sparser with thin mycelia. After 72 h of incubation at 25 °C, the growth measured 85–90 mm on PDA and V8A but 75–83 mm on CMA. Hyphal swellings were globose in shape, located intercalarily or terminally, and measured (16.8–)20.4–27.5(–29.8) (av. 23.9) µm ($n = 50$) (Figure 1G,H). Oospores were mostly spherical, hyaline, and measured (18.3–)20.2–25.3(–26.6) (av. 22.8) µm ($n = 50$) in diameter (Figure 1I). The antheridia were transparent and either monoclinous or hypogynous. The morphological characters closely resembled those described for *Globisporangium ultimum* (Trow) Uzuhashi, Tojo & Kakish [3].

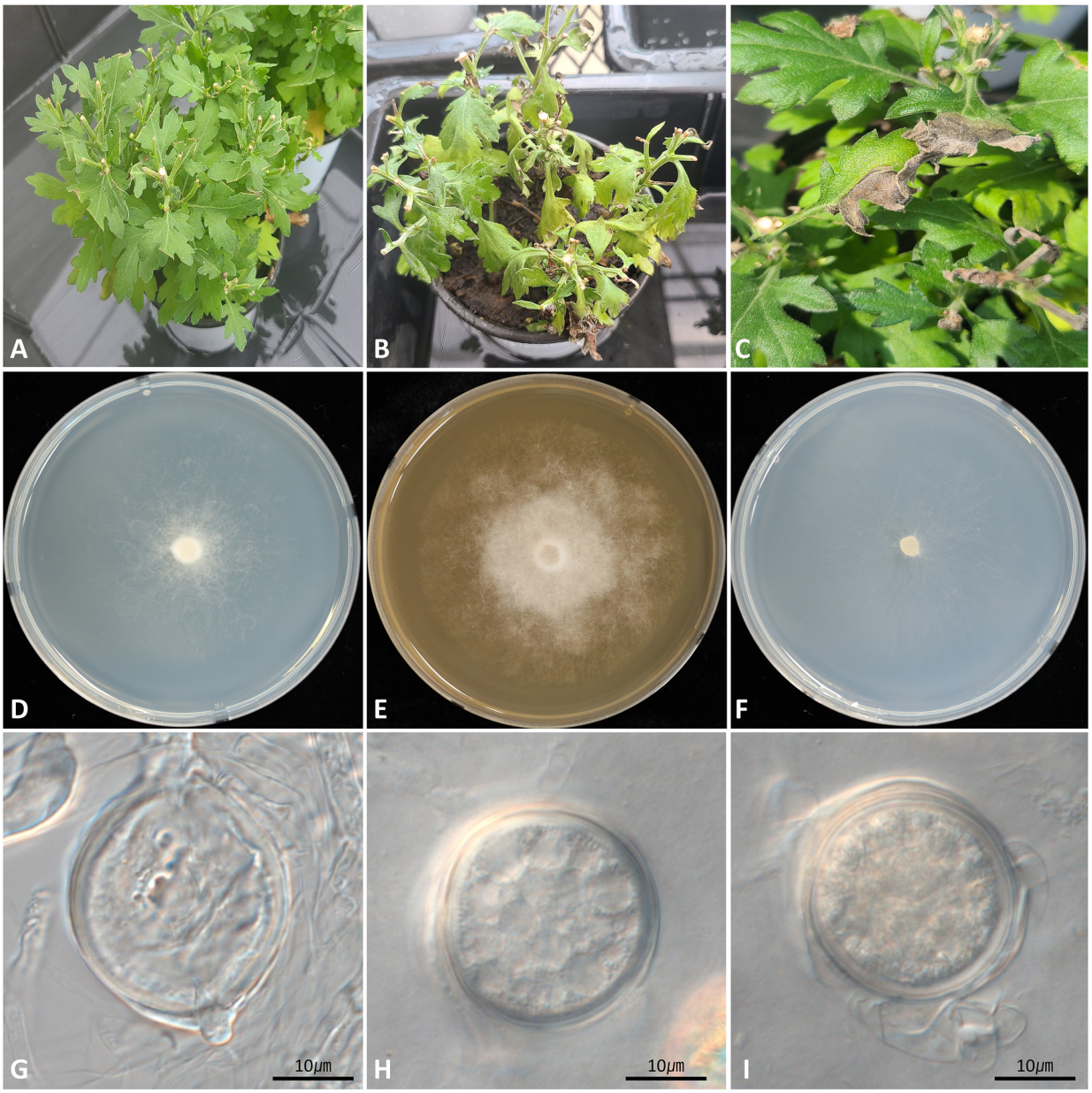

Figure 2. Disease symptoms and morphological characteristics of *Phytopythium helicoides* KACC 42226 on chrysanthemum (*chrysanthemum morifolium*). (A) healthy chrysanthemum. (B) Stem rot and leaf blight symptoms. (C) Close-up view of affected leaves. (D-F) Cultural characteristics on potato dextrose agar (D), V8 agar (E), and cornmeal agar (F) after 72 h at 25 °C. (G) Spherical sporangium. (H & I) Globose oospore.

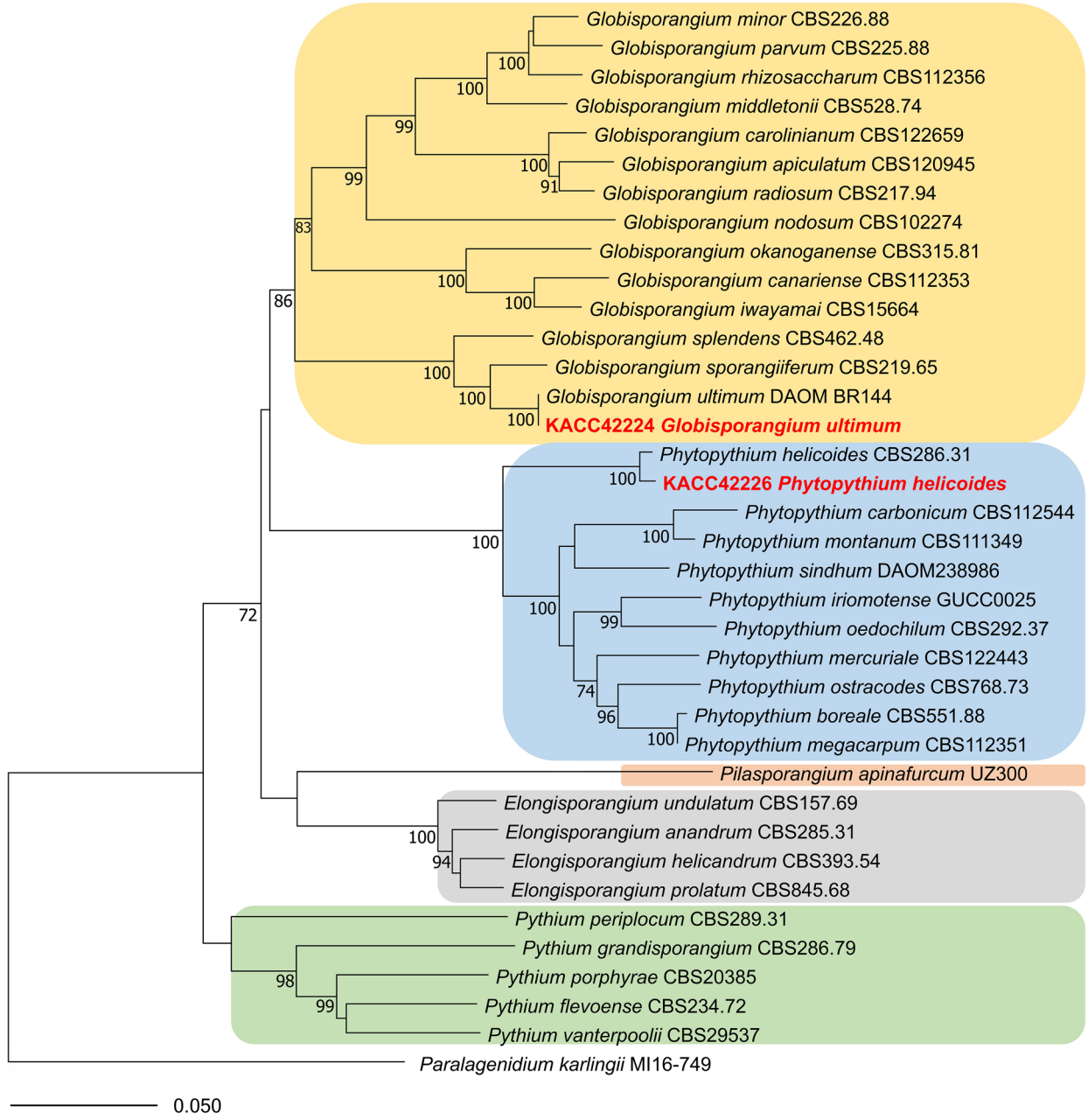

Figure 3. Phylogenetic tree of *Globisporangium* and *Phytopythium* species from the minimum evolution analysis based on a concatenated alignment of the ITS rDNA, *cox*1, and *cox*2 mtDNA sequences. Bootstrapping values (minimum evolution BP/maximum likelihood BP) higher than 70% were given above or below the branches (1,000 replicates). The Korean isolates were shown in bold red. *Paralagenidium karlingii* was used as an outgroup. The scale bar equals the number of nucleotide substitutions per site.

The colonies of KACC42226 grew colorlessly in a radiate pattern on all three media, PDA (Figure 2D), V8A (Figure 2E), and CMA (Figure 2F). On PDA and CMA, little to no aerial mycelium was observed, while on V8A, aerial mycelium was present on the center and layered over the medium. After 72 h of incubation at 25 °C, the colony growth measured 70–85 mm on PDA, 80–85 mm on V8A, and 65–75 mm on CMA. Papillate sporangia were formed on V8A containing the soil extract. The sporangia were spherical or ellipsoidal, measuring (30.5–)32.2–36.1(–38.5) x (28.1–)29.5–33.73(–35.5) (av. 34.06 × 31.84) um ($n = 50$) (Figure 2G). Oospores were hyaline, spherical, and measured (22.4–)24.3–29.3(–30.8) (av. 26.8) um ($n = 50$) (Figure 2H,I). The antheridia were hyaline and either monoclinous or hypogynous in structure. The morphological features matched *Phytopythium helicoides* (Drechsler) Abad, de Cock, Bala, Robideau, Lodhi & Lévesque [32].

3.3. Molecular phylogeny

Through a BLASTn search of the ITS, *cox*1, and *cox*2 sequences, KACC 42224 isolate showed high

Table 1. Sensitivity range and mean value of effective concentrations to inhibit mycelial growth of *Globisporangium ultimum* KACC 42224 and *Phytopythium helicoides* KACC 42224 by EC50 values for five anti-oomycete fungicides (metalaxyl, ethaboxam, fluazinam, dimethomorph, and picarbutrazox).

Fungicide	Frac code	Target site	EC50 (μg/mL)	
			G. ultimum KACC 42224	*P. helicoides* KACC 42226
Metalaxyl	4	RNA polymerase	1.98759 (1.71144–2.29926)	0.29183 (0.17600–0.45630)
Ethaboxam	22	Tubulin polymerization	2.11283 (2.04696–2.17773)	31.70823 (17.85208–61.66769)
Fluazinam	29	Uncouplers of oxidative phosphorylation	23.73889 (21.87540–25.42800)	67.40539 (37.22705–114.66779)
Dimethomorph	40	Cellulose synthase	25476.96229 (18554.50700–30965.56001)	795.97247 (471.53522–1115.71952)
Picarbutrazox	U17	Unknown	0.00014 (0.00007–0.00021)	0.00375 (0.00264–0.00536)

sequence similarities with the reference strain of *G. ultimum* DAOM BR144 across all three markers: ITS sequence at 820/820 bp (AY598657; 100%), *cox*1 at 658/659 bp (KJ639195; 99.84%), and *cox*2 at 528/529 bp (KJ639195; 99.81%). The isolate KACC 42226 matched the ex-type sequences of *P. helicoides* CBS286.31 in the ITS at 745/758 bp (AB725878, 98.28%), *cox*1 at 669/673 bp (AB690645, 99.41%), and *cox*1 at 531/535 bp (AB690675, 99.25%).

For phylogenetic analysis of the two KACC isolates, the sequences of the three markers were aligned and concatenated. In both ML and ME trees (Figure 3), KACC 42224 and 42226 were closely related to members of *Globisporangium* and *Phytopythium*, respectively, with high bootstrap supports. Further, KACC 42224 formed a well-supported group with the reference sequence of *G. ultimum*, while KACC 42226 grouped with *P. helicoides*, supported by the maximum BS value.

3.4. Pathogenicity

Six days after inoculation with *G. ultimum* KACC 42224, the typical stem and leaf blights, beginning from the basal part and spreading throughout the plant, and severe necrotic root rot were observed on chrysanthemums. Eight days after inoculation, the plants inoculated with *P. helicoides* KACC 42226 developed dark brown lesions on stems and leaves, wilting of the aboveground parts, and root rot. The symptoms were consistent with those initially observed on chrysanthemums in the field. All six inoculated plants died within two weeks after the appearance of the disease. No symptoms were observed in control plants. The inoculated oomycetes were re-isolated from diseased stems and roots and identified by morphological and sequence analyses, fulfilling Koch's postulates.

3.5. Fungicidal sensitivity

The responses of *G. ultimum* KACC 42224 and *P. helicoides* KACC 42226 against five anti-oomycete fungicides (metalaxyl, ethaboxam, fluazinam, dimethomorph, and picarbutrazox) revealed different patterns of sensitivity and resistance (Table 1, Figure 4). Picarbutrazox demonstrated the highest inhibitory activity against both isolates, with EC50 values of 0.00002 μg/mL for *G. ultimum* and 0.00169 μg/mL for *P. helicoides*. Metalaxyl showed moderate efficacy for both isolates, with EC50 values indicating sensitivity for *P. helicoides* (0.29183 μg/mL) but reduced sensitivity for *G. ultimum* (1.98759 μg/mL). Similarly, ethaboxam and fluazinam exhibited intermediate effectiveness, with variability in sensitivity levels between the two species. In contrast, both isolates resisted dimethomorph, with high EC50 values of 23.73889 μg/mL for *G. ultimum* and 795.97247 μg/mL for *P. helicoides*.

4. Discussion

Chrysanthemums (*Chrysanthemum* spp.) are globally recognized as economically and culturally valuable ornamental plants. However, their cultivation is often affected by diseases caused by oomycetes, such as *Globisporangium*, *Phytopythium*, and *Pythium*. The present study is the first report of root and stem rot diseases caused by *Globisporangium ultimum* and *Phytopythium helicoides* on chrysanthemums in Korea. These findings represent a critical advancement in chrysanthemum cultivation by providing a comprehensive knowledge of pathogen identification through morphological characterization, molecular phylogenetic analysis, and fungicide sensitivity testing. Previously, similar diseases caused by five oomycete species, *G. ultimum* var. *ultimum* (as *Pythium ultimum* var. *ultimum*), *Phytopythium helicoides* (as

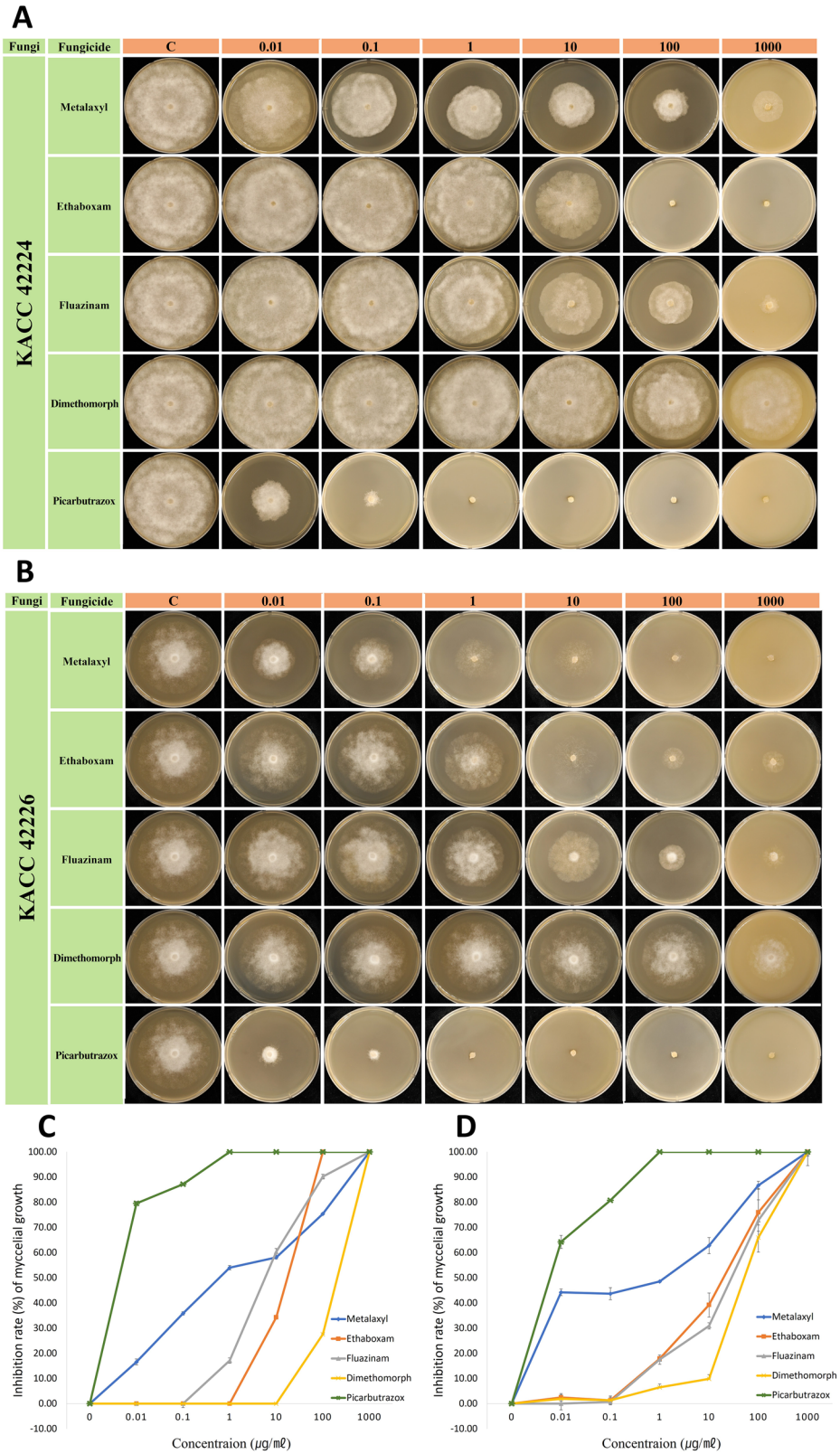

Figure 4. Mycelial growth of *Globisporangium ultimum* KACC 42224 (A,C) and *Phytopythium helicoides* KACC 42226 (B,D) against five anti-oomycete fungicides (metalaxyl, ethaboxam, fluazinam, dimethomorph, and picarbutrazox). V8A (20%) media contains different concentrations (0, 0.01, 0.1, 1, 10, 100, and 1000 ug/mL) of each fungicide. Agar plugs sourced from seven-day-old colonies were inoculated on V8A, with daily measurements of mycelial diameter until the control group reached a diameter of 60 mm.

Pythium helicoides), *Pythium dissotocum* Drechsler, *Phytopythium oedochilum* (Drechsler) Abad, de Cock, Bala, Robideau, Lodhi & Lévesque (as *Pythium oedochilum* Drechsler), and *Globisporangium sylvaticum* (W.A. Campb. & F.F.Hendrix) Uzuhashi, Tojo & Kakish. (as *Pythium sylvaticum* W.A. Campb. & F.F. Hendrix), have been reported on chrysanthemum in Japan. However, this study did not perform

molecular phylogenetic analysis or fungicidal sensitivity testing [33]. The occurrence of morphologically similar pathogens affecting chrysanthemum underscores the importance of molecular tools to ensure accurate identification and diagnosis.

Phytopythium helicoides has become an emerging concern in crop cultivation due to its broad host range of plant families, including chrysanthemum [28]. Additionally, this species exhibits remarkable adaptability to different environmental conditions [34,35]. Its detrimental effects are especially evident under high humidity and dense plant population conditions, making it a significant threat to ornamental horticulture [28,35,36].

Globisporangium ultimum is an economically important pathogen, causing damping-off and root rot in over 300 host species, including major crops like corn, soybean, and wheat [37,38]. This species has previously caused root and stem rot on chrysanthemums in Japan [33], the Netherlands [39,40] and the USA [41–43]. Its global presence in fields, ponds, and decomposing vegetation is driven by its ability to grow saprotrophically in soil and plant residue [44].

Fungicide sensitivity assays demonstrated picarbutrazox as the most effective agent against both pathogens. This finding aligns with previous results highlighting the broad-spectrum efficacy of picarbutrazox against oomycete pathogens [45,46]. Conversely, both species are resistant to dimethomorph, which was consistent with those observed in other species of *Globisporangium*, *Phytopythium*, and *Pythium* [47,48], although it exhibits high activity against other plant pathogenic oomycetes, like *Phytophthora* and downy mildews (Peronosporaceae) [48–51]. Variability in sensitivity to other fungicides (metalaxyl, ethaboxam, and fluazinam) emphasizes the need for integrated management strategies, including fungicide rotation. Therefore, picarbutrazox is a promising candidate for managing *G. ultimum* and *P. helicoides* in chrysanthemum cultivation.

This study enhances our understanding of oomycete-related diseases occurring on chrysanthemums, specifically focusing on those caused by *G. ultimum* and *P. helicoides*. Integrating molecular phylogenetics and fungicide sensitivity testing offers a reliable framework for pathogen identification and introduces picarbutrazox as an effective fungicide to ensure the health and productivity of chrysanthemums.

Informed consent

All authors have reviewed the manuscript and approved its submission.

Disclosure statement

The authors do not have any conflict of interest, and there are no competing financial and non-financial interests.

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Data availability statement

Sequences from this study were registered to GenBank.

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