

Short Article

Oomycetes associated with cucurbit rhizospheres in Iran: A new record of *Pythium tardicrescens*

Fatemeh Salmaninezhad¹, Pouria Sekandarpour¹, Reza Mostowfizadeh-Ghalemfarsa¹

Department of Plant Protection, School of Agriculture, Shiraz University, Shiraz, Iran

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ABSTRACT

Cucurbits are widely cultivated in Iran, particularly under intensive greenhouse production, where soilborne oomycetes may contribute to root and crown diseases. During a survey of cucurbit production systems in Fars Province in 2025, symptomatic root and crown tissues, rhizosphere soils, plant debris, and irrigation water were collected from cucumber, cantaloupe, muskmelon, squash, and watermelon. Oomycetes were isolated using selective media and baiting methods, and representative isolates were characterized based on cultural and morphological features, cardinal temperatures, pathogenicity assays, and molecular phylogenetic analyses. Among recovered oomycete isolates, seven were identified as *Phytophthora inundata*, *Phytophthora litorale*, and *Pythium tardicrescens*. Molecular analyses confirmed their placement in Clade 6 of *Phytophthora*, Clade 1 of *Phytophthora*, and Clade B of *Pythium sensu stricto*, respectively. Five isolates of *P. tardicrescens* were recovered from diseased squash rhizosphere soil, representing the first record of this species from Iran. The species was characterized by slow radial growth, delayed formation of reproductive structures, filamentous to lobate sporangia, globose terminal oogonia, monoclinal or paragynous antheridia, and aplerotic zoospores. A single isolate of *Ph. inundata* was recovered from cucumber rhizosphere soil, representing the first association of this species with cucumber worldwide. *Phytophthora litorale* was also recovered from cucumber rhizosphere soil. None of the isolates caused symptoms in cucurbit seedlings tested under the experimental conditions used. These findings document *Py. tardicrescens* in Iran for the first time and a new cucumber association for *Ph. inundata* and highlight the need for broader ecological and pathogenicity studies to clarify their roles in cucurbit production systems.

KEYWORDS

Cucurbitaceae, Oomycota, Pathogenicity, Phylogeny, Taxonomy.

INTRODUCTION

Oomycetes inhabiting crop rhizospheres are ecologically significant components of belowground communities, where they interact with roots, organic substrates, and other microorganisms (Pérez-Sierra et al. 2022). In cucurbit production systems, these organisms may function as latent or active pathogens, transient colonizers, or members of the broader rhizosphere microbiome (Hatami et al. 2013, Parkunan and Ji 2013). Documenting their occurrence is therefore important for understanding plant health dynamics, improving disease surveillance, and strengthening agricultural biosecurity in intensively cultivated soils.

Phytophthora inundata Brasier, Sánch. Hern. & S.A. Kirk is distributed mainly in Europe, but it has also been reported from India, Iran, Australia, South America, and North America, where it infects the roots and collars of trees, shrubs, alfalfa, olive, willow, and grapevine in wet or flooded soils (Brasier and Sanchez-Hernandez 2003, Abad et al. 2023a). *Phytophthora litorale* (Nechw.) Abad, de Cock, K. Bala, Robideau, A.M. Lodhi & Lévesque has been reported as a plant-associated oomycete and is a serious pathogen of oriental plane (*Platanus orientalis* L.) in Turkey, causing stem and branch cankers, root and collar rot, rapid tree decline, and mortality (Derviş et al. 2020). *Pythium tardicrescens* Vanterp. has been detected in association with cereal-growing environments and can cause root and crown rot, damping-off, and seedling disease (Bickel et al. 2025), although its global distribution and host range remain less well documented

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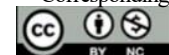
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Corresponding Author: Reza Mostowfizadeh-Ghalemfarsa; Email: rmostofi@shirazu.ac.ir

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than those of the other two species. Collectively, these oomycetes may have economic importance through damage to forest and urban trees, ornamental plants, turfgrass, and agricultural crops, particularly under poorly drained or waterlogged conditions.

Despite the agricultural importance of cucurbits, information on rhizosphere-associated oomycetes remains limited in many regions. In Iran, previous studies have largely focused on conspicuous and economically important diseases, whereas the diversity of naturally occurring oomycetes in cucurbit rhizospheres has received comparatively little attention. Recording additional regional occurrences is essential for refining knowledge of species distributions, clarifying ecological associations, and informing assessments of potential future disease risk.

To address the underexplored aspect of cucurbit-associated oomycete diversity, the present study investigated oomycetes associated with the rhizosphere of cucurbit crops in Fars Province using an integrative approach combining cultural characteristics, morphology, and molecular phylogenetic analyses. This work aims to improve current knowledge of the oomycete communities associated with cucurbit rhizospheres and to document their occurrence in an important agricultural region of Iran.

MATERIALS AND METHODS

During 2025, a total of 39 sampling sites were surveyed in Fars Province, including nine sites in Shiraz County, five in Kazerun, three in Arsanjan, 15 in Beyza, two in Marvdasht, and five in Dasht-e Arjan. Samples were collected from 23 cucumber, two cantaloupe, five muskmelon, seven squash, and one watermelon production unit. In total, 134 samples were collected, comprising symptomatic root and crown tissues, rhizosphere soil, plant debris, and irrigation water. Isolation from plant tissues was performed on CMA-PARP (Jeffers and Martin 1986), and oomycetes from soil were recovered using leaf- and grass-baiting assays, following the protocols of Jeffers and Martin (1986) and related baiting methods (Pérez-Sierra et al. 2022). Asexual and sexual structures were induced and examined on organic substrates and culture media as described previously (Fang et al. 2017, van der Plaats-Niterink 1981, Erwin and Ribeiro 1996). Colony morphology, radial growth, and cardinal temperatures were assessed on standard agar media using established methods for oomycete characterization (van der Plaats-Niterink 1981, Erwin and Ribeiro 1996). Morphological measurements were based on 50 structures per isolate, and cultures were maintained on cornmeal agar slants at 15 °C for subsequent analyses.

Genomic DNA was extracted from freeze-dried mycelium grown in potato extract broth using the DNG PLUS DNA extraction kit, following Mirsoleimani and Mostowfizadeh-Shalamfarsa (2013). For *Pythium sensu stricto*, the *βtub*, *cox1*, and *cox2* loci were amplified using standard primers and PCR conditions (Hudspeth et al. 2000, Villa et al. 2006, Robideau et al. 2011), and amplicons were sequenced by Codon Genetic Group. For *Phytophthora* and *Phytophythium* isolates, only the *cox1* locus was amplified and sequenced. Sequences were edited in Geneious Prime 2022, aligned with MAFFT v.7 (Katoh et al. 2019), and tested for phylogenetic congruence using the Partition Homogeneity Test (Incongruence Length Difference test) implemented in PAUP* 4.0a136 (Swofford and Sullivan 2003). The test was conducted with 1000 partition-replicate searches using heuristic searches. Phylogenetic analyses were performed using Bayesian Inference in MrBayes 3.1 via Tracer (Mishra et al. 2023). In addition, Maximum Likelihood and Minimum Evolution analyses were also conducted with 1000 bootstrap replicates, with *Elongisporangium anandrum* (Drechsler) Uzuhasi, Tojo & Kakishige as the outgroup. Trees were visualized and edited in MEGA 12 (Kumar et al. 2024), and all newly generated sequences were deposited in GenBank.

Pathogenicity tests were performed on seedlings of cucumber, cantaloupe, muskmelon, squash, and watermelon using vermiculite-hempseed inoculum prepared according to Banihashemi (1989). In summary, for each isolate, 200 g of vermiculite was mixed with 120 mL of hempseed extract (60 g ground hempseed L⁻¹ distilled water) and sterilized three times at 121 °C for 20 min at 24-h intervals (Banihashemi 1989). The mixture was inoculated with twenty 6-mm plugs from actively growing margins of 3-day-old CMA cultures and incubated at 25 °C for four weeks, with shaking every 4–5 days. Controls received non-colonized CMA plugs. Pre- and post-emergence damping-off assays were conducted in sterile soil: sand substrate as described previously (Banihashemi 1989), with non-colonized vermiculite-hempseed substrate used as the control. Plants were maintained under waterlogged conditions for 24 h, incubated at 25 °C, and monitored for two weeks for seedling mortality, wilting, stunting, and root rot symptoms. The assays were independently repeated twice and evaluated under blind conditions.

RESULTS AND DISCUSSION

Among the isolates recovered from the rhizosphere of cucurbit plants exhibiting root rot, crown rot, and yellowing symptoms, morphological characteristics identified *Phytophthora inundata* (one isolate from diseased cucumber rhizosphere soil), *Phytophythium litorale* (one isolate from diseased cucumber rhizosphere soil), and *Pythium tardicrescens* (five isolates from diseased squash rhizosphere soil) (Fig. 1; Table 1). Molecular analyses confirmed these identifications and supported their placement in Clade 6a of *Phytophthora* for *Ph. inundata* (Abad et al. 2023b), Clade 1 of *Phytophythium* for *Pp. litorale* (Baten et al. 2014), and Clade B of *Pythium sensu stricto* for *Py. tardicrescens* (Lévesque and de Cock 2004) (Fig. 1).

None of the isolates caused detectable symptoms on the tested cucurbit seedlings under the experimental conditions used. These results indicate that the tested isolates did not induce disease under the conditions examined; however, they do not exclude isolate- or species-specific pathogenicity under different environmental conditions, host developmental stages, inoculum pressures, or soil under different environmental conditions. The single isolate assigned to *Pp. litorale* tested here should not be generalized to the species, because pathogenicity and aggressiveness may vary among isolates. The recovery of these oomycetes from symptomatic rhizosphere samples may reflect secondary colonization, latent infection, weak pathogenicity, or association with disease complexes. Further studies using multiple isolates, host cultivars, and species-specific environmental conditions are needed to clarify their ecological and pathogenic roles.

Among the recovered taxa, *Py. tardicrescens* is particularly noteworthy because it represents a new record for the oomycete biota of Iran. It was characterized by filamentous, slightly inflated to toruloid and lobate sporangia, globose terminal oogonia (av. 26.5 ± 0.9 (22.7–27.3) μm in diam) with smooth surface, a single sac-shaped monoclinal or paragynous antheridium (av. 11.2 ± 0.3 (9.5–13.7) $\times$ 7.8 ± 0.5 (6.3–10.2) μm), and globose, aplerotic oospores (av. 22.8 ± 0.6 (21.0–26.6) μm in diam) with walls up to 2 ± 0.1 μm thick (Fig. 2). This species is closely related to *Py. scleroteichum* Drechsler, but differs in sporangial and growth morphology. In agreement with previous reports, *Py. tardicrescens* showed very slow growth (0.5 mm per day) and delayed production of reproductive structures, which were formed only after approximately three months. Cardinal temperatures were 5, 20, and 30 °C for minimum, optimum, and maximum growth, respectively.

The recovery of *Ph. inundata* from cucumber is also significant, as this appears to be the first report of this species in association with cucumber worldwide. In Iran, it was previously reported from rice, sugar beet, *Solanum nigrum* L., and pistachio (Safaeifarahani et al. 2013, Salmaninezhad and Mostowfizadeh-Ghalamfarsa 2017). *Phytophthora litorale* has previously been reported from cucumber and squash (Parkunan and J 2013; Alboasi et al. 2018) and was described as a strong pathogen of squash in some studies; however, the isolate recovered here was non-pathogenic under our experimental conditions.

In conclusion, this study expands the known diversity of cucurbit-associated oomycetes in Iran and documents *Py. tardicrescens* as a new national record. Further studies should include broader sampling and pathogenicity assays under different environmental conditions to better clarify the ecological roles and disease potential of these taxa.

Table 1. List of the isolates obtained in this study with their GenBank accession numbers.

Species	Isolate	Date	Host (Matrix)	Location	Longitude	Latitude	GenBank Accession no.		
							<i>βtub</i>	<i>cox1</i>	<i>cox2</i>
<i>Phytophthora inundata</i>									
	CSPH03	Nov. 2025	<i>Cucumis sativus</i> (rhizosphere soil)	Beyza	29.96380371	52.36211680	-	PZ713512	-
<i>Phytophthium litorale</i>									
	CSPP12	Nov. 2025	<i>Cucumis sativus</i> (rhizosphere soil)	Beyza	29.96084423	52.35113731	-	PZ713513	-
<i>Pythium tardicrescens</i>									
	CPT03	Oct. 2025	<i>Cucumis pepo</i> (rhizosphere soil)	Dasht-e Arjan	30.08008238	51.52921542	-	-	-
	CPT11	Oct. 2025	<i>Cucumis pepo</i> (rhizosphere soil)	Dasht-e Arjan	30.08008239	51.52921536	PZ533845	PZ533837	PZ533841
	CPT17	Oct. 2025	<i>Cucumis pepo</i> (rhizosphere soil)	Dasht-e Arjan	30.08008234	51.52921530	-	-	-
	CPT99	Oct. 2025	<i>Cucumis pepo</i> (rhizosphere soil)	Dasht-e Arjan	30.08008239	51.52921546	-	-	-
	CPT03	Oct. 2025	<i>Cucumis pepo</i> (rhizosphere soil)	Dasht-e Arjan	30.08008238	51.52921542	-	-	-

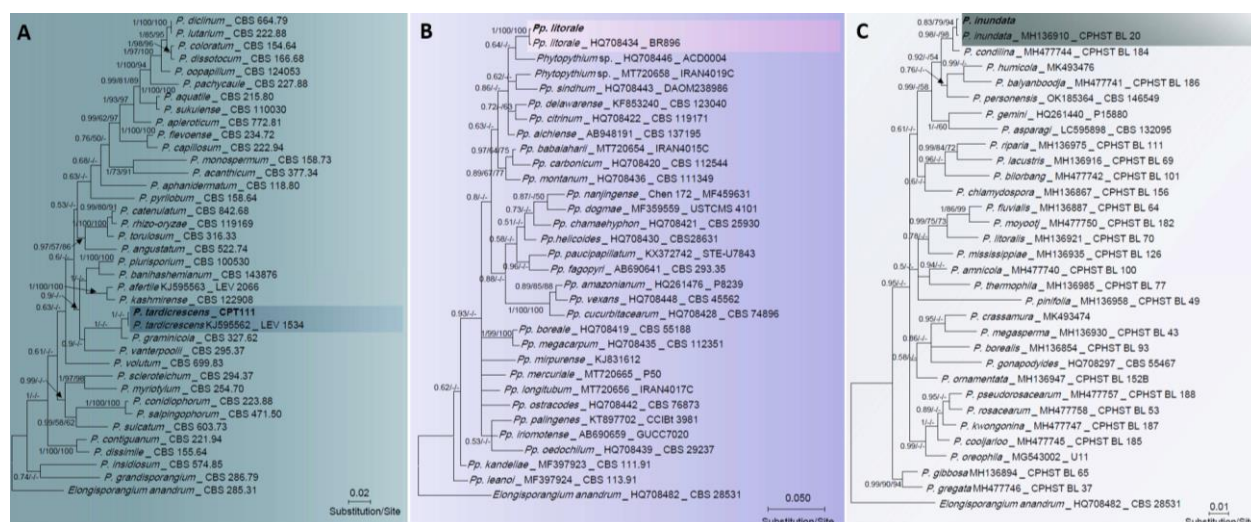


Fig. 1. Phylogenetic relationships of oomycetes species from cucurbits in this study. (A) Phylogenetic relationships of *Pythium sensu stricto* species from cucurbits and 36 previously described *Pythium* spp. based on Bayesian analyses of a concatenated alignment of nuclear (*βtub*) and mitochondrial (*cox1* and *cox2*) loci. (B) Phylogenetic relationships of *Phytopythium* species from cucurbits and 30 previously described *Phytopythium* spp. based on Bayesian analyses of the alignment of *cox1* sequences. (C) Phylogenetic relationships of *Phytophthora* species from cucurbits and 30 previously described *Phytophthora* spp. from Clade 6 based on Bayesian analyses of the alignment of *cox1* sequences. Numbers above the branches represent Bayesian posterior probabilities and bootstrap support based on the Maximum Likelihood and Minimum Evolution analyses, in the respective order. Isolates used in this study are shown in bold.

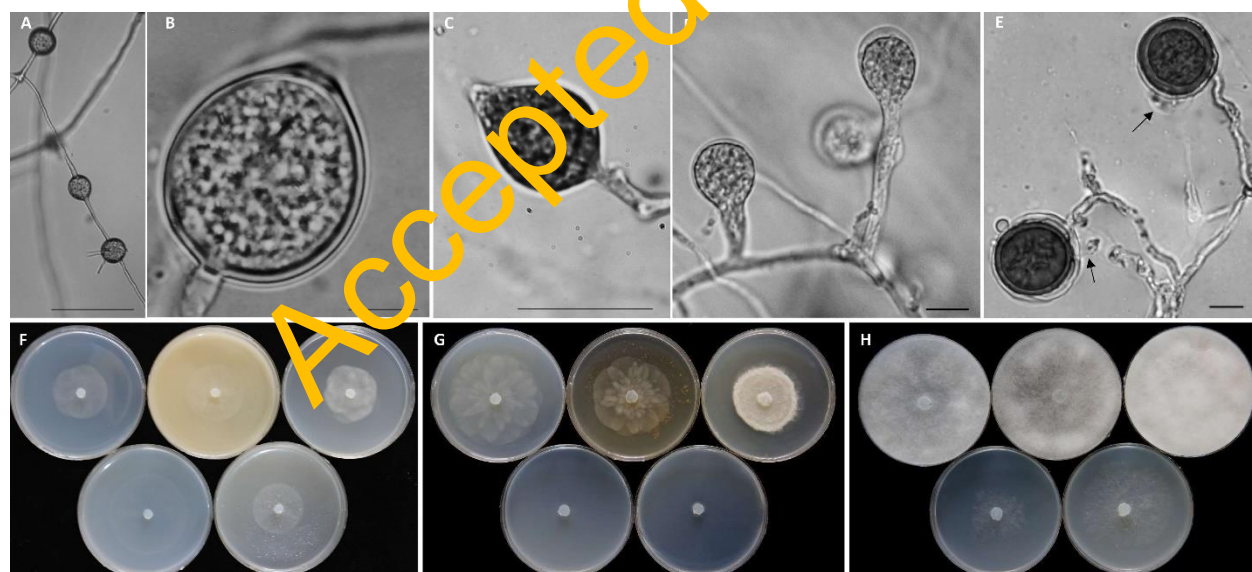


Fig. 2. Morphology of the recovered species from cucurbits in this study. (A, B) *Phytophthora inundata*. (A) globose and catenulated hyphal swellings. (B) ovoid sporangium. (C) *Phytopythium litorale*'s sporangium. (D, E) *Pythium tardicrescens*. (D) filamentous sporangia with lobate elements. (E) aplerotic oospores with single monoclinal antheridium (arrows). (F–H) Colony morphology of different species on various media at 25 °C after 48 hours. (Top from left to right): carrot agar, malt extract agar and potato-dextrose agar. Bottom (from left to right): hempseed agar and cornmeal agar. (F) *Phytophthora inundata*. (G) *Phytopythium litorale*. (H) *Pythium tardicrescens*.

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AUTHOR CONTRIBUTION

Fatemeh Salmaninezhad: Funding acquisition, Investigation, Data curation, Formal analysis, Visualization, Validation, Writing, original draft, Writing, review and editing; Pouria Sekandarpour: Investigation, Visualization, Validation, Writing, review and editing; Reza Mostowfizadeh-Ghalamfarsa: Conceptualization, Funding acquisition, Supervision, Validation, Writing, original draft, Writing, review and editing.

DATA AVAILABILITY

All datasets generated during this study are available from the corresponding author upon request.

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DECLARATION

The authors declare no competing interests.

ETHICAL APPROVAL

This article does not contain any studies with human participants or animals by any of the authors.

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Pythium tardicrescens اُمیست‌های همراه با فراریشه‌ی کدوییان: گزارشی جدید از

فاطمه سلمانی نژاد، پوریا سکندرپور، رضا مستوفی زاده قلمفرسا ✉
بخش گیاه پزشکی، دانشکده کشاورزی، دانشگاه شیراز، شیراز، ایران



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چکیده

گیاهان خانواده کدوییان به‌طور گسترده در ایران، به‌ویژه در سامانه‌های تولید متراکم گلخانه‌ای، کشت می‌شوند؛ شرایطی که در آن آُمیست‌های خاک‌برد می‌توانند در بروز بیماری‌های ریشه و طوقه نقش داشته باشند. طی پایش سامانه‌های تولید کدوییان در استان فارس در سال ۱۴۰۴، بافت‌ها، ریشه و طوقه دارای علائم بیماری، خاک فراریشه، بقایای گیاهی و آب آبیاری از مزارع و گلخانه‌های خیار، طالبی، خربزه، کدو و هندوانه جمع‌آوری شدند. جداسازی آُمیست‌ها با استفاده از محیط‌های کشت انتخابی و روش‌های طعمه‌گذاری انجام شد و جدایه‌های مشخص بر اساس ویژگی‌های پرگنه، صفات ریخت‌شناختی، دماهای اصلی رشد، آزمون‌های بیماری‌زایی و واکاوی‌های فیلوژنتیکی شناسایی شدند. از مجموع جدایه‌های آُمیستی به‌دست‌آمده، هفت جدایه به‌عنوان *Pythium tardicrescens*، *Phytophthora inundata*، *Phytophthora* جنس 6a، تبار ۱ جنس *Phytophthora* و تبار B جنس *Pythium sensu stricto* تأیید جایگاه آن‌ها را در تبار 6a جنس *Pythium*، تبار ۱ جنس *Phytophthora* و تبار B جنس *Pythium sensu stricto* تأیید کردند. پنج جدایه‌ی *Py. tardicrescens* از خاک فراریشه‌ی کدو بیمار به‌دست آمد که نخستین گزارش این گونه از ایران محسوب می‌شود. این گونه با رشد شعاعی‌کُند، تشکیل دیر هنگام ساختارهای تولید مثل، اسپورانژیوم‌های رشته‌ای تالپ‌دار، آُگونیم‌های انتهایی و کروی، آنتریدیوم‌های تک‌بُن و پراماده و آُسپورهای ناپرساز مشخص شد. یک جدایه‌ی *Ph. inundata* نیز از خاک فراریشه‌ی خیار جداسازی شد که نخستین گزارش همراهی این گونه با خیار در جهان به‌شمار می‌رود. همچنین، *Pp. litorale* از خاک فراریشه‌ی خیار به‌دست آمد. هیچ‌یک از جدایه‌ها تحت شرایط آزمایشی مورد استفاده، در سامانه‌های کدوییان علائم بیماری ایجاد نکردند. این یافته‌ها برای نخستین بار حضور *Py. tardicrescens* را در ایران و همچنین ارتباط جدایه *Ph. inundata* را با خیار مستند کرده است و بر ضرورت انجام مطالعات گسترده‌تر بوم‌شناختی و بیماری‌زایی برای روشن‌شدن نقش آن‌ها در سامانه‌های تولید کدوییان تأکید می‌کند.

واژگان کلیدی: بیماری زای، تاکسونومی، فیلوژنی، *Oomycota*, *Cucurbitaceae*.