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New European distribution of *Coleosporium inulae* (Coleosporiaceae) on *Dittrichia graveolens* (Asteraceae) and considerations for weed biological control

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Abstract

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As part of a classical biological control programme, investigating potential plant pathogens is one way to control alien weeds. This research study reports the first observation of the rust fungus *Coleosporium inulae* in Cyprus, France, and Portugal on the Asteraceae *Dittrichia graveolens* (stinkwort). *Dittrichia graveolens*, originating from North Africa and Mediterranean Europe, is reported as an invasive alien weed in many parts of the world, like the western USA, South Africa, and central and northern Europe. The authors collected samples from three European countries and conducted molecular identification to confirm the identity of the fungus. The results showed that the sequences obtained from the samples were closely related to other *Coleosporium inulae* sequences reported on *Inula* and *Pinus* species. The symptoms observed on the infected plants ranged from mild to severe, with some populations exhibiting high infection levels and plant mortality. The authors discuss the potential use of *Coleosporium inulae* as a biocontrol agent for *Dittrichia graveolens* but note that the heteroecious life cycle of the fungus, which requires two unrelated host plants, may complicate its development as a biocontrol agent outside the borders of Europe. The study extends the known distribution of *Coleosporium inulae* and provides insights into the natural enemies of the invasive weed *Dittrichia graveolens* in its native range. Further development is needed to investigate the host specificity and potential impact of *Coleosporium inulae* on non-target plant species.

Keywords: Basidiomycota, invasion, pathogen, Pucciniomycetes, rust, stinkwort, weeds.

INTRODUCTION

The genus *Dittrichia* (Asteraceae, Inuleae) comprises two species, *Dittrichia viscosa* (L.) Greuter, and *Dittrichia graveolens* (L.) Greuter that are both native to Eurasia (Greuter, 2006; NGRP, 2013). *Dittrichia graveolens*, known as stinkwort, is of particular interest as it has been introduced to several continents, including North America, where it is considered an invasive alien species. *Dittrichia graveolens*'s worst USA invasion is in California, where it was first reported from the San Jose area in 1984 (Preston, 1997). By 2012, it had spread to 36 counties (Brownsley et al., 2013), and by 2024, to

49 of California's 58 counties (CCH, 2024). Modelling studies indicate that most of *Dittrichia graveolens* ecological niche in California is still unfilled (Lustenhouwer & Parker, 2022). It is now present in at least six other USA states and has been classified as a major invader nationally by USDA-APHIS. *Dittrichia graveolens* is also a successful invader in Europe, where it moved from the Mediterranean basin towards central and Northern Europe like Romania, Poland, the Czech Republic, The Netherlands, Lithuania, etc. (Lustenhouwer & Parker, 2022; Roy et al., 2020; Gudžinskas, 2024). *Dittrichia graveolens* spreads on roadsides and highways and then invades the banks of canals, reservoirs and creeks, as well as row crop edges, tree crop and vineyard plantings, pastures and wildfire scars, threatening crop and livestock production, water resources and biodiversity. *Dittrichia graveolens* thrive in high-light, disturbed habitats and can tolerate a wide range of soil types (Lustenhouwer et al., 2024).

Among all management strategies for tackling the spread of *Dittrichia graveolens*, classical biological control is currently prioritised as considered safe and sustainable (Suckling & Sforza, 2014). As an initial step in any classical biological control programme, field surveys, also known as foreign exploration in the native range of the target invasive species, are a prerequisite (Borowiec & Sforza, 2022). This field investigation observes and collects natural enemies, including arthropods and plant pathogens. Among plant pathogens, rust fungi occupy a particular role as they are longer considered in classical biological control (Barton, 2012; Patejuk et al., 2024). They are often restricted to a single species with high impact damage on the target weed, such as *Puccinia chondrillina* Bubak & Syd. on rush skeleton weed, *Chondrilla juncea* L. (Hasan & Wapshere, 1973). Within the Asteraceae, the fungal pathogen *Puccinia spegazzinii* de Toni was introduced from Tropical America to various Asian countries against the weed *Mikania micrantha* Kunth. (Sforza, 2021).

Rust fungi (Pucciniales) are one of the largest groups of plant pathogens and the most damaging to plants worldwide (Kemen et al., 2015; Lorrain et al., 2019). Within the *Coleosporium* group, Asteraceae species are the most impacted family, with 110 species reported as hosts in Europe (Helfer, 2013). *Dittrichia graveolens* is listed as one of the hosts for *Coleosporium inulae* (G. Kunze) E. Fisch., which is also reported from 22 Asteraceae species, mainly from the Inuleae tribe (Helfer, 2013). *Coleosporium inulae* belongs to a complex of 20 *Coleosporium* species gathered into the *Coleosporium tussilaginis* complex (Klenke & Scholler, 2015). It has mainly been reported from Pinaceae as primary hosts, including but not limited to *Pinus mugo* Turra, *Pinus nigra* J.F. Arnold, *Pinus nigra* subsp. *laricio* Palib ex Maire*, Pinus pinaster* Aiton*, Pinus sylvestris* L. (Helfer, 2013; Ellis, 2024). The European species of the genus *Coleosporium* are impossible to distinguish morphologically (Helfer, 2013). Over the past decades, mycologists have intensely debated about having a single species of *Coleosporium tussilaginis* (Pers.) Tul. (Termorshuizen & Swertz, 2011), while Klenke & Scholler (2015) have advocated all species as independent. A consensus has been proposed by Helfer (2013) to grouping all described species into *formae speciales* of *Coleosporium tussilaginis*. If we consider the latter consensus, *Coleosporium tussilaginis* f. sp. *inulae* Helfer, 2013 (syn. *Coleosporium inulae* Rabenhorst, 1851) was first observed on *Pinus halepensis* Mill., and on Asteraceae in the tribe Inuleae particularly on *Dittrichia* and *Inula* genera, but there is limited information about the hosts (Helfer, 2013; Beenken et al., 2017). As the majority of Pucciniales, *Coleosporium inulae* is a heteroecious fungus that requires two specific and unrelated plant hosts to complete its life cycle by shifting between the aecial host from *Pinus* genus and the telial host from the Asteraceae family (EFSA, 2023). In the frame of a biocontrol programme against the alien weed *Dittrichia graveolens*, the current study will present new records of *Coleosporium inulae* on *Dittrichia graveolens* in Europe with considerations on the potential use of this rust fungus as a biocontrol candidate.

MATERIALS AND METHODS

Collection

Three collecting trips were scheduled in the autumn of 2023 and summer of 2024 to look for natural enemies of *Dittrichia graveolens*. A population of *Dittrichia graveolens* infected by rust was observed in the west of the island of Cyprus (34°57'44" N, 32°27'22" E) on 14 October 2023, one in Portugal at ca. 30 km northeast of Porto (41°15'21" N,

8°12'54" E) on 9 November 2024 and one in Southern France (43°33'41.81" N, 4°8'32.72" E) on 27 August 2024. Each population was found in fallow lands on road edges. For each location, ten leaves and stems presenting urediniospores were preserved in Eppendorf vials in 95% ethanol until molecular identification. Symptoms were also recorded. A voucher specimen from France was deposited at the Herbarium of the University of Montpellier (MPU), France, under the registration number MPU1471183.

Molecular identification

The collected samples were air-dried and then observed using a binocular microscope to collect spores with a scalpel for DNA extraction. Spores were transferred to an MP FastPrep Lysing matrix Tubes A or G in 400 µL of lysing buffer and disrupted in a tissue lyser instrument (FastPrep-24 instrument, MP Biomedicals) using programme mouse femur. Then, DNA was extracted using the Qiagen DNeasy Plant Mini Kit following the manufacturer's instructions. The DNA was used to amplify the 18S-ITS1–5.8S-ITS2 rDNA gene region with the two primer pairs: ITS1F/ITS4B (Gardes & Bruns, 1993) and NL1/NL4 (Kurtzman & Robnett, 1997). PCR were run in a CFX96 system (Biorad) in 25 µL PCR reaction containing 0.5 µL of each primer (10 µM), 0.5 µL of dNTP mix (10 mM each), 2.5 µL of CoralLoad 10× PCR Buffer, 0.2 µL of Taq DNA Polymerase, 18.8 µL of ddH2O, and 2µL of 1/10 diluted DNA. For the ITS1/ITS4B primer pair, PCR conditions were as follows: 94°C for 3 min; 35 cycles of 94°C for 30 s, 57°C for 60 s, 72°C for 60 s, finalising with an extension of 10 min at 72°C.

For the NL1/NL4 primer pair, PCR conditions were as follows: 94°C for 3 min; five cycles of 94°C for 30 s, 52°C for 60 s and 72°C for 60 s, 35 cycles of 94°C for 30 s, 54°C for 60 s and 72°C for 60s, finalising with an extension of 10 min at 72°C. PCR products were visualised in a 1% agarose gel (TAE buffer 0.5X) and compared to a 1 kb molecular weight marker (Smart Ladder 10 kb). PCR products were sequenced using amplification primers. Raw sequence data were cleaned and aligned using BioEdit and MEGA11 (Tamura et al., 2021). A similar search and identification was undertaken using blastn against the nr/Nr nucleotide collection on GenBank (National Center for Biotechnology Information). The obtained sequences were deposited in GenBank (Accession numbers: PP574452-PP574453; PQ451776). Phylogenetic analysis was conducted using ClustalW as implemented in MEGA11 (Tamura et al., 2021). The evolutionary history was inferred using the Neighbor-Joining method (Saitou & Nei, 1987). The optimal tree was shown. The percentage of replicate trees in which the associated taxa clustered together in the bootstrap test (500 replicates) was shown above the branches (Felsenstein, 1985). The tree was drawn to scale, with branch lengths in the same units as those of the evolutionary distances used to infer the phylogenetic tree. The evolutionary distances were computed using the Tamura 3-parameter method (Tamura, 1992) and are in the units of the number of base substitutions per site. The rate variation among sites was modelled with a gamma distribution (shape parameter = 1). This analysis involved 24 nucleotide sequences. All positions with less than 95% site coverage were eliminated, i.e., fewer than 5% alignment gaps, missing data, and ambiguous bases were allowed at any position (partial deletion option). There were a total of 478 positions in the final dataset.

Photography and microscopy

Only samples collected from France were observed under a stereo microscope Keyence VHX-7000 with various lenses. Fresh leaves with rust symptoms were directly photographed in one or two dimensions. Uredinia were scraped from rust-diseased *Dittrichia graveolens* plants, and urediniospores were observed and measured (n = 50) under an optical microscope (Leica DMLB). Values were reported with the mean ± SE and the minimum and maximum values in brackets. Digital images were obtained with a PATH4K microscope digital camera.

RESULTS

Disease symptoms

From the field, the main symptoms induced by *Coleosporium inulae* on the telial host *Dittrichia graveolens* were orange-yellow uredinia (Fig. 1, A, C, D) on the lower and upper side (less common) of

the leaves and on stems (Fig. 1, E–F). Uredinia were polymorphic (Fig. 1, F, H, I), and urediniospores had a circular or a cylindrical shape (Fig. 1, I) with mean urediniospores size 28.20 (21.92–36.97) ± SE 3.06 × 20.69 (17.20–24.58) ± SE 1.8 µm, n = 50 (Fig. 1, G). Spermagonia and aecia were not observed. Infection by *Coleosporium inulae* could be observed in summer (France) until late autumn (France, Cyprus, Portugal). No symptoms were reported on flowerheads during all vegetative cycles (Fig. 1, C–D). In the fields of Cyprus and France, we noticed early necrotic dark areas developing on the leaf surface next to uredenia (Fig. 1, E), leading to a very severe and general infection to the whole plant with leaf distortion, blackening of stems and leaves, leading to mortality as early as late August in France and Cyprus (Fig. 1 B). More than 90% (visually estimated) of a 400 m^2 field with *Dittrichia graveolens* in Cyprus was infected (Fig. 1 B). The symptoms observed in Portugal were similar (Fig. 1, D), but on a minimal number of plants compared to Cyprus and France.

Molecular characterisation

Sequences obtained from samples collected in Cyprus and France were 100% identical and shared 99.77% identity with the one from Portugal, which differs in two base pairs. Homology search assigned all three sequences to *Coleosporium inulae* and revealed 99.53% identity to sequence of *Coleosporium inulae* reported in Switzerland on *Inula salicina* (GenBank KY810470) and 99.16% with an isolate from Germany on *Pinus sylvestris* (GenBank KY783673). Sequences of *Coleosporium inulae* and other sequences from related taxa were retrieved from GenBank to conduct phylogenetic analysis. The phylogenetic tree constructed using the Neighbour-Joining method showed that the sequences obtained in this study grouped into a single clade with other *Coleosporium inulae* sequences obtained from telial host plants belonging to *Inula* or *Dittrichia* genera and the aecial host plant *Pinus sylvestris* (Fig. 2).

DISCUSSION

The current study shows new hits for the distribution of *Coleosporium inulae on Dittrichia graveolens* across the Mediterranean basin. This confirms the widespread status of this rust fungus. Its impact on *Dittrichia graveolens* stands is variable in intensity, with red spots on few leaves in most of the populations surveyed. Still, the one observed in Cyprus exhibited severe symptoms leading to death of the plants. This heterogeneity in field symptom expression cannot be explained at this stage. One possibility could be the presence (Cyprus) or absence (France, Portugal) of reinfections among secondary hosts, e.g. *Dittrichia graveolens* and other species in the Inulae tribe. For example, *Coleosporium ipomoeae* (Schwein.) Burrill, another heteroecious fungus, can infect *Ipomea* sp. by producing urediniospores that reinfect multiple secondary hosts, with up to 15 asexual generations occurring during the summer (Chappell & Rausher, 2016).

Based on the updated literature, the high host plant diversity for *Coleosporium tussilaginis* f. sp. *inulae* (Helfer, 2013) would not be compatible with a biocontrol programme. However, Blanz & Zwetko (2018) have noticed some inconsistency in the shape of urediniospores in the *Coleosporium tussilaginis* cluster and suggest that "*infection and molecular studies are promising"* for sorting out species from *formae speciales*. Some new species with narrower hosts could arise from additional studies. Interestingly, despite the large geographical distances between Cyprus and Western European collecting sites, we showed a high homogeneity in the *Coleosporium inulae* sequences. In addition, our sequences fall within a large cluster with *Coleosporium inulae* recorded from Germany, Greece and Switzerland. However, besides this observed molecular similarity within *Coleosporium inulae* sequences obtained from six European countries, we cannot exclude the existence of genotypes of *Coleosporium inulae* that would be more specific toward one single host plant, namely *Dittrichia graveolens*, as has been demonstrated in *Coleosporium ipomoeae* (Chappell & Rausher, 2016).

Cross-inoculations between *Coleosporium inulae* collected on *Dittrichia graveolens* at a specific site and host plants of different species, i.e. *Inula* sp. and *Dittrichia* sp., would provide valuable information on the specificity of a particular pathogen genotype. However, its heteroecious cycle is the main constraint to considering *Coleosporium inulae* as a potential biocontrol agent. In this study, the aecial host (carrying aecidiospores) in the three countries

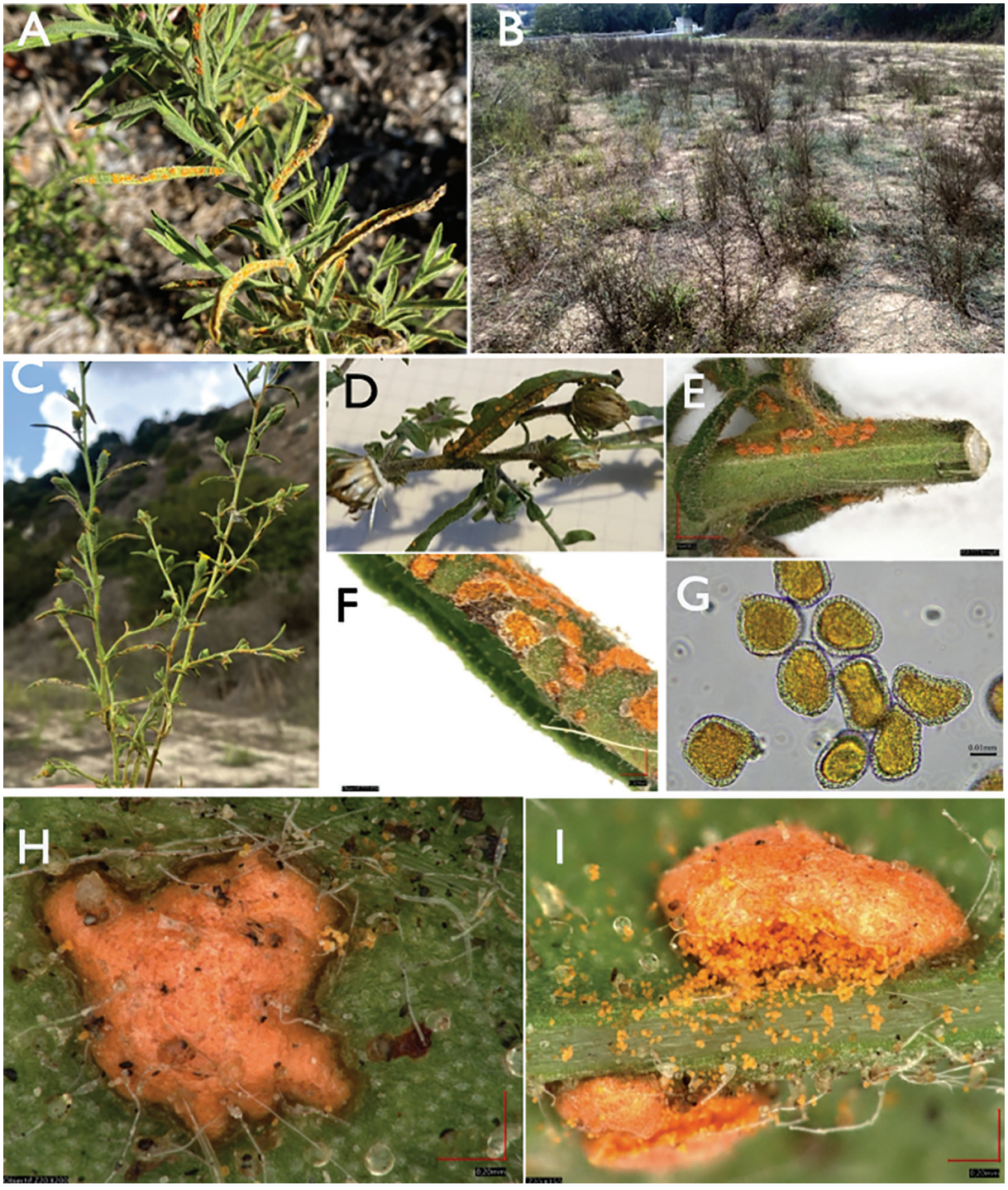

Fig. 1. A – **s**ymptoms of *Coleosporium inulae* on leaves of *Dittrichia graveolens* at Le Grau du Roi (France); B – population of *Dittrichia graveolens* infected by *Coleosporium inulae* at different phenological stages like green plants and black dead plants; C – *Dittrichia graveolens* infected by *Coleosporium inulae* on leaves during the flowering stage in Cyprus; D – *Dittrichia graveolens* infected by *Coleosporium inulae* on leaves during the seeding stage in Portugal; E – infected stem of *Dittrichia graveolens*; F – uredinia and necrotic areas in dark brown colour; G – urediniospores of *Coleosporium inulae* under an optical microscope; H – closed uredinium on the leaf surface; I – open uredinium with spores spreading on the leaf surface. Photographs of uredinia (E–I, except G) taken using Keyence VHX-7000 stereo microscope (Photographs by R.F.H. Sforza (A–I) and M. Tannières (G).

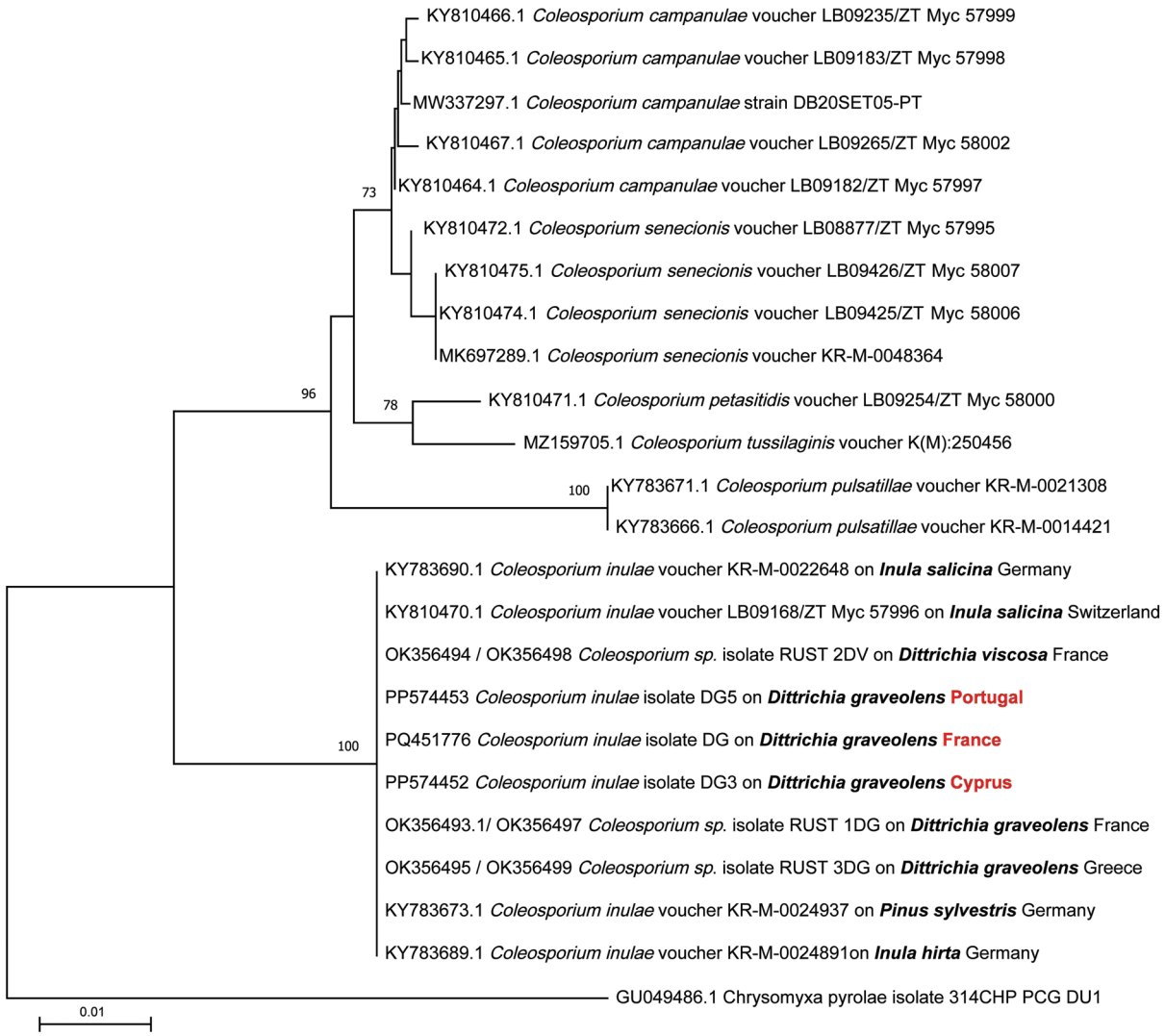

Fig. 2. The phylogenetic tree of *Coleosporium* species includes our sequences from Portugal, France and Cyprus (in red).

surveyed (France, Portugal and Cyprus) is still unknown. However, Pinaceae species are likely natural primary hosts (Helfer, 2013). This host alternating on pine trees may complicate further studies on host specificity to evaluate the impact of *Coleosporium inulae* on *Dittrichia graveolens* and closely related species in a biological control programme. To date, *Coleosporium* species have been considered for biocontrol purposes, such as *Coleosporium ipomoeae* on *Ipomoea fistulosa* Mart. ex Choisy in Brazil (Vieira et al., 2004), or *Coleosporium* sp. on *Ailanthus altissima* (Mill.) in China (Ding et al., 2006).

The current study is still preliminary but will lead to indoor tests with the French inoculum of *Coleosporium inulae* to fulfil Koch's postulates and investigate the host specificity among non-target species in the Inuleae tribe. As discussed above, the infection of undesired *Pinus* species in the case of classical biocontrol in the USA with a European rust strain remains a serious issue with minimal positive outcomes. However, one way would be to consider classical biological control within European countries that are becoming invaded with *Dittrichia graveolens* (e.g. central Europe, like Slovakia, the Czech Republik, Poland, The Netherlands, Lithuania, etc.) (Lustenhouwer & Parker, 2022; Roy et al., 2020; Gudžinskas, 2024) that may share similar *Pinus* species, like *Pinus sylvestris* L. (Bruxaux et al., 2024),

that the country of origin of the current candidate *Coleosporium inulae*. Investigating in the countries from central Europe would also be worthwhile to study local infection with an already on-site *Coleosporium inulae* strain to prevent the spillover phenomenon, where introduced species can become invasive themselves (Patejuk et al., 2024). In a recent study, Gudžinskas (2024) has listed no less than 12 sympatric plant species surrounding *Dittrichia graveolens* in Lithuania, but none belong to the Inuleae tribe. As *Coleosporium inulae* was collected and morphologically identified from plants belonging at 96% to the Inuleae tribe (Helfer, 2013), this would minimise the risk of an adverse impact. *Coleosporium inulae* has already been recorded from 28 European countries, including Lithuania and Poland, which might provide local rust strains for attacking invasive populations of *Dittrichia graveolens* in northern Europe (Helfer, 2013). In that perspective, one preliminary step would be to document, in laboratory and field conditions, the host specificity of each strain of *Coleosporium inulae* that would be used for field release to prevent non-target impacts and be equally damaging and safe (Tanner et al., 2005). Then, once inoculated, urediniospores spread through the population by wind and convection currents, giving them high mobility (Morin et al., 2012), will naturally colonise the invaded environment.

Based on the successful and widespread contamination of a *Dittrichia graveolens* plot by *Coleosporium inulae* in western Cyprus, one might think that there is a strong potential for inundative release of a liquid suspension of urediniospores (Tanner et al., 2005; Tan et al., 2024) at a defined concentration over invaded populations in central and northern Europe.

Although the use of *Coleosporium inulae* as a biocontrol agent seems complex due to its heteroecious life cycle, the overall findings extend our knowledge on the distribution and the composition of the assemblage of natural enemies of *Dittrichia graveolens* in the native range.

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