ACTA SCIENTIARUM POLONORUM

Acta Sci. Pol. Hortorum Cultus, 25(5) 2026, 81–90

https://czasopisma.up.lublin.pl/index.php/asphc ISSN 1644-0692 e-ISSN 2545-1405 https://doi.org/10.24326/asphc.2026.5742

REVIEW PAPER

Received: 11.07.2026
Accepted: 2.10.2026
Issue published: 30.10.2026

OCCURRENCE AND PROPERTIES OF ENDOPHYTIC FUNGI OF THYME (*Thymus* spp.)

Beata Zimowska[1], Rosario Nicoletti[2]

ABSTRACT

Endophytic fungi constitute an important yet still poorly explored component of the microbiome of thyme (*Thymus* spp.). This review summarizes the current knowledge on their diversity, ecological functions, and biotechnological potential based on literature published up to April 2026. Reported endophytes represent a diverse taxonomic community, comprising 49 genera and 53 species most of which belong to common ascomycete genera, such as *Alternaria*, *Fusarium*, *Colletotrichum*, *Aspergillus*, *Penicillium*, *Phoma*, and *Trichoderma*. Current evidence from experiments carried out *in planta* indicates that these microorganisms may contribute to plant growth promotion, enhanced tolerance to abiotic stress, modulation of essential oil production, and protection against plant pathogens through the synthesis of bioactive metabolites and volatile organic compounds. Moreover, in *in vitro* assays several isolates have demonstrated antimicrobial, antioxidant, cytotoxic, and enzyme-producing activities, highlighting their promising applications in sustainable agriculture and biotechnology. Although significant progress has been achieved, many aspects of the ecology, host specificity, and functional interactions of thyme-associated fungal endophytes remain insufficiently understood.

Keywords: thyme, Lamiaceae, endophytes, essential oils, defensive mutualism, growth promotion

INTRODUCTION

Endophytic fungi are polyphyletic microorganisms that inhabit plants without inducing overt negative effects on their health, eventually establishing mutualistic relationships with the host. For a long time, the widespread assumption that pathogens basically were the only microorganisms capable of colonizing living plant tissues has delayed recognition that endophytic fungi are constantly associated with plants and can significantly influence their ecological fitness. Currently, they are regarded as a reservoir of unexplored biodiversity, awaiting to be exploited as plant protection agents or growth promoters, as well as for a variety of biotechnological applications [Nicoletti and Fiorentino 2015, Yadav et al. 2022]. Indeed, many studies have shown that these microbial associates may improve plant fitness through various interactions with agents of biotic adversities, such as antibiosis, parasitism, competition for space and nutrients, and the promotion of tolerance and resistance mechanisms [Rabiey et al. 2019, Morelli et al. 2020]. Moreover, their recognized role in growth promotion supports their consideration as genuine and effective plant probiotics [Pandey et al. 2022]. Beyond the intrinsic effects/properties of single strains or species, a more comprehensive ecological approach should consider that endophytes may perform these functions in the form of interacting consortia with other components of the plant microbiome [Adeleke et al. 2022].

[1] University of Life Sciences, Department of Plant Protection, Leszczyńskiego 7, 20-069 Lublin, Poland, https://orcid.org/0000-0001-5524-7623; corresponding author: beata.zimowska@up.edu.pl
[2] Council for Agricultural Research and Economics, Research Center Olive, Fruit and Citrus Crops, Via Torrino, 81100 Caserta, Italy, https://orcid.org/0000-0002-3049-4641

© Copyright by the Author(s), 2026
Licensee University of Life Sciences in Lublin – Publishing House, Lublin, Poland
This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution 4.0 International license.

As with other medicinal plants, the cultivation of thyme (*Thymus vulgaris* and other *Thymus* spp.) has recently expanded, owing to its increasing use in gastronomy and the cosmetic industry [Nieto 2020, Halat et al. 2022, Waheed et al. 2024]. This ongoing boost especially concerns the organic farms, where adherence to the principles of integrated pest management is particularly important. Thus, insights into the organization of the plant associated microbes are crucial to improve our understanding of their ecological role, as well as to promote practical applications. Unlike endophytic bacteria, whose interactions with thyme have recently been the subject of several studies [Checcucci et al. 2017, Mohamad et al. 2020, 2022, Musa et al. 2020, Abdel-Hamid et al. 2021, Delbari et al. 2023, Zhao et al. 2023], the impact of endophytic fungi is less studied and recognized. In addition to endophytism in the strict sense, some fungal species have been reported to participate in a tritrophic association including gall midges of the genus *Asphondylia* (Diptera, Cecidomyidae) [Malagaris 2011, Zimowska et al. 2017, 2020, 2021]. This paper provides an overview of the occurrence and properties of the endophytic symbionts associated with thyme, based on the examination of the literature published until April 2026. To this end, we searched the Google Scholar and PubMed databases using the terms 'thyme endophytic fungi' and '*Thymus* endophytic fungi', without any time restriction and excluding only unpublished dissertations and degree theses.

Botanical notes on *Thymus* L.

The genus *Thymus* L. is one of the most diverse and taxonomically challenging groups within the family Lamiaceae. Belonging to the tribe Mentheae and subtribe Menthinae, the genus comprises approximately 220–250 species of perennial aromatic herbs and dwarf shrubs distributed primarily throughout the Mediterranean basin and adjacent regions of Europe, North Africa, Macaronesia, and temperate Asia extending eastwards to the Himalayas [Morales 2002, Drew and Sytsma 2012]. The Mediterranean basin represents the principal center of diversification of *Thymus*, where repeated geological, climatic, and ecological processes have promoted extensive speciation and local endemism. Major diversity hotspots occur in the Iberian peninsula, southern France, Italy, the Balkan peninsula, Greece, Anatolia, and the Caucasus, while secondary centers of diversification extend into the Irano-Turanian region and western Asia [Morales 2002, Celep and Dirmenci 2017, Bartolucci and Nachychko 2025, Bahadori et al. 2026].

Modern molecular studies generally support the monophyly of *Thymus*, although relationships among infrageneric groups remain incompletely resolved and continue to be refined through phylogenomic analyses [Soorni et al. 2019, Nieto-Lugilde et al. 2026].

The complexity of *Thymus* taxonomy arises from a combination of extensive morphological variability, ecological specialization, local endemism, hybridization, polyploidization, and the proliferation of names introduced during the eighteenth and nineteenth centuries. As botanical exploration intensified across Europe and the Mediterranean region, numerous taxa were described based on subtle differences in vegetative or floral morphology, generating extensive synonymy and uncertain species circumscriptions. Consequently, modern taxonomic studies have focused on stabilizing nomenclature through typification and critical revision of historical names. Important advances in this regard were achieved by Bartolucci et al. [2013], who clarified the application of several names through lectotypification and taxonomic annotations, and by Bartolucci and Nachychko [2025], whose comprehensive revision for the Euro+Med PlantBase provided updated nomenclature, typifications, synonymies, and distributional data for the genus.

Morphological plasticity is particularly pronounced and frequently obscures taxonomic boundaries. Plant size, growth form, leaf morphology, pubescence, and inflorescence architecture may vary substantially in response to environmental conditions including altitude, substrate, grazing pressure, drought intensity, and exposure. Consequently, populations belonging to a single species may exhibit remarkable phenotypic divergence across ecological gradients, whereas unrelated taxa occupying similar habitats may converge morphologically [Morales 2002, Federici et al. 2013].

Hybridization represents another major source of taxonomic complexity. Natural hybrids have been documented throughout the genus, particularly in regions where closely related species occur sympatrically. Hybrid populations often display intermediate morphological characteristics and mixed phytochemical profiles, complicating species identification and obscuring evolutionary relationships. Furthermore, several species complexes exhibit extensive polyploid variation, including diploid, tetraploid, and higher polyploid cytotypes. Polyploidization has long been recognized as an important evolutionary mechanism

within *Thymus*, but recent genomic investigations have demonstrated that interploidy gene flow may be far more widespread than previously assumed

The advent of molecular systematics has greatly improved understanding of evolutionary relationships within the genus, revealing the limitations of the traditional morphology-based classifications. Federici et al. [2013], using DNA barcoding approaches, demonstrated that standard plant barcode markers often fail to discriminate closely related species of *Thymus*, reflecting recent evolutionary divergence, incomplete lineage sorting, and shared ancestral polymorphism. Their results emphasized the need for integrative approaches combining molecular and morphological evidence. More recently, advances in phylogenomics have provided unprecedented insights into species relationships and diversification processes. A comprehensive genomic study of *Thymus* sect. *Mastichina* demonstrated that patterns of morphological variation, ecological niche differentiation, and genomic structure do not always coincide, revealing extensive historical introgression and complex evolutionary histories among the currently recognized taxa [Nieto-Lugilde et al. 2026]. These findings suggest that species boundaries within some groups of *Thymus* are considerably more dynamic and permeable than previously assumed.

The genus is also renowned for its extraordinary chemical diversity. *Thymus* species produce a wide range of essential oils (EOs), including thymol, carvacrol, linalool, geraniol, borneol, γ-terpinene, and *p*-cymene. These compounds play important ecological roles in defense against herbivores and pathogens and determine the economic significance of thyme species in medicine, food preservation, cosmetics, and perfumery [Etri and Pluhár 2024]. Chemotaxonomic studies have traditionally been used to support species delimitation; however, growing evidence indicates that phytochemical variation does not necessarily correspond to taxonomic boundaries. Najar et al. [2021] demonstrated the persistence of distinct thymol and linalool chemotypes within cultivated populations of *T. vulgaris* in central Italy, while Del Valle et al. [2026] showed that EO composition is shaped by a complex interaction between genetic background and environmental conditions. Consequently, although phytochemical profiles remain valuable taxonomic characters, they should not be used independently for species recognition.

Occurrence of endophytic fungi in *Thymus* spp.

A list of the fungal species so far identified as endophytic associates of *Thymus* spp. is provided in Table 1, along with details on the geographical locations and the part of the plant from which isolations were carried out. Most of the findings refer to direct isolation in axenic cultures, after external sterilization of the tissues excised from the plants. However, in one case the report was based on direct microscopic observation; particularly, the arbuscular mycorrhizal fungi *Acaulospora gedanensis* and three *Glomus*-like species (namely, *Entrophospora claroidea*, *Planticonsortium tenue* and *Rhizophagus fasciculatus*) were identified in the roots of *T. vulgaris* plants growing at the Garden of Medicinal Plants of the Jagiellonian University in Kraków (Poland), along with resting spores of *Olpidium* sp. and dark septate endophytes [Zubek and Błaszkowski 2009]. Taxonomic identification of the accessions in Table 1 was based exclusively on morphological characters, with two exceptions: an isolate ascribed to *Trichoderma samuelsii* (Sordariomycetes, Hypocreales), as resulting from the sequence homology of three selected molecular markers (ITS, *tef1* and *rpb2*) [Ma et al. 2023], and an isolate classified as *Neopestalotiopsis aotearoa* (Sordariomycetes, Amphisphaeriales) based on 18S rDNA sequence homology [Abdelhamid et al. 2024]. However, in the latter case it must be considered that 18S is insufficient as a marker for a reliable species identification [López et al. 2026].

The available data do not allow us to make conjectures on any specific or systematic association with *Thymus* spp. of a defined fungal species. Within a sample of 11 endophytic fungi recovered from *T. vulgaris* at the Garden of Medicinal and Aromatic Plants of the Agriculture Research Centre in Giza (Egypt), *Aspergillus terreus* was the most frequently recovered species, represented by five isolates [Ali et al. 2018]. In an investigation carried out in Austria *Colletotrichum gloeosporioides* and *Ascochyta* sp. were found to be the dominant endophytic fungi, respectively in leaves and stems of *Thymus serpyllum* and *Thymus polytrichus* (currently *Thymus praecox* subsp. *polytrichus*), while *Alternaria alternata* was the most frequent species recovered from *Thymus capitatus* (syn. *Thymbra capitata*), *Thymus herba-barona* and *Thymus richardii* at the island of Mallorca, Spain [Fisher et al. 1992]. As a whole, more than 400 isolates from about 30 species were obtained in this study carried out over 30 years ago, which still represents the largest survey of endophytic fungi conducted on thyme.

Table 1. Fungi reported for endophytic occurrence in *Thymus* spp.

Fungal species	*Thymus* species *	Location	Reference
Acaulospora gedanensis	*T. vulgaris* R	Kraków, Poland	Zubek and Błaszkowski 2009
*Allophoma tropica***	*T. eriocalyx* L	Hamedan, Iran	Masumi et al. 2015
Alternaria alternata	*T. capitatus* L-S, *T. herba-barona* S, *T. richardii* S	Mallorca, Spain	Fisher et al. 1992
	T. eriocalyx L-S, *T. fallax* L, *T. kotschyanus* S, *T. lancifolius* L	Hamedan, Iran	Masumi et al. 2015
	T. vulgaris S	Alsharqia, Egypt	Olama et al. 2023
*Alternaria atra***	*T. vulgaris* S	Hamedan, Iran	Masumi et al. 2015
Alternaria franseriae	*T. eriocalyx* L, *T. kotschyanus* L, *T. lancifolius* L	Hamedan, Iran	Masumi et al. 2015
*Alternaria gossypina*** *(A. tangelonis)*	*T. eriocalyx* L-S, *T. kotschyanus* L-S, *T. lancifolius* L	Hamedan, Iran	Masumi et al. 2015
Alternaria sp.	*T. capitatus* S, *T. herba-barona* S, *T. richardii* S	Mallorca, Spain	Fisher et al. 1992
	T. polytrichus L	Altaussee, Austria	
	T. eriocalyx L, *T. lancifolius* L	Hamedan, Iran	Masumi et al. 2015
	T. algeriensis R	Bordj Bou Arreridj, Algeria	Zerroug and Sadrati 2022
	T. vulgaris S	Alsharqia, Egypt	Olama et al. 2023
Anthostomella sp.	*T. capitatus* S, *T. richardii* S	Mallorca, Spain	Fisher et al. 1992
Ascochyta sp.	*T. polytrichus* L-S, *T. serpyllum* L-S	Altaussee, Austria	Fisher et al. 1992
	T. richardii S	Mallorca, Spain	
Aspergillus japonicus	*T. vulgaris* L	Giza, Egypt	Ali et al. 2018
Aspergillus sp.	*T. fallax* L	Hamedan, Iran	Masumi et al. 2015
	T. algeriensis R	Bordj Bou Arreridj, Algeria	Zerroug and Sadrati 2022
Aspergillus terreus	*T. vulgaris* L	Giza, Egypt	Ali et al. 2018
Asteromella sp.	*T. polytrichus* L	Altaussee, Austria	Fisher et al. 1992
Aureobasidium pullulans	*T. serpyllum* L	Altaussee, Austria	Fisher et al. 1992
Aureobasidium sp.	*T. capitatus* S	Mallorca, Spain	Fisher et al. 1992
Boeremia exigua var. *exigua***	*T. vulgaris* L-R-S	Fajsławice, Poland	Machowicz-Stefaniak et al. 2002
Botrytis cinerea	*T. serpyllum* S	Altaussee, Austria	Fisher et al. 1992
Chaetosphaeronema sp.	*Thymus* sp. S	Hamedan, Iran	Mirzaei et al. 2023
Cladosporium cladosporioides	*T. eriocalyx* L, *T. lancifolius* L	Hamedan, Iran	Masumi et al. 2015
Cladosporium oxysporum	*T. serpyllum* L	Altaussee, Austria	Fisher et al. 1992
Cladosporium tenuissimum	*T. polytrichus* L-S	Altaussee, Austria	Fisher et al. 1992
	T. capitatus S, *T. herba-barona* L	Mallorca, Spain	
Cladosporium variabile	*T. eriocalyx* L, *T. kotschyanus* L	Hamedan, Iran	Masumi et al. 2015
Colletotrichum dematium	*T. polytrichus* S	Altaussee, Austria	Fisher et al. 1992
	T. herba-barona S	Mallorca, Spain	
Colletotrichum gloeosporioides	*T. serpyllum* L-S	Altaussee, Austria	Fisher et al. 1992
Colletotrichum sp.	*T. kotschyanus* L-R	Hamedan, Iran	Masumi et al. 2015
Coniochaeta tetraspora	*T. capitatus* L-S, *T. richardii* S	Mallorca, Spain	Fisher et al. 1992
Curvularia akaii	*T. eriocalyx* S, *T. kotschyanus* S	Hamedan, Iran	Masumi et al. 2015
Cylindrocarpon sp.	*T. eriocalyx* R	Hamedan, Iran	Masumi et al. 2015
dark septate endophytes	*T. vulgaris* R	Kraków, Poland	Zubek and Błaszkowski 2009
Diaporthe sp.**	*T. polytrichus* L, *T. serpyllum* L	Altaussee, Austria	Fisher et al. 1992
*Didymella glomerata***	*T. vulgaris* L-R-S	Fajsławice, Poland	Machowicz-Stefaniak et al. 2002
	T. eriocalyx L	Hamedan, Iran	Masumi et al. 2015
*Didymella pomorum***	*T. capitatus* L-S	Mallorca, Spain	Fisher et al. 1992
Diplodia sp.	*T. capitatus* S	Mallorca, Spain	Fisher et al. 1992
*Ectophoma multirostrata***	*T. vulgaris* L-R-S	Fajsławice, Poland	Machowicz-Stefaniak et al. 2002
*Ectophoma pomi***	*T. kotschyanus* L-S	Hamedan, Iran	Masumi et al. 2015
*Entrophospora claroidea***	*T. vulgaris* R	Kraków, Poland	Zubek and Błaszkowski 2009
Fusarium acuminatum	*T. eriocalyx* S	Hamedan, Iran	Masumi et al. 2015
Fusarium equiseti	*T. eriocalyx* S	Hamedan, Iran	Masumi et al. 2015
Fusarium javanicum	*T. fallax* R	Hamedan, Iran	Masumi et al. 2015
Fusarium lateritium	*T. eriocalyx* S	Hamedan, Iran	Masumi et al. 2015
Fusarium oxysporum	*T. daenensis* L, *T. kotschyanus* S	Hamedan, Iran	Masumi et al. 2015

Fungal species	*Thymus* species *	Location	Reference
Fusarium reticulatum	*T. eriocalyx* F-S	Hamedan, Iran	Masumi et al. 2015
Fusarium sp.	*T. eriocalyx* L, *T. kotschyanus* R	Hamedan, Iran	Masumi et al. 2015
	T. algeriensis R	Bordj Bou Arreridj, Algeria	Zerroug and Sadrati 2022
	T. vulgaris S	Alsharqia, Egypt	Olama et al. 2023
Fusarium subglutinans	*T. eriocalyx* S	Hamedan, Iran	Masumi et al. 2015
Fusarium tricinctum	*T. polytrichus* S	Altaussee, Austria	Fisher et al. 1992
Gilmaniella humicola	*T. richardii* S	Mallorca, Spain	Fisher et al. 1992
Godronia sp.**	*T. herba-barona* S, *T. richardii* S	Mallorca, Spain	Fisher et al. 1992
*Heterophoma nobilis***	*T. vulgaris* L-R-S	Fajsławice, Poland	Machowicz-Stefaniak et al. 2002
Hormonema sp.	*T. richardii* S	Mallorca, Spain	Fisher et al. 1992
Hypoxylon sp.**	*T. capitatus* S, *T. richardii* S	Mallorca, Spain	Fisher et al. 1992
Mycelia sterilia	*T. polytrichus* L, *T. serpyllum* L-S	Altaussee, Austria	Fisher et al. 1992
	T. capitatus S, *T. herba-barona* L-S, *T. richardii* L-S	Mallorca, Spain	
	T. vulgaris L	Giza, Egypt	Ali et al. 2018
	T. daenensis R, *T. eriocalyx* F-L-R-S, *T. kotschyanus* R-S, *T. lancifolius* L, *T. vulgaris* S	Hamedan, Iran	Masumi et al. 2015
Neopestalotiopsis aotearoa	*T. vulgaris* S	Mansoura, Egypt	Abdelhamid et al. 2024
Olpidium sp.	*T. vulgaris* R	Kraków, Poland	Zubek and Błaszkowski 2009
*Paraboeremia selaginellae***	*T. eriocalyx* L	Hamedan, Iran	Masumi et al. 2015
*Paraphoma chrysanthemicola***	*T. eriocalyx* F	Hamedan, Iran	Masumi et al. 2015
Penicillium chrysogenum	*T. vulgaris* L	Giza, Egypt	Ali et al. 2018
Penicillium sp.	*T. algeriensis* S	Bordj Bou Arreridj, Algeria	Zerroug and Sadrati 2022
Phialophora sp.	*T. richardii* L-S	Mallorca, Spain	Fisher et al. 1992
Phoma haematocycla	*T. daenensis* L	Hamedan, Iran	Masumi et al. 2015
Phoma sp.	*T. polytrichus* L-S, *T. serpyllum* L-S	Altaussee, Austria	Fisher et al. 1992
	T. capitatus S, *T. herba-barona* L-S, *T. richardii* L-S	Mallorca, Spain	
	T. eriocalyx S	Hamedan, Iran	Masumi et al. 2015
	T. algeriensis L	Bordj Bou Arreridj, Algeria	Zerroug and Sadrati 2022
*Planticonsortium tenue***	*T. vulgaris* R	Kraków, Poland	Zubek and Błaszkowski 2009
*Plenodomus pimpinellae***	*T. eriocalyx* S	Hamedan, Iran	Masumi et al. 2015
*Pyrenophora dematioidea***	*T. daenensis* L	Hamedan, Iran	Masumi et al. 2015
*Pyrenophora tetrarrhenae***	*T. eriocalyx* S	Hamedan, Iran	Masumi et al. 2015
*Rhizophagus fasciculatus***	*T. vulgaris* R	Kraków, Poland	Zubek and Błaszkowski 2009
Rhizopus sp.	*T. algeriensis* R	Bordj Bou Arreridj, Algeria	Zerroug and Sadrati 2022
*Sclerophomella glaucii***	*T. vulgaris* L-R-S	Fajsławice, Poland	Machowicz-Stefaniak et al. 2002
Septoria sp.	*T. polytrichus* L-S, *T. serpyllum* L-S	Altaussee, Austria	Fisher et al. 1992
	T. capitatus S, *T. richardii* L	Mallorca, Spain	
Sordaria fimicola	*T. richardii* S	Mallorca, Spain	Fisher et al. 1992
Sporormiella intermedia	*T. richardii* L	Mallorca, Spain	Fisher et al. 1992
Stemphylium sp.	*T. lancifolius* L	Hamedan, Iran	Masumi et al. 2015
*Stemphylium vesicarium***	*T. capitatus* S, *T. richardii* S	Mallorca, Spain	Fisher et al. 1992
*Subplenodomus valerianae***	*T. eriocalyx* R, *T. kotschyanus* L-S	Hamedan, Iran	Masumi et al. 2015
Taeniolella stilbospora	*T. herba-barona* S	Mallorca, Spain	Fisher et al. 1992
Trichoderma harzianum	*T. serpyllum* S	Altaussee, Austria	Fisher et al. 1992
Trichoderma samuelsii	*T. mongolicus*	Yinchuan, China	Ma et al. 2023
unidentified yeasts	*T. eriocalyx* L-S, *T. fallax* S, *T. lancifolius* S	Hamedan, Iran Central and Western Iran	Masumi et al. 2015 Masumi et al. 2015b
*Westerdykella capitulum***	*T. vulgaris* L-R-S	Fajsławice, Poland	Machowicz-Stefaniak et al. 2002
	T. eriocalyx L	Hamedan, Iran	Masumi et al. 2015

* *T. lancifolius* and *T. polytrichus* are now regarded as subspecies of *T. daenensis* and *T. praecox*, respectively.
** For these records, the species names were updated according to Mycobank.
F: flower; L: leaf; R: root; S: stem

Another large set of isolates (95) was collected in a study carried out in the Hamedan province of Iran considering six *Thymus* species: once more, *A. alternata* was the most common endophyte with 16 isolates recovered from all the above-ground plant parts, followed by several species identified within the genera *Fusarium* and *Phoma sensu lato* [Masumi et al. 2015a]. Fungi belonging to the above three genera were again the most frequent in an investigation carried out on *Thymus algeriensis* in Algeria [Zerroug and Sadrati 2022], while *Alternaria* and *Fusarium* were the only genera represented in a small sample of five isolates recovered from *T. vulgaris* in Egypt [Olama et al. 2023]. Moreover, earlier investigations on field-grown *T. vulgaris* in the Lublin region of Poland documented a diverse assemblage of *Phoma sensu lato* fungi colonizing shoots, leaves and, less frequently, roots of *T. vulgaris*. Several species were identified that have been recently renamed after taxonomic revision, with the new binomial indicated in brackets: *Phoma capitulum* (= *Westerdykella capitulum*), *P. glaucii* (= *Sclerophomella glaucii*), *P. dictamnicola* (= *Heterophoma nobilis*), *P. glomerata* (= *Didymella glomerata*), *P. multirostrata* var. *microspora* (= *Ectophoma multirostrata*), and *P. exigua* var. *exigua* (*Boeremia exigua* var. *exigua*) [Machowicz-Stefaniak et al. 2002]. Subsequent pathogenicity studies demonstrated that, among these taxa, only *P. exigua* var. *exigua* was confirmed as an occasional (facultative) pathogen of thyme, causing reduced seed germination, seedling damping-off, and necrosis of roots and hypocotyls following artificial inoculation [Machowicz-Stefaniak et. al. 2008], whereas the remaining species were reported only as endophytic colonizers, without any evidence of pathogenicity. Besides *Phoma* [Zimowska 2022], *Alternaria* and *Fusarium* are also under revision with reference to the recent concepts in fungal taxonomy [Li et al. 2022, Crous et al. 2022]; hence, a re-interpretation according to the updated nomenclature is desirable and appropriate for the available data concerning these genera, which have also been reported among the most common endophytic associates of many other plant species [Ahmed et al. 2023, Nicoletti et al. 2020, Manathunga et al. 2024, Nicoletti and Zimowska 2023].

Biochemical and ecological properties of endophytic fungi in *Thymus* spp.

It is a key issue in mycological research to accurately investigate the biochemical properties of endophytic fungi in view of possible biotechnological exploitation [Gupta et al. 2023, Agrawal and Bhatt 2023]. Indeed, secondary metabolites are regarded as the main factor influencing the interspecific relationships established with both the plant host and all components of its associated microbiome, with substantial effects on plant growth and protection. With reference to *Thymus* spp., it has been shown that the EOs contained in the leaf glandular tissues represent one of the primary selective factors shaping the endophytic community composition [Checcucci et al. 2017].

As also demonstrated on several crop species, the beneficial effects of two well-known endophytic basidiomycetes belonging to the Sebacinales, namely *Serendipita* (= *Sebacina*) *vermifera* and *Serendipita* (= *Piriformospora*) *indica* [Ray and Craven 2016, Saleem et al. 2022], have been documented on *T. vulgaris* plants cultured *in vitro* and *in vivo*. Besides an increase in height and root length, as well as in fresh and dry weights of shoots and roots, oil yield was found to be enhanced in all the inoculated plants, and its analysis carried out by means of gas chromatography coupled with mass spectrometry (GC-MS) showed a notably increased content of thymol along with a decrease in its isomer carvacrol [Dolatabadi et al. 2011].

At least in part, the growth-promoting effects induced by Sebacinales are attributed to the direct and indirect production of auxins and other phytohormones. In this respect, more circumstantial evidence has been obtained for an isolate of *N. aotearoa* from *T. vulgaris*, which was found to produce indole-3-acetic acid (IAA) at a concentration of 11.16 µg mL^{-1} [Abdelhamid et al. 2024]. On the other hand, the inoculation with fungal endophytes isolated from other Lamiaceae species was found to significantly improve growth, chlorophyll, and carotenoid content in thyme plants under drought stress. Moreover, lipid peroxidation levels were significantly reduced, and the higher activity of antioxidant enzymes and improved redox state of glutathione were considered to be crucial for the increased resistance to drought [Kamyab et al. 2024].

Besides influencing EO production and composition in the host plants, endophytic fungi of thyme may also directly synthesize these compounds. This is the case of a strain of *A. alternata* isolated from *T. vulgaris* in Egypt producing an array of volatile organic compounds (VOCs), some of which were common to the host plant [Olama et al. 2023]. Moreover, ethyl acetate extracts from culture of a strain of *A. terreus*, again from *T. vulgaris* in Egypt, were found to contain carvacrol and thymol in higher concentrations than

those determined in the host plant. Other compounds characteristic of the EOs were detected in the GC-MS analysis, such as terpineol, α-phellandrene, camphene, α-pinene, isopregol, dihydrocarveol, borneol, citronellal, humulene, ascaridole, geraniol, caryophyllene, cedrenol, along with some mycotoxins, namely aflatoxin G2, cyclopaldic acid, nivalenol, and typical plant secondary metabolites, such as glaucine, scoparone, scrophulein, trispherine, luteolin, trimethylquercetin and other flavonoids. This compound assortment accounts for the notable antioxidant properties determined for the culture extract of this strain, as well as for the cytotoxicity against HEPG-2 hepatoma cells, with an IC_{50} value of 3.53 ±0.4 μg mL^{-1} [Ali et al. 2018]. In addition, high antibacterial and antifungal activities against *Escherichia coli, Staphylococcus aureus*, *Aspergillus flavus* and *Candida albicans* were documented for the culture extract of this strain by the same research group [El-Ela Sayed et al. 2020].

An endophytic isolate of *T. samuelsii* recovered from the stem of *Thymus mongolicus* displayed antagonistic activity in a co-culture experiment towards a panel of eight pathogenic fungi, including *A. alternata*, *Alternaria solani*, *Botrytis cinerea*, *Cytospora mali*, *Fusarium graminearum*, *Fusarium oxysporum*, *Fusarium sambucinum*, and *Neocosmospora solani*, with inhibition rates ranging between 31.0% and 68.5%. However, the antifungal activity of its fermentation broth and crude extract was low. GC-MS analysis showed that VOCs were the key antifungal compounds released in the co-cultures, with the main component identified as 6-pentyl-2H-pyran-2-one [Ma et al. 2023].

In a study including 89 endophytic isolates from several *Thymus* spp., some strains stood out for their antimicrobial effects, as assayed either directly or through their culture extracts; that is, strains of *Fusarium subglutinans*, *Fusarium equiseti*, *Fusarium javanicum*, *Fusarium lateritium*, *F. oxysporum*, *A. alternata*, *Allophoma tropica*, *Subplenodomus valerianae* and *Chaetosphaeronema* sp. displaying inhibitory effects against *B. cinerea*. The latter strain was the only one to show clear antibacterial effects in assays carried out against a panel of four strains belonging to *E. coli*, *S. aureus*, *Xanthomonas arboricola* pv. *juglandis* and *Streptomyces scabies*; conversely, a higher effectiveness was displayed by the culture extracts of *F. equiseti* and *F. lateritium* against *S. aureus*, and of *A. alternata*, *F. equiseti*, *F. oxysporum*, *F. subglutinans* and *S. valerianae* against *S. scabies* [Mirzaei and Masumi 2023]. In a previous study by the same research group, six strains of unidentified yeasts collected from three *Thymus* spp. also showed limited antifungal effects (14.70–37.25% growth inhibition) against *B. cinerea* [Masumi et al. 2015b].

Additional data on the antimicrobial properties have been collected for several endophytic isolates which were only identified at the genus level. This list includes a panel of 16 isolates belonging to the genera *Aspergillus*, *Alternaria*, *Fusarium*, *Penicillium*, *Phoma* and *Rhizopus*, which exhibited varying degrees of antibacterial and antifungal activities *in vitro* against *Bacillus cereus*, *Enterococcus faecalis*, *E. coli*, *Pseudomonas aeruginosa*, *Salmonella typhimurium*, *S. aureus*, *Fusarium caeruleum*, *F. oxysporum* and *Phytophthora infestans* [Zerroug and Sadrati 2022].

Finally, some extent of antimicrobial properties were documented for the ethyl acetate culture extracts of isolates of *Alternaria* and *Fusarium* collected from *T. vulgaris* in Egypt; in particular, this refers to antibacterial activity in assays carried out against *Bacillus subtilis*, *P. aeruginosa* and *S. aureus*, as well as to antifungal activity against *Aspergillus niger* and *C. albicans*. Moreover, these extracts were determined to possess antioxidant properties in assays based on the diphenyl-2-picryl hydrazyl (DPPH) radical scavenging activity, with IC_{50} values up to 36.80 μg mL^{-1} [Olama et al. 2023].

Besides the implications related to the antimicrobial, cytotoxic and antioxidant properties, potential biotechnological exploitation may also concern the production of enzymes. In this respect, in the screening of a set of 89 endophytic isolates from several *Thymus* spp. collected in Western Iran high levels of asparaginase and amylase production were recorded from strains of *F. subglutinans* and *Curvularia akaii*, respectively [Masumi et al. 2014].

CONCLUSIONS

This paper provides an overview of the current knowledge on the diversity, ecological functions, and biotechnological potential of endophytic fungi associated with *Thymus* species. These fungi represent a taxonomically diverse community comprising 49 genera and 53 species, mostly belonging to common

ascomycete genera such as *Alternaria*, *Fusarium*, *Colletotrichum*, and *Phoma*; considering that most identifications were based on morphological characters, a more rigorous taxonomic reassessment would be desirable. The currently available data are limited, and do not allow to establish if any species has developed a mutualistic association reflecting ecological significance. Nevertheless, some of these microorganisms have proved to be able to modulate production of EOs and contribute to plant growth promotion, enhanced tolerance to abiotic stress, and protection against plant pathogens through the synthesis of bioactive metabolites and volatile organic compounds. Moreover, several isolates have been demonstrated antimicrobial, antioxidant, and cytotoxic activities, deserving further assessments with a view to their effective application in sustainable agriculture and biotechnology. On the other hand, the occurrence of potential pathogens and species known as mycotoxin producers calls for additional work aimed at verifying their safety with respect to both plant and human health.

Future research in the field should focus particularly on the culture-independent characterization of the fungal endophytic communities, the standardization of sampling and isolation methods, the use of appropriate molecular markers for the isolate identification and the deposition of the obtained DNA sequences in recognized public repositories, and a more detailed investigation of host and organ specificity. Moreover, it is desirable that the experimental protocols be designed to more diffusely include controlled inoculation assays, field validation, and biosafety screening.

SOURCE OF FUNDING

This manuscript was prepared in the context of the research activity carried out within the project 'Valutazione di Bioformulati per la Difesa e Produzione delle Piante Officinali e Potenziale Applicazione dei Fitoestratti come Biopesticidi e Biostimolanti (Biofficinali)', financed by the Italian Ministry of Agriculture, Food Sovereignty and Forestry.

The manuscript also received financial support by SUBB.WOK.19.019.RIO.

CONFLICT OF INEREST

The authors declare no conflict of interest.

DECLARATION OF THE USE OF GENERATIVE AI TOOLS IN THE PROCESS OF PREPARING THE PAPER

The authors declare that no genAI tools were used in the process of preparing the paper.

AUTHORS CONTRIBUTION

The authors contributed in equal parts to collecting information and writing this paper.

REFERENCES

Abdelhamid, S.A., Abo Elsoud, M.M., El-Baz, A.F. et al. (2024). Optimisation of indole acetic acid production by *Neopestalotiopsis aotearoa* endophyte isolated from *Thymus vulgaris* and its impact on seed germination of *Ocimum basilicum*. BMC Biotechnol. 24(1), 46. https://doi.org/10.1186/s12896-024-00872-3

Abdel-Hamid, M.S., Fouda, A., El-Ela, H.K.A. et al. (2021). Plant growth-promoting properties of bacterial endophytes isolated from roots of *Thymus vulgaris* L. and investigate their role as biofertilizers to enhance the essential oil contents. Biomol. Concepts 12(1), 175–196. https://doi.org/10.1515/bmc-2021-0019

Adeleke, B.S., Fadiji, A.E., Ayilara, M.S. et al. (2022). Strategies to enhance the use of endophytes as bioinoculants in agriculture. Horticulturae 8(6), 498. https://doi.org/10.3390/horticulturae8060498

Agrawal, S., Bhatt, A. (2023). Microbial endophytes: emerging trends and biotechnological applications. Curr. Microbiol. 80(8), 249. https://doi.org/10.1007/s00284-023-03349-2

Ahmed, A.M., Mahmoud, B.K., Millán-Aguiñaga, N. et al. (2023). The endophytic *Fusarium* strains: a treasure trove of natural products. RSC Advan. 13(2), 1339–1369. https://doi.org/10.1039/d2ra04126j

Ali, E.A.M., Aziz Ahmed, A.A., El-Ela Sayed, M.A. et al. (2018). Antioxidant activity and cytotoxicity of extracts of *Thymus vulgaris* L. and their associated endophytic fungi. Egypt. J. Experim. Biol. 14(1), 107–116. https://doi.org/10.5455/egyjebb.20180122025355

Bahadori, S., Attar, F., Osaloo, S.K. et al. (2026). Biogeographical and taxonomic insights into Iranian *Thymus* (Lamiaceae): *Thymus coriifolius*, and *T. jankae* and *T. syriacus*. Phytotaxa 744(2), 103–122. https://doi.org/10.11646/phytotaxa.744.2.1

Bartolucci, F., Nachychko, V. (2025). The Euro+Med treatment of *Thymus* (Lamiaceae): nomenclature, typification of names and distribution updates. Willdenowia 55(1), 295–304. https://doi.org/10.3372/wi.55.14

Bartolucci, F., Peruzzi, L., Passalacqua, N. (2013). Typification of names and taxonomic notes within the genus *Thymus* L. (Lamiaceae). Taxon 62(6), 1308–1314. https://doi.org/10.12705/626.1

Celep, F., Dirmenci, T. (2017). Systematic and biogeographic overview of Lamiaceae in Turkey. Nat. Volat. Essent. Oils 4(4), 14–27. https://izlik.org/JA62MN24YT

Checcucci, A., Maida, I., Bacci, G. et al. (2017). Is the plant-associated microbiota of *Thymus* spp. adapted to plant essential oil? Res. Microbiol. 168(3), 276–282. https://doi.org/10.1016/j.resmic.2016.11.004

Crous, P.W., Sandoval-Denis, M., Costa, M.M. et al. (2022). *Fusarium* and allied fusarioid taxa (FUSA). 1. Fungal Syst. Evol. 9(1), 161–200. https://doi.org/10.3114/fuse.2022.09.08

Delbari, Y., Mohassel, Y., Kakaei, E. et al. (2023). Identification and anti-bacterial property of endophytic actinobacteria from *Thymes kotschyanus, Allium hooshidaryae*, and *Cerasus microcarpa*. Sci. Rep. 13(1), 13145. https://doi.org/10.1038/s41598-023-40478-x

Del Valle, J.C., Martín-Carretié, E.M., García-Cárdenas, F.J. et al. (2026). Ecological and genetic determinants of essential oil diversity in Mediterranean *Thymus*. Biochem. Syst. Ecol. 127, 105260. https://doi.org/10.1016/j.bse.2026.105260

Dolatabadi, H.K., Goltapeh, E.M., Moieni, A. et al. (2011). Effect of *Piriformospora indica* and *Sebacina vermifera* on plant growth and essential oil yield in *Thymus vulgaris* in vitro and in vivo experiments. Symbiosis 53(1), 29–35. https://doi.org/10.1007/s13199-010-0104-0

Drew, B.T., Sytsma, K.J. (2012). Phylogenetics, biogeography, and staminal evolution in the tribe Mentheae (Lamiaceae). Am. J. Bot. 99(5), 933–953. https://doi.org/10.3732/ajb.1100549

El-Ela Sayed, M.A., Ali E.A.M., Aziz Ahmed, A.A. et al. (2020). Antimicrobial activity of *Thymus vulgaris* L. and associated endophytes extracts. Egypt. J. Experim. Biol. 16(2), 141. https://doi.org/10.5455/egyjebb.20200709014142

Etri, K., Pluhár, Z. (2024). Exploring chemical variability in the essential oils of the *Thymus* genus. Plants 13(10), 1375. https://doi.org/10.3390/plants13101375

Federici, S., Galimberti, A., Bartolucci, F. et al. (2013). DNA barcoding to analyse taxonomically complex groups in plants: the case of *Thymus* (Lamiaceae). Bot. J. Linnean Soc. 171(4), 687–699. https://doi.org/10.1111/boj.12034

Fisher, P.J., Petrini, O., Amezquita, M.M. (1992). Endophytic fungi from Alpine and Mediterranean species of *Thymus*. Nova Hedwigia 55(3–4), 473–477.

García-Cárdenas, F.J., Ortiz, M.Á., del Valle, J.C. et al. (2026). Patterns of interploidy admixture in polyploid complexes: insights from *Thymus* sect. *Mastichina* (Lamiaceae). Mol. Ecol. 35(3), e70259. https://doi.org/10.1111/mec.70259

Gupta, A., Meshram, V., Gupta, M. et al. (2023). Fungal endophytes: Microfactories of novel bioactive compounds with therapeutic interventions. A comprehensive review on the biotechnological developments in the field of fungal endophytic biology over the last decade. Biomolecules 13(7), 1038. https://doi.org/10.3390/biom13071038

Halat, D.H., Krayem, M., Khaled, S. et al. (2022). A focused insight into thyme: Biological, chemical, and therapeutic properties of an indigenous Mediterranean herb. Nutrients 14(10), 2104. https://doi.org/10.3390/nu14102104

Kamyab, A., Samsampour, D., Ahmadinasab, N., Bagheri, A. (2024). Lamiaceae family-derived endophytic fungi: induced tolerance to drought stress in *Thymus vulgaris* plants. BMC Plant Biol. 24(1), 1104. https://doi.org/10.1186/s12870-024-05764-4

Li, J.F., Jiang, H.B., Jeewon, R. et al. (2022). *Alternaria*: Update on species limits, evolution, multi-locus phylogeny, and classification. Stud. Fungi 8(1), 1–61. http://doi.org/sif-0024-0001

López, P., Pastrana, A.M., Marin, M.V. et al. (2026). Molecular characterization reveals three *Neopestalotiopsis* species causing strawberry disease outbreaks in Spain. Front. Plant Sci. 17, 1830265. https://doi.org/10.3389/fpls.2026.1830265

Ma, L., Qu, H., Guo, Z. et al. (2023). Identification and antifungal activity of endophytic fungus *Trichoderma samuelsii* 2-63 strain from *Thymus mongolicus* Ronn. Chin. J. Pest. Sci. 25(2), 377–387. https://doi.org/10.16801/j.issn.1008-7303.2023.0012

Machowicz-Stefaniak, Z., Zimowska, B., Zalewska, E. (2002). Fungi colonizing various organs of thyme (*Thymus vulgaris* L.) cultivated in the region of Lublin. Acta Agrobot. 55(1), 185–197.

Machowicz-Stefaniak, Z., Zimowska, B., Zalewska, E. (2008). The occurrence and pathogenicity of *Phoma exigua* Desm. var. *exigua* for selected species of herbs. Acta Agrobot. 61(2), 157–166. https://doi.org/10.5586/aa.2008.044

Malagaris, P. (2011). Biology and ecology of *Asphondylia coridothymi* (Diptera: Cecidomyiidae) inducing galls on *Coridothymus capitatus* on the island of Samos, Greece. Acta Soc. Zool. Bohem. 75, 239–251.

Manathunga, K.K., Gunasekara, N.W., Meegahakumbura, M.K. et al. (2024). Exploring endophytic fungi as natural antagonists against fungal pathogens of food crops. J. Fungi 10(9), 606. https://doi.org/10.3390/jof10090606

Masumi, S., Mirzaei, S., Kalvandi, R. et al. (2014). Asparaginase and amylase activity of thyme endophytic fungi. J. Crop Prot. 3(5), 655–662. https://doi.org/10.48311/jcp.2014.1176

Masumi, S., Mirzaei, S., Zafari, D. et al. (2015a). Isolation, identification and biodiversity of endophytic fungi of *Thymus*. Progr. Biol. Sci. 5(1), 43–50.

Masumi, S., Mirzaei, S., Zafari, D. et al. (2015b). Bioactivity of endophytic bacteria and yeasts isolated from *Thymus*. Progr. Biol. Sci. 5(1), 33–42.

Mirzaei, S., Masumi, S. (2023). The antimicrobial activity of endophytic fungi isolated from *Thymus* spp. J. Med. Plants By-prod. 1, 117–124. https://doi.org/10.22092/jmpb.2022.342405.1192

Mohamad, O.A.A., Ma, J.B., Liu, Y.H. et al. (2020). Beneficial endophytic bacterial populations associated with medicinal plant *Thymus vulgaris* alleviate salt stress and confer resistance to *Fusarium oxysporum*. Front. Plant Sci. 11, 47. https://doi.org/10.3389/fpls.2020.00047

Mohamad, O.A.A., Liu, Y.H., Huang, Y. et al. (2022). The metabolic potential of endophytic actinobacteria associated with medicinal plant *Thymus roseus* as a plant-growth stimulator. Microorganisms 10(9), 1802. https://doi.org/10.3390/microorganisms10091802

Morales, R. (2002). The history, botany and taxonomy of the genus *Thymus.* In: Thyme: The Genus *Thymus*, Stahl-Biskup, E., Sáez, F. (eds.). Taylor & Francis, London, 1–44.

Morelli, M., Bahar, O., Papadopoulou, K.K. et al. (2020). Role of endophytes in plant health and defense against pathogens. Front. Plant Sci. 11, 1312. https://doi.org/10.3389/fpls.2020.01312

Musa, Z., Ma, J., Egamberdieva, D. et al. (2020). Diversity and antimicrobial potential of cultivable endophytic actinobacteria associated with the medicinal plant *Thymus roseus*. Front. Microbiol. 11, 191. https://doi.org/10.3389/fmicb.2020.00191

Najar, B., Pistelli, L., Ferri, B. et al. (2021). Crop yield and essential oil composition of two *Thymus vulgaris* chemotypes along three years of organic cultivation in a hilly area of central Italy. Molecules 26(16), 5109. https://doi.org/10.3390/molecules26165109

Nicoletti, R., Di Vaio, C., Cirillo, C. (2020). Endophytic fungi of olive tree. Microorganisms 8(9), 1321. https://doi.org/10.3390/microorganisms8091321

Nicoletti, R., Fiorentino, A. (2015). Plant bioactive metabolites and drugs produced by endophytic fungi of Spermatophyta. Agriculture 5(4), 918–970. https://doi.org/10.3390/agriculture5040918

Nicoletti, R., Zimowska, B. (2023). Endophytic fungi of hazelnut (*Corylus avellana*). Plant Prot. Sci. 59(2), 107–123. https://doi.org/10.17221/133/2022-PPS

Nieto, G. (2020). A review on applications and uses of *Thymus* in the food industry. Plants 9(8), 961. https://doi.org/10.3390/plants9080961

Nieto-Lugilde, D., Del Valle, J.C., Martín-Carretié, E.M. et al. (2026). Genomic structure, introgression, niche overlap, and morphological variation challenges species delimitation in *Thymus* sect. *Mastichina*. Ann. Bot. 138(4), 1194–1209. https://doi.org/10.1093/aob/mcag151

Olama, S.M., Sheata, R., El Shiekh, H. et al. (2023). Phytochemistry and biodiversity of endophytic fungal metabolites isolated from medicinal plants. Al-Azhar J. Agric. Res. 48(2), 42–58. https://doi.org/10.21608/ajar.2024.224023.1198

Pandey, S.S., Jain, R., Bhardwaj, P. et al. (2022). Plant probiotics–endophytes pivotal to plant health. Microbiol. Res. 263, 127148. https://doi.org/10.1016/j.micres.2022.127148

Rabiey, M., Hailey, L.E., Roy, S.R. et al. (2019). Endophytes vs tree pathogens and pests: can they be used as biological control agents to improve tree health? Eur. J. Plant Pathol. 155(3), 711–729. https://doi.org/10.1007/s10658-019-01814-y

Ray, P., Craven, K.D. (2016). *Sebacina vermifera*: a unique root symbiont with vast agronomic potential. World J. Microbiol. Biotechnol. 32(1), 16. https://doi.org/10.1007/s11274-015-1970-7

Saleem, S., Sekara, A., Pokluda, R. (2022). *Serendipita indica* – A review from agricultural point of view. Plants 11(24), 3417. https://doi.org/10.3390/plants11243417

Soorni, A., Borna, T., Alemardan, A. et al. (2019). Transcriptome landscape variation in the genus *Thymus.* Genes 10(8), 620. https://doi.org/10.3390/genes10080620

Waheed, M., Hussain, M.B., Saeed, F. et al. (2024). Phytochemical profiling and therapeutic potential of thyme (*Thymus* spp.): A medicinal herb. Food Sci. Nutri. 12(12), 9893–9912. https://doi.org/10.1002/fsn3.4563

Yadav, A.N., Kour, D., Kaur, T. et al. (2022). Endophytic fungal communities and their biotechnological implications for agro-environmental sustainability. Folia Microbiol. 67(2), 203–232. https://doi.org/10.1007/s12223-021-00939-0

Zerroug, A., Sadrati, N. (2022). Endophytic fungi isolated from *Thymus algeriensis* with good antimicrobial activities. Turk. J. Agric. Food Sci. Technol. 10(10), 1789–1798. https://doi.org/10.24925/turjaf.v10i10.1789-1798.5395

Zhao, M., Su, H., Huang, Y. et al. (2023). Plant growth-promoting properties and anti-fungal activity of endophytic bacterial strains isolated from *Thymus altaicus* and *Salvia deserta* in arid lands. J. Arid Land 15(11), 1405–1420. https://doi.org/10.1007/s40333-023-0071-y

Zimowska, B. (2022). *Phoma* on medicinal and aromatic plants. In: *Phoma:* Diversity, taxonomy, bioactivities, and nanotechnology. Springer International Publishing, Cham, 37–55.

Zimowska, B., Becchimanzi, A., Krol, E.D. et al. (2021). New *Cladosporium* species from normal and galled flowers of Lamiaceae. Pathogens 10(3), 369. https://doi.org/10.3390/pathogens10030369

Zimowska, B., Okoń, S., Becchimanzi, A. et al. (2020). Phylogenetic characterization of *Botryosphaeria* strains associated with *Asphondylia* galls on species of Lamiaceae. Diversity 12(2), 41. https://doi.org/10.3390/d12020041

Zimowska, B., Viggiani, G., Nicoletti, R. et al. (2017). First report of the gall midge *Asphondylia serpylli* on thyme (*Thymus vulgaris*), and identification of the associated fungal symbiont. Ann. Appl. Biol. 171(1), 89–94. https://doi.org/10.1111/aab.12360

Zubek, S., Błaszkowski, J. (2009). Medicinal plants as hosts of arbuscular mycorrhizal fungi and dark septate endophytes. Phytochem. Rev. 8(3), 571–580. https://doi.org/10.1007/s11101-009-9135-7