



Evidence for selective pathogenicity of *Globisporangium coniferarum* in coniferous urban trees

Fatemeh Salmaninezhad^{id}, Pouria Sekandarpour^{id}, Reza Mostowfizadeh-Ghalamfarsa^{✉ id}

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

✉ Corresponding authors: rmostofi@shirazu.ac.ir

Article Info.	Abstract
Article type: Original article Article history: Received 03 May 2026 Received in revised form 18 May 2026 Accepted 24 May 2026 Available Online 25 May 2026 Keywords: <i>Globisporangium coniferarum</i>, Host specificity, Oomycete pathogenicity, Root and crown rot, Urban forestry.	Urban trees are vital to sustainable cities but are increasingly affected by abiotic stressors that increase their susceptibility to biotic factors. Among these, oomycetes of the genus <i>Globisporangium</i> are important agents of root diseases that manifest symptoms in both root and foliar systems, particularly under poorly drained and intensively irrigated conditions. This study evaluated the pathogenicity of <i>Globisporangium coniferarum</i>, a recently described species from Iran, on seedlings of <i>Acer</i> sp., <i>Cupressus sempervirens</i>, <i>Eucalyptus obliqua</i>, <i>Morus alba</i>, <i>Pinus eldarica</i>, and <i>Salix alba</i> under greenhouse conditions. Inoculations were performed using a vermiculite-based inoculum applied to the crown region, and disease development was assessed over eight weeks based on disease symptom expression, plant growth traits, tissue colonization frequency, and pathogen re-isolation. Clear decline symptoms developed only in inoculated <i>P. eldarica</i> and <i>C. sempervirens</i>, which showed reduced vigor, foliar discoloration, crown thinning, and root necrosis. These species also exhibited significant reductions in most measured growth traits compared with non-inoculated controls. In contrast, <i>Acer</i> sp., <i>E. obliqua</i>, <i>M. alba</i>, and <i>S. alba</i> remained symptomless and showed no significant growth reduction compared with control treatments. Colonization assays revealed significant host-dependent differences, with the highest root and crown colonization in <i>P. eldarica</i>, <i>C. sempervirens</i>, and <i>Acer</i> sp., intermediate colonization in <i>E. obliqua</i>, and minimal colonization in <i>M. alba</i> and <i>S. alba</i>. Koch's postulates were fulfilled by re-isolation and molecular confirmation of the pathogen using the <i>cox1</i> gene. These findings demonstrate marked host-dependent pathogenicity in <i>G. coniferarum</i> and identify coniferous potential hosts, particularly <i>P. eldarica</i> and <i>C. sempervirens</i>, as the most susceptible.
Cite this article: Salmaninezhad, F., Sekandarpour, P., & Mostowfizadeh-Ghalamfarsa, R. (2026). Evidence for selective pathogenicity of <i>Globisporangium coniferarum</i> in coniferous urban trees. <i>Journal of Advances in Plant Protection</i>, 3(1), 1–8.	
© The Author(s).	
Publisher: Shahid Bahonar University of Kerman	

Introduction

Urban trees are integral components of sustainable cities, delivering essential ecological and socio-environmental services, including microclimate regulation, air quality improvement, and enhancement of human well-being (Dwyer et al., 1991). However, trees growing in urban environments are subjected to chronic stressors such as soil compaction, restricted rooting volume, drought, salinity, and mechanical disturbance, which predispose them to physiological decline and increase their vulnerability to biotic agents including soilborne pathogens (Raum et al., 2023).

Among these pathogens, oomycetes in the genus *Globisporangium* are increasingly recognized as important agents of root and collar rot in woody plants, particularly under conditions of soil saturation and poor drainage (Vettraino et al., 2025; Salmaninezhad et al., 2026). In arid and semi-arid regions such as Iran, a wide range of coniferous and broadleaf tree species are extensively planted in urban and peri-urban landscapes due to their relative drought tolerance and adaptability to harsh environmental conditions. Recent observations of decline symptoms, such as reduced vigor, crown thinning, and progressive dieback, across several of these tree species have raised concerns regarding the

potential involvement of soilborne oomycetes in urban tree health decline. *Globisporangium coniferarum* Salmanin. & Mostowf., described in 2022 as a novel species within Clade G of *Pythium sensu lato*, was originally isolated from declining conifers (i.e., *Cupressus sempervirens* L., *Hesperocyparis arizonica* (Greene) Bartel, and *Pinus eldarica* Ten.) and *Quercus* spp. and characterized based on both morphological traits and multilocus molecular analyses (Salmaninezhad et al., 2022). Its documented association with symptomatic woody hosts, together with its phylogenetic placement among predominantly root-infecting taxa, indicates a potential role in complex decline syndromes affecting urban and ornamental trees. In Iranian urban green spaces, widespread irrigation practices combined with compacted and poorly drained soils create environmental conditions highly conducive to oomycete survival, reproduction, and dispersal. Therefore, investigating the pathogenic association of *G. coniferarum* with decline symptoms across susceptible urban tree species is essential to clarify its role in disease etiology and to inform evidence-based management strategies for sustainable urban forestry.

Material and Methods

Pathogenicity tests

As part of a comprehensive assessment of the pathogenic potential of *Globisporangium* species associated with ornamental and urban trees in Iran, isolates of *G. coniferarum* (Supplementary Table S1) were evaluated for pathogenicity on seedlings of *Acer* sp., *Cupressus sempervirens* L., *Eucalyptus obliqua* L'Hér., *Morus alba* L., *Pinus eldarica* Medw., and *Salix alba* L. under controlled greenhouse conditions.

Inoculum preparation

Inoculum production was carried out following the protocol described by Banihashemi (1989). Briefly, 10 agar plugs (5 mm diameter) excised from the actively growing margins of *G. coniferarum* colonies cultivated on cornmeal agar (CMA; cornmeal extract 40 g L⁻¹, agar 15 g L⁻¹) (Jeffers & Martin, 1968) were transferred to 200 mg of autoclaved vermiculite supplemented with hempseed extract (60 g L⁻¹). The inoculum was incubated in darkness at 25 °C for four weeks, with daily homogenization to ensure uniform colonization. Sterile agar plugs processed identically were used for non-inoculated control treatments.

Inoculation

For pathogenicity assays, six-month- to one-year-old seedlings of *Acer* sp., *C. sempervirens*, *E. obliqua*, *M. alba*, *P. eldarica*, and *S. alba* were selected. Inoculation was performed according to the crown-infestation method described by Banihashemi (1989), whereby 30 mg of colonized vermiculite inoculum was applied directly to the crown region and subsequently covered with sterile soil. Inoculated and control plants were maintained at 25 ± 1 °C under a 16-h photoperiod and approximately 70% relative humidity for eight weeks and irrigated daily with 100 mL of sterile water. At the conclusion of the experiment, development of disease symptoms was evaluated using both visual symptom assessment and quantitative measurements. As for quantitative measurements, nine plant traits, including root wet weight, root dry weight, foliage wet weight, foliage dry weight, biomass wet weight, biomass dry weight, stem diameter, root length, and plant height were measured two months after inoculation. For each treatment, three independent replicates (each consisting of one seedling) were used.

Host colonization

To determine the extent of host colonization, roots and crown tissues from inoculated plants were thoroughly washed, surface cleaned, and sectioned into 2 mm fragments. For each host species, 30 tissue segments per sample were plated onto 80 mm Petri dishes containing CMA-PARP selective medium, with three replicates per treatment (Jeffers & Martin, 1968). Plates were examined for oomycete growth between 12 and 48 h post-incubation. Colonization frequency (Cf%) was calculated using the formula $Cf = (N_{col}/N_t) \times 100$, where N_{col} represents the number of segments colonized by *G. coniferarum* and N_t denotes the total number of segments assessed (Sessa et al., 2018).

Statistical analyses

Colonization data for root and crown tissues were analyzed separately. Because the percentage data were bounded and did not meet assumptions of normality or homogeneity of variance, the aligned rank transform (ART) procedure was used to conduct non-parametric factorial analyses. ART-ANOVA was performed with host species as the fixed factor. When a significant main effect was detected, pairwise comparisons were carried out using estimated marginal means with Tukey adjustment for multiple comparisons. Compact letter displays were generated to summarize statistically homogeneous groups and were incorporated into the plots to support the interpretation of host responses. All

statistical analyses and visualizations were conducted in R (ver. 4.5.2; R Core Team 2025), using the packages ARTool (ver. 0.11.2; Kay et al., 2025) for aligned rank transform procedures, Estimated Marginal Means (emmeans) (ver. 2.0.1; Lenth & Piaskowski, 2025) for marginal means and post-hoc tests, multcomp (ver. 1.4.29; Hothorn et al., 2008) for compact letter display generation, dplyr (ver. 1.1.4) for data processing, and ggplot2 (ver. 3.5.2; Wickham, 2016) for graphical output.

All statistical analyses were conducted in R (ver. 4.5.2; R Core Team 2025). The effects of inoculation with *G. coniferarum* on plant performance were evaluated across six host species. For each of the nine measured plant traits, including root wet weight, root dry weight, foliage wet weight, foliage dry weight, biomass wet weight, biomass dry weight, stem diameter, root length, and plant height, a two-way analysis of variance was performed with host species, treatment, and their interaction included as fixed effects. The treatment factor consisted of control and *G. coniferarum*-inoculated plants. When significant main effects or interactions were detected, post-hoc pairwise comparisons between treatments within each host species were conducted using Tukey's Honest Significant Difference (HSD) test. Compact letter displays derived from these post-hoc tests were used to summarize statistically significant differences at the 0.05 probability level. All figures were generated using ggplot2 (ver. 3.5.2; Wickham, 2016). The R packages used for data analysis and visualization included stats (R Core Team 2025) for analysis of variance, ggplot2 for graphical output, dplyr and tidyr in the tidyverse package (version 2.0.0; Wickham et al., 2019) for data manipulation.

To fulfill Koch's postulates, *G. coniferarum* was re-isolated from symptomatic root and crown tissues and confirmed morphologically and molecularly. Genomic DNA was extracted from re-isolated cultures following Mirsoleimani and Mostowfizadeh-Ghalamfarsa (2013). Molecular identification was performed by amplification of the mitochondrial cytochrome c oxidase subunit II (cox2) region using universal primers (Villa et al., 2006), and PCR products were sequenced at the Codon Genetic Research Center (Tehran, Iran). Sequence data were used to verify the identity of the re-isolated isolates as *G. coniferarum* by performing BLAST searches against reference sequences in GenBank (<https://www.ncbi.nlm.nih.gov/blastn>).

Results

Development of disease symptoms

Two months after inoculation with *G. coniferarum*, inoculated plants of *P. eldarica* and *C. sempervirens* exhibited clear decline symptoms compared with non-inoculated controls. Inoculated seedlings showed reduced vigor, crown thinning, and visible foliar discoloration, while control plants remained healthy and symptomless. Root systems of inoculated plants were poorly developed and exhibited necrosis and decay symptoms, consistent with oomycete-induced root dysfunction. In contrast, control plants displayed intact root architecture and normal foliage development, indicating that the observed symptoms were associated with pathogen infection. Inoculated plants of *Acer* sp., *E. obliqua*, *M. alba*, and *S. alba* did not show any symptoms compared to the controls (Fig. 1 and Fig. 2).



Fig. 1. Results of the pathogenicity test of *Globisporangium coniferarum* isolate GbCu04-2 on roots of conifers after two months in this study. (A-B) *Pinus eldarica*. (A) Uninoculated control; (B) Severe root rot symptom; (C-D) *Cupressus sempervirens*; (C) Uninoculated control; (D) Root rot and severe reduction symptoms in root volume. Bar = 20 mm.



Fig. 2. Results of the pathogenicity test of *Globisporangium coniferarum* isolate GbCu04-2 on foliage of the conifers in this study after two months. (A-B) *Pinus eldarica*. (A) Uninoculated control; (B) Severe decline, yellowing, and reduction symptoms in foliage volume; (C-D) *Cupressus sempervirens*. (C) Uninoculated control. (D) Severe yellowing and decline symptoms. Bar = 200 mm.

Effects of *G. coniferarum* on plant traits

Inoculation with *G. coniferarum* affected plant traits in a host-dependent manner. Significant differences between inoculated and control plants were detected only in *P. eldarica* and *C. sempervirens* (Fig. 3; [Supplementary Table S2](#)). No significant treatment effects were observed for *Acer* sp., *E. obliqua*, *M. alba*, or *S. alba* for any of the measured traits. In *C. sempervirens*, inoculated plants differed significantly from control plants for all measured traits, including root wet weight, root dry weight, foliage wet weight, foliage dry weight, biomass wet weight, biomass dry weight, stem diameter, root length, and plant height. In *P. eldarica*, significant differences between inoculated and control plants were detected for root wet weight, root dry weight, foliage wet weight, foliage dry weight, biomass wet weight, biomass dry weight, root length, and plant height. Stem diameter did not differ significantly between treatments in this species. For *Acer* sp., *E. obliqua*, *M. alba*, and *S. alba*, inoculated and control plants did not differ significantly for any of the nine measured traits.

Root and crown colonization by *G. coniferarum* in plant species

Root colonization by *G. coniferarum* differed significantly among the host species, as indicated by the ART-ANOVA ($P < 0.001$) (Fig. 4; [Supplementary Table S3](#)). *Pinus eldarica*, *C. sempervirens*, and *Acer* sp. exhibited the highest colonization frequencies, while *M. alba* and *S. alba* showed little to no colonization (Fig. 4). *Eucalyptus obliqua* displayed an intermediate level of susceptibility, falling between the high- and low-colonization groups. These patterns were supported by the post-hoc comparisons and compact letter displays, which distinguished three statistically meaningful categories of host response. Crown tissues exhibited similar but slightly attenuated patterns of host colonization. The host effect was significant (ART-ANOVA, $F_{5,12} = 10.12$, $P < 0.001$), with *P. eldarica*, *C. sempervirens*, and *Acer* sp. showing the highest crown colonization frequencies. *Morus alba* and *S. alba* again showed minimal colonization, and *E. obliqua* maintained an intermediate response. Pairwise comparisons revealed that the strongest statistical

contrasts occurred between the highly colonized hosts and those showing negligible colonization, with *E. obliqua* remaining statistically intermediate. The compact letter display derived from the emmeans results

clearly separated hosts into high, intermediate, and low colonization categories, consistent with the biological observations..

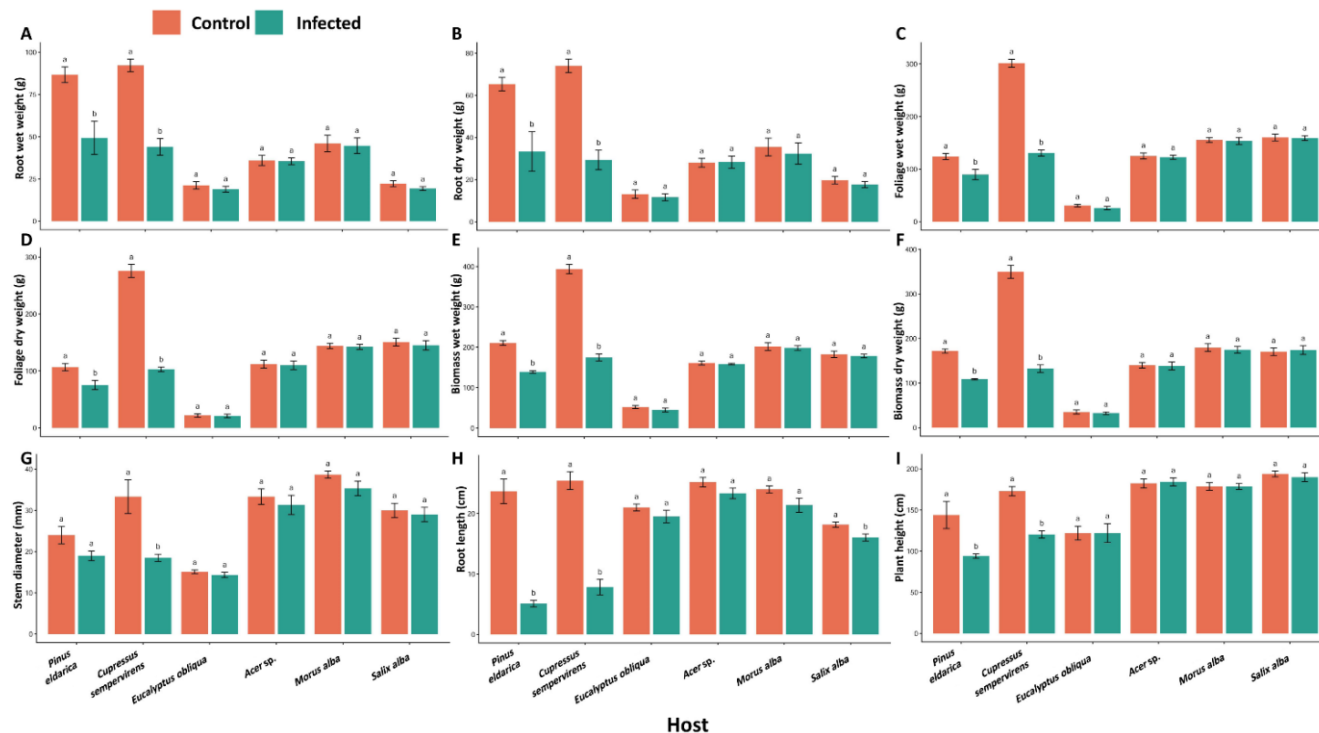


Fig. 3. Impact of *G. coniferarum* infection on growth and biomass parameters across six host species. Comparison between uninoculated control and infected groups for: (A) Root wet weight, (B) Root dry weight, (C) Foliage wet weight, (D) Foliage dry weight, (E) Biomass wet weight, (F) Biomass dry weight, (G) Stem diameter, (H) Root length, and (I) Plant height. The host species included *Pinus eldarica*, *Cupressus sempervirens*, *Eucalyptus obliqua*, *Acer sp.*, *Morus alba*, and *Salix alba*. Bars represent the mean value, and error bars indicate the standard error of the mean ($\pm$ SE) of three replicates. Different lowercase letters above the bars denote significant differences between the control and infected treatments within each host species according to Tukey's HSD test at $P < 0.05$.

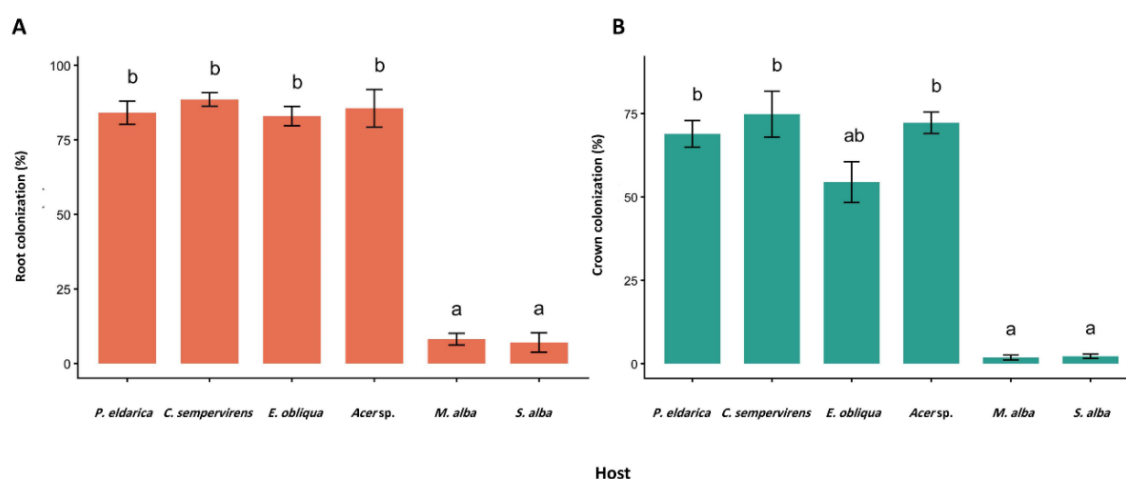


Fig. 4. Root and crown colonization (%) of six host species by *Globisporangium coniferarum*. (A) Root colonization and (B) Crown colonization were compared among *Pinus eldarica*, *Cupressus sempervirens*, *Eucalyptus obliqua*, *Acer sp.*, *Morus alba*, and *Salix alba*. Bars represent mean $\pm$ SE. Different lowercase letters above bars indicate significant differences among host species based on aligned rank transform ANOVA (ART ANOVA), followed by post hoc multiple comparisons at $P < 0.05$.

Discussion

The present study demonstrates that *G. coniferarum* exhibits host-dependent pathogenicity, with the conifer species tested showing the greatest susceptibility under the experimental conditions. This agrees with previous reports indicating that *Globisporangium* spp., such as *G. barbulae*, *G. izadpanahii*, *G. oryzicola* and related oomycetes, such as *Pythium arrhenomanes* and *P. catenulatum* are primarily soilborne root pathogens whose disease expression is strongly influenced by host identity, root susceptibility, and environmental conditions such as excessive moisture and poor soil aeration (Erwin & Ribeiro, 1996; Ueta & Tojo, 2016; Uzuhashi et al., 2017; Schmidt et al., 2020; Salmaninezhad et al., 2026). The stronger disease response observed in conifers is also consistent with the association of *G. izadpanahii* with *P. eldarica* reported by Salmaninezhad et al. (2026).

A key finding of this study is that pathogen recovery did not consistently correlate with symptom expression, indicating the possibility of asymptomatic or latent colonization in certain hosts. This suggests that colonization and pathogenicity may be partially uncoupled, as reported for several soilborne oomycetes, such as *G. barbulae*, *G. oryzicola*, and *G. uncinatum* where asymptomatic colonization may occur before disease expression or may only become damaging under stress conditions (Erwin & Ribeiro, 1996; Ueta & Tojo, 2016; Uzuhashi et al., 2017; Koike et al., 2024). Therefore, some broadleaf hosts may act as tolerant or weakly susceptible hosts, whereas susceptible conifers may experience greater root dysfunction and seedling decline following infection. The ability of oomycetes to colonize host tissues asymptotically is well established and should not be regarded as atypical. Similar incongruities between the source of isolation and observed pathogenic behavior have been documented in several oomycete lineages, including Clade D taxa of *Pythium sensu stricto*, where repeated isolation from plant-associated substrates has not consistently correlated with disease expression or sustained pathogenic colonization (Lévesque & de Cock, 2004; Uzuhashi et al., 2010). Accordingly, recovery from root tissues alone cannot be considered definitive evidence of an actively pathogenic or endophytic lifestyle. Rather, *G. coniferarum* may engage in a transient or context-dependent association with host tissues, the outcome of which is likely mediated by environmental conditions, host developmental stage, tissue susceptibility, inoculum density, and interactions with the surrounding root

microbiome. Comparable patterns have been reported in phylogenetically related oomycete taxa that exhibit limited or inconsistent colonization despite their detection in plant tissues by molecular- or culture-based methods (Bala et al., 2010; Robideau et al., 2011; Salmaninezhad & Mostowfizadeh-Ghalamfarsa, 2019; Salmaninezhad et al., 2024; Boie et al., 2024). Therefore, the recovery of *G. coniferarum* from *Acer* sp. roots in the present study indicates that the pathogen was able to establish within host tissues, but this colonization was not associated with visible symptoms or measurable growth reduction under the tested conditions.

The predominance of root infection over crown invasion further supports the role of *G. coniferarum* as a root-associated pathogen. This pattern is consistent with the biology of many *Globisporangium* species, such as *G. barbulae* and *G. oryzicola*, which commonly infect fine roots and cortical tissues, leading to impaired water and nutrient uptake rather than rapid systemic invasion (Ueta & Tojo, 2016; Uzuhashi et al., 2017). From a practical perspective, these results suggest that *G. coniferarum* should be considered a selective risk factor for susceptible woody hosts, particularly in nurseries and urban landscapes where irrigation, compacted soil, and poor drainage may favor oomycete activity. Future studies should evaluate this pathogen under combined abiotic stress conditions to clarify its role as either a primary pathogen or part of a broader decline complex. In addition, because pathogenicity in oomycetes may vary among isolates within a single species (Ueta & Tojo, 2016; Veterano et al., 2018), further assays including multiple isolates of *G. coniferarum* are needed to determine the extent of intraspecific variability in host responses and virulence. Based on the results of the present study, *G. coniferarum* should be regarded as an opportunistic to moderately aggressive soilborne pathogen with host-dependent pathogenicity, rather than a uniformly aggressive parasite across all tested hosts. In recent years, the increasing number of reports of *Globisporangium* species from diverse hosts and habitats has highlighted the growing importance of this genus in plant health, particularly in agricultural, ornamental, nursery, and urban landscape systems (Uzuhashi et al., 2017). During the past decade, more than eight novel *Globisporangium* species, together with more than ten previously described species, have been reported from Iran (Salmaninezhad et al., 2022; Rezaei et al., 2024; Ahadi et al., 2024; Salmaninezhad et al., 2024; Ahadi et al., 2025), indicating that the diversity of this genus in the country is likely still underestimated. This rapid increase in records may reflect both improved taxonomic and molecular

identification efforts and the ecological suitability of Iranian agroecosystems, nurseries, irrigated landscapes, and urban green spaces for the establishment and spread of soilborne oomycetes. The frequent recovery of *Globisporangium* species from declining plants, rhizosphere soils, irrigation-associated environments, and ornamental hosts suggests that these organisms may represent an important but still insufficiently characterized component of soilborne disease complexes in Iran.

Conclusion

Overall, this study provides initial evidence that *G. coniferarum* may contribute to decline problems in susceptible woody plants, particularly under nursery or landscape conditions favorable to oomycete development. Its impact appears to depend on the host–pathogen interaction rather than the simple presence of the organism alone. Further work incorporating additional isolates, host species, and environmental stress factors will be essential to better define its ecological role, pathogenic potential, and management significance.

Acknowledgments

The authors acknowledge Shiraz University and the Iranian National Scientific Foundation for their financial support of this study.

Ethical Approval and Consent

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

CRedit author statement

F. Salmaninezhad: Conceptualization, Funding acquisition, Investigation, Methodology, Visualization, Validation, Data curation, Formal Analysis, Writing – original draft, Writing – review & editing. **P. Sekandarpour:** Formal analysis, Investigation, Methodology, Validation, Writing – review & editing. **R. Mostowfizadeh-Ghalemfarsa:** Conceptualization, Funding acquisition, Project administration, Resources, Supervision, Validation, Writing – review & editing.

Funding

This study was funded by the Iran National Science Foundation (INSF, award number: 4044515).

Data Availability

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

Conflict of interest

The authors declare no conflicts of interest.

References

- Ahadi, R., Alizadeh, A., Chenari Bouket, A., Masigol, H., & Grossart, H. P. (2025). Multigene phylogeny, morphology, and pathogenicity uncover two novel *Globisporangium* species (Oomycota) from freshwater habitats in northwestern Iran. *Frontiers in Microbiology*, 16, 1615096. <https://doi.org/10.3389/fmicb.2025.1615096>.
- Ahadi, R., Bouket, A. C., Alizadeh, A., Masigol, H., & Grossart, H. P. (2024). *Globisporangium tabrizense* sp. nov., *Globisporangium mahabadense* sp. nov., and *Pythium bostanabadense* sp. nov. (Oomycota), three new species from Iranian aquatic environments. *Scientific Reports*, 14(1), 31701. <https://doi.org/10.1038/s41598-024-81651-0>.
- Bala, K., Robideau, G. P., Désaulniers, N., De Cock, A. W. A. M., & Lévesque, C. A. (2010). Taxonomy, DNA barcoding and phylogeny of three new species of *Pythium* from Canada. *Persoonia-Molecular Phylogeny and Evolution of Fungi*, 25(1), 22–31. <https://doi.org/10.3767/003158510x524754>.
- Banihashemi, Z. (1989). Study of pistachio gummosis in southern provinces of Iran. In *Proceedings of the 9th Iranian Plant Protection Congress*, Mashhad, Iran. pp. 87.
- Boie, W., Schemmel, M., Ye, W., Hasler, M., Goll, M., Verreet, J. A., & Cai, D. (2024). An assessment of the species diversity and disease potential of *Pythium* communities in Europe. *Nature Communications*, 15(1), 8369. <https://doi.org/10.1038/s41467-024-52761-0>.
- Dwyer, J. F., Schroeder, H. W., & Gobster, P. H. (1991). The significance of urban trees and forests: toward a deeper understanding of values. *Journal of Arboriculture*, 17 (10), 276–284. <https://doi.org/10.48044/jauf.1991.062>.
- Erwin, D. C., & Ribeiro, O. K. (1996). *Phytophthora diseases worldwide*. American Phytopathological Society (APS) publish.
- Hothorn, T., Bretz, F., & Westfall, P. (2008). Simultaneous inference in general parametric models. *Biometrical Journal*, 50(3), 346–363. <https://doi.org/10.1002/bimj.200810425>.
- Jeffers, S. N., & Martin, S. B. (1986). Comparison of two media selective for *Phytophthora* and *Pythium* species. *Plant Disease*, 70(11), 1038–1043. <https://doi.org/10.1094/pd-70-1038>.
- Koike, S. T., Stanghellini, H., Tsuchida, C., & Guerrero, J. (2024). First report of *Globisporangium uncinulatum* (syn. *Pythium uncinulatum*) causing

- Pythium* wilt of artichoke in California. *Plant Disease*, 108(4), 1118. <https://doi.org/10.1094/pdis-10-23-2078-pdn>.
- Kay, M., Elkin, L. A., Higgins, J. J., & Wobbrock, J. O. (2025). *ARTool: Aligned rank transform for nonparametric factorial ANOVAs* (R package version 0.11.2). <https://doi.org/10.5281/zenodo.594511>
- Lenth, R., & Piaskowski, J. (2025). *Emmeans: Estimated marginal means, aka least-squares means* (R package version 2.0.1). <https://doi.org/10.32614/CRAN.package.emmeans>.
- Mirsoleimani, Z., & Mostowfizadeh-Ghalemfarsa, R. (2013). Characterization of *Phytophthora pistaciae*, the causal agent of pistachio gummosis, based on host range, morphology and ribosomal genome. *Phytopathologia Mediterranea*, 53, 501–506. <https://www.jstor.org/stable/42685429>.
- Raum, S., Collins, C. M., Urquhart, J., Potter, C., Pauleit, S., & Egerer, M. (2023). Tree insect pests and pathogens: a global systematic review of their impacts in urban areas. *Urban Ecosystems*, 26(2), 587–604. <https://doi.org/10.1007/s11252-022-01317-5>.
- Rezaei, S., Abrinbana, M., & Ghosta, Y. (2024). Diversity of mycoparasitic *Pythium sensu stricto* and *Globisporangium* species in West Azarbaijan province of Iran. *Annals of Applied Biology*, 185(1), 58–72. <https://doi.org/10.1111/aab.12918>.
- Robideau, G. P., de Cock, A. W. A. M., Coffey, M. D., Volgmayr, H., Brouwer, H., Bala, K., Chitty, D. W., Desaulniers, N., Eggertson, Q. A., Gachon, C. M., Hu, C. H., Kupper, F. C., Rintoul, T. L., Sarhan, E., Verstappen, E. C., Zhang, Y., Bonants, P. J., Ristaino, J. B., & Lévesque, A. C. (2011). DNA barcoding of oomycetes with cytochrome c oxidase subunit I and internal transcribed spacer. *Molecular Ecology Resources*, 11(6), 1002–1011. <https://doi.org/10.1111/j.1755-0998.2011.03041.x>.
- Salmaninezhad, F., Aloï, F., Pane, A., Mostowfizadeh-Ghalemfarsa, R., & Cacciola, S. O. (2022). *Globisporangium coniferarum* sp. nov., a new species associated with conifers and *Quercus* sp. *Fungal Systematics and Evolution*, 10, 127–137. <https://doi.org/10.3114/fuse.2022.10.05>.
- Salmaninezhad, F., & Mostowfizadeh-Ghalemfarsa, R. (2019). Three new *Pythium* species from rice paddy fields. *Mycologia*, 111(2), 274–290. <https://doi.org/10.1080/00275514.2018.1543486>.
- Salmaninezhad, F., Mostowfizadeh-Ghalemfarsa, R., & Cacciola, S. O. (2024). *Pythium banihashemianum* sp. nov. and *Globisporangium izadpanahii* sp. nov.: Two New Oomycete Species from Rice Paddies in Iran. *Journal of Fungi*, 10(6), 405. <https://doi.org/10.3390/jof10060405>.
- Salmaninezhad, F., Sekandarpour, P., & Mostowfizadeh-Ghalemfarsa, R. (2026). First evidence of pathogenicity of *Globisporangium izadpanahii* on *Pinus eldarica*. *Journal of Plant Pathology*, 108, 785–790. <https://doi.org/10.1007/s42161-025-02080-0>.
- Schmidt, C. S., Leclercq, A., Pfeiffer, T., Goessling, J. W., Orlik, M., Jamshidi, B., Saar, K., Sellman, J., Siepe, I., & Koch, E. (2020). Pathogenicity of *Pythium* species to maize. *European Journal of Plant Pathology*, 158(2), 335–347. <https://doi.org/10.1007/s10658-020-02076-9>.
- Sessa, L., Abreo, E., & Lupo, S. (2018). Diversity of fungal latent pathogens and true endophytes associated with fruit trees in Uruguay. *Journal of Phytopathology*, 166(9), 633–647. <https://doi.org/10.1111/jph.12726>.
- Ueta, S., & Tojo, M. (2016). *Pythium barbulae* sp. nov. isolated from the moss, *Barbula unguiculata*: Morphology, molecular phylogeny and pathogenicity. *Mycoscience*, 57, 11–19. <http://dx.doi.org/10.1016/j.myc.2015.07.002>.
- Uzuhashi, S., Hata, K., Matsuura, S., & Tojo, M. (2017). *Globisporangium oryzicola* sp. nov., causing poor seedling establishment of directly seeded rice. *Antonie van Leeuwenhoek*, 110, 543–552. <https://doi.org/10.1007/s10482-016-0822-2>.
- Veterano, S. T., Coffua, L. S., Mena- Ali, J. I., & Blair, J. E. (2018). *Pythium yorkensis* sp. nov., a potential soybean pathogen from southeastern Pennsylvania, USA. *Plant Pathology*, 67(3), 619–625. <https://doi.org/10.1111/ppa.12779>.
- Vettraino, A. M., Narduzzi, M., & Antonelli, C. (2025). Isolation and characterization of *Globisporangium glomeratum* (syn. *Pythium glomeratum*) from declining holm oak in a historical garden. *Pathogens*, 14(10), 960. <https://doi.org/10.3390/pathogens14100960>.
- Villa, N. O., Kageyama, K., Asano, T., & Suga, H. (2006). Phylogenetic relationships of *Pythium* and *Phytophthora* species based on ITA rDNA, cytochrome oxidase II and β - tubuline gene sequences. *Mycologia*, 98, 410–422. <https://doi.org/10.3852/mycologia.98.3.410>.
- Wickham, H. (2016). Programming with ggplot2. In *Ggplot2: elegant graphics for data analysis* (pp. 241–253). Cham: Springer International Publishing. <https://doi.org/10.1007/978-3-319-24277-4>.
- Wickham, H., Averick, M., Bryan, J., Chang, W., McGowan, L. D., François, R., Grolemund, G., Hayes, A., Henry, L., Hester, J., Kuhn, M., Pedersen, T. L., Miller, E., Bache, S. M., Müller, K., Ooms, J., Robinson, D., Seidel, D. P., Spinu, V., ... Yutani, H. (2019). Welcome to the tidyverse. *Journal of Open Source Software*, 4(43), 1686. <https://doi.org/10.21105/joss.01686>.