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RESEARCH NOTE

Holomorph Morphology and Molecular Phylogeny of *Erysiphe zelkovae* Found on *Zelkova serrata* in Korea

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ABSTRACT

Erysiphe zelkovae is one of the main pathogens causing significant damage to *Zelkova serrata* in East Asia. Despite the global diversity of *Zelkova* spp., *E. zelkovae* has been reported only on *Z. serrata* from East Asian countries (Japan, China, and Korea). Mycological information regarding this fungus is insufficient in terms of sequenced nucleotides and detailed morphological characteristics. This study presents a detailed characterization of the holomorph of *E. zelkovae* and its taxonomic placement through molecular phylogenetic analyses using the internal transcribed spacer region and large subunit gene sequences from three representative Korean specimens. This study confirmed the identity of *E. zelkovae* as a distinct species among the *Erysiphe* section *Uncinula* species on host plants belonging to the family Ulmaceae.

Keywords: Cannabaceae, *Celtis*, *Erysiphe kusanoi*, Ulmaceae, *Uncinula zelkovae*

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The genus *Zelkova* Spach, belonging to the family Ulmaceae, consists of six species distributed across Europe and East Asia. Although *Zelkova* species are widespread, only *Zelkova serrata* (Thunb.) Makino has been reported as a host for powdery mildew fungus *Erysiphe zelkovae* (Henn.) U. Braun [as '*zelkowae*'], which is also encountered only in East Asian countries, such as Japan, China, and Korea [1]. Furthermore, *E. zelkovae* is the only known powdery mildew pathogen found on *Zelkova* globally. Traditionally, the powdery mildew pathogen of *Z. serrata* was identified as a variety of *Uncinula kusanoi* Syd. & P. Syd. [currently *Erysiphe kusanoi* (Syd. & P. Syd.) U. Braun & S. Takam.] based on the similarities in their morphological traits [2,3]. Japanese scientists followed this concept and recorded *Zelkova* powdery mildew as *U. kusanoi* var. *zelkovae* (P. Henn) U. Braun [4]. In Korea, *E. zelkovae* was first recorded as *Uncinula zelkovae* P. Henn. [5]. Shin [5] recognized *U. zelkovae* as a distinct species differing from *U. kusanoi* var. *zelkovae* on the basis of the number of ascospores in an ascus, while also emphasizing the close affinity of the anamorph morphology of the two powdery mildew species.

Erysiphe kusanoi is an obligate parasite of *Celtis* L. species [1]. Previously, *Celtis* spp. were classified within the elm (Ulmaceae) family, but were later transferred to the Cannabaceae (hemp) based on the molecular phylogenetic analysis [6]. Both the Ulmaceae and Cannabaceae families belong to the order Rosales; therefore, the molecular and morphological similarities of *E. zelkovae* and *E. kusanoi* can be understood within the framework of the phylogenetic relationship between host families. Considering the above-mentioned issues between these two powdery mildew species, detailed mycological characterization is required to distinguish them. Furthermore, a single sequence from a Japanese specimen (MUMH 403) for the internal transcribed spacer (ITS) and large subunit ribosomal DNA (LSU) regions provides insufficient molecular evidence to recognize *E. zelkovae* as a distinct species. Therefore, this study aimed to characterize the holomorph morphology of *E. zelkovae* in detail, to elucidate its molecular phylogenetic position using ITS and LSU sequence data derived from Korean specimens, and to compare its phylogenetic relationships with other closely related *Erysiphe* powdery mildews.

A total of 28 powdery mildew specimens associated with *Z. serrata* were collected from multiple localities in Korea and are currently preserved at the Korea University Herbarium (KUS). Accession numbers for the specimens are listed as follows: KUS-F15571 (Oct 27, 1998; Seoul), F15636 (Nov 03, 1998; Seoul), F17168 (Oct 22, 1998; Namyangju), F17795 (Oct 09, 2000; Dongducheon), F22395 (Oct 28, 2006; Jinju), F23620 (Aug 29, 2008; Gongju), F24645 (Sep 20, 2009; Mungyeong), F25070 (Jul 18, 2010; Jecheon), F25084 (Jul 19, 2010; Youngwol), F25252 (Aug 08, 2010; Dongducheon), F25511 (Oct 18, 2010; Pocheon), F27062 (Oct 06, 2012; Seoul), F27952 (Jul 25, 2014; Hongcheon), F28198 (Sep 22, 2014; Jinju), F28249 (Sep 25, 2014; Busan), F28349 (Oct 09, 2014; Miryang), F28389 (Oct 14, 2014; Hongcheon), F28549 (Nov 27, 2014; Ulsan), F28912 (Oct 12, 2015; Yangpyeong), F29630 (Oct 27, 2016; Yangpyeong), F30353 (Nov 09, 2017; Daegu), F30809 (Sep 11, 2018; Hongcheon), F31296 (Oct 15, 2019; Daegu), F33414 (Oct 23, 2022; Imsil), F33898 (Oct 23, 2023; Uijeongbu), F33905 (Oct 23, 2023; Seoul), F34384 (Oct 21, 2024; Namyangju), F34444 (Nov 15, 2024; Paju), and F34595 (Aug 21, 2025; Chuncheon).

The morphological features of the powdery mildew pathogen were examined using an Olympus BX50 light microscope (Olympus, Tokyo, Japan), and images were captured using a Zeiss AX10 microscope equipped with an AxioCam MRc5 camera (Carl Zeiss, Oberkochen, Germany). Microscopic observations and measurements were primarily conducted on fresh specimens. The lactic acid technique was used to examine the dried herbarium materials [7]. For each diagnostic structure, quantitative assessment was based on 30 measurements.

Mycelial mats with conidiophores and conidia were amphigenous and abundantly epigenous, forming circular to irregular white colonies (Fig. 1A). In the later stages of the disease, chasmothecia were formed abundantly on the lower side of the leaves (Fig. 1B, C). The appressoria on the mycelia were moderately lobed to multi-lobed (Fig. 1D, E). Conidiophores emerging from the side of the hyphae were 55–87 × 7–9 μm, and producing conidia singly, followed by 1–2(–3) cells (Fig. 1F–I). Foot cells of conidiophores were curved or L-shaped from the basal part, cylindrical, and 18–32 μm long. Conidia were hyaline, cylindrically ovoid to oblong, variable in shape and size, 26–36 × 13–16 μm (length/width ratio = 2.0–2.8), occupied by vacuoles and oil drops, and lacking distinct fibrosin bodies (Fig. 1J). Germ tubes were produced at the perihilar position of the conidia (Fig. 1K, L). Chasmothecia were amphigenous, abundantly hypogenous, scattered to gregarious, dark brown, depressed globose, and 91–125 μm in diameter, and containing 4–7 asci per chasmothecium (Fig. 1M, N). Chasmothecial appendages were positioned in the lower half of the chasmothecium, numerous, 12–24 in number, not branched, substraight to mildly curved, apex circinate to uncinate, 4–6 μm wide but up to 9 μm wide at the uncinate part, 1–1.5 times as long as the chasmothecial diameter, aseptate, and hyaline throughout (Fig. 1O). Asci were obovoid, saccate, subsessile, 42–56 × 32–42 μm, and moderately thick-walled, thinner at the upper part (Fig. 1P, Q). Ascospores were 3–4 in an ascus, oval to cylindrically ovoid, 24–30 × 11–14 μm (length/width ratio = 1.8–2.2), and containing oil drops (Fig. 1R, S).

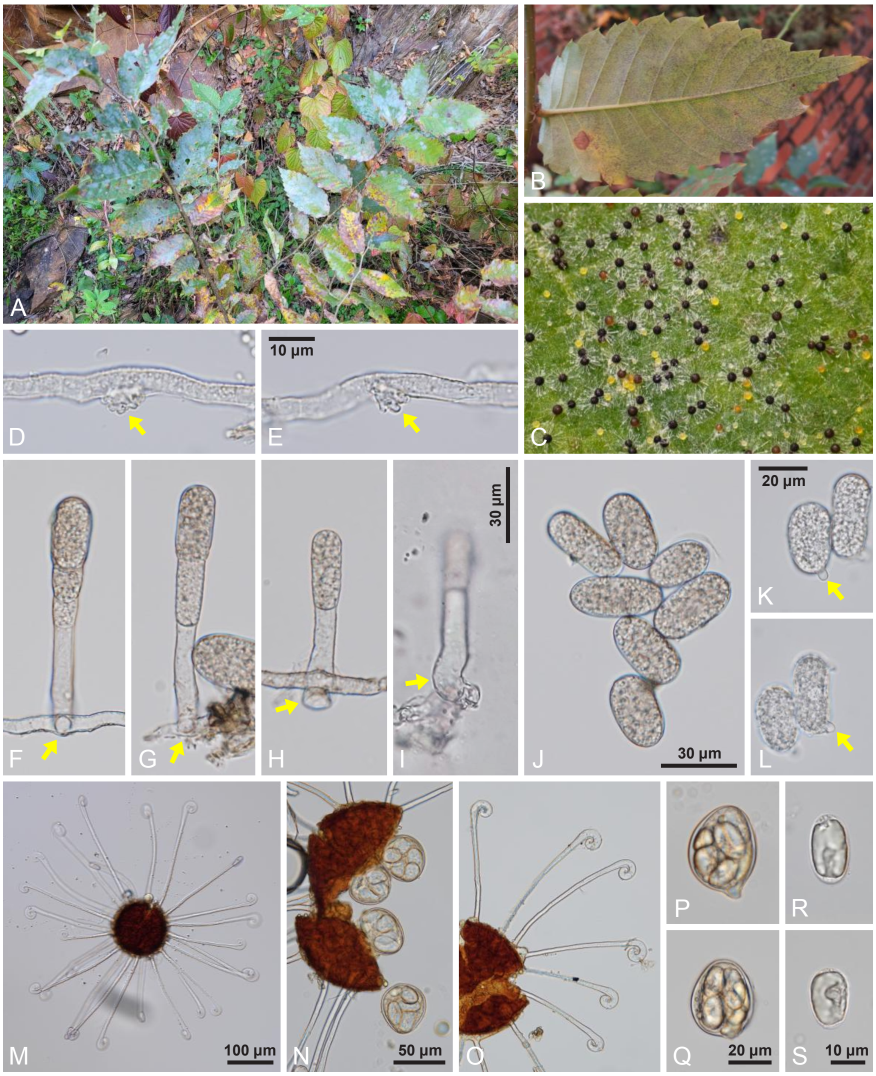

Fig. 1. *Erysiphe zelkovae*, a powdery mildew fungus found on *Zelkova serrata* (KUS-F34595). A: Powdery mildew symptoms on the leaves. B: Chasmothecia of *E. zelkovae* formed on the lower leaf surface. C: Close-up view of chasmothecia. Note yellowish, immature chasmothecia. D and E: Appressoria formed on the hyphae (arrows). F–I: Conidiophores. Note the lower part of conidiophores emerging from the side of creeping hyphae (arrows). J: Conidia. K and L: Conidia germinating (arrows). M: Chasmothecium with appendages. N: Asci protruding from the chasmothecium. O: Chasmothecial appendages with enlarged apex. P and Q: Mature asci. R and S: Ascospores.

To confirm the morphology-based identification, genomic DNA was obtained from three herbarium samples (KUS-F30809, F31296, and F33414). The LSU gene and ITS region, including the 5.8S rDNA gene, were amplified and sequenced using the primer pairs PM3/NLP2 and ITS1/PM6, respectively [8]. Forward and reverse reads were combined in MEGA11 [9], and the resulting sequences were submitted to the National Center for Biotechnology Information database (accession numbers: PX916213–PX916215 for ITS, and PX916216–PX916218 for LSU). Sequence similarity searches were performed against the GenBank database using BLASTn search tool. The results showed 100% identity in the ITS region with the sequences of *E. zelkovae* (AB475121) and in the LSU region with *E. zelkovae* (AB475114). The sequences of the LSU region were found to be 98.3% similar to those of *E. nothofagi* (AB378736) and 97.4% to *Erysiphe* sp. (OQ221121). To determine the phylogenetic placement of *E. zelkovae* among other closely related uncinuloid powdery mildews, a concatenated dataset of ITS and LSU sequences was assembled using MEGA11 for 20 *Erysiphe* sequences, including 17 sequences retrieved from GenBank. Sequence of *Erysiphe patagoniaca* Havryl. & S. Takam. (AB378747) was used as an outgroup taxon. Maximum parsimony (MP) analysis was conducted in PAUP* 4.0.a using the heuristic searches with the “tree-bisection-reconstruction” algorithm and 100 random sequence additions. All characters were treated as unordered and unweighted, and gaps were interpreted as missing data [10]. Tree statistics, including tree length, consistency index, retention index, and rescaled consistency index, were calculated. The analyzed alignment comprised 20 sequences spanning 870 characters, including 69 variable sites (7.9%) and 101 parsimony-informative sites (11.6%). Moreover, a maximum likelihood (ML) tree was constructed using raxmlGUI 2.0.13 based on the GAMMA model and GTR substitution [11]. Bootstrap (BS) support values were estimated from 1,000 replicates for both MP and ML analyses. In the inferred topology, all three sequences generated in this study formed a separate clade together with *E. zelkovae*, supported by 100% BS values from both analyses (Fig. 2). Based on the resulting phylogenetic tree presented in this study, it can be assumed that *E. zelkovae* and *Erysiphe* powdery mildews on *Celtis* spp. diverged from the same ancestor, which explains the similarities in their morphology.

Erysiphe zelkovae was first described as *Uncinula zelkovae* in 1901, based on a Japanese sample from *Zelkova serrata* [12]. Later, this species was reduced to a variety rank of *U. kusanoi*, as *U. kusanoi* var. *zelkovae* [2]. In accordance with the change in generic concepts within the Erysiphaceae, this fungus was renamed *Erysiphe kusanoi* var. *zelkovae* (Henn) U. Braun [12]. In 2009, Heluta et al. [13] provided the first sequence data for *E. kusanoi* var. *zelkovae* based on a Japanese specimen, suggesting that the *Zelkova* mildew pathogen (*E. kusanoi* var. *zelkovae*) be differentiated from the typical *Celtis* mildew pathogen (*E. kusanoi* var. *kusanoi*). No additional sequence data for *Zelkova* mildew were obtained. In 2012, the fungus was elevated to the species level as *Erysiphe zelkovae* based on the morphological differences from typical *Erysiphe kusanoi* and the taxonomic position of the host genera [1]. Therefore, the current study provides the first sequence data from Korean samples and supports the concept of *E. zelkovae* sensu Braun by confirming 99–100% similarity between the Japanese data and three Korean sequences. In conclusion, this study confirmed the identity of *E. zelkovae* as a distinct species in the genus *Erysiphe* section *Uncinula* species on diverse ulmaceous host plants [1,14].

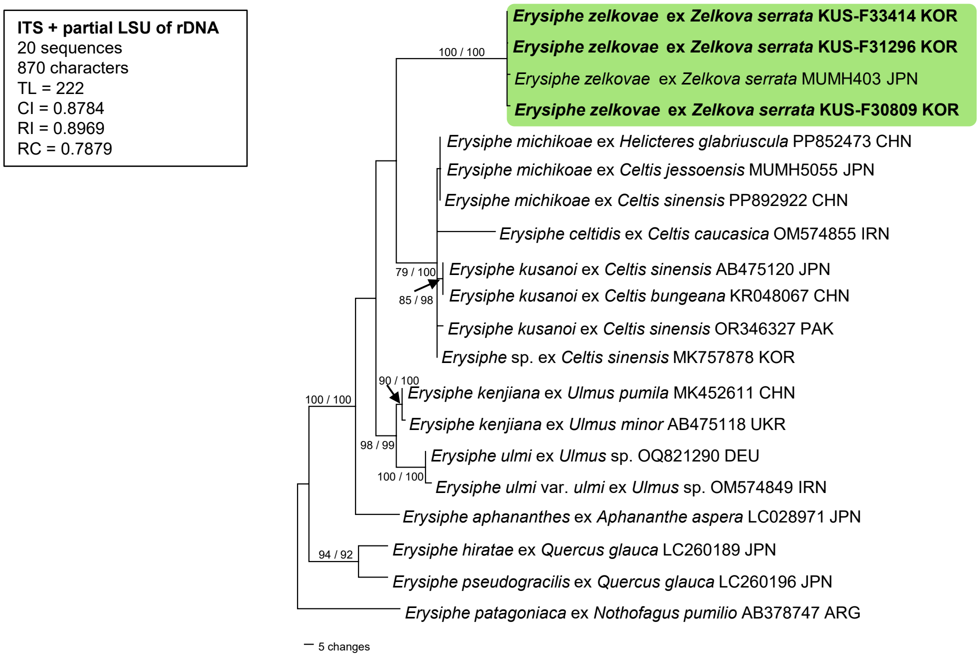

Fig. 2. Phylogenetic position of *Erysiphe zelkovae* among other closely related species of the *Erysiphe* sect. *Uncinula* is presented in the maximum parsimony tree derived from a combined data matrix of internal transcribed spacer (ITS) and large subunit ribosomal DNA (LSU) sequences. The sequence of *E. patagoniaca* (AB378747) is an outgroup here. Isolates obtained in this study are highlighted in bold. Bootstrap values (> 70%) obtained from the maximum parsimony and maximum likelihood analyses are indicated on the related branches, respectively. TL: tree length; CI: consistency index; RI: retention index; RC: rescaled consistency index.

CONFLICT OF INTEREST

The authors declare that there are no conflicts of interest.

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