







RESEARCH NOTE

Characterization of *Cercospora flagellaris* sensu stricto on its Original Host, *Phytolacca americana*, Based on Korean Collections

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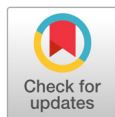
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ABSTRACT

Cercospora cf. *flagellaris* is one of the unresolved species complexes within the genus *Cercospora*. Despite recent advances in molecular approaches for species delimitation using multigene sequence analysis, the identity of *C. flagellaris* remains unclear. As new records are accumulated, the complexity of this species group increases, encompassing hosts from a wide range of plant families. *Phytolacca americana*, a species native to North America and later introduced to East Asia, was the original host of this fungus. Since 1991, leaf spot diseases caused by *C. flagellaris* have been consistently reported in Korea. In this study, we summarized all isolates identified as *C. flagellaris* from *P. americana* in Korea to date, to infer their morphological and molecular phylogenetic identities and to understand the true identity of this fungus. All isolates were morphologically and molecularly examined, illustrated, and their phylogenetic placement was demonstrated in a tree inferred from multigene sequence analyses.

Keywords: Leaf spot disease, Multigene analysis, Mycosphaerellaceae, Species complex



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The genus *Cercospora* Fresen. ex Fuckel (Mycosphaerellaceae) contains numerous economically and ecologically important plant pathogenic fungi that cause leaf spot disease on various plants, including angiosperms, gymnosperms, and ferns [1–5]. The current concept of the genus was established in 2013, proposing the use of multilocus sequence analysis for species delimitation within the genus [4]. Since then, several protein-coding genes, such as actin (*actA*), β -tubulin (*tub2*), calmodulin (*cmdA*), glyceraldehyde-3-phosphate dehydrogenase (*gapdh*), histone H3 (*his3*), translation elongation factor 1- α (*tef1*), and RNA polymerase II second largest subunit (*rpb2*), along with the internal transcribed spacer (ITS) region of the rDNA, have been investigated [6].

Among the poorly known and fastidious species of *Cercospora* and cercosporoid fungi, *C. flagellaris* Ellis & G. Martin remains unresolved, and its taxonomy has become increasingly complex with the emergence

of new reports globally. This fungus was first described in 1882 as a leaf spot pathogen of *Phytolacca decandra* L. (currently *Phytolacca americana* L.) in North America, which is the native range of the host [7]. Numerous isolates that phylogenetically cluster within the *flagellaris* group have been designated as *confer* (cf.) *flagellaris* owing to several uncertainties. Bakshi et al. [6] noted that the cf. *flagellaris* group can be divided into three distinct clades based on analyses of eight gene loci in molecular phylogenetics. However, this remains insufficient for species delimitation because of overlaps in morphology and host ranges among these clades within the group. Currently, the number of *C. cf. flagellaris* isolates from various hosts continues to expand, encompassing plants from diverse families [4,8,9]. However, *C. flagellaris* s. str. on *Phytolacca* spp. has been reported in North America and East Asia, with the exception of Ethiopia [10,11]. To date, only three isolates of *C. flagellaris* have been analyzed using multigene sequence data by Groenewald et al. [4], all of which originated from Korean samples of *P. americana*.

In Korea, this fungus was first reported on *Phytolacca esculenta* Van Houtte [12], followed by a report on *P. americana* [13]. The authors noted abundant hypophyllous fructification of the fungus on some samples that co-occurred with epiphyllous fructification. They compared their findings with Chupp's description of American specimens, which were characterized by epiphyllous caespituli.

The first step in resolving the complexity of the *flagellaris* group was to elucidate the morphology and molecular phylogeny of true *C. flagellaris* on its original host. Therefore, this study aimed to reassess and integrate previous records with newly obtained collections of *C. flagellaris* on *P. americana* in Korea. By combining morphological examinations with multigene phylogenetic analyses, this study sought to clarify the identity of true *C. flagellaris* on its original host.

The samples used in this study are listed in Table 1, along with their collection dates, localities, strains, and sequence deposition IDs in the relevant databases. All collected samples were preserved at the Herbaria of Korea University (labeled as KUS-F, Seoul, Korea) and Jeonbuk National University (as JBNU-F, Jeonju, Korea). For morphological characterization of *C. flagellaris*, fungal structures were examined and photographed using a Zeiss AX10 microscope equipped with an AxioCam MRc5 camera (Carl Zeiss, Oberkochen, Germany). The size of each diagnostic feature was determined based on at least 20–30 measurements. To obtain single-spore isolates, conidia collected from young lesions were mounted on a drop of sterile water and streaked onto 2% water agar (WA; Junsei, Tokyo, Japan) plates supplemented with 100 mg/L streptomycin sulfate. The plates were incubated at 25°C. After 2 days, the germinating conidia were transferred to 2% potato dextrose agar (PDA; Difco, Detroit, MI, USA) plates to obtain a pure culture. Colony color was determined using Raynar color charts [14]. The obtained strains were deposited in the Korean Agricultural Culture Collection (KACC; Wanju, Korea).

All examined specimens were consistent with the leaf symptoms and fungal morphology. Initial lesions on the affected leaves were circular to irregular, brown to pale brown, and more or less sunken in the middle. As the spots enlarged with narrow borders, they became tan, creamy white, and even grayish with heavy fructification. Discrete lesions were mainly less than 6 mm in diameter, occasionally confluent, and cottony with numerous conidiophores and conidia (Fig. 1A, B). Stromata were small to medium, poorly developed,

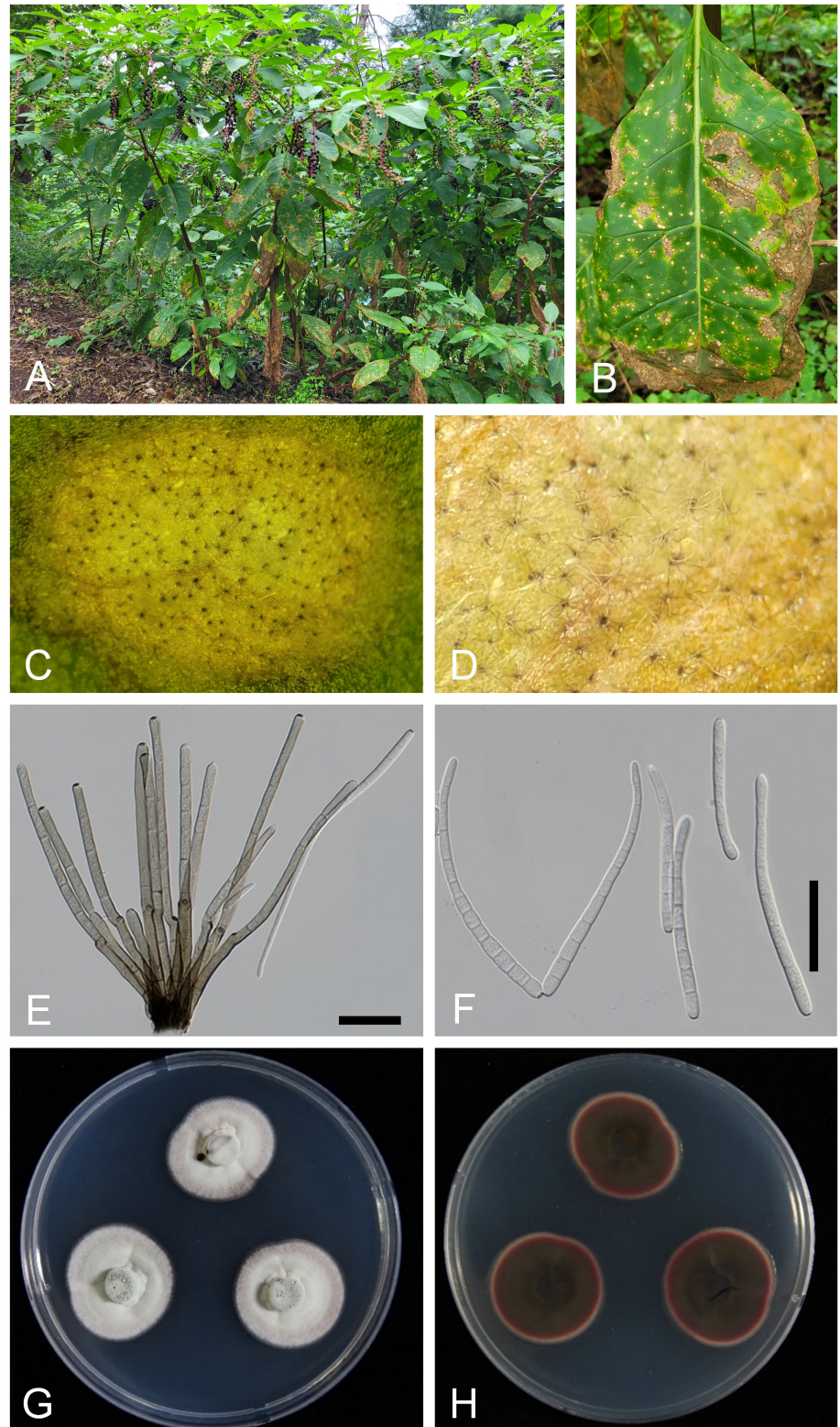


Fig. 1. *Cercospora flagellaris* s. str. on *Phytolacca americana* (micrographs were obtained from the sample JBNU-F0463). A: Infected plants showing leaf spots in the field; B: Young and mature leaf spots coalescing into necrotic lesions on the affected leaf; C: Close-up view of the leaf spot; D: Close-up view of fructification under a stereo microscope; E: Conidiophore; F: Conidia; G: One-week-old colonies grown on potato dextrose agar (PDA) at 25°C (obverse surface); H: Reverse surface of the same colony. Scale bars = 30 μ m.

sometimes only occupying stomatal openings, brown to dark brown, 10–24 μm in diameter, and composed of several dark brown cells (Fig. 1C, D). Conidiophores were 8–16 in a divergent fascicle, emerging through stomatal openings in the early stage or from the cuticle of the upper leaf surface in the later stages of disease development. They were usually not branched, mildly or abruptly geniculated 1–4 times, olivaceous brown throughout or paler upwards, variable in length, $30\text{--}265 \times 3\text{--}5 \mu\text{m}$, and 0–5-septate (Fig. 1E). Conidial scars on conidiophores were conspicuous, apical, or at the position of geniculations, and 3–5 μm in diameter. Conidiogenesis was holoblastic, with terminal conidiogenous cells. Conidia were solitary, acicular-filiform, straight to mildly curved, hyaline, 4–12-septate, $40\text{--}160 \times 3.0\text{--}4.5 \mu\text{m}$, with conspicuously thickened and darkened hila, base truncate to subtruncate, and apex obtuse (Fig. 1F).

Two-week-old colonies grown on PDA at 25°C were 35–43 mm in diameter, with entire edge, the obverse surface was radially striate and cottony white in color, with a slightly pinkish margin. The reverse of the colonies was bloody red, and pinkish near the margin (Fig. 1G, H). The aforementioned morphological characteristics align with those of *C. flagellaris* reported by Chupp from North American samples [7] and Katsuki and Kobayashi from Japanese materials [15].

Genomic DNA was extracted from mycelia obtained from 2- or 3-week-old colonies using Maglisto™ 5M kits (Bioneer, Daejeon, Korea) according to the manufacturer's guidelines. Nucleotide sequences of the ITS region and protein-coding genes such as *actA*, *cmdA*, *tef1*, and *his3* were amplified and sequenced using ITS5/ITS4, ACT-512F/ACT-783R, CAL-228F/CAL-737R, EF1-728F/EF1-986R, and CylH3F/CylH3R, respectively [16–18]. The PCR products were purified and sequenced using the same primers from Bioneer Inc. (Daejeon, Korea). The obtained forward and reverse sequences were inspected using BioEdit 7.2.5 [19], then assembled in MEGA 11 [20], and concatenated data were deposited in GenBank (Table 1).

Table 1. Information on Korean specimens of *Cercospora flagellaris* on *Phytolacca americana* used in this study

Voucher specimen number	Collection date	Collection place	KACC accession number	GenBank accession number				
				ITS	<i>actA</i>	<i>cmdA</i>	<i>his3</i>	<i>tef1</i>
KUS-F22958	2 Oct 2007	Suwon	43108	PX022570	PX072443	PX072447	PX072453	PX072459
KUS-F33049	13 Jul 2022	Wanju	410484	PX022571	PX072444	PX072450	PX072454	PX072460
KUS-F33087	20 Jul 2022	Imsil	410485	PX022572	PX072445	PX072451	PX072455	PX072461
KUS-F33169	4 Sep 2022	Jinan	410486	PX022573	PX072446	PX072452	PX072456	PX072462
JBNU-F0285	2 Nov 2023	Wanju	-	PX022574	PX072441	PX072448	PX072457	PX072463
JBNU-F0463	27 Aug 2024	Buan	-	PX022575	PX072442	PX072449	PX072458	PX072464

KACC: Korean Agricultural Culture Collection, Rural Development Administration; ITS: internal transcribed spacer; *actA*: actin; *cmdA*: calmodulin; *his3*: histone H3; *tef1*: translation elongation factor 1-alpha.

Multigene phylogenetic analyses were performed using a combined dataset of five genes. In total, 50 sequences of isolates were used, of which six were obtained in this study. *Septoria provencialis* (CBS 118910) was designated as an outgroup [9]. Information on the sequences used in the phylogenetic analyses is provided in Supplementary Table. Each gene was first aligned individually in MEGA 11 using the MUSCLE algorithm [20] and then concatenated into a single multilocus dataset of ITS+*tef1*+*act*+*cmdA*+*his3* using SequenceMatrix software [21]. Character set partition was as follows: ITS 1–480, *tef1* 481–789, *actA* 790–1,003, *cmdA* 1,004–1,299, and *his3* 1,300–1,677 bp. The final data matrix

consisted of 50 sequences and 1,677 characters. Character-based methods, maximum parsimony (MP), and maximum likelihood (ML) were used to generate phylogenetic trees in PAUP*4.0a using a heuristic search option and in raxmlGUI 2.0.14 using GTR+G [22,23]. Bootstrap analyses were performed with 1,000 replicates to evaluate the robustness of the internal branches [24].

The nucleotide sequences of ITS, *actA*, *cmdA*, *his3*, and *tef1* were determined for six *Cercospora* strains isolated from *P. americana* in this study. We manually compared the genetic identities of these isolates with each other and with three previously reported *Phytolacca*-derived isolates (CPC 10684, CPC 10124, and CBS 132674). The ITS, *cmdA*, *his3*, and *tef1* sequences were identical among all six strains, whereas the ITS and *his3* sequences were identical to those of the three previously reported isolates. However, a single nucleotide polymorphism (SNP) was detected in the *actA* gene (226 bp), where adenine (A) was replaced by guanine (G) in KACC 43108 and 410484, distinguishing these two isolates from the remaining four and three isolates. A BLASTn search showed 100% identity to *C. cf. flagellaris* for ITS (KT193679), *actA* (DQ835121, JX143112, JX143123), *cmdA* (OQ773733, OQ773748), *his3* (JX142625, JX142626, DQ835175), and *tef1* (JX143360, JX143362).

The tree topologies generated by the MP and ML analyses were consistent. In total, 34 trees were retained from parsimony analysis. All nucleotide substitutions were equally weighted and unordered, and gaps were treated as missing data. Of the 1,677 total characters, 159 (9.4%) were variable and parsimony-uninformative, and 238 (14.1%) were informative for parsimony analysis. Tree scores were calculated, including tree length (TL = 774), consistency index (CI = 0.6589), retention index (RI = 0.7805), and rescaled consistency index (RC = 0.5143). Phylogenetic analysis revealed that all isolates obtained from *P. americana*, including six newly generated and three previously deposited sequences (CBS 132674, CPC 10124, and CPC 10684), formed a well-supported monophyletic subclade within the broader *C. cf. flagellaris* lineage (Fig. 2). This subclade was strongly supported (79/82% BS), indicating that it was a genetically coherent group. In contrast, other isolates identified as *C. cf. flagellaris*, which were derived from diverse host plants, such as *Amaranthus hybridus*, *Cichorium intybus*, *Sigesbeckia pubescens*, were distributed across several more heterogeneous and weakly supported branches. This branching pattern suggests that *C. cf. flagellaris* is a species complex with considerable host-associated divergences. The consistent clustering of *Phytolacca*-derived isolates into distinct and well-supported lineages supports the hypothesis that these isolates represent *C. flagellaris* sensu stricto (s. str.).

P. americana (Phytolaccaceae), commonly known as the American pokeweed, is native to North America. It is now widely distributed in North America, South America, Africa, and several countries in Asia [25]. This plant was introduced to Korea in the 1950s and is currently distributed across various locations on the peninsula, including areas near factories and vacant lots [26]. To date, *C. flagellaris* s. str. is native to North America and has become invasive in Japan, Korea [12,13,15,27], and Taiwan [28]. Phylogenetic analysis based on multiple genes is required for this fungus from American samples to prove the true identity of *C. flagellaris*. As this species was originally described as a leaf spot fungus on *P. americana*, the concept of *C. flagellaris* should be limited to isolates obtained from *Phytolacca* species. Therefore, we propose that *C. flagellaris* s. str. as a standard for the isolates. This is the first comprehensive documentation of *C. flagellaris* on *P. americana* in Korea.

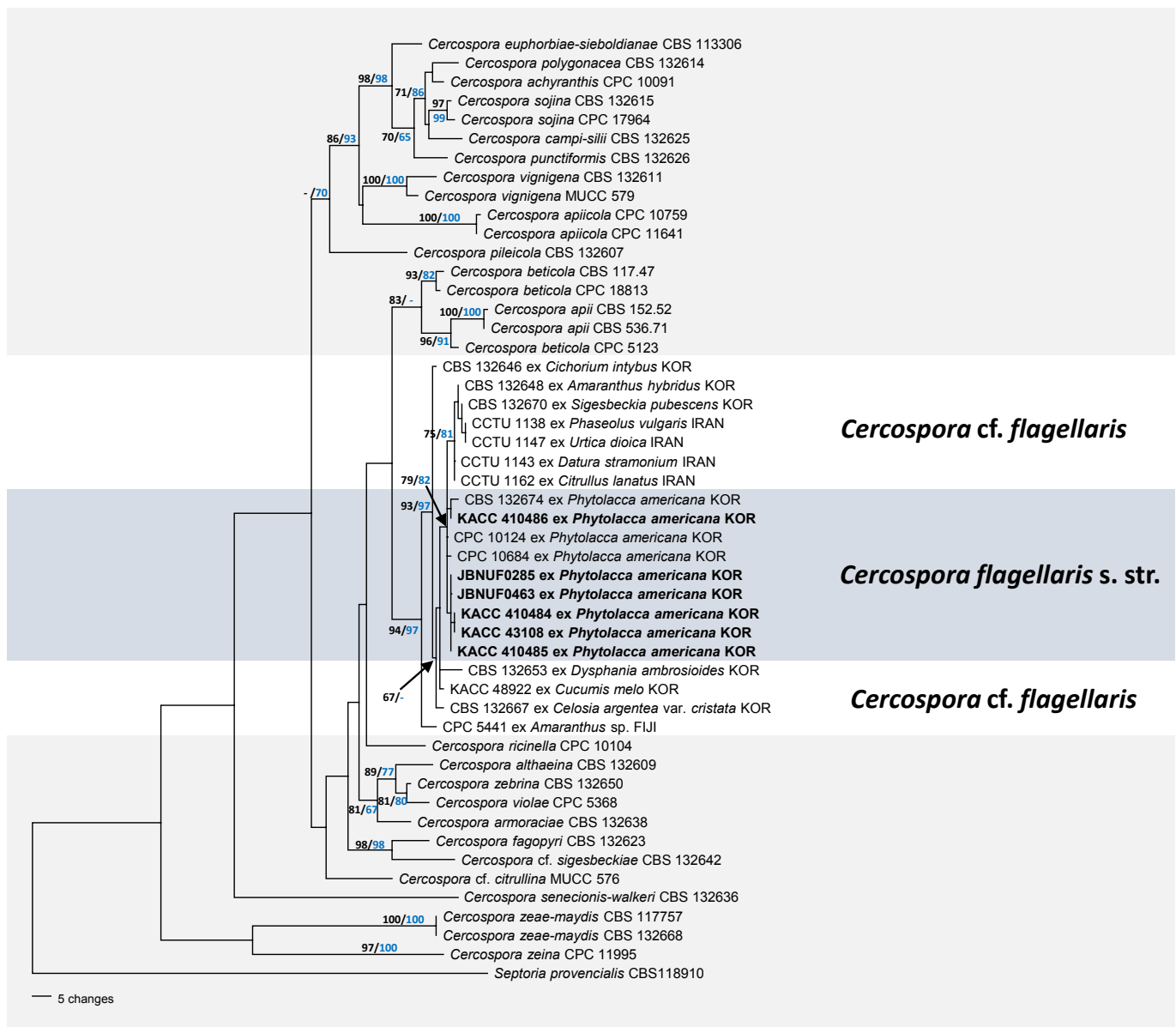


Fig. 2. Parsimonious tree of *Cercospora* highlighting *C. flagellaris*. The tree was generated from a combined multigene dataset of ITS + *tef1* + *actA* + *cmdA* + *his3*, comprising 50 sequences and 1,677 characters. All isolates obtained in this study are indicated in bold. The branching patterns and topologies of the trees from the maximum parsimony (MP) and maximum likelihood (ML) analyses were consistent. Bootstrap values (>70%) obtained using MP (black) and ML (blue) are displayed on the branch. ITS: internal transcribed spacer; *actA*: actin; *cmdA*: calmodulin; *his3*: histone H3; *tef1*: translation elongation factor 1-alpha.

CONFLICT OF INTEREST

No potential conflict of interest was reported by the author(s).

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Supplementary table. Information on sequences derived from various *Cercospora* isolates used in the phylogenetic analyses.

Fungus	Isolate ID	Host	Country	GenBank ID number					Ref.
				ITS	actA	cmdA	his3	tefl	
<i>C. achyranthis</i>	CPC 10091	<i>Achyranthes japonica</i>	Korea	JX143524	JX143032	JX142786	JX142540	JX143278	[4]
<i>C. althaeina</i>	CBS 132609	<i>Althaea rosea</i>	Korea	JX143529	JX143037	JX142791	JX142545	JX143283	[4]
<i>C. apii</i>	CBS 536.71	<i>Apium graveolens</i>	Romania	AY752133	AY752194	AY752225	AY752256	AY752166	[4]
	CBS 152.52	<i>Beta vulgaris</i>	Netherlands	AY840515	AY840446	AY840413	AY840380	AY840482	[4]
<i>C. apiicola</i>	CPC 11641	<i>Apium</i> sp.	Greece	DQ233340	DQ233392	DQ233418	DQ233440	DQ233366	[4]
	CPC 10759	<i>Apium graveolens</i>	Korea	AY840544	AY840475	AY840442	AY840409	AY840511	[4]
<i>C. amoraciae</i>	CBS 132638	<i>Barbarea orthoceras</i>	Korea	JX143542	JX143050	JX142804	JX142558	JX143296	[4]
<i>C. beticola</i>	CBS 117.47	<i>Beta vulgaris</i>	Czech Republic	DQ233322	DQ233374	DQ233400	DQ233426	DQ233348	[4]
	CPC 18813	<i>Beta vulgaris</i>	USA	JX143556	JX143064	JX142818	JX142572	JX143310	[4]
	CPC 5123	<i>Apium graveolens</i>	New Zealand	DQ233327	DQ233379	AY752226	AY752257	DQ233353	[4]
<i>C. campi-silii</i>	CBS 132625	<i>Impatiens noli-tangere</i>	Korea	JX143561	JX143069	JX142823	JX142577	JX143315	[4]
<i>C. cf. citrulina</i>	MUCC 576	<i>Citrullus lanatus</i>	Japan	JX143579	JX143091	JX142845	JX142599	JX143337	[4]
<i>C. euphorbiae-sieboldianae</i>	CBS 113306	<i>Euphorbia sieboldiana</i>	Korea	JX143593	JX143105	JX142859	JX142613	JX143351	[4]
<i>C. fagopyri</i>	CBS 132623	<i>Fagopyrum esculentum</i>	Korea	NR_147263	JX143106	JX142860	JX142614	JX143352	[4]
<i>C. flagellaris</i> s.str.	CPC 10684	<i>Phytolacca americana</i>	Korea	JX143610	JX143123	JX142877	JX142631	JX143369	[4]
	CPC 10124	<i>P. americana</i>	Korea	JX143608	JX143120	JX142874	JX142628	JX143366	[4]
	CBS 132674	<i>P. americana</i>	Korea	JX143606	JX143118	JX142872	JX142626	JX143364	[4]
<i>C. cf. flagellaris</i>	CPC 5441	<i>Amaranthus</i> sp.	Fiji	JX143611	JX143124	JX142878	JX142632	JX143370	[4]
	CBS 132648	<i>Amaranthus hybridus</i>	Korea	JX143602	JX143114	JX142868	JX142622	JX143360	[4]
	CBS 132667	<i>Celosia argentea</i> var. <i>cristata</i>	Korea	JX143604	JX143116	JX142870	JX142624	JX143362	[4]
<i>C. cf. flagellaris</i>	CBS 132646	<i>Cichorium intybus</i>	Korea	JX143601	JX143113	JX142867	JX142621	JX143359	[4]
	CCTU 1162	<i>Citrullus lanatus</i>	Iran	KJ886496	KJ886013	KJ885852	KJ886174	KJ886335	[8]
	KACC 48922	<i>Cucumis melo</i>	Korea	MN945227	MN945229	MN945230	MN945231	MN945228	[20]
	CCTU 1143	<i>Datura stramonium</i>	Iran	KJ886484	KJ886001	KJ885840	KJ886162	KJ886323	[8]
	CBS 132653	<i>Dysphania ambrosioides</i>	Korea	JX143603	JX143115	JX142869	JX142623	JX143361	[4]
	CCTU 1138	<i>Phaseolus vulgaris</i>	Iran	KJ886479	KJ885996	KJ885835	KJ886157	KJ886318	[8]
	CBS 132670	<i>Sigesbeckia pubescens</i>	Korea	JX143605	JX143117	JX142871	JX142625	JX143363	[4]
	CCTU 1147	<i>Urtica dioica</i>	Iran	KJ886486	KJ886003	KJ885842	KJ886164	KJ886325	[8]
	CBS 132607	<i>Pilea pumila</i>	Korea	JX143634	JX143147	JX142901	JX142655	JX143393	[4]
	CBS 132614	<i>Persicaria longiseta</i>	Korea	JX143637	JX143150	JX142904	JX142658	JX143396	[4]
<i>C. polygonacea</i>	CBS 132626	<i>Cynanchum wilfordii</i>	Korea	JX143638	JX143151	JX142905	JX142659	JX143397	[4]
<i>C. punctiformis</i>	CPC 10104	<i>Ricinus communis</i>	Korea	JX143647	JX143160	JX142914	JX142668	JX143406	[4]
<i>C. ricinella</i>	CBS 132636	<i>Senecio walkeri</i>	Laos	JX143649	JX143162	JX142916	JX142670	JX143408	[4]
<i>C. senecionis-walkeri</i>	CBS 132642	<i>Pilea pumila</i>	Korea	JX143654	JX143167	JX142921	JX142675	JX143413	[4]
<i>C. cf. sigesbeckiae</i>	CBS 132615	<i>Glycine soja</i>	Korea	JX143659	JX143173	JX142927	JX142681	JX143419	[4]
	CPC 17964	<i>Glycine max</i>	Argentina	JX143662	JX143176	JX142930	JX142684	JX143422	[4]
<i>C. vignigena</i>	CBS 132611	<i>Vigna unguiculata</i>	Korea	JX143734	JX143247	JX143001	JX142755	JX143493	[4]
	MUCC 579	<i>Vigna unguiculata</i>	Japan	JX143736	JX143249	JX143003	JX142757	JX143495	[4]
<i>C. zebrina</i>	CBS 132650	<i>Trifolium repens</i>	Korea	JX143751	JX143267	JX143021	JX142775	JX143513	[4]
<i>C. zea-maydis</i>	CBS 117757	<i>Zea mays</i>	USA	DQ185074	DQ185098	DQ185110	DQ185122	DQ185086	[4]
	CBS 132668	<i>Zea mays</i>	China	JX143742	JX143255	JX143009	JX142763	JX143501	[4]
<i>C. zeina</i>	CPC 11995	<i>Zea mays</i>	South Africa	DQ185081	DQ185105	DQ185117	DQ185129	DQ185093	[4]
<i>C. violae</i>	CPC 5368	<i>Viola odorata</i>	New Zealand	JX143738	JX143251	JX143005	JX142759	JX143497	[4]
<i>Septoria provencialis</i>	CBS 118910	<i>Eucalyptus</i> sp.	France	DQ303096	JX143276	JX143030	JX142784	JX143522	[20]

ITS: internal transcribed spacer; *actA*: actin; *cmdA*: calmodulin; *his3*: histone H3; *tefl*: translation elongation factor 1-alpha.