RESEARCH ARTICLE

Polyphasic Characterization of *Taphrina deformans*, the Causal Agent of Peach Leaf Curl in Korea

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ABSTRACT

Taphrina deformans, a plant pathogenic fungal species belonging to the family Taphrinaceae, is associated with leaf curl on peach (*Prunus persica*). Although *T. deformans* has a worldwide distribution and has been reported in Korea since 1928, Korean isolates have never been comprehensively characterized. Using a polyphasic approach integrating morphological, physiological, and molecular phylogenetic analyses, Korean isolates obtained from symptomatic peach leaves were identified as *T. deformans*. This study confirms the early report of *T. deformans* in Korea and provides the detailed morphological, physiological, and genetic information needed to accurately identify this ascomycetous yeast species.

Keywords: Identification, Phylogeny, Physiology, *Prunus persica*, Taphrinaceae

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INTRODUCTION

Taphrina (Taphrinaceae, Taphrinales) comprises dimorphic ascomycetous fungi that infect a broad range of vascular plant hosts [1–4]. During their sexual stage, the fungus develops dikaryotic hyphae within living host tissues, intercellularly, subcuticularly, or under the epidermis, and produces naked asci on the surface of diseased organs. Infection causes hypertrophy and deformation, resulting in symptoms such as fruit pockets, leaf blotch, leaf curl, leaf gall, tongue gall, and witches' brooms [1–4]. In the asexual stage, *Taphrina* species exhibit yeast-like growth, reproducing by budding, and can be cultured on artificial media under laboratory conditions [1–4].

Traditionally, species in *Taphrina* have been delineated based on host association, disease symptoms, and morphological characteristics, including the size and shape of asci, ascospores, and stalk cells [1–3]. More recently, molecular phylogenetic analysis has become an essential tool for species identification and classification. The internal transcribed spacer (ITS) region of the ribosomal RNA (rRNA) gene, the D1 and D2 domains of the 26S rRNA gene, and the mitochondrial small subunit ribosomal RNA (*rns*) gene

are the molecular markers most commonly used for phylogenetic studies of *Taphrina*, as they provide improved species delimitation and taxonomic resolution [4–8]. Based on these combined morphological and molecular data, approximately 30 species are currently recognized in the genus [4,9].

Taphrina deformans, the causal agent of leaf curl on almond (*Prunus dulcis* (Mill.) D.A. Webb) and peach (*P. persica* (L.) Batsch), currently has a worldwide distribution [2,4]. However, in Korea, records of peach leaf curl are based primarily on historical specimens collected prior to the advent of molecular analysis, and only limited morphological examinations have been performed; thus, the pathogen's identity has not been confirmed using a modern polyphasic approach [10].

Peach is a major fruit crop cultivated in countries worldwide, including Korea, where its production ranks fourth among domestic fruit crops [11,12]. In addition to its agricultural importance, peach-based agroforestry systems have been recognized for their potential in degraded land restoration, soil erosion control, slope stabilization, and the enhancement of ecosystem services [13,14]. However, peach is highly susceptible to peach leaf curl caused by *T. deformans*. The disease reduces photosynthetic activity and induces premature defoliation, and severe outbreaks may affect up to 90% of the tree's shoots, substantially reducing fruit production and tree vigor [15,16]. In Korea, peach leaf curl is regularly observed in peach orchards and is recognized as one of the major diseases affecting peach production [17].

The objective of this study was to definitively identify the fungus associated with peach leaf curl through disease symptom observations and morphological characterization, together with molecular phylogenetic analyses. In addition, the physiological characteristics of the isolates were investigated to provide further taxonomic evidence for the classification of these ascomycetous yeasts.

MATERIALS AND METHODS

Sampling and fungal isolation

Leaves of *Prunus persica* exhibiting curls were collected from orchards in Jeonju (35°52′36″N, 127°06′38″E); Osan (37°09′57″N, 127°03′29″E); Dongdaemun-gu, Seoul (37°35′35″N, 127°02′40″E); Wanju (35°49′35″N, 127°01′48″E); Jongno-gu, Seoul (37°34′39″N, 126°59′35″E); and Seongbuk-gu, Seoul (37°36′40″N, 127°00′02″E). After collection, samples were immediately transported to the laboratory under refrigerated conditions, and specimen preparation, microscopic observation, and fungal isolation were conducted aseptically within 6 hr to minimize changes in sample condition. Voucher specimens were deposited in the Korea University Mycological Herbarium (KUS-F) (Table 1).

Table 1. Voucher specimen numbers, culture collection information, and NCBI GenBank accession numbers for the *Taphrina* isolates examined in this study

KUS-F voucher no.	Locality	Collection date	KACC accession no.	NCBI GenBank accession no.		
				ITS	D1/D2	*rns*
KUS-F35004	Jeonju-si, Jeollabuk-do	6 May 2021	Not deposited	Not submitted		
KUS-F35005	Osan-si, Gyeonggi-do	13 May 2021	KACC 411353	PZ626205	PZ626210	PZ630116
KUS-F35006	Dongdaemun-gu, Seoul	1 Jun 2021	Not deposited	Not submitted		
KUS-F35007	Wanju-gun, Jeollabuk-do	29 Apr 2024	KACC 411354	PZ626206	PZ626209	PZ630115
KUS-F35008	Jongno-gu, Seoul	28 May 2024	Not deposited	Not submitted		
KUS-F35009	Seongbuk-gu, Seoul	4 Jun 2025	KACC 411352	PZ626208	PZ626211	PZ630117

KUS-F: Korea University Mycological Herbarium; KACC: Korean Agricultural Culture Collection; NCBI: National Center for Biotechnology Information; ITS: Internal transcribed spacer region of the rRNA gene; D1/D2: D1/D2 domains of 26S rRNA gene; *rns*: Mitochondrial small subunit ribosomal RNA gene.

Pure cultures were obtained using a spore-drop isolation method. Approximately 3 mm² sections bearing hymenium tissue were cut from the margins of leaves with a sterile scalpel and affixed to the inner side of a Petri dish lid. Spores were then allowed to fall onto glucose–peptone–yeast extract (GPY) agar (2% glucose, 1% peptone, 0.5% yeast extract, and 2% agar) [18]. The lid was rotated every 2 hr, and the new position of the tissue section was marked to identify the corresponding spore deposition site. After incubation at 21°C for 5 days, individual colonies appearing at the marked sites were transferred to yeast malt (YM) agar using a sterile loop. Samples from each isolate were preserved at −80°C in 20% glycerol, and three representative isolates were deposited in the Korean Agricultural Culture Collection (KACC) (Table 1).

Morphological examination

Morphological characteristics were examined using freshly collected tissues. Fungal structures, including ascogenous cells, asci with stalk cells, ascospores, and blastospores, were characterized under a compound light microscope (Olympus BX53-32XDIC equipped with a DP74 camera, Olympus, Tokyo, Japan). For each morphological feature, at least 50 individual structures were measured.

DNA sequencing and phylogenetic analysis

Genomic DNA was extracted from 7-day-old cultures grown on YM agar using the Quick-DNA Fungal/Bacterial Miniprep Kit (Zymo Research, Irvine, CA, USA). The ITS region, D1/D2 domains of the 26S rRNA gene, and *rns* gene were amplified with the primer pairs ITS1/ITS4, NL1/NL4, and SSU1/SSU5, respectively (Table 2). Polymerase chain reactions were carried out using PCR Master Mix, 2× (Promega, Madison, WI, USA), and the amplified products were sequenced through a DNA sequencing service (Cosmogenetech, Seoul, Korea). The obtained sequences were edited using Chromas version 2.6.6 (Technelysium Pty Ltd., South Brisbane, Australia) and aligned in BioEdit version 7.2.5 [21]. The assembled ITS region, D1/D2 domain, and *rns* gene sequences were deposited in the National Center for Biotechnology Information (NCBI) GenBank database (Table 1). Sequence similarity searches were conducted against the GenBank database using BLAST [22].

For phylogenetic analysis, a total of 60 sequences representing 38 *Taphrina* species were obtained

from the NCBI GenBank and National Agriculture and Food Research Organization (Japan) Genebank databases, with *Protomyces inouyei* (HA 1353) selected as the outgroup [4,8]. The ITS, D1/D2, and *rns* sequences were concatenated in MEGA 11 [23] and aligned using the MAFFT online service version 7.0 [24]. Candidate nucleotide substitution models were evaluated with jModelTest version 2.1.10 [25], and the best-fitting model was chosen based on the Akaike information criterion [26]. A maximum likelihood phylogenetic analysis was conducted using PhyML version 3.0 [27], with branch support assessed using 1,000 bootstrap resamples.

Table 2. Primer pairs used to amplify the ITS, D1/D2, and *rns* regions

Primer	Primer sequence (5′–3′)	Target region	Reference
ITS1	TCCGTAGGTGAACCTGCGG	ITS region (of rDNA)	[19]
ITS4	TCCTCCGCTTATTGATATGC		
NL1	GCATATCAATAAGCGGAGGAAAAG	D1/D2 domain (of LSU rDNA)	[20]
NL4	GGTCCGTGTTTCAAGACGG		
SSU1	GTGCCAGCAGTCGCGGTAATAC	*rns* gene (of mtDNA)	[7]
SSU5	CAGGTTCCCCTACAGTAACTGTATTTCAACTT		

ITS: internal transcribed spacer; rDNA: ribosomal DNA; D1/D2: D1/D2 domains of the 26S rRNA gene; LSU: large subunit; *rns*: mitochondrial small subunit ribosomal RNA gene; mtDNA: mitochondrial DNA.

Physiological characterization

The physiological characteristics of the strains were investigated according to the standard procedures described by Kurtzman et al. [18]. Carbon assimilation was evaluated for 41 carbon sources in 16 × 125 mm test tubes containing 5 mL of liquid medium, and nitrogen assimilation was assessed for 9 nitrogen sources on solid media in 90 × 15 mm Petri dishes. All assays were performed at 21°C, with 21-day incubation periods for carbon assimilation tests and 14-day incubation periods for nitrogen assimilation tests. Urea hydrolysis and tolerance to 0.01% cycloheximide were examined in liquid medium using 16 × 125 mm test tubes. In addition, the diazonium blue B (DBB) color reaction and growth at 20, 25, and 30°C on YM agar were evaluated. Lastly, the production of starch-like polysaccharides was assessed using both liquid and solid media. All tests were carried out independently in triplicate to ensure the reproducibility of the results (Fig. S1).

RESULTS

Disease symptoms

During field surveys conducted across six regions of South Korea, we detected leaf curl symptoms on *Prunus persica* in all six regions beginning in mid-May (Fig. 1A). Symptoms initially appeared as small reddish swellings on young leaves (Fig. 1B). As the disease progressed, the affected tissues became enlarged and thickened, resulting in leaf curl and distortion, with the development of an amphigenous white hymenial layer (Fig. 1C). In advanced stages, the affected tissues turned brown and became necrotic, and in severe cases the symptoms extended over nearly the entire leaf (Fig. 1D).

Morphological characteristics

The sexual state developed on diseased leaves as a hymenial layer (Fig. 1E–G). Ascogenous cells, 10–20 × 6.5–13 μm in size, that developed into immature asci were observed on the epidermal surface (Fig. 1E). As development progressed, a mature naked ascus layer formed on both sides of the infected leaf lesions (Fig. 1F, G). Asci were cylindrical with a rounded apical region, hyaline, and 22–38 × 9–15 μm in size (n = 50) (Fig. 1H). Each ascus contained eight biseriately arranged ascospores, and budding within the ascus was frequently observed (Fig. 1H). Stalk cells were not observed in the present study. Ascospores were hyaline, globose to subglobose, and ovate or obovate, measuring 6–10 × 5–7 μm (n = 50) (Fig. 1I). After 7 days of incubation on YM agar at 21°C, an asexual, blastospore-producing yeast-like state derived from ascospores was observed. Blastospores were subglobose, ovate, or elliptical and reproduced by budding (Fig. 1J). On YM agar, cultures produced yeast-like growth along streaking lines, forming smooth, butyrous colonies with a yellowish-cream to pinkish-cream coloration (Fig. 1K).

Molecular phylogeny

The ITS, D1/D2, and *rns* sequences were identical among all Korean isolates. BLAST searches against the NCBI GenBank database indicated that these isolates' ITS and D1/D2 domain regions shared 100% sequence identity with those of the type strain of *T. deformans*, CBS 356.35^{T}, isolated from *Prunus persica* in the Netherlands (accession no. NR_160071 for ITS and accession no. AF492038 for D1/D2 domain).

For the ML phylogenetic analysis, the final alignment consisted of 60 sequences and 2,315 characters, comprising the concatenated ITS, D1/D2, and *rns* sequences, and the best-fit nucleotide substitution model was GTR+I+G. The phylogeny showed that all *Taphrina deformans* isolates, including the Korean strains, the type strain CBS 356.35^{T}, and additional reference strains (CBS 355.35, NRRL-T470, PYCC 5894, and MAFF 242963), formed a single, well-supported clade (Fig. 2).

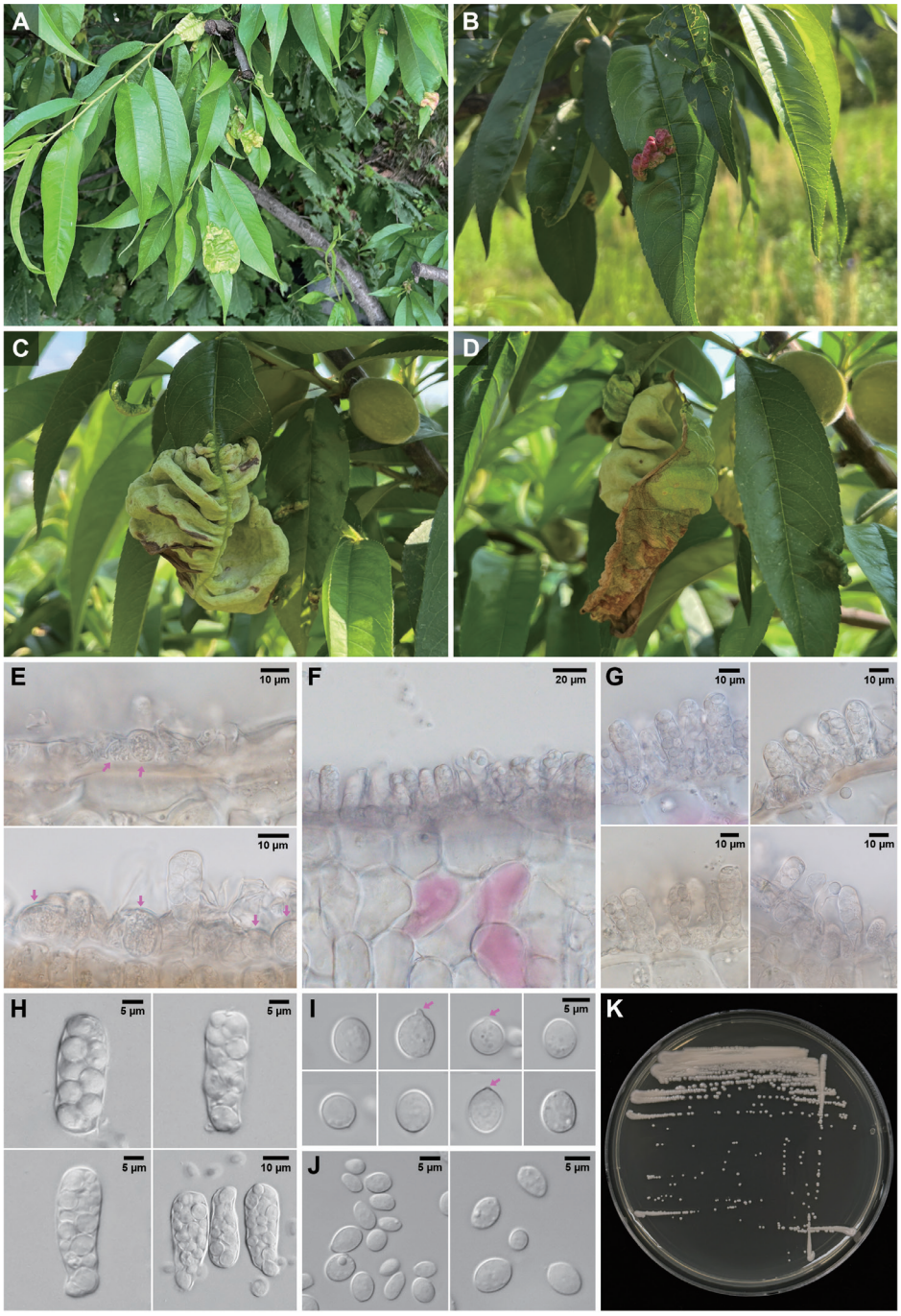

Fig. 1. Images showing the symptomatic features and morphological characteristics of the leaf curl pathogen on *Prunus persica*. A–D: leaf curl symptoms on *P. persica* infected with *T. deformans* in mid-May; E: ascogenous cells observed on the surface of infected leaves (arrows); F and G: cross-sectional views of the naked ascus layer; H: asci; I: ascospores, with budding indicated by arrows; J: blastospores; and K: colonies grown on yeast malt agar at 21℃ for 7 days.

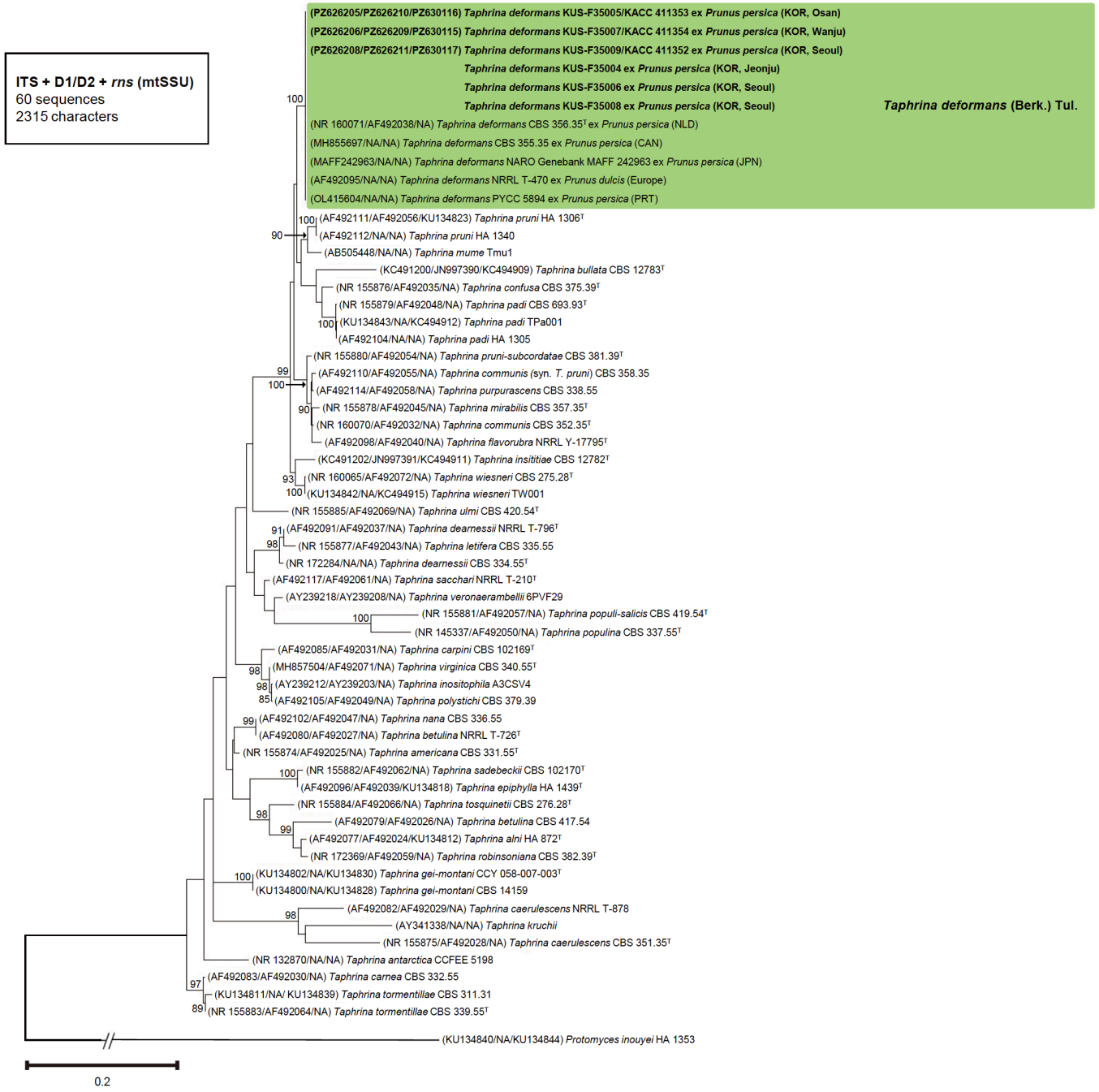

Fig. 2. Phylogenetic tree of *Taphrina deformans* (green box) and related *Taphrina* species, inferred from the concatenated ITS, D1/D2, and *rns* sequences of 38 *Taphrina* species using the maximum likelihood method based on the GTR+I+G nucleotide substitution model in PhyML version 3.0. Bootstrap support values > 70%, obtained from 1,000 replicates, are shown above the corresponding nodes. The isolates obtained in this study are shown in bold, and type strains are indicated by a superscript T. The scale bar represents 0.2 nucleotide substitutions per site, and "NA" indicates that the sequence data were unavailable. ITS: internal transcribed spacer; D1/D2: D1/D2 domains of the 26S rRNA gene; *rns*: mitochondrial small subunit ribosomal RNA gene; GTR+I+G: general time reversible model with a proportion of invariable sites and gamma-distributed rate heterogeneity.

Physiological characterization

Out of 41 tested carbon compounds, 13 were assimilated (+) by all three assessed strains: D-glucose, D-xylose, D-arabinose, sucrose, trehalose, cellobiose, salicin, raffinose, glycerol, xylitol, D-glucitol, D-mannitol, and fructose. The remaining 28 were not (−): D-galactose; L-sorbose; D-glucosamine; D-ribose; L-arabinose; L-rhamnose; maltose; α-methyl-D-glucoside; arbutin; melibiose; lactose; melezitose; inulin; soluble starch; erythritol; ribitol; galactitol; *myo*-inositol; D-glucono-1,5-lactone; D-glucuronate; DL-lactate; succinate; citrate; methanol; ethanol; N-acetyl-D-glucosamine; L-malate; and hexadecane. Out of nine tested nitrogen compounds, three, nitrate (potassium), D-glucosamine, and ammonium sulfate, were assimilated (+), whereas nitrite (sodium), ethylamine, L-lysine, cadaverine, creatinine, and N-acetyl-D-glucosamine were not (−). No growth was observed in the vitamin-free medium or the medium containing 0.01% cycloheximide (−), and the DBB reaction was negative (−). In temperature growth tests, growth occurred at 20°C and 25°C but not at 30°C (Table 3).

Table 3. Comparison of physiological characteristics between Korean isolates and reference strains of *Taphrina deformans*

Physiological characteristic - C: Carbon source - N: Nitrogen source	Previous study [4]	This study		
	Taphrina deformans	*Taphrina deformans* (Korean isolates)		
		KACC 411352	KACC 411353	KACC 411354
C1 D-Glucose	+	+	+	+
C2 D-Galactose	−	−	−	−
C3 L-Sorbose	v	−	−	−
C4 D-Glucosamine	−	−	−	−
C5 D-Ribose	−	−	−	−
C6 D-Xylose	+	+	+	+
C7 L-Arabinose	−	−	−	−
C8 D-Arabinose	−	+	+	+
C9 L-Rhamnose	−	−	−	−
C10 Sucrose	v	+	+	+
C11 Maltose	−	−	−	−
C12 Trehalose	v	+	+	+
C13 α-methyl-D-glucoside	−	−	−	−
C14 Cellobiose	+	+	+	+
C15 Salicin	+	+	+	+
C16 Arbutin	nd	−	−	−
C17 Melibiose	−	−	−	−
C18 Lactose	−	−	−	−
C19 Raffinose	−	+	+	+
C20 Melezitose	−	−	−	−
C21 Inulin	−	−	−	−
C22 Soluble starch	v	−	−	−
C23 Glycerol	v	+	+	+
C24 Erythritol	−	−	−	−
C25 Ribitol	−	−	−	−
C26 Xylitol	v	+	+	+
C27 D-Glucitol	+	+	+	+
C28 D-Mannitol	+	+	+	+
C29 Galactitol	−	−	−	−
C30 *myo*-Inositol	−	−	−	−

Table 3. Comparison of physiological characteristics between Korean isolates and reference strains of *Taphrina deformans*(continued)

Physiological characteristic - C: Carbon source - N: Nitrogen source	Previous study [4]	This study		
	Taphrina deformans	*Taphrina deformans* (Korean isolates)		
		KACC 411352	KACC 411353	KACC 411354
C31 D-Glucono-1,5-lactone	v	−	−	−
C32 D-Glucuronate	−	−	−	−
C33 DL-Lactate	−	−	−	−
C34 Succinate	v	−	−	−
C35 Citrate	−	−	−	−
C36 Methanol	−	−	−	−
C37 Ethanol	v	−	−	−
C38 *N*-Acetyl-D-glucosamine	nd	−	−	−
C39 L-Malate	v	−	−	−
C40 Fructose	nd	+	+	+
C41 Hexadecane	nd	−	−	−
N1 Nitrate (Potassium)	v	+	+	+
N2 Nitrite (Sodium)	v	−	−	−
N3 Ethylamine	−	−	−	−
N4 L-Lysine	−	−	−	−
N5 Cadaverine	v	−	−	−
N7 Creatinine	nd	−	−	−
N8 D-Glucosamine	−	+	+	+
N9 *N*-Acetyl-D-glucosamine	nd	−	−	−
NP Ammonium sulfate	+	+	+	+
0.01% Cycloheximide resistance	−	−	−	−
Starch formation	v	+	+	+
Urea hydrolysis	+	+	+	+
DBB reaction	−	−	−	−
Vitamin-free medium	−/w	−	−	−
20℃	+	+	+	+
25℃	+	+	+	+
30℃	−	−	−	−

Physiological data for *T. deformans* from a previous study [4] represent the combined results from six strains, including three isolates from peach (CBS 356.35^{T}, NRRL T-857, and PYCC 5894) and three isolates from almond (PYCC 5908, PYCC 5909, and PYCC 5910) [4].
KACC: Korean Agricultural Culture Collection; DBB: diazonium blue B.
Growth reaction symbols/abbreviations include + (positive), − (negative), w (weak), v (variable), and nd (no data).

DISCUSSION

To date, there have been 12 records of the genus *Taphrina* in Korea, comprising eight species reported from nine host tree species (Table 4). However, most of these records are from specimens identified primarily based on disease symptoms and information from early international literature, particularly reports from Japan, without comprehensive analyses of the morphological, molecular, or physiological characteristics of the causal pathogens. Among the 12 *Taphrina* records in Korea, six originated from surveys conducted during the Japanese colonial period, including the record of *T. deformans* associated with leaf curl on *Prunus persica*. A *Taphrina* species associated with plum pockets was recently identified based on ITS and SSU sequences [28]. However, its identity requires further confirmation through molecular

and physiological comparisons including additional isolates associated with the disease in other regions. Consequently, for most *Taphrina* species in Korea, reliable information on their occurrence, taxonomy, and biological characteristics is still needed.

Table 4. *Taphrina* species reported in Korea and their molecular characterization status.

Pathogen	Disease	Host	Year	Genotyped
Taphrina mume	Leaf curl	*Prunus mume*	1928	X
Taphrina wiesneri	Witches' broom	*Prunus jamasakura*	1928	X
Taphrina deformans	Leaf curl	*Prunus persica*	1928	X
Taphrina nikkoensis	Leaf spot	*Acer triflorum*	1943	X
Taphrina mume	Leaf curl	*Prunus armeniaca*	1928	X
Taphrina caerulescens	Leaf blister	*Quercus mongolica*	1943	X
Taphrina pruni	Plum pocket	*Prunus avium*	1961	X
Taphrina alni-incanae	Not assigned	*Alnus japonica*	1986	X
Taphrina japonica	Witches' broom	*Alnus japonica*	1940	X
Taphrina deformans	Plum pocket	*Prunus salicina*	2020	O
Taphrina pruni	Plum pocket	*Prunus salicina*	1928	X
Taphrina caerulescens	Leaf blister	*Quercus* spp.	1943	X

This table was compiled based on the List of Plant Diseases in Korea [10].
X: not genotyped; O: genotyped.

The symptomatic features of peach leaf curl we observed in Korea are consistent with those reported for *T. deformans* worldwide [1–4]. The morphological characteristics of the Korean isolates also agree with the descriptions of *T. deformans* provided by Mix [2], particularly in the sizes of asci (17–56 × 7–15 μm) and ascospores (3–7 × 3–7 μm), the amphigenous development of the ascus layer, and the frequent budding of ascospores within the asci. Furthermore, the colony morphologies, yeast-like colonies with a yellowish-cream to pinkish-cream coloration, were consistent with those detailed in previous descriptions of *T. deformans* [4]. Based on disease symptoms, morphological characteristics, and molecular phylogenetic analyses, the leaf curl pathogen associated with *P. persica* in Korea was identified as *T. deformans*. However, stalk cells supporting the asci, which have been reported in previous descriptions of *T. deformans* [2,4], were not observed in the Korean isolates examined here. Interestingly, Campbell had reported *T. deformans* asci lacking stalk cells in the earlier description [29], but Mix subsequently confirmed typical stalk cells in specimens collected from the same host tree [2]. For some *Taphrina* species, a stalk cell (basal cell) is later cut off from the ascus proper and is thus absent in the mature ascus [2]. Therefore, the absence of stalk cells in the present isolates may reflect the developmental stage of the asci, suggesting that stalk cells are observable during a specific stage of ascus development.

A previous physiological study of *T. deformans* was based on six strains, including CBS 356.35^{T}, NRRL T-857, and PYCC 5894 isolated from peach (*Prunus persica*), as well as PYCC 5908, PYCC 5909, and PYCC 5910 isolated from almond (*P. dulcis*) (Table 3) [4]. However, many physiological traits were reported as variable (v), limiting our ability to make direct comparisons among individual isolates. In contrast, the three Korean isolates examined in the present study (KACC 411352, KACC 411353, and KACC 411354) exhibited identical physiological characteristics, showing consistently positive reactions

(+) for sucrose, trehalose, glycerol, xylitol, nitrate (potassium), and starch formation, and consistently negative reactions (−) for L-sorbose, soluble starch, D-glucono-1,5-lactone, succinate, ethanol, L-malate, nitrite (sodium), and cadaverine, all of which had previously been reported as variable (v). This consistent physiological profile for *T. deformans* strains isolated from *Prunus persica* in Korea will serve as a valuable reference for future studies investigating intraspecific physiological variation across different hosts and geographic regions.

The present study confirmed that the Korean peach leaf curl pathogen is *Taphrina deformans* based on morphological characteristics and molecular phylogenetic analyses. Comprehensive morphological and physiological profiles and molecular characteristics were documented for the Korean isolates, together with detailed descriptions of disease symptoms. These findings provide a valuable reference for future studies on the taxonomy, diversity, and epidemiology of *Taphrina* species in Korea.

SUPPLEMENTARY MATERIAL

The following supplementary material is available on the journal's website:

• Supplementary Fig. S1. Example images from the physiological tests of Korean *Taphrina deformans* isolates KACC 411352, KACC 411353, and KACC 411354.

CONFLICT OF INTEREST

The authors declare that there are no conflicts of interest.

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