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Endophytic fungi of hazelnut (*Corylus avellana*)

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Abstract: Results of a vast research activity carried out worldwide in the last decades have demonstrated that endophytic fungi hold a fundamental role in improving plant fitness based on their aptitudes as growth promoters and/or defensive mutualists. These properties may have applicative perspectives in crop production, particularly for tree species such as hazelnut (*Corylus avellana*), which is mostly cropped extensively in semi-natural contexts of highland regions throughout the temperate zones. The available data on the occurrence, ecological roles, and applications in biotechnology of endophytic fungi associated with hazelnuts are revised in this paper in view to provide a reference supporting future investigations and projects aimed at exploiting the potential of this component of the plant microbiome.

Keywords: endophytes; crop management; biodiversity; plant mycobiome; defensive mutualism; Betulaceae

Endophytic fungi are polyphyletic microorganisms that inhabit plant tissues without inducing disease symptoms, and eventually establish mutualistic relationships with their hosts. After having been generally overlooked as a component of ecosystems, in the last decades they have been revalued by the scientific community and are now regarded as a trove of unexplored biodiversity (Nicoletti & Fiorentino 2015; Yadav et al. 2022). Indeed, many studies have shown that these microbial associates may improve plant fitness through various kinds of interactions with agents of biotic adversities, such as antibiosis, parasitism, competition for space and nutrients, and promotion of tolerance/resistance mechanisms (Rabiev et al. 2019; Morelli et al. 2020). Moreover, their emerging role in growth promotion stimulates their consideration as real and effective plant probiotics (Pandey et al. 2022). Besides the intrinsic effects/properties of single strains/species, a more comprehensive ecological approach should consider that endophytes may also play these functional roles in the form of interacting consortia with other components of the plant microbiome (Adeleke et al. 2022).

The above properties may have applicative perspectives in agriculture, particularly in extensive farming of tree crops, such as hazelnut (*Corylus avellana* L.), which are basically limited to devoted geographic areas and climatic contexts. So far, scant information has been achieved on the pos-

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sible impact of the endophytic microbiome in hazelnut production. Hence, circumstantial data on these symbionts, their aptitude to promote plant growth and to perform an ecological antagonistic role against key pathogens and pests can provide indications on how they actively contribute to hazelnut fitness and may allow to reduce, or even suppress, the pesticides input in the perspective of pursuing an ecologically-friendly crop management. In this review, the available information on the occurrence and properties of endophytic fungi of hazelnut is examined in view of supporting desirable initiatives and the development of effective strategies for the practical exploitation of this valuable component of biodiversity.

Occurrence

The examination of the existing literature reveals that so far limited work has been done dealing with the characterization of the assemblage of endophytic fungi associated with hazelnuts, particularly in leading producer countries such as Italy and Turkey, which provide about 80% of the world production (Silvestri et al. 2021; Nicoletti et al. 2022). A comparative investigation carried out in forest areas of Estonia showed that trees of *C. avellana* and grey alder [*Alnus incana* L. (Moench.)] share many of the endophytic fungi which could be identified by means of high-throughput DNA sequencing (Küngas et al. 2020). Even the leaf rust agent *Melampsoridium hiratsukanum*, known as an obligate biotroph pathogen developing its life cycle between alder and larch (Moricca et al. 2021), was detected in all sampled hazelnut organs. As a general trait in this study, the kind of plant organ resulted to correlate to the pattern of the associated endophytic species better than the tree species. Over 80 species were identified within a wider range of operational taxonomic units (OTU) (Table 1), including fungi known as hazelnut pathogens (e.g. the powdery mildew agents *Erysiphe penicillata* and *Phyllactinia guttata*), pathogens of other crops (e.g. *Colletotrichum godetiae*, *Cyphellophora sessilis*, *Exobasidium gracile*, *Microcyclosporella mali*, *Mycosphaerella sumatrensis*, *Paraleptosphaeria praetermissa*, *Ramularia* spp.), lignicolous/corticolous Agaricomycetes (e.g. *Ganoderma applanatum*, *Lachnella villosa*, *Pluteus cervinus*) and Leotiomycetes (e.g. *Lachnum fuscescens*, *Mollisia ventosa*, *Pezicula ericae*), yeasts (e.g. *Buckleyzyma aurantiaca*, *Filobasidium wieringae*, *Microstroma phylloplanum*) and lichens (e.g. *Bacidia neosquamulosa*, *Bacidina arnoldiana*, *Buellia griseovirens*, *Lecania nagelii*, *Ostropa barbara*, *Phlyctis argena*, *Physcia tenella*). Fungi such as *Annulohypoxylon multiforme*, *Daldinia petriniae*, *Gnomonia gnomon*, *Hypoxylon* spp. are of common endophytic occurrence on Betulaceae (Sogonov et al. 2008; Carmona et al. 2009; Stadler et al. 2014; Lambert et al. 2021), while *Diatrypella pulvinata*, *Amphisphaeria* (= *Lepteutypa*) *fuckelii*, *Massaria conspurcata*, *Mollisia ventosa*, *Pestalotia* (= *Monochaetia*) *kansensis* and *Pezicula ericae* have been reported as endophytes of other forest plants. Along with many species with an unknown ecological role, several species were found which commonly occur as saprophytes in diverse environments. Not surprisingly, species of many genera of common endophytic occurrence, such as *Aspergillus, Cladosporium, Fusarium, Penicillium, Talaromyces, Trichoderma*, could not be detected since this study was based on amplification of rDNA-ITS sequences, which have limited relevance for identification of these fungi at the species level (Dou et al. 2020; Houbraken et al. 2020; Becchimanzi et al. 2021; O'Donnell et al. 2022); hence, it is quite likely that sequences corresponding to these fungi were annotated as unidentifiable according to the criteria for taxonomic ascription followed by the authors (Küngas et al. 2020).

In fact, some species belonging to the above genera were identified in another investigation carried out in six regions of northern Iran, which was based on preliminary isolation of endophytic fungi (Kashanian et al. 2021). Of course, data collected in this study are also limited in numerical terms, by reason of the inability of many fungi to grow on the isolation medium or to overcome competition with other associated fast-growing species. In addition to fungi only identified at the genus level, such as *Diaporthe*, *Exophiala*, *Fusarium* and *Talaromyces* spp., the species *Alternaria alternata*, *Cladosporium sphaerospermum*, *Epicoccum nigrum*, *Fusarium fujikuroi*, *Fusarium proliferatum*, *Gnomoniopsis castaneae* (= *G. smithogilvyi*), *Neocucurbitaria unguis-hominis*, *Penicillium chrysogenum* and *Penicillium citrinum* were found at all locations as a result of isolations from different plant tissues. Most of these species are quite common saprophytes spreading in a wide range of ecological contexts and have previous records concerning their endophytic occurrence (Nicoletti

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Table 1. Fungal species reported as endophytic associates of hazelnut (*Corylus avellana*)

Species	Source	Reference
Acremonium sp.	root; Sichuan (China)	Yang et al. 2019
Alatosessilispora bibrachiata	branch, leaf, trunk; Estonia	Küngas et al. 2020
Alternaria alternata	leaf, root, stem; northern Iran stem; northwestern Iran	Kashanian et al. 2021 Mohammadi Ballakuti et al. 2022
Alternaria infectoria	branch, leaf, trunk; Estonia	Küngas et al. 2020
Alternaria sp.	branch, leaf, trunk; Estonia	Küngas et al. 2020
Amphisphaeria fuckelii	branch, leaf; Estonia	Küngas et al. 2020
Angustimassarina populi	leaf, stem; northern Iran	Kashanian et al. 2021
Angustimassarina sp.	leaf; Ardabil (Iran)	Kashanian et al. 2021
Annulohypoxylon multiforme	branch, leaf, trunk; Estonia	Küngas et al. 2020
*Apiospora arundinis**	leaf; northwestern Iran	Mohammadi Ballakuti et al. 2022
Apodus sp.	root; Sichuan (China)	Yang et al. 2019
Archaeorhizomyces sp.	root; Sichuan (China)	Yang et al. 2019
Arthrobotrys sp.	root; Sichuan (China)	Yang et al. 2019
Arthrocatena sp.	branch, leaf, trunk; Estonia	Küngas et al. 2020
Aspergillus microcysticus	leaf; northwestern Iran	Mohammadi Ballakuti et al. 2022
Aspergillus sp.	root; Sichuan (China)	Yang et al. 2019
Aureobasidium pullulans	leaf; Astroni Nature Reserve (Italy)	NIH 2022
Aureobasidium sp.	root; Sichuan (China) branch, leaf, trunk; Estonia	Yang et al. 2019 Küngas et al. 2020
Bacidia neosquamulosa	leaf, trunk; Estonia	Küngas et al. 2020
Bacidia sp.	root; Sichuan (China)	Yang et al. 2019
Bacidina arnoldiana	branch, leaf, trunk; Estonia	Küngas et al. 2020
Basidiobolus sp.	root; Sichuan (China)	Yang et al. 2019
Bjerkandera adusta	root, stem; northern Iran	Kashanian et al. 2021
Buckleyzyma aurantiaca	branch, leaf, trunk; Estonia	Küngas et al. 2020
Buellia griseovirens	branch, leaf; Estonia	Küngas et al. 2020
Bullera sp.	root; Sichuan (China)	Yang et al. 2019
Camarosporomyces flavigenus	leaf; Iran	Salehi et al. 2020a
Candida sp.	root; Sichuan (China)	Yang et al. 2019
Cenangiopsis raghavanii	branch, leaf; Estonia	Küngas et al. 2020
Cercospora sp.	leaf, root, stem; northern Iran	Kashanian et al. 2021
Chaetomium sp.	root; Sichuan (China)	Yang et al. 2019
Chloridium sp.	root; Sichuan (China)	Yang et al. 2019
Cladophialophora sp.	branch, leaf, trunk; Estonia	Küngas et al. 2020
Cladosporium cladosporioides	branch, leaf, trunk; Estonia	Küngas et al. 2020
Cladosporium herbarum	leaf, root, stem; northern Iran	Kashanian et al. 2021
Cladosporium perangustum	branch; Astroni Nature Reserve (Italy)	†
Cladosporium sphaerospermum	leaf, root, stem; northern Iran	Kashanian et al. 2021
Cladosporium tenuissimum	leaf, root, stem; northern Iran	Kashanian et al. 2021
Cladosporium variabile	leaf; northwestern Iran	Mohammadi Ballakuti et al. 2022
Clavulina sp.	root; Sichuan (China)	Li et al. 2019; Yang et al. 2019
Colletotrichum godetiae	branch, leaf; Estonia	Küngas et al. 2020
Coniosporium sp.	root; Sichuan (China)	Li et al. 2019

Table 1 to be continued

Species	Source	Reference
Coniothyrium telephii	stem; northwestern Iran	Mohammadi Ballakuti et al. 2022
Coprinellus disseminatus	branch, leaf, trunk; Estonia	Küngas et al. 2020
Coprinellus micaceus	branch, leaf, trunk; Estonia	Küngas et al. 2020
Cordyceps sp.	root; Sichuan (China)	Yang et al. 2019
Crassiperidium octosporum	leaf, stem; northern Iran	Kashanian et al. 2021
Cryptococcus sp.	root; Sichuan (China)	Yang et al. 2019
Cryptosporella pacifica	branch, leaf, trunk; Estonia	Küngas et al. 2020
Cryptosporiopsis tarraconensis	leaf; northwestern Iran	Mohammadi Ballakuti et al. 2022
Cyphellophora sessilis	branch, leaf, trunk; Estonia	Küngas et al. 2020
Cystobasidium sp.	branch, leaf, trunk; Estonia	Küngas et al. 2020
Daldinia petriniae	branch, leaf, trunk; Estonia	Küngas et al. 2020
*Dendrothyrium variisporum**	inflorescence; northwestern Iran	Mohammadi Ballakuti et al. 2022
Devriesia sp.	branch, leaf, trunk; Estonia	Küngas et al. 2020
Diaporthe amygdali	root; Ordu-Akçatepe (Turkey)	Akay et al. 2011, 2014
Diaporthe sp.	branch, leaf, trunk; Estonia leaf, root, stem; northern Iran	Küngas et al. 2020 Kashanian et al. 2021
Diaporthella sp.	branch, leaf; Estonia	Küngas et al. 2020
Diatrypella pulvinata	branch, leaf; Estonia	Küngas et al. 2020
Dioszegia sp.	branch, leaf, trunk; Estonia	Küngas et al. 2020
Elsinoe sp.	branch, leaf, trunk; Estonia	Küngas et al. 2020
Entoloma sp.	root; Sichuan (China)	Yang et al. 2019
Epicoccum nigrum	leaf, root, stem; northern Iran leaf; northwestern Iran	Kashanian et al. 2021 Mohammadi Ballakuti et al. 2022
Erysiphe penicillata	branch, leaf, trunk; Estonia	Küngas et al. 2020
Erysiphe sp.	root; Sichuan (China)	Yang et al. 2019
Exobasidium gracile	branch, leaf, trunk; Estonia	Küngas et al. 2020
Exophiala sp.	leaf, root, stem; northern Iran	Kashanian et al. 2021
Filobasidium wieringae	branch, leaf, trunk; Estonia	Küngas et al. 2020
Fusarium equiseti	leaf; Zanjan (Iran)	Kashanian et al. 2021
Fusarium fujikuroi	leaf, root, stem; northern Iran leaf; northwestern Iran	Kashanian et al. 2021 Mohammadi Ballakuti et al. 2022
Fusarium graminearum	leaf, root, stem; northern Iran	Kashanian et al. 2021
Fusarium oxysporum	leaf; Ordu-Akçatepe (Turkey)	Akay et al. 2014
Fusarium proliferatum	leaf, root, stem; northern Iran	Kashanian et al. 2021
Fusarium sp.	root; Sichuan (China) leaf, root; northern Iran	Yang et al. 2019 Kashanian et al. 2021
Fusarium tricinctum	leaf; northwestern Iran	Mohammadi Ballakuti et al. 2022
Ganoderma applanatum	branch, leaf, trunk; Estonia	Küngas et al. 2020
Geosmithia sp.	root; Sichuan (China)	Yang et al. 2019
Gnomonia gnomon	branch, leaf, trunk; Estonia	Küngas et al. 2020
Gnomoniopsis castaneae	leaf, root, stem; northern Iran	Kashanian et al. 2021
Gnomoniopsis idaeicola	leaf; Ardabil (Iran)	Kashanian et al. 2021
Guehomyces sp.	root; Sichuan (China)	Yang et al. 2019
Hirsutella sp.	root; Sichuan (China)	Yang et al. 2019

Table 1 to be continued

Species	Source	Reference
Humicola sp.	root; Sichuan (China)	Li et al. 2019; Yang et al. 2019
Hymenochaete sp.	root; Sichuan (China)	Li et al. 2019; Yang et al. 2019
Hypoxylon fuscum	branch, leaf, trunk; Estonia	Küngas et al. 2020
Hypoxylon laschii	branch, leaf; Estonia	Küngas et al. 2020
Hypoxylon rubiginosum	branch, leaf, trunk; Estonia	Küngas et al. 2020
Ilyonectria sp.	root; Sichuan (China)	Li et al. 2019; Yang et al. 2019
Kuehneromyces sp.	branch, leaf, trunk; Estonia	Küngas et al. 2020
Lachnella villosa	branch, leaf, trunk; Estonia	Küngas et al. 2020
Lachnum fuscescens	branch, leaf; Estonia	Küngas et al. 2020
Lecania nagelii	branch, leaf, trunk; Estonia	Küngas et al. 2020
Leptogium sp.	root; Sichuan (China)	Yang et al. 2019
Leptosphaeria sp.	branch, leaf, trunk; Estonia	Küngas et al. 2020
Lulwoana sp.	root; Sichuan (China)	Yang et al. 2019
Lycoperdon perlatum	branch, leaf; Estonia	Küngas et al. 2020
Lycoperdon umbrinum	branch, leaf; Estonia	Küngas et al. 2020
Malassezia sp.	root; Sichuan (China)	Yang et al. 2019
*Malbranchea albolutea**	leaf; northwestern Iran	Mohammadi Ballakuti et al. 2022
Massaria conspurcata	branch, leaf; Estonia	Küngas et al. 2020
Meira geulakonigae	stem; northwestern Iran	Mohammadi Ballakuti et al. 2022
Meira sp.	branch, leaf; Estonia	Küngas et al. 2020
Melampsoridium hiratsukanum	branch, leaf, trunk; Estonia	Küngas et al. 2020
Melanconium hedericola	leaf; northwestern Iran branch; Astroni Nature Reserve (Italy)	Mohammadi Ballakuti et al. 2022 †
Microcyclosporella mali	trunk; Estonia	Küngas et al. 2020
Microdochium (*Monographella*) sp.	root; Sichuan (China)	Li et al. 2019; Yang et al. 2019
Microstroma phylloplanum	branch, leaf, trunk; Estonia	Küngas et al. 2020
Mollisia ventosa	branch, leaf, trunk; Estonia	Küngas et al. 2020
Mortierella sp.	root; Sichuan (China)	Yang et al. 2019
Muriphaeosphaeria sp.	branch, leaf; Estonia	Küngas et al. 2020
Mycosphaerella sp.	branch, leaf, trunk; Estonia	Küngas et al. 2020
Mycosphaerella sumatrensis	trunk; Estonia	Küngas et al. 2020
Myriococcum sp.	root; Sichuan (China)	Yang et al. 2019
Myrothecium sp.	root; Sichuan (China)	Yang et al. 2019
Neocucurbitaria unguis-hominis	leaf, root, stem; northern Iran	Kashanian et al. 2021
Neopestalotiopsis vitis	leaf; northwestern Iran	Mohammadi Ballakuti et al. 2022
Neosetophoma sp.	branch, leaf, trunk; Estonia	Küngas et al. 2020
Nothophoma quercina	leaf, root, stem; northern Iran	Kashanian et al. 2021
Ophiognomonia sp.	branch, leaf, trunk; Estonia	Küngas et al. 2020
Ophiostoma sp.	root; Sichuan (China)	Li et al. 2019
Ostropa barbara	branch, leaf; Estonia	Küngas et al. 2020
Paraconiothyrium brasiliense	bark; Iran	Salehi et al. 2019a
Paraconiothyrium sporulosum	root; Golestan (Iran)	Kashanian et al. 2021
Paraleptosphaeria praetermissa	branch, leaf, trunk; Estonia	Küngas et al. 2020
Penicillium aurantiogriseum	nut; Aurora (Oregon, USA)	Yang et al. 2014

Table 1 to be continued

Species	Source	Reference
Penicillium chrysogenum	leaf, root, stem; northern Iran	Kashanian et al. 2021
Penicillium citrinum	leaf, root, stem; northern Iran	Kashanian et al. 2021
Penicillium expansum	nut; Aurora (Oregon, USA)	NIH 2022
Penicillium rubens	leaf; northwestern Iran	Mohammadi Ballakuti et al. 2022
Penicillium sp.	root; Sichuan (China)	Li et al. 2019; Yang et al. 2019
*Pestalotia kansensis**	branch, leaf, trunk; Estonia	Küngas et al. 2020
Pestalotiopsis sp.	branch, leaf, trunk; Estonia leaf; Ashiu (Japan)	Küngas et al. 2020 NIH 2022
Pezicula ericae	branch, leaf, trunk; Estonia	Küngas et al. 2020
Phaeoacremonium sp.	root; Sichuan (China)	Li et al. 2019; Yang et al. 2019
Phaeomoniella sp.	branch, leaf, trunk; Estonia	Küngas et al. 2020
Phialocephala sp.	branch, leaf, trunk; Estonia	Küngas et al. 2020
Phlyctis argena	branch, leaf, trunk; Estonia	Küngas et al. 2020
Phoma herbarum	branch, leaf, trunk; Estonia	Küngas et al. 2020
Phoma sp.	root; Sichuan (China) branch, leaf, trunk; Estonia	Yang et al. 2019 Küngas et al. 2020
Phyllactinia guttata	leaf; Estonia	Küngas et al. 2020
Physcia tenella	branch, leaf, trunk; Estonia	Küngas et al. 2020
Pichia sp.	root; Sichuan (China)	Yang et al. 2019
Pluteus cervinus	branch, leaf, trunk; Estonia	Küngas et al. 2020
Podospora sp.	root; Sichuan (China)	Li et al. 2019; Yang et al. 2019
Pseudocyphellaria sp.	root; Sichuan (China)	Yang et al. 2019
Pseudofabraea sp.	branch, leaf, trunk; Estonia	Küngas et al. 2020
Pseudovalsaria sp.	branch, leaf, trunk; Estonia	Küngas et al. 2020
Purpureocillium lilacinum	leaf, root, stem; northern Iran	Kashanian et al. 2021
Pyrenochaetopsis sp.	root, stem; northern Iran	Kashanian et al. 2021
Ramularia bellunensis	leaf; Estonia	Küngas et al. 2020
Ramularia heraclei	branch, leaf, trunk; Estonia	Küngas et al. 2020
Ramularia hydrangeae-macrophyllae	leaf, trunk; Estonia	Küngas et al. 2020
Ramularia mali	inflorescence; northwestern Iran	Mohammadi Ballakuti et al. 2022
Ramularia sp.	branch, leaf, trunk; Estonia	Küngas et al. 2020
Ramularia tovarae	branch, leaf, trunk; Estonia	Küngas et al. 2020
Sarcosphaera sp.	root; Sichuan (China)	Yang et al. 2019
Schizangiella sp.	root; Sichuan (China)	Yang et al. 2019
Scleroderma sp.	root; Sichuan (China)	Li et al. 2019; Yang et al. 2019
Septobasidium carestianum	branch, leaf, trunk; Estonia	Küngas et al. 2020
*Similiphoma crystallifera**	leaf; northwestern Iran	Mohammadi Ballakuti et al. 2022
Simplicillium sp.	root; Sichuan (China)	Yang et al. 2019
Staphylotrichum sp.	root; Sichuan (China)	Yang et al. 2019
Stemphylium vesicarium	leaf; northwestern Iran	Mohammadi Ballakuti et al. 2022
Talaromyces amestolkiae	root; Qazvin (Iran)	Kashanian et al. 2021
Talaromyces sp.	root; Sichuan (China) leaf, root, stem; northern Iran	Yang et al. 2019 Kashanian et al. 2021
Taphrina sp.	branch, leaf, trunk; Estonia	Küngas et al. 2020

Table 1 to be continued

Species	Source	Reference
Thelephora sp.	root; Sichuan (China)	Yang et al. 2019
Tomentella sp.	root; Sichuan (China)	Yang et al. 2019
Trechispora sp.	root; Sichuan (China)	Li et al. 2019; Yang et al. 2019
Trichoderma harzianum	stem; United Kingdom	NIH 2022
Trichoderma sp.	root; Sichuan (China)	Yang et al. 2019
Trichomerium dioscoreae	branch, leaf, trunk; Estonia	Küngas et al. 2020
Trichomerium sp.	branch, leaf, trunk; Estonia	Küngas et al. 2020
Tuber sp.	root; Sichuan (China)	Li et al. 2019; Yang et al. 2019
Umbelopsis isabellina	branch, leaf; Estonia	Küngas et al. 2020
Umbelopsis sp.	root; Sichuan (China)	Yang et al. 2019
Villophora sp.	root; Sichuan (China)	Yang et al. 2019
Vishniacozyma carnescens	branch, leaf, trunk; Estonia	Küngas et al. 2020
Vishniacozyma foliicola	branch, leaf, trunk; Estonia	Küngas et al. 2020
Vishniacozyma victoriae	branch, leaf, trunk; Estonia	Küngas et al. 2020
Zygophiala sp.	branch, leaf, trunk; Estonia	Küngas et al. 2020

*These species are reported with their currently accepted names

†Original finding by the authors in the course of an investigation currently in progress in Italy

et al. 2014, 2020; Imazaki & Kadota 2015; Nicoletti 2019; Zimowska et al. 2020). Other species are also quite common, having been found at four or five of the six investigational sites, i.e. *Angustimassarina populi*, *Bjerkandera adusta*, *Cladosporium herbarum*, *Cladosporium tenuissimum*, *Crassiperidium octosporum*, *Fusarium graminearum*, *Nothophoma quercina* and *Purpureocillium lilacinum*, while *Gnomoniopsis idaeicola*, *Paraconiothyrium sporulosum* (= *Paraphaeosphaeria sporulosa*) and *Talaromyces amestolkiae* were recovered at just a single site. Some of them are known as pathogens of forest plants, which may result into an epidemiological impact. For instance, *C. octosporum* is a recently discovered pathogen of *Fagus crenata* (Matsumura et al. 2018), while *N. quercina* is reported as an agent of cankers and leaf spots on *Quercus* spp. and many unrelated plants growing in a wide range of environmental conditions (Chen et al. 2015; Vettraino et al. 2017).

Another recent investigation carried out in northwestern Iran by an independent research group has been more specifically addressed to identify endophytic fungi able to produce taxane compounds (Mohammadi Ballakuti et al. 2022). Unfortunately, just 18 strains were identified at the species level out of about 250 isolates obtained, including species already reported in the previous investigation, such as *A. alternata, E. nigrum* and *F. fujikuroi*. Along with some infrequent species, such as *Malbranchea albolutea* (= *Auxarthron alboluteum*) and *Similiphoma crystallifera*, and a couple of species of known endophytic occurrence [i.e. *Dendrothyrium variisporum* (= *Kalmusia variispora*) and *Meira geulakonigae*], other isolates were recovered of fungi which are widespread in every environment, such as *Aspergillus, Penicillium* and *Cladosporium*. Other species are known as pathogens of crops, such as *Apiospora* (= *Arthrinium*) *arundinis, Neopestalotiopsis vitis* and *Stemphylium vesicarium*, or forest plants, such as the already mentioned *C. octosporum* (Matsumura et al. 2018). More endophytic fungi were recovered in another Iranian study with the purpose of verifying their possible effect on eliciting taxol production in hazel cells *in vitro*, but identification was only reported for a strain of *Camarosporomyces flavigenus* (Salehi et al. 2020a).

A few examples deserve to be mentioned of how studies concerning endophytic fungi may help in collecting additional data on the occurrence and ecological role of species which otherwise would be recorded as rare or infrequent. Among the species listed in Table 1, *Alatosessilispora bibrachiata* is occasionally reported as an aquatic fungus dwelling in humid substrates, such as fallen leaves (Ando

1992); *Cenangiopsis raghavanii*, described as a corticolous fungus of *Juniperus* in Montenegro (Perić et al. 2015); *Angustimassarina populi*, described as a saprobic or fungicolous species (Thambugala et al. 2015); *Cryptosporella pacifica*, described as an associate of two *Alnus* spp. in the Pacific Northwest of the United States of America (Mejía et al. 2011); and *Trichomerium dioscoreae*, described from isolates from leaf spots on *Dioscorea* sp. in Japan (Crous et al. 2014). Interestingly, another recently described species, *Melanconium hedericola* (Crous et al. 2014), has been recovered from two far geographic contexts, calling for its possible more widespread association with hazelnuts.

Overall, Table 1 includes a total of 181 fungal taxa so far reported as hazelnut endophytes, of which 100 were identified at the species level. Likewise resulting on other tree species (Nicoletti 2019; Nicoletti et al. 2020, 2021), the Ascomycota prevail in taxonomic terms. Particularly, there are 37 genera from 23 families in the Sordariomycetes, 30 genera from 18 families in the Dothideomycetes, 10 genera from seven families in the Eurotiomycetes, 10 genera from eight families in the Lecanoromycetes, 10 genera from six families in the Leotiomycetes, while the Pezizomycetes, the Orbiliomycetes, the Saccharomycotina and the Taphrinomycotina are less represented, each with one or two genera (Figure 1). As for the Basidiomycota, the taxonomic assortment resulting from the current findings includes 14 genera in 13 families belonging to the Agaricomycetes and six genera/families in the Tremellomycetes, while the Pucciniomycotina and the Ustilaginomycotina are less represented, each with four genera (Figure 2). Finally, the phyla Basidiobolomycota (genera *Basidiobolus* and *Schizangiella*), and Mucoromycota (genera *Mortierella* and *Umbelopsis*) are just occasionally represented. For the time being, these data indicate that there is no correspondence possibly supporting a more systematic association or a special role by any taxa reported for endophytic occurrence on hazelnut.

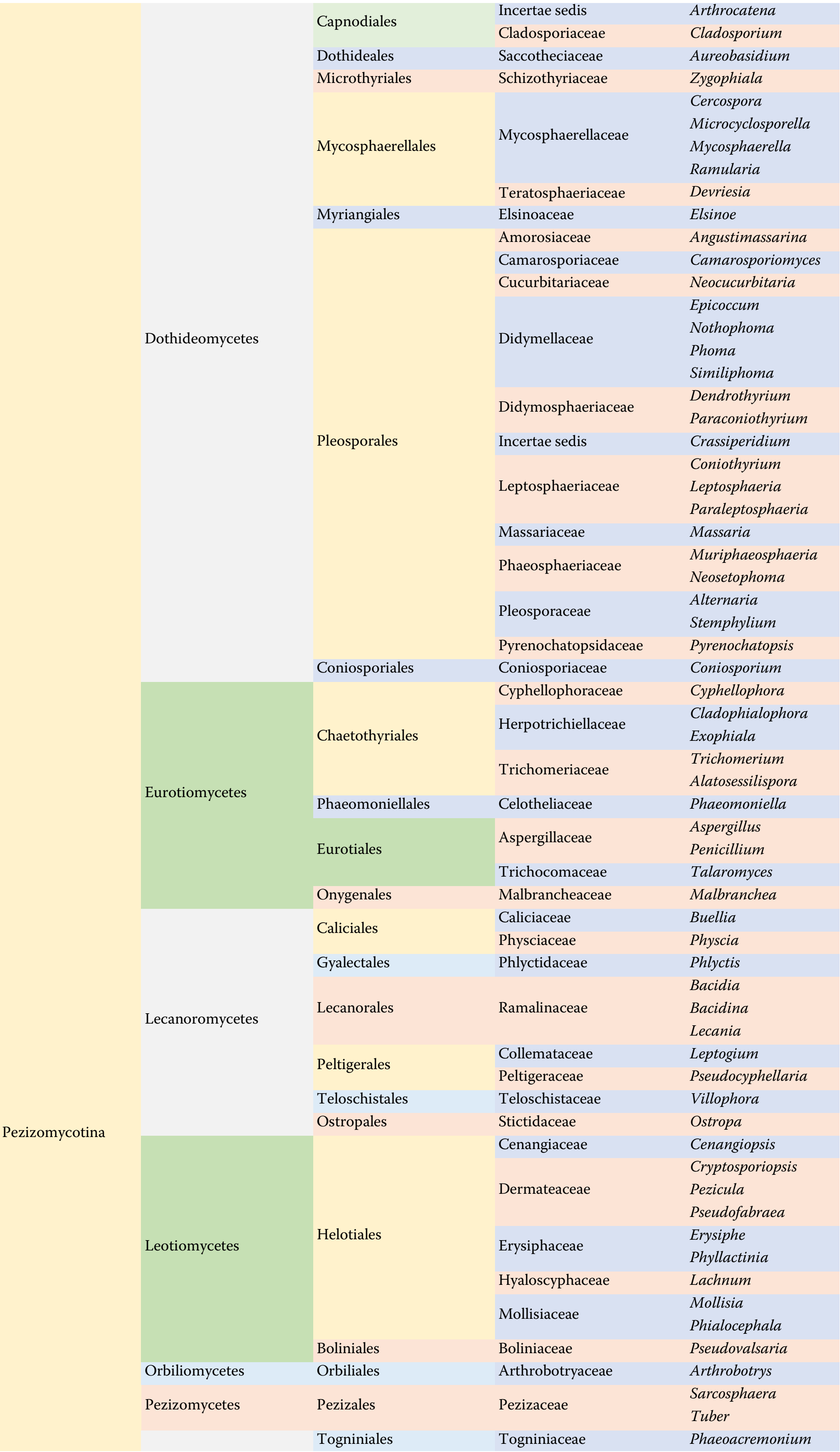
On the other hand, no definite association can be inferred with the plant organ; rather, it seems that most endophytic fungi are generalist in their capacity to colonize hazelnut. In fact, their presence was detected in all three organs examined (branch, leaf, trunk) for 60 out of 81 taxa in the Estonian study (Küngas et al. 2020), and for 16 out of 28 taxa in the Iranian study based on isolations from leaves, roots and stems (Kashanian et al. 2021).

Implications in crop management

Data on occurrence of endophytic fungi of hazelnuts have been collected from sterilized plant parts, which ensures that they were either developing or dormant inside living tissues rather than being external contaminant. However, respecting this methodological constraint is not sufficient for inferring their ecological role and which kind of interaction is established with the host plant. Indeed, many pathogens of trees, especially those cropped in extensive contexts, are reported to possibly colonize their hosts endophytically, without external manifestation. This silent presence could be interpreted either in terms of detection during the latency period, or considering that some species only express their pathogenic potential when plants undergo environmental stress, or when some biological factors, intrinsic or extrinsic (e.g., naturally occurring antagonists), fail to exert their defensive role (Schulz & Boyle 2005; Nicoletti et al. 2021). Whatever the reason of the presence of potential pathogens in healthy plant tissues, it is evident that the indication that they can be constantly associated in a given context and represent a potential threat is very useful for risk assessment and must be taken into account in crop management.

In this respect, the endophytic occurrence of obligate pathogens which may require fungicide treatments, such as the agents of powdery mildew, deserves to be attentively investigated in farms. These fungi were not only detected in the above-ground parts in the Estonian study (Küngas et al. 2020), but even in roots (as *Erysiphe* sp.) in the investigation by Yang et al. (2019). Of course, roots are not an infection site for these pathogens; hence, this finding could represent an indication for a more general aptitude by powdery mildew agents to survive and spread endophytically in the plant in the absence of leaves.

On another instance, the fact that powdery mildew agents may be forced to persist in a semi-quiescent stage could be due to the contemporary presence of antagonists in the host tissues. As an example, many *Cladosporium* spp. may act as hyperparasites of powdery mildews (Dolińska & Schollenberger 2012) and a variety of plant pathogenic fungi (Heuchert et al. 2005), also thanks to a widespread capacity to produce antifungal compounds (Salvatore et al. 2021). More species/genera are reported in Table 1 which could be involved in defensive mutualism on hazelnut; this is the case of *E. nigrum, Chaetomium,*



Pezizomycotina	Dothideomycetes	Capnodiales	Incertae sedis	*Arthrocatena*
			Cladosporiaceae	*Cladosporium*
		Dothideales	Saccotheciaceae	*Aureobasidium*
		Microthyriales	Schizothyriaceae	*Zygophiala*
		Mycosphaerellales	Mycosphaerellaceae	*Cercospora*
				Microcyclosporella
				Mycosphaerella
				Ramularia
			Teratosphaeriaceae	*Devriesia*
		Myriangiales	Elsinoaceae	*Elsinoe*
		Pleosporales	Amorosiaceae	*Angustimassarina*
			Camarosporiaceae	*Camarosporiomyces*
			Cucurbitariaceae	*Neocucurbitaria*
			Didymellaceae	*Epicoccum*
				Nothophoma
				Phoma
				Similiphoma
			Didymosphaeriaceae	*Dendrothyrium*
				Paraconiothyrium
			Incertae sedis	*Crassiperidium*
			Leptosphaeriaceae	*Coniothyrium*
				Leptosphaeria
				Paraleptosphaeria
			Massariaceae	*Massaria*
			Phaeosphaeriaceae	*Muriphaeosphaeria*
				Neosetophoma
			Pleosporaceae	*Alternaria*
				Stemphylium
			Pyrenochatopsidaceae	*Pyrenochatopsis*
		Coniosporiales	Coniosporiaceae	*Coniosporium*
	Eurotiomycetes	Chaetothyriales	Cyphellophoraceae	*Cyphellophora*
			Herpotrichiellaceae	*Cladophialophora*
				Exophiala
			Trichomeriaceae	*Trichomerium*
				Alatosessilispora
		Phaeomoniellales	Celotheliaceae	*Phaeomoniella*
		Eurotiales	Aspergillaceae	*Aspergillus*
				Penicillium
			Trichocomaceae	*Talaromyces*
		Onygenales	Malbrancheaceae	*Malbranchea*
	Lecanoromycetes	Caliciales	Caliciaceae	*Buellia*
			Physciaceae	*Physcia*
		Gyalectales	Phlyctidaceae	*Phlyctis*
		Lecanorales	Ramalinaceae	*Bacidia*
				Bacidina
				Lecania
		Peltigerales	Collemataceae	*Leptogium*
			Peltigeraceae	*Pseudocyphellaria*
		Teloschistales	Teloschistaceae	*Villophora*
		Ostropales	Stictidaceae	*Ostropa*
	Leotiomycetes	Helotiales	Cenangiaceae	*Cenangiopsis*
			Dermateaceae	*Cryptosporiopsis*
				Pezicula
				Pseudofabraea
			Erysiphaceae	*Erysiphe*
				Phyllactinia
			Hyaloscyphaceae	*Lachnum*
			Mollisiaceae	*Mollisia*
				Phialocephala
		Boliniales	Boliniaceae	*Pseudovalsaria*
	Orbiliomycetes	Orbiliales	Arthrobotryaceae	*Arthrobotrys*
	Pezizomycetes	Pezizales	Pezizaceae	*Sarcosphaera*
				Tuber
		Togniniales	Togniniaceae	*Phaeoacremonium*

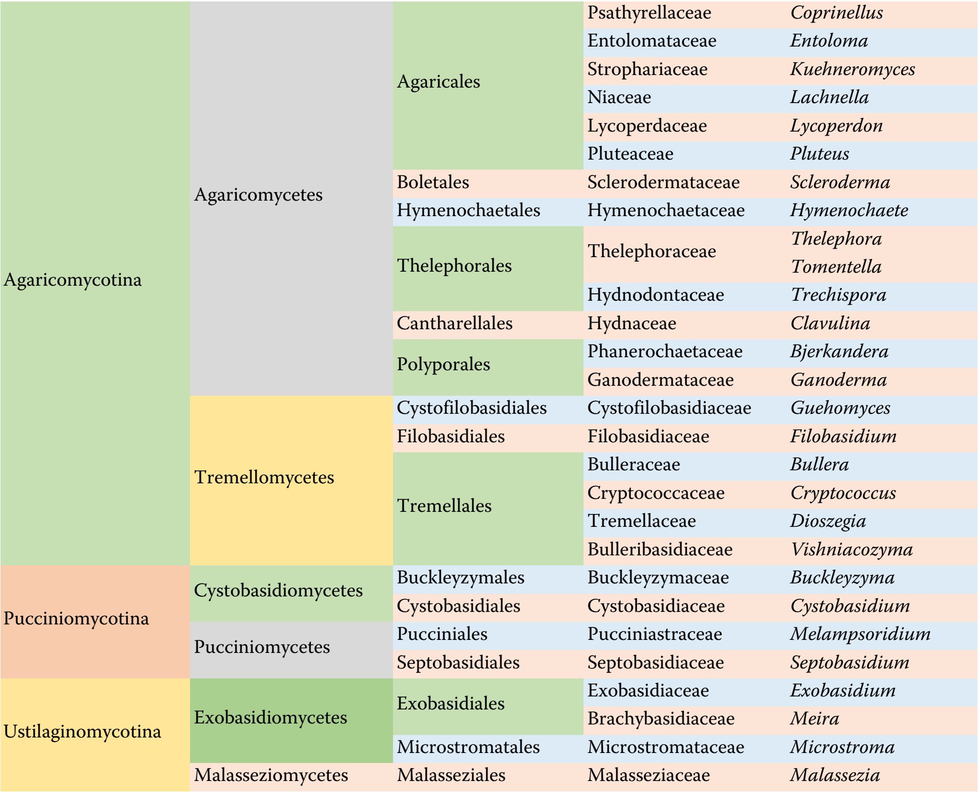
Figure 1. Taxonomic assortment of Ascomycota genera reported as endophytic in hazelnut

Pezizomycotina	Sordariomycetes	Diaporthales	Gnomoniaceae	*Cryptosporella*
				Gnomonia
				Gnomoniopsis
				Ophiognomonia
			Melanconidaceae	*Melanconium*
			Valsaceae	*Diaporthe*
				Diaporthella
		Glomerellales	Glomerellaceae	*Colletotrichum*
		Hypocreales	Bionectriaceae	*Geosmithia*
			Cordycipitaceae	*Cordyceps*
				Simplicillium
			Hypocreaceae	*Acremonium*
				Trichoderma
			Nectriaceae	*Fusarium*
				Ilyonectria
			Ophiocordycipitaceae	*Hirsutella*
				Purpureocillium
			Stachybotryaceae	*Myrothecium*
		Chaetosphaeriales	Chaetosphaeriaceae	*Chloridium*
		Ophiostomatales	Ophiostomataceae	*Ophiostoma*
		Sordariales	Chaetomiaceae	*Chaetomium*
				Humicola
				Staphylotrichum
			Podosporaceae	*Podospora*
			Sordariaceae	*Apodus*
		Amphisphaeriales	Amphisphaeriaceae	*Amphisphaeria*
				Pestalotia
			Pestalotiopsidaceae	*Neopestalotiopsis*
				Pestalotiopsis
		Xylariales	Apiosporaceae	*Apiospora*
			Diatrypaceae	*Diatrypella*
			Hypoxylaceae	*Annulohypoxylon*
				Daldinia
				Hypoxylon
			Microdochiaceae	*Microdochium*
		Lulworthiales	Lulworthiaceae	*Lulwoana*
Saccharomycotina	Saccharomycetes	Saccharomycetales	Saccharomycetaceae	*Candida*
				Pichia
Taphrinomycotina	Archaeorhizomycetes	Archaeorhizomycetales	Archaeorhizomycetaceae	*Archaeorhizomyces*
	Taphrinomycetes	Taphrinales	Taphrinomycetaceae	*Taphrina*

Figure 1 to be continued

Talaromyces and *Trichoderma*, which are credited for application in biological control of many plant pathogens on various crops (Thambugala et al. 2020; Alfiky & Weisskopf 2021), while *P. lilacinum* and *Arthrobotrys* are mainly known as nematophagous (Yang & Zhang 2014), and *Cordyceps, Hirsutella, Simplicillium* as entomopathogens (Nicoletti & Becchimanzi 2020). Particularly, the role of endophytic entomopathogens is increasingly appreciated for its general impact in plant protection (Mantzoukas & Eliopoulos 2020; Nicoletti & Becchimanzi 2020, 2021); on hazelnut, it deserves to be carefully investigated with reference to the high economic incidence on production by insects such as weevils (*Curculio* spp.) and stink bugs (Heteroptera: Pentatomidae, Coreidae) (Hamidi et al. 2022; Shanovich & Aukema 2022).

More pathogens are implicitly included in the series of fungi only identified at the genus level. This may be the case of *Pestalotiopsis guepinii*, known as an agent of twig blight (Türkkan et al. 2011), with reference to the findings of *Pestalotiopsis* sp. in Estonia and Japan. Among these genera, *Diaporthe* (Sordariomycetes, Diaporthales, Valsaceae) deserves further insights on its occurrence in hazelnuts. After the affirmation of the principle 'one fungus, one name' in fungal taxonomy, this genus includes species which were previously better known under the anamorphic name *Phomopsis* (Udayanga et al. 2012). The first report of these fungi on hazelnut dates back to about one century ago, when *Phomopsis avellana* was described from a specimen collected in Olomouc (Czechia) (Petrak 1921). However, this classification should be re-examined



Agaricomycotina	Agaricomycetes	Agaricales	Psathyrellaceae	*Coprinellus*
			Entolomataceae	*Entoloma*
			Strophariaceae	*Kuehneromyces*
			Niaceae	*Lachnella*
			Lycoperdaceae	*Lycoperdon*
			Pluteaceae	*Pluteus*
		Boletales	Sclerodermataceae	*Scleroderma*
		Hymenochaetales	Hymenochaetaceae	*Hymenochaete*
		Thelephorales	Thelephoraceae	*Thelephora*
				Tomentella
			Hydnodontaceae	*Trechispora*
		Cantharellales	Hydnaceae	*Clavulina*
		Polyporales	Phanerochaetaceae	*Bjerkandera*
			Ganodermataceae	*Ganoderma*
	Tremellomycetes	Cystofilobasidiales	Cystofilobasidiaceae	*Guehomyces*
		Filobasidiales	Filobasidiaceae	*Filobasidium*
		Tremellales	Bulleraceae	*Bullera*
			Cryptococcaceae	*Cryptococcus*
			Tremellaceae	*Dioszegia*
			Bulleribasidiaceae	*Vishniacozyma*
Pucciniomycotina	Cystobasidiomycetes	Buckleyzymales	Buckleyzymaceae	*Buckleyzyma*
		Cystobasidiales	Cystobasidiaceae	*Cystobasidium*
	Pucciniomycetes	Pucciniales	Pucciniastraceae	*Melampsoridium*
		Septobasidiales	Septobasidiaceae	*Septobasidium*
Ustilaginomycotina	Exobasidiomycetes	Exobasidiales	Exobasidiaceae	*Exobasidium*
			Brachybasidiaceae	*Meira*
		Microstromatales	Microstromataceae	*Microstroma*
	Malasseziomycetes	Malasseziales	Malasseziaceae	*Malassezia*

Figure 2. Taxonomic assortment of Basidiomycota genera reported as endophytic in hazelnut

in light of the modern taxonomic schemes, considering that at that time it was routine to refer names of fungi to the host plant in the absence of the capacity to promptly compare new isolates with previously described species of the same genus. Given this uncertainty, a revision of *Diaporthe-Phomopsis* published in 2013 mentions just a single species in association with hazelnuts, that is *D. decedens* from specimens collected in Austria and Sweden (Gomes et al. 2013). Additional findings have been reported in the last decade, starting with *D. amygdali* which, besides an endophytic strain from Turkey (Akay et al. 2011), has been found inciting formation of galls on twigs and branches of *C. avellana* in Iran (Mirabolfathi et al. 2013). More recently the species *D. australafricana* and *D. eres* have been recovered from cankers on *C. avellana*, respectively in Chile (Guerrero & Pérez 2013) and Oregon (Wiman et al. 2019), and the new species *D. coryli* and *D. corylicola* along with *D. eres* have been isolated in China from cankers on plants of *Corylus mandshurica* Maxim. and *Corylus heterophylla* Trautv. (Yang et al. 2020; Gao et al. 2021). Besides the woody organs, *Diaporthe* spp. may infect the nuts throughout their developmental stages, causing necrotic surface spots, internal browning and molding of the kernel. These product defects have been referred to *D. rudis* in an investigation carried out in Oregon (Pscheidt et al. 2019), while a more comprehensive study implemented in Turkey disclosed a varied species assortment, including *D. unshiuensis*, *D. oculi*, *D. pseudooculi*, *D. arecae*, *D. hongkongensis*, and the *D. sojae* and *D. eres* species complexes, with the latter being the most frequent (Arciuolo et al. 2020). *Diaporthe-Phomopsis* spp. are known for widespread endophytic occurrence, and the evidence is strong that most species are not specifically associated to plant species/families but spread horizontally throughout a given ecological context (Gomes et al. 2013; Carrieri et al. 2014; Nicoletti 2019; Küngas et al. 2020); hence, the endophytic aptitude of these fungi deserves to be accurately monitored in view of preventing the possible onset of disease, particularly in consequence of the stressful effects deriving by the ongoing climatic changes. This may also depend on the ecological association with other fungi; in fact, *Phomopsis* spp. were reported to cause gray necrosis of nuts in association with *Alternaria* spp. (Belisario et al. 2004; Duran et al.

2020), including *A. alternata* which is also mentioned for endophytic occurrence (Table 1).

Another species in the Valsaceae, *Anisogramma anomala*, is known to cause the eastern filbert blight of *C. avellana* in north America, which symptoms consist in rapidly expanding cankers and branch dieback; conversely, this fungus is a non-lethal endemic pathogen of the autochthonous species *Corylus americana* Walter (Johnson et al. 1996). Due to the stealthy spread tendency of *A. anomala*, which so far has not been reported in the territory of the European Union (EFSA Panel et al. 2018), methods for its rapid identification in plant tissues have been developed (Cai et al. 2013) which may enable to detect it in asymptomatic tissues and to shed light on its eventual endophytic aptitude.

Two more species identified as foliar endophytes in Iran may present pathogenic implications. *Cryptosporiopsis tarraconensis* is specific to hazelnuts where it causes bud rot (Gené et al. 1990; Tagliavento et al. 2021), and leaf brown spot (Roohvarzi et al. 2013), while *Gnomoniopsis idaeicola* has been reported as a frequent associate in hazelnut kernels (Pscheidt et al. 2019). Although hazelnuts are often harvested after falling to the ground, which may lead to their contamination with soil microbes, it would be worth ascertaining if the occurrence in molded nuts of *G. idaeicola* and eventually other fungi may rather be consequential to their primary endophytic settlement. Mild pathogenic aptitude on hazelnuts has been documented in Sardinia for *G. castaneae*, inciting cankers on twigs and branches (Linaldeddu et al. 2016). This species is mainly known as a pathogen of chestnut, representing one of the most recently affirmed threats of this forest crop (Lione et al. 2019), where it was also reported to be able to develop endophytically (Nicoletti et al. 2021). The finding that it can also occur as an endophyte of hazelnut, which often shares the same agro-climatic contexts as chestnuts, stimulates further consideration about the epidemiological impact of this adaptability.

This concept is also valid in the case of *Fusarium*, which is considered one of the most important genera of plant pathogenic fungi, known as disease agents of an extremely wide range of crops (O'Donnell et al. 2022). On hazelnut *Fusarium lateritium* is reported as the causal agent of twig canker (Belisario et al. 2005) and nut gray necrosis (Vitale et al. 2011). However, the introduction of methods based on DNA sequencing in the classification of *Fusaria* has pointed out that identification of isolates based on morphology or biochemical characters can be misleading (Manganiello et al. 2019); so that a revision is currently in progress in view of attaining to a correct taxonomic identification of isolates, which are often provisionally ascribed to species complexes (O'Donnell et al. 2022). In fact, a recent study showed an isolate from symptomatic hazelnuts to be more closely related to the *Fusarium tricinctum* species complex in phylogenetic terms (Turco et al. 2021). Along with a few more *Fusarium* spp., *F. tricinctum* was isolated as an endophyte in Iran (Table 1), which can be indicative of a more widespread association with hazelnut calling for insights on the real nature of ecological relationships between the two symbionts.

Besides pathogens, there is another functional category of fungi possibly resulting in investigations on the endophytic associates of hazelnut, that has notable influence on the host metabolism with obvious effects on growth and health: the mycorrhizae. A couple of studies carried out in Sichuan (China) have focused on the microbial communities associated with ectomycorrhizae in hazelnut plants inoculated with the Chinese white truffle (*Tuber panzhihuanense*) (Yang et al. 2019) and the bianchetto truffle (*Tuber borchii*) (Li et al. 2019). In both these studies identification was limited at the genus level, by reason of the previously discussed taxonomic approximation resulting after the use of ITS sequences. In the first case, a higher number of genera was found in association with the inoculated plants, with increased abundance of some taxa (e.g. *Monographella*), and lower presence of several pathogenic and competitive mycorrhizal fungi (e.g. *Phaeoacremonium*, *Podospora*, *Hymenochaete*, *Ilyonectria*, *Trechispora*). The latter effect was observed in the second study too, particularly with reference to *Ilyonectria*, *Podospora* and *Hymenochaete*, while the presence of other genera (e.g. *Humicola, Trechispora*) increased. Both studies provide preliminary indications of favourable effects of a higher diversity of the endophytic associates on mycorrhization and plant health.

Implications in biotechnology

The limited studies carried out so far on hazelnut endophytes reflect quite limited applications in biotechnology. Undoubtedly, the most substantial one consists in the exploitation of endophytic fungi in production of the blockbuster antitumor drug paclitaxel. In fact, although primarily extracted from yews (*Taxus* spp.) and as a product of their endophytes (Nicoletti & Fiorentino 2015; Gallego-Jara et al. 2020), the issue of paclitaxel (taxol) production has become of primary interest for hazelnuts too, starting with the finding that it can be obtained from cell cultures, nutshells and leaves of this plant, along with other taxanes (Bestoso et al. 2006; Ottaggio et al. 2008). As it happened with yews, this discovery stimulated investigations on the possible production through fermentation by employing hazelnut endophytes. This search led to the finding of an endophytic strain of *Penicillium aurantiogriseum* holding this remarkable property; its genome was sequenced, enabling to demonstrate that taxol synthesis by this fungus follows a partially different biochemical pathway (Yang et al. 2014). Subsequently, it has been shown that endophytic fungi are able to elicit taxane synthesis in hazel cell cultures; particularly, a strain of *Paraconiothyrium brasiliense* from hazelnut and a strain of *Chaetomium globosum* from common yew (*Taxus baccata*) (Salehi et al. 2019a). Likewise, culture filtrate and cell extract of a hazelnut endophytic strain of *C. flavigenus* were found to be effective in eliciting taxol synthesis in the cell suspension culture of *C. avellana* (Salehi et al. 2020a, b). The reverse eliciting effect was also observed by the extract from hazel cell cultures, which stimulated taxol biosynthesis by another endophytic strain of yew identified as *E. nigrum*; yields were even higher in co-cultures of hazelnut cells with this strain (Salehi et al. 2018, 2019b).

The potential of the endophytic fungi of hazelnut in the pharmaceutical field may not be limited to issues related to paclitaxel production. In fact, a leaf isolate of *Diaporthe* (= *Phomopsis*) *amygdali* was found to produce two α-pyrone derivatives, that is a novel compound named 4-butoxy-6-(1-hydroxypentyl)-5,6-dihydro-2H-pyran-2-one and the known (-)pestalotin; both products displayed moderate cytotoxic activity against a panel of human cancer cell lines (Akay et al. 2011, 2014), joining the huge list of fungal products awaiting for further characterization as antitumor drugs (Nicoletti 2021).

CONCLUSION

Climate change, pollution, ecosystem collapses, biodiversity loss, food security and depletion of natural sources of plants used for biotechnological purposes are some of the biggest threats facing humanity currently and in the next decades. In this alarming scenario, all attempts to enhance studies on endophytic fungi and their applicative perspectives in plant protection and biotechnology are desirable to counteract the negative impact on the environment and human welfare, following the paradigm of sustainable agriculture. Above all, endophytes hold great dexterity for biological control of cryptogamic diseases by exerting a range of antagonistic effects against their agents. On hazelnut, these properties may be particularly exploited as an alternative to copper products, which have been announced to be phased out in the European Union due to the harmful effects on humans and the negative impact on soil structure and biodiversity in agricultural habitats (Tamm et al. 2022).

Note: For authorities of the fungal species names, please check information at the Index Fungorum (www.indexfungorum.org/names/names.asp).

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