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# Advances in endophytic fungi research: a data analysis of 25 years of achievements and challenges

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## ABSTRACT

Research on fungal endophytes has demonstrated the ability to improve crop performance and protect host plants against diverse biotic and abiotic stresses. Yet, despite the exponential growth of this topic, a whole outline to reflect the relevance and extent of each study type is missing. Hence, we performed an analysis of all available literature to expose the characteristics and limitations of this research field. Our results suggested that, overall, there is still a tendency to study the most known models in plant-fungal-stress combinations (ascomycetous fungi, grasses, abiotic stress). Fungal endophytes in dicot plants or against biotic stress, though promising, are still quite unexplored. All these data could lead future studies to assess less considered study factors that might help discern the beneficial effects of fungal endophytes with more extent and accuracy.

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## 1. Introduction

Current studies about global food and agriculture revealed that world production may need to be increased by 60%–110% before 2050 to avoid food shortage. However, yields are no longer improving on 24–39% of most important crop-land areas (Schmidhuber and Tubiello 2007; Edgerton 2009). Along with the demand for increased production, we need to preserve the environment and promote biodiversity in agronomic ecosystems, mainly by reducing the use of pesticides and making better use of agricultural inputs and resources: land, water, fertilizers and energy. In this context, the use of beneficial microorganisms to improve crop performance and reduce the need for chemical inputs has become a realistic alternative that is gaining interest among researchers and the industry (Lugtenberg et al. 2016; Singh and Trivedi 2017; Llorens et al. 2019).

Microorganisms are widely reported to be naturally associated with plants. Despite the fact that the presence of living microorganisms inside plants has been known since the beginning of the last century, its attention only increased in the last decades with the discovery of their ecological significance and their ability to produce metabolites that could modulate the physiology of the host plant or be of pharmacological interest (Mattoo and Nonzom 2021). Given these circumstances, the term ‘plant microbiome’ (Hardoim et al. 2015) is on the rise, and the living microorganisms that are in association with plants are investigated with rising intensity.

In this way, one of the emerging areas of study is around fungal endophytes. Plant-associated fungi are typically classified as either pathogenic, saprotrophic, epiphytic, mycorrhizal or endophytic (Porrás-Alfaro and Bayman 2011). Yet, most, if not all, plants have symbiotic fungi, either epiphytic, endophytic or mycorrhizal (Rodríguez et al. 2009).

With the evolution of research regarding endophytic microorganisms, fungal endophytes have held several definitions (Schulz and Boyle 2005; Hyde and Soytong 2008). In this case, the most accepted consideration establishes endophytic fungi as those fungi that reside entirely within plant tissues, without causing apparent symptoms of disease (Tan and Zou 2001; Rodríguez et al. 2009). These endophytes also differ from mycorrhizae in that there’s no localized and specialized hyphae or synchronized plant-fungus development (Brundrett 2006).

Despite the broad diversity of the group, fungal endophytes have been conventionally divided into two categories, clavicipitaceous and non-clavicipitaceous, and four classes (Rodríguez et al. 2009) based on their symbiotic and ecological patterns. Clavicipitaceous endophytes, also called class 1 endophytes, belong to Clavicipitaceae (Hypocreales; Ascomycota) and are restricted to a narrow range of hosts, but they can colonize the whole plant and transmit vertically and horizontally. On the contrary, non-clavicipitaceous endophytes, which comprise Class 2, Class 3, and Class 4, are characterized by colonizing a broad range of hosts, which include both monocot and dicot plants. Class 2 is formed by ascomycetes or basidiomycetes fungi and can be found in any part of the plant and transmitted both vertically and horizontally. Opposed to Class 2, endophytes in Class 3 and Class 4 are restricted to shoots or roots, respectively. Class 3 includes a diverse group of fungi that is transmitted horizontally, whereas Class 4 includes a specific group of sterile fungi also known as dark septate endophytes, which manifest melanized septa (Rodríguez et al. 2009).

In addition, the diversity of microbial symbionts varies on a host plant and environmental conditions including biogeography, as seen in Kivlin et al. (2017). Yet, endophyte diversity is not the only complex aspect of endophytes, since the

relation between the host plant and its fungal endophytes is also intricate (Saikkonen et al. 1998). Although their interaction commonly provides nutrients and stress or competition tolerance to a degree, Schulz and Boyle (2005) hypothesized that there is a continuum of antagonistic interactions and no neutral interactions, and each relationship differs from another. Thus, understanding the nature and particularities of the interactions between endophytes and host plants and how they affect the host could be key to improving agricultural management.

Recent studies have shown that the microbiome has an impact on different aspects of the host plant, such as improving tolerance to drought, heat, or saline stress, reducing susceptibility to diseases, and increasing vigor (Weiß et al. 2016; Llorens et al. 2019). For instance, species that improve the growth of certain types of grass (*Panicum virgatum* or rod grass) for the production of biofuels or species that protect maize from fungal pathogens have been reported. Moreover, it has also been described that certain species from wild herbs, when transferred to wheat and tomato, are capable of improving the growth of these plants under conditions of heat and salinity stress (Redman et al. 1986; Rodriguez et al. 2008). The mechanisms by which the endophytic microorganisms improve the performance and the resistance of the plants could be divided into direct and indirect mechanisms. The direct mechanisms include compounds that are directly secreted by the endophyte that have a straightforward effect. These mechanisms comprise secretion of antibiotics, lytic enzymes, phytohormones, indolic compounds or direct competition of the niche. On the other hand, indirect mechanisms include plant responses induced by the presence of the endophyte. These mechanisms include the stimulation of Induced systemic resistance (ISR) and Systemic acquired resistance (SAR) or the stimulation of plant secondary metabolites (Fadji and Babalola 2020).

The ability and feasibility of improving plant performance and resistance to different stressors using fungal endophytes have fomented the interest in this research area. However, the possibilities of research on different fungi, hosts, stressors, and many other variables give almost endless combinations that can lead to the underestimation of some areas. The rising attention given to microbial symbiosis in the scientific community is reflected in the high number of publications regarding this topic, including several reviews (Tan and Zou 2001; Gautam and Avasthi 2019; Pozo et al. 2021) and some meta-analysis (Mayerhofer et al. 2013; Dastogeer 2018). Yet, many are focused on a specific aspect of symbiosis, such as induction of resistance or production of metabolites, and some don't focus on the fungal endophytes.

Now, we have at our disposal the data of many types of study about endophytic fungi, but what is the magnitude of each one? What is the relevance of one type of endophyte compared to others? In order to know to what extent a study category is relevant, we would need a clear description of the whole research field. We hereby introduce a precise interpretation of the data observed in fungal endophytes' studies to demonstrate the state and tendency of the field by analyzing published literature. In this work, the objective was to contrast the main study aspects and find some minor categories of research that are usually overlooked. The following questions were addressed:

- What is the diversity of the studied fungal endophytes and their host plants?
- Which are the potential endophyte effects that are addressed in the studies? Were the results positive?
- What aspects of fungal endophytes are extensively investigated and what ones are scarcely studied?

## 2. Methodology

### 2.1. Study design

We conducted a systematic analysis of literature published about the effect of fungal endophytes in plants. The structure of the analysis process was performed following the Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) guidelines.

### 2.2. Literature search

#### 2.2.1. Eligibility criteria and search methodology

To obtain the metadata that would allow analyzing the current status of fungal endophyte studies we performed a literature search on the Scopus database in 2021, including all the articles published up to December 2021.

The following terminology was used for the search:

- *Endophyte*
- *Plant OR grass*: This term was included to avoid research with no inoculation in plants.
- *Fungi*: Fungus, fungal, and variations were included.
- *Stress OR tolerance*: To find the purpose of the endophytes
- NOT *mycorrhiza*: Excluded mycorrhizal fungi to find strict endophytic fungus.

The terminology was looked for in title-abstracts and keywords of articles.

A second search was conducted afterward for growth-promoting endophytes. This time, the keyword for 'stress or tolerance' was changed to 'growth.'

Other non-vital roles like phytoremediation, fruiting characteristics and such can be of great interest for specific host plants or environment but are not as globally significant as the main roles previously discussed, hence their absence in our literature search.

#### 2.2.2. Study selection and criteria for inclusion

Results from both search queries were merged, and then examined to ensure the relevance of the publications for our topic concerns. In order to achieve equality of the results, references with the following conditions were removed:

- (a) studying endophyte presence and identity without further application,
- (b) focusing on the cattle industry,
- (c) aiming to particularly identify the mechanism of the host-endophyte relation,
- (d) not fulfilling the search requirements due to other unspecific reasons, and
- (e) not having its original source available or verifiable.

From the selected manuscripts, the information provided about the fungal endophytes, the host plants, the type of

stress studied, and the results were included in the final analysis. In addition, highly similar articles such as in same authors, endophyte and host, were only counted once, including all the results from them.

### 2.2.3. Data collection

Subsequently, the references were exported to an MS Excel spreadsheet for further analysis. To compare selected articles, the data was broken down into different sets:

- (1) The fungal endophytes' species, or at least their genus, DSE, unidentified fungi, or the use of all microbiome of a plant was recorded as such if appropriate.
- (2) Original host plants' species, from which the endophytes were isolated. Their condition as wild or cultivated plants was distinguished, and endophytes that were not isolated in the current study had this section unfilled to avoid duplicates.
- (3) Study host plants' species, whether the endophyte is inoculated in the same host plant from which it was isolated, or a new host. Their condition as wild or cultivated plants was noted.
- (4) Method used to produce endophyte-free plants, if pertinent. This section does not account for surface sterilization, since it's a widespread procedure that occurs in most, if not all, studies.
- (5) Tested effects of the endophytes.
- (6) Experimental results, whether the endophytes conferred clearly beneficial effects, had some varying impact, or had no significant or negative effects on the host plant.

When several species were used, they were all registered. Taxonomic synonymy was avoided by assigning only the current taxonomic name, as consulted in the NCBI database at the moment of the analysis.

Furthermore, to simplify results, we recorded some data into groups:

- (1) Fungal endophytes' division. Ascomycota, Basidiomycota, and Mucoromycota. When fungi of different phyla were reported in the same article, it was considered that the article worked with various phyla.
- (2) Original host plants' family.
- (3) Study plants' family.
- (4) Function group of the endophyte. The potential effects were classified into one of these categories: abiotic stress tolerance, biotic stress tolerance, growth promotion, other effects, or several of them. When growth promotion was assessed under stress conditions, only the stress tolerance effect was considered.

### 2.3. Study quality and risk of bias

This meta-analysis aims to perform a qualitative analysis of the currently available literature. In this way, it is necessary to consider that, due to the diversity and complexity of the analyzed studies, comparing experiments with different study parameters is not always feasible. Therefore, for the purpose of this work, the simplest and clearest variables have been compared.

It is also important to address the issue of independence of the analyzed studies since the search results include papers

that are part of the same study or research group and only differ on either study parameters or research progression. To avoid inaccuracy caused by counting dependent items as independent ones, a set of papers from the same study or research group was considered as a single independent item with several study parameters.

We are aware of the possible bias committed by considering only those articles that use the word 'endophyte' in the title, keywords, or abstract, excluding some potential useful reports. Yet, opposite bias could also happen, since there might be articles that elaborate on endophytic organisms only in the main text, hence remaining out of the current research and analysis. All this said, the only way to correct such bias would be reading all articles with the word 'endophyte' in the main text and selecting those that meet the other criteria for inclusion, which effort we considered as unmanageable for the purpose of this work.

## 3. Results and discussion

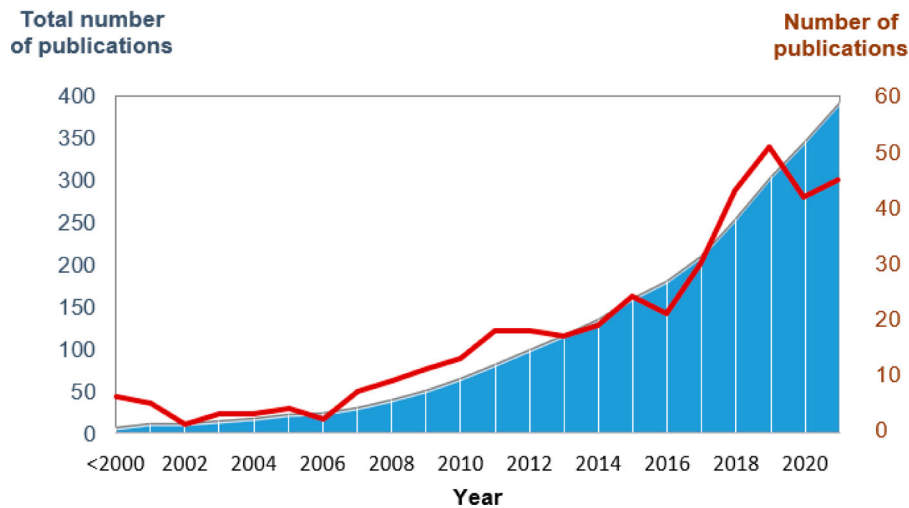
Beneficial microorganisms play an important role in plant performance and adaptation to adverse conditions. Among them, the interest in fungal endophytes has raised in the last decades due to their ability to produce secondary metabolites that could protect the host plant against herbivory (Bultman and Bell 2003; Shiba and Sugawara 2005). More recently, it also has been observed that fungal endophytes could play other roles related to plant protection against stress conditions (Waller et al. 2005; Hossain et al. 2017), increasing the interest of the researchers in this emerging area.

In order to confirm and analyze the state of fungal endophytes' studies, we performed two literature searches that retrieved around 1138 online references for the first one, covering stress tolerance, and 418 for the second one, focused on growth promotion. After the pertinent reductions described in the methodology section of this paper, we elaborated a database with a sum of 392 papers, containing scientific publications that range from the year 1988 to December 2021.

The preliminary analysis of the gathered literature proves the rising tendency of this research area, as observed in the graphic slope of Figure 1. This figure shows how this study field has been increasing steadily since 2006, and how the number of publications on this topic in the last 5 years is higher than the number of publications before 2017. However, it has been also observed that, in the last year analyzed, the number of publications that fulfill our search criteria has been slightly lower. On the other hand, an enhancement of articles with related topics as the study of plant microbiomes has increased. Thus, this makes clear the outstanding performance of fungal endophytes as a research field and the ongoing attention given to these microorganisms by the research community.

The literature we examined usually had a common way of working, with experiments arranged following next steps: isolation of endophytes from a host of interest or acquisition from a provider, selection of most relevant endophyte or few endophytes, inoculation in the plant, and evaluation of its effects in growth promotion or against some kind of stress. In the following sections, we show our analysis of the relevant aspects and other details of interest of the reviewed papers.

### Accumulative number of articles belonging to the literature search



**Figure 1.** Number and accumulative number of published articles identified in the present literature research until 2021. Right-side axis belong to graphic line; Left-side axis belong to graphic area.

### 3.1. Fungal endophytes and their diversity

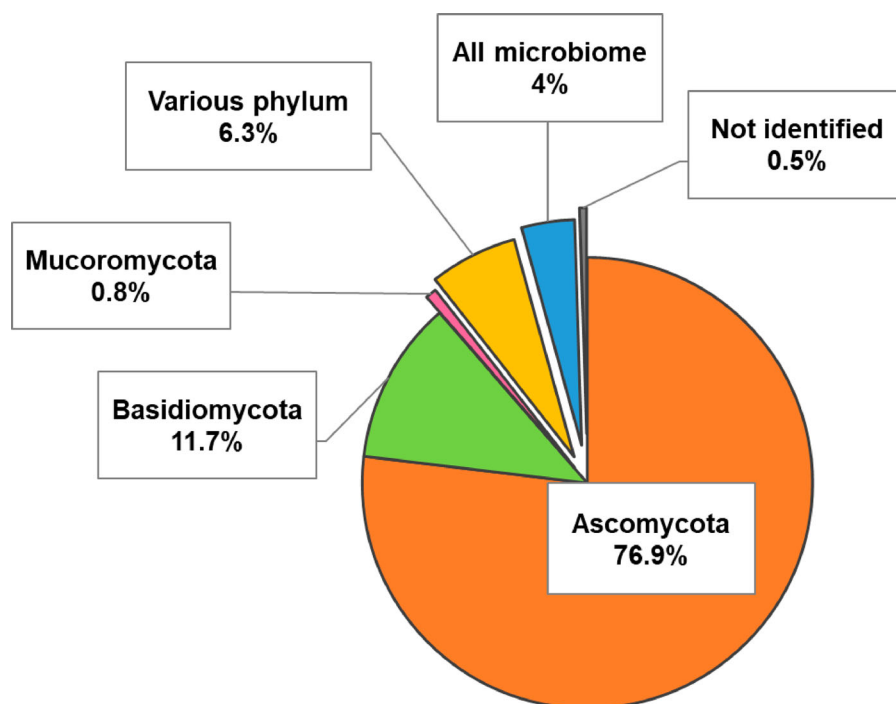
Studies usually state the fungal strain used in their experiments, either specified by the provider or obtained by identifying the isolates of a host plant. Yet, 21% of the literature did not completely identify the endophyte, leaving the determination at the genus level or potential candidates. This might be caused by several reasons: not finding total coincidence with any species on fungal databases, focusing on the role of the endophyte rather than its identity, etc.

Tested endophytes are categorized at the division level in Figure 2, and genera frequency is shown in Figure 3(a). Also, though it was outside the scope of the study, root endophytes seemed to be more commonly studied, followed by leaf and stem endophytes. Our analysis showed that the vast majority

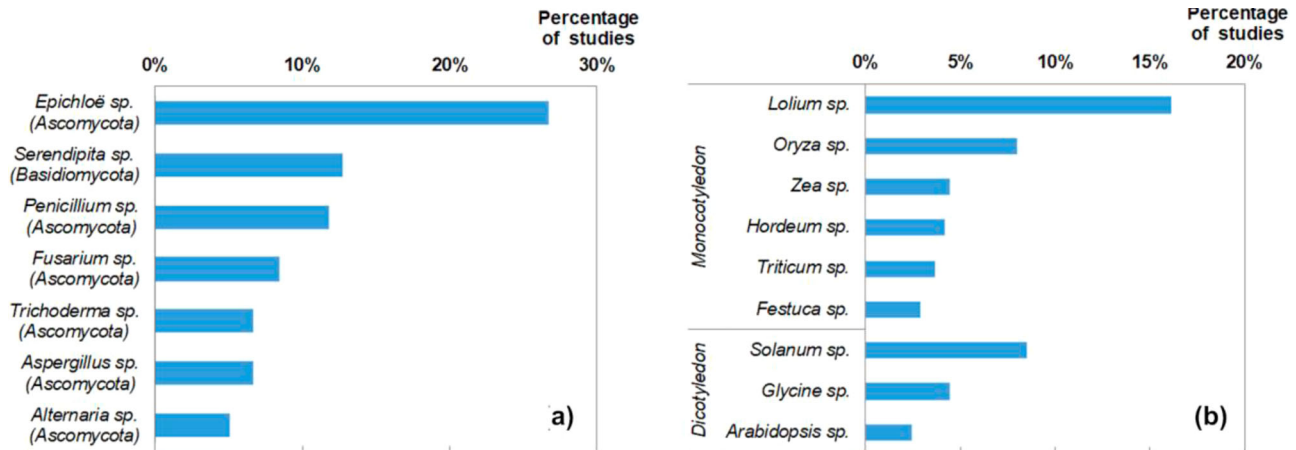
of the studies are focused on Ascomycota, which turned out to be almost 80% of the database results, while Basidiomycota covered around 12%, and Mucoromycota barely added up to another 1% of the results.

Ascomycota’s prevalence is not surprising, since ascomycetes fungi are the commonest in nature. In this category, we can find genera such as *Epichloë*, *Penicillium*, *Trichoderma*, *Fusarium*, *Aspergillus*, and *Alternaria*.

The relevancy of *Epichloë*, also known as *Neotyphodium* or *Acremonium* in past literature for its asexual morphs, goes back to 1988 when it was discovered. It is considered the first reported endophytic fungi, and it is beyond question the most known fungal endophyte genus since it extensively colonizes widespread forage grasses, such as *Lolium spp.*



**Figure 2.** Fungal endophyte phyla recurrence in literature research.



**Figure 3.** Most common endophyte genera (a) and study plant genera (b) found in literature research.

(Scharndl et al. 2004). As seen in reviewed articles, studies about *Epichloë* are usually focused on plants as forage or turf, and there are no studies about inoculation of this Class 1 endophyte in non-host plants due to its limited host range. West et al. (1988) observed that endophyte-infected *Lolium arundinaceum* gained tolerance to drought and nematode infection and Elmi and Robbins (2000) and other posterior works confirmed those premises relating both stresses. *Lolium perenne* as endophyte host has therefore been studied to demonstrate, for instance, tolerance to drought and nitrogen deficit (Ravel et al. 1997), to heavy metals like zinc (Monnet et al. 2001) or predators like rice leaf bug (Shiba and Sugawara 2005).

Another recurrent genus of Ascomycota endophytes is *Penicillium* for the ability to improve growth and abiotic stress resistance, with species like *P. janthinellum* (Khan et al. 2014) or *P. funiculosum* (Khan et al. 2011). Likewise, *Fusarium* is not only studied for abiotic resistance ability but to confer biotic resistance, with special regard to pathogenic *F. oxysporum* strains (Ting et al. 2008; Nefzi et al. 2019).

Some of the articles refer to the use of dark septate endophytes (DSE). This definition was used for the first time by Read and Haselwandter (1981) to describe a diverse group of ascomycetous endophytes with melanin hyphae that live in roots without causing any visible symptoms. Subsequently, numerous researchers have used this informal term without further classification. Even so, few articles describe the use of DSE and identify the fungi as *Alternaria* sp. or *Penicillium* sp.

In contrast to the diversity of ascomycetous endophytes exposed in the publications, basidiomycetes, and mucoromycetes have been less studied according to our literature database. One exception to this is the basidiomycete *Serendipita indica*, previously known as *Piriformospora indica*. *S. indica* was firstly reported in 1998 (Verma et al. 1998), discovered in desert soil from India, and found to be similar to arbuscular mycorrhizal fungi (AMF), yet, as opposed to them, it was able to grow in axenic culture (Varma et al. 2001). And, unlike *Epichloë*, it has been since widely tested in both monocots and dicots. The most common benefits of this endophyte have been reported to be growth promotion (Sahay and Varma 1999; Rai et al. 2001; Bagde et al. 2011; Satheesan et al. 2012; Noora et al. 2017), as well as inducing resistance

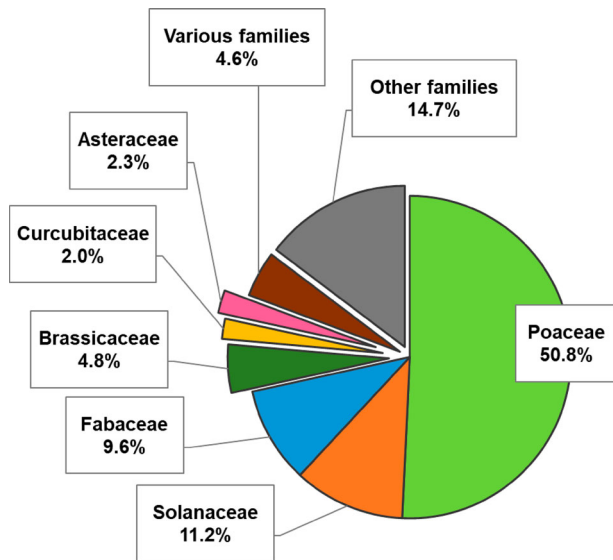
against abiotic stress such as drought (Sherameti et al. 2008; Hosseini et al. 2017; Hussin et al. 2017; Ahmadvand and Hajinia 2018) and salinity (Waller et al. 2005; Sinclair et al. 2013; Abdelaziz et al. 2017; Li et al. 2017; Sharma et al. 2017). Some studies also report a beneficial role against pathogens (Cosme et al. 2016; Lin et al. 2019), but this field is less studied.

Not a considerable amount of studies worked with multiple endophytes at once. Some articles referred to various endophytes from different phyla (6%), through the application of various potential endophytes or a selection from the microbiome of the host plant. In this case, studies use a consortium of fungal strains, though using a consortium of both bacterial and fungal strains like done by Varkkey et al. (2018) was apparently more common. Furthermore, a scarce number of studies worked with the whole microbiome from a plant (4%). We hypothesize that the scarcity of these types of study is a sign of researchers considering beneficial properties provided by individual endophytes more relevant than their interactions within plant tissue. This, at the same time, is probably due to the complications that involve studying several endophytic species at once since, according to Kivlin et al. (2013), since the interactions depend on not clear conditions, there is the danger of underestimating or overestimating the global effects of a group of endophytes.

### 3.2. Host plant and their diversity

Results of the analysis regarding endophyte host plants are illustrated in Figure 4. Poaceae family dominates the studies with half of the literature results (51%). The other half refers mostly to a diversity of host plants, usually of economic relevance, and only a few studies refer their experiments to several plant families.

As seen in Figure 3(b), ryegrass (*Lolium* sp.) stands out among the recurrent host plants. This grass genus, which includes *Lolium perenne*, *Lolium arundinaceum*, and *Lolium multiflorum*, has been included in more than 16% of the total number of articles. We consider that the main reasons for this might be its wide range, importance in the cattle sector, and identity as host of *Epichloë* endophytes. Another well-used monocot in literature is rice (*Oryza sativa*). This is one of the most relevant food crops in the world and is inoculated with non-host endophytes in order to obtain



**Figure 4.** Family of study host plant recurrence in literature research.

growth enhancement and abiotic stress tolerance. Other species from the Poaceae family commonly mentioned are barley (*Hordeum vulgare*), maize (*Zea mays*), common wheat (*Triticum aestivum*), and red fescue (*Festuca rubra*) in order of recurrence. All of them are extensively cultivated species, and barley and red fescue, along with some close relatives, are also commonly infected with *Epichloë sp.*

Monocots are surely the prevalent plant group of interest, since they are of great economic and cultural relevance and are relatively easy to work with. However, dicot plants as endophyte hosts have yet a lot of unrevealed potential. Around 30% of the studies covered species that belong to families with relevance as food resources such as *Solanaceae*, *Fabaceae*, *Brassicaceae*, and *Cucurbitaceae*. Among these, the most used species are tomato (*Solanum lycopersicum*) and soybean (*Glycine max*), which take part in around 9% and 5% of the articles, respectively. Both species hold great economic value similar to the previously mentioned monocots, yet are seldom used as biological models in front of biotic stress.

The remaining studies in the database worked with plants that have significance either as ornamental plants, ecological models, or sources for other goods such as medicine, lumber, or resin. In addition to these, a few articles (barely 4%) need to be considered for applying endophytes to several plant species that belong to different families.

Finally, the environment in which plants grow and where the experiments are conducted can also have an impact on the reliability of the results. Although field experiments would be the most realistic approach for the studies (Rai et al. 2001; Zhou et al. 2018), it is difficult to perform this kind of experiments because of the complexity of all the factors that get involved in it. Instead, most publications referred to growth chambers and greenhouses to carry out their experiments. On the opposite, a couple of studies (5%) performed their experiments only in vitro bioassays (Dovana et al. 2015; Khan et al. 2017), usually with mutant rice. This last kind of studies has particularly controlled environmental conditions and further experiments would be required to test the effects of the endophytes on the behavior and interactions of the host plant under more realistic conditions.

### 3.3. Host plant and study plant conditions

Since the original host plant of the studied endophytes may differ from the study's host plant, the information regarding their conditions was recorded (Figure 5).

Around 30% of the studies referred to host plants from wild origin (Li et al. 2017; Li et al. 2018). We consider studying endophytes from nature-adapted plants of great significance due to their biodiversity and wide-ranging microbiome. Those endophytes are also typically acquired from locations with extreme environmental conditions such as deserts to assess their potential role in adverse conditions. On the contrary, only 18% of study plants were clearly traditional or wild plants, against 53% of the studies that inoculated cultivated species. This confirms that finding endophytes from wild origin to use them as means to improve the behavior of crops is more relevant than discerning their role in a natural environment.

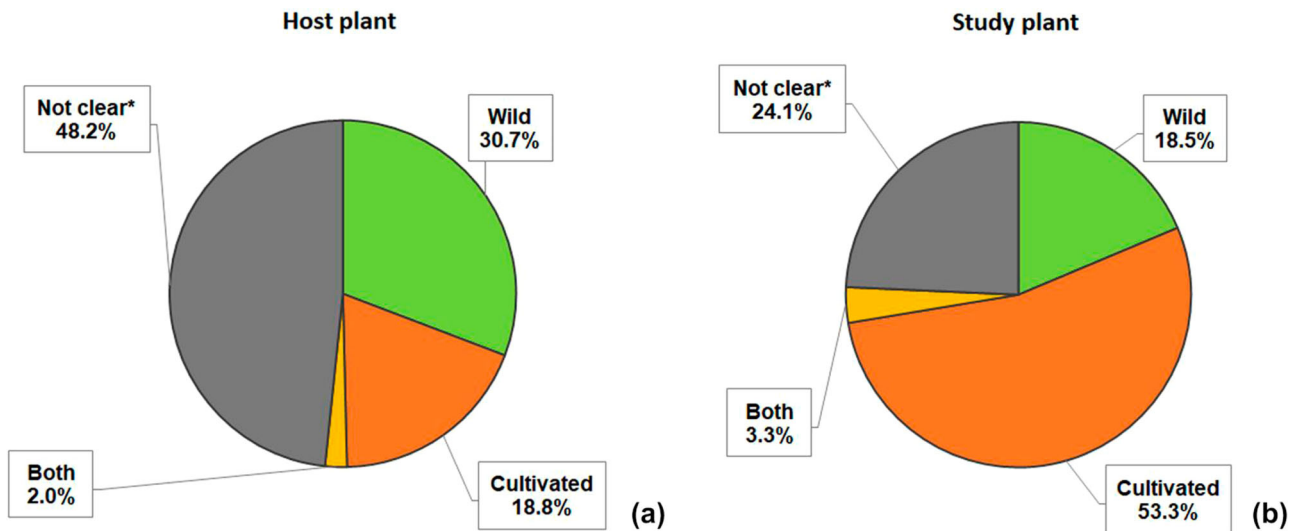
In 52% of the articles, isolating the fungal endophyte strains was an integral part of the study. In the other cases, the strains were either isolated in previous work of the research group or provided by microbial banks or another entity.

On another note, we compared the identity of the host and study plant. In this case, we could see that the fungal endophyte was inoculated to the same host plant species from which it was isolated in at least 48% of the articles, while at least 25% of them used a different species of host plants in the experiments. Inoculation of the same plant species from which the endophyte was isolated is, possibly, an indicator of the interest in exploring the effect of the endophyte on its natural host.

There also was a tendency to use some methods in order to produce endophyte-free plants, but this seems to be of decreasing importance in the more recent studies. These methods are specified in Table 1, and focus on obtaining plants that are cleared up from any microbiota to avoid interference with the endophyte of interest. Among these treatments, systemic fungicide treatment prevailed (11%), especially in the early years of research. However, these practices have been discontinued since, presumably due to the need of considering interaction within the plant microbiome in order to ascertain the effect of the study endophyte. Likewise, heat treatment use has almost disappeared nowadays (4%). In this case, the reason may be the possible negative impact of heat treatment in seed germination and future plant physiologic aspects and performance. The only method that is still used with the same incidence as before is the individual selection of study material (6%). This is a procedure that usually makes use of microscopy to identify the presence or absence of the study endophyte to classify their plant material. In the end, these treatments are not used anymore on a current basis, and most of the studies (73%) tend to not apply them. This includes the great number of publications where inoculated plants differ from the original host plant of the study endophyte and the other studies that only resort to surface sterilization of the seeds before inoculation.

### 3.4. Role of fungal endophytes in studied plants

Plants are always exposed to multiple environmental factors and many of them can result in biological stress, an adverse condition that inhibits their normal functioning (Jones and



**Figure 5.** Host plant origin in literature research. (\*) Not stated or endophyte is whether from soil, previously isolated or provided by a bank.

Jones 1989). However, fungal endophytes can also affect multiple aspects of the host plant's life cycle. It has been extensively reported how fungal endophytes can alter host physiology under stress and confer tolerance to host plants by enhancing activation of the host's defense system (Tidke et al. 2017; Shankar Naik 2019). The diverse effects that endophytes trigger in their host plants can range from growth improvement to protection against cattle. Thus, the effects are not straightforward and there is a whole range of benefits that could be induced in the plant and play a critical role in their resilience (Rodriguez et al. 2009; Mei and Flinn 2010; White and Torres 2010).

**Table 1.** Used method to obtain endophyte-free plants besides surface sterilization.

Recurrence	Method	Description	Potential consequences
12%	Fungicide	Application of chemical compounds such as propiconazole or systemic fungicide like benomyl to seed plants.	Harm to physiologic functions and growth of the plants.
4%	Heat	Application of high temperatures to seed plants, with specific conditions that are previously tested. Temperature is higher than 50°C, either with hot water or in oven, for a period between an hour and a week.	Physical damage and germination difficulty of seeds, physiologic alteration of plants.
1%	Storage	Infected seeds are stored at room temperature for a long period of time, which sometimes result in a loss of endophyte infection.	Incomplete removal of the fungal endophyte from the seeds.
6%	Selection	Individual selection of seeds, either as an option provided from seed bank or after examination by microscopy.	Error in detection of endophyte strain.
77%	None	There's no method applied to eliminate endophytes from plant besides surface sterilization of the used seeds.	Not considered.

In this study, studied effects of fungal endophytes are sorted as seen in Figure 6. Resistance against abiotic stress is the most studied condition (57%), followed by growth promotion (20%) and resistance against biotic stress (15%). The remaining articles experimented with several types of plant stress conditions (8%).

In the following sections, we check the specific results for each type of stress, taking into account individual results for the studies.

#### 3.4.1. Effect of fungal endophytes under abiotic stress

With the advance of climate change, plants are severely exposed to abiotic stress, both physical and chemical. Abiotic stress is defined, according to Ben-Ari and Lavi (2012), as the negative impact of non-living factors on living organisms in a specific environment. These conditions, such as water deficit, extreme temperature, soil salinity and heavy metal contamination are common adversities that affect crop productivity worldwide.

In this context, endophytes can play a significant role in conferring stress tolerance to host plants by altering water relations, osmolyte production, and synthesis of hormones and reactive oxygen species (ROS) (Shankar Naik 2019). Thus, we believe that countering the extensive consequences of global warming and contamination is one of the main goals of studying fungal endophytes. The interest in the potential induction of resistance against abiotic stress is reflected in a high number of the analyzed articles in the current review (55%). The specific stress conditions tested in each study are classified and presented in Figure 7(a).

Water stress takes part in 40% of the studies, and this being the most studied condition is expected since drought is the most widespread limiting factor for plant productivity (Kane 2011; Ahmadvand and Hajinia 2018; Kavroulakis et al. 2018; Kuzhuppillymyal-Prabhakarankutty et al. 2020). Following water stress, heavy metals (Bilal et al. 2018; Ikram et al. 2018) and salinity stress (Radhakrishnan et al. 2015; Wang et al. 2020) were also recurrently studied, with each covering 22% and 18% of the studies about abiotic stress, respectively. These are the commonest source of soil contamination, and both are capable of interfering with vital cellular processes and causing severe injuries to plants (Munns and Tester 2008; Yadav 2010).



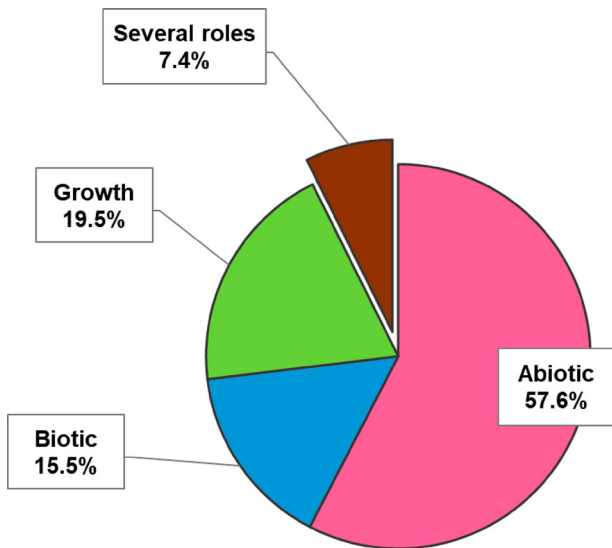


Figure 6. Potential roles of fungal endophytes studied in literature research.

The remaining articles dealt with temperature stress, nutrient availability, cutting and other minor categories. It is known that plants subjected to extreme temperature stress alter processes that critically affect development and growth (Bokszczanin and Frągkostefanakis 2013). However, it is surprising there isn't a considerable amount of studies about the stress caused by temperature change, albeit the importance of its environmental effects. In this way, Acuña-Rodríguez et al. (2020) consider cold stress as a substantial gap in this study field, and according to their analysis, microbial symbionts confer more benefits at low temperatures.

### 3.4.2. Effect of fungal endophytes under biotic stress

Another relevant condition that can affect plants severely is biotic stress. Biotic stress refers to the negative impact caused by other living organisms, usually plant pathogens like insects, nematodes, pathogenic bacteria, and fungi or competitive plants or weeds (Gull et al. 2019). Plants respond to this type of stress with defense mechanisms of their immune system, generating chemical compounds such as salicylic acid (SA) or jasmonic acid (JA), producing proteins and enzymes, increasing cell lignification and other morphological or structural barriers (Madani et al. 2018).

In order to confront biotic stress, endophytic symbioses can play an important role, since these associations are

reported to affect the performance and behavior of pathogenic organisms (Hartley and Gange 2009; Shankar Naik 2019). In this way, entomopathogenic fungi (EPF) are common in terrestrial environments and can be important natural regulators of insect and arachnid populations (Chandler 2017).

However, the analysis reveals that, compared to abiotic stress, endophyte roles regarding biotic stress are much less studied. Less than 20% of articles studied the role of endophytes for biotic stress resistance. Biotic stressors (Figure 7b) mainly cover fungal pathogens (Waqas et al. 2015), insects (Cosme et al. 2016), and soil nematodes (Liarzi et al. 2016). Fungi pathogens are present in 41% of studies, while insects add up to 23% and nematodes to 16%. Thus, the main tested effect of fungal endophytes is to confer protection against other fungi, presumably pathogenic, and probably anticipating a competition for the ecological niche (Oliva et al. 2021).

Interestingly, the effect of fungal endophytes against bacterial pathogens was rarely evaluated (6%). In spite of that, manuscripts describing the protective effect of fungal endophytes against bacterial pathogens usually report good control of the disease. For instance, Lin et al. (2019) observed that plants treated with *Serendipita indica* and infected with the bacterial pathogen *Ralstonia solanacearum* showed an enhanced response of the Jasmonic acid pathway and the expression of *VSP*, *PR1* and *PR5* genes.

### 3.4.3. Effect of fungal endophytes in promoting growth

Aside from detrimental abiotic and biotic stress conditions, the growth properties of plants are the main concern in crops. Fungal endophytes, along with bacterial endophytes and mycorrhizae, are associated with the transfer of nutrients and minerals in the host plant (Shankar Naik 2019), so they are biological treatments that can improve different aspects of the plant life cycle. In this way, Plant Growth Promoting Fungi (PGPF) are known as beneficial fungi in close interaction with plants, inducing an enhancement of the plant performance by alteration of physiological pathways and molecular mechanism regulation. They're also associated with induced systemic resistance (ISR) through the ability to enhance nutrient uptake and phytohormone production (Hossain et al. 2017).

Therefore, fungal endophytes have been extensively studied for their beneficial properties and potential to

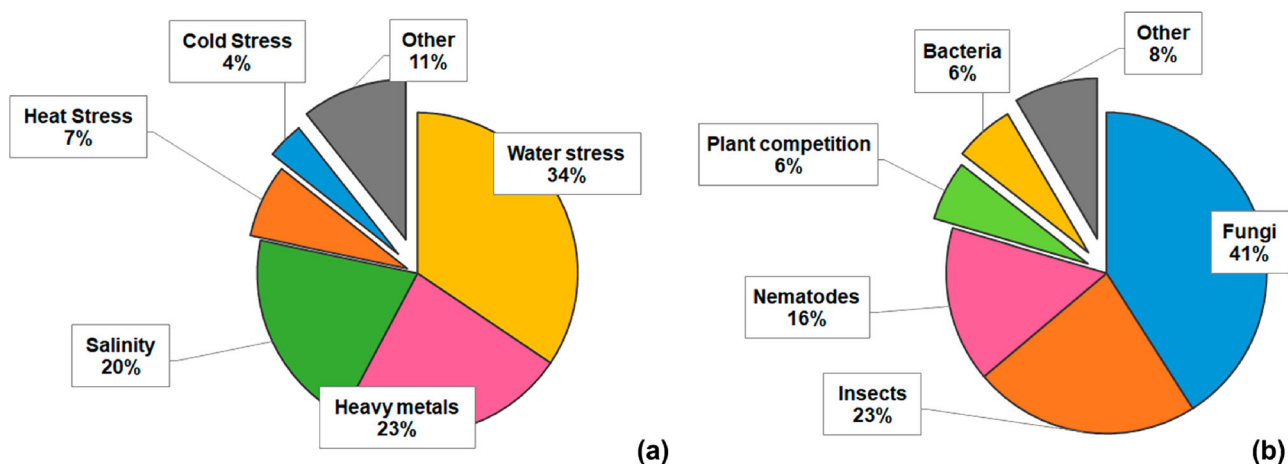


Figure 7. Most studied potential roles of fungal endophytes in front of abiotic (a) and biotic (b) stresses.

enhance productivity for crop plants. The literature research conducted in this paper reveals that studies focused on PGPF take near 20% of the fungal endophyte investigation, covering both in vitro and in field application on plants. These reports cover their beneficial effects on germination (Vujanovic et al. 2016), nutrient uptake (Khayamim et al. 2011), host plant vigor, biomass (Al-Hosni et al. 2018), and fruit production (Rho et al. 2020), all in accordance with an ecological agriculture approach.

Among the studies that assess growth promotion, 80% of the research is done in absence of pathogens in stable environmental conditions, while the other 20% further studied the effects of the same endophytes when the host plants were exposed to abiotic or biotic stress. The latter scenario is especially useful since it allows comparison of effects both on stable and stress conditions. It should be reminded that the effects on growth promotion only under stress conditions are not accounted for in this section since it has no stable conditions to be compared to.

### 3.5. Results of efficacy

Research results are decisive to know the real impact of the experimental studies. As expected, most analyzed articles in the current review report beneficial roles of the studied endophytes, irrespective of the magnitude of the effects. We categorized these results as good, neutral or variable. We expected to find a high number of positive results since there is a preference for reporting positive results and keeping the negative ones unpublished (Mehta 2019).

Around a quarter of the studies agreed that the effects on the host and environmental factors are variable, to the extent that some endophytes could negatively affect the host plant in some way. This potential negative impact is likewise reported in a small number of articles that were not able to provide positive results. This usually occurred in experiments that focus on finding new effects of previously known endophytic fungi, such as *Epichloë* spp., inoculating it on non-host plants and/or under new conditions (Hall et al. 2014; Heineck et al. 2018). It is to be noted that the particular conditions of the experiments can affect the reliability of the study comparisons (Arnold 2007). For instance, as observed by Singh et al. (2016) with *Serendipita indica*, growth media can influence the relationship between the fungal endophytes and their host plant. Yokoya et al. (2017) also showed how habitats with suboptimal conditions have more endophytes that prove to be beneficial to their host plant. Regardless, we consider these results to be key in providing knowledge about research limitations since they indicate what can be avoided in future studies.

## 4. Conclusions and future prospects

This work has analyzed the current structure of fungal endophyte research, focused on the organization and variables of the studies that aim to find beneficial effects of fungal endophytes on a host plant. This field of study has been on the rising trend for 20 years now and has worked mostly on Ascomycota fungi, with ubiquitous and widely known endophytes such as *Epichloë* spp. We here confirmed that only a few fungal species are recurrently studied as endophytes, while there is a broad spectrum of novel, potentially

interesting endophytic fungi that have only been sporadically studied. Moreover, less than 10% of the studies deal with several endophytes, implying a shortage of studies regarding the symbioses interaction and the high difficulty attached to them. Furthermore, other analyzed aspects of the study also denote certain gaps. In particular, host plants are still mainly monocots like *Lolium* spp., leaving fair room to improve on dicots' studies. Wild species are frequently used as a source of fungal endophytes but quite less as study plants. The potential effects of fungal endophytes are most commonly tested on cultivated species (between 51% and 80%) and assessed in front of abiotic stress (around 57%), especially on drought conditions. A relevant abiotic scenario that is surprisingly barely studied is stress caused by temperature changes (11%), especially cold stress. Biotic stress experiments, in turn, only appear in 15% of the literature, and among the biotic factors, fungal pathogens are the most studied, while other biotic factors like bacterial pathogens are scarcely covered. On another note, resorting to procedures to ensure endophyte-free plants has decreased lately. The majority of the studies use growth chambers or greenhouse experiments, while field studies are very limited. Lastly, we found that more than 25% of the studies reported neutral, variable, or negative effects from some endophytes, which denotes the difficulty of this experimental research.

The results showed in this work highlight the interest in the field of the use of fungal endophytes to improve the plant performance, but also uncover certain areas are still understudied such as protection against bacterial diseases. Despite that, the use of fungal endophytes is still in its beginning and presents some interesting questions for future studies such as: what is the effect of an introduced endophyte in the plant microbiome?, could it affect other functions besides the studied ones? Could different fungal endophytes be combined in a synthetic community to achieve a broad spectrum of protection? Is the observed effect caused by the presence of the endophyte or by its secreted metabolites? If the latter, could it be possible to mimick the effect using endophyte exudates?

Taken together, fungal endophytes and their interaction with their host plant are still an intricate subject, with effects that vary from mutualist to pathogenic depending on several factors. Nonetheless, their relevance as a potential source of growth promotion and stress tolerance is unquestionably recognized, and their beneficial effects on plant physiology are reported across several endophytes and host plants. The results presented here demonstrate the incidence and direction of fungal endophyte research, and also prove the presence of some unexplored subjects in the field, especially regarding dicot plants and against biotic stress.

### Declarations

#### Data availability statement for basic data sharing policy

All reviewed articles in the present manuscript are accessible through Scopus® database and checked on 30st December 2021. The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

## Competing interests

The authors declare there are no conflicts of interest that are relevant to the content of this manuscript.

## Disclosure statement

No potential conflict of interest was reported by the author(s).

## Author contributions

Conceptualization: LLX, BV, PGA, EL; data collection: LLX, EL; methodology: LLX, EL; formal analysis: LLX; writing—original draft: LLX, EL; writing—review and editing: LLX, BV, PGA, EL; funding acquisition: BV, PGA and EL.

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