

Seed pathology of non-domesticated species of tropical ecosystems

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ABSTRACT: Seed pathology is an area of study that began in the last century and has been developing since then, with increasing contribution especially to agricultural production systems. However, in the environmental area, studies began much later, but showed equal importance, especially for plant restoration and germplasm conservation programs. In this review, information about the knowledge on the pathology of seeds of non-domesticated species from tropical ecosystems is presented and the benefits and gaps of these studies are discussed.

Index terms: forest seeds, seed-borne diseases, wild species.

RESUMO: A patologia de sementes é uma área de estudos que se iniciou no século passado e vem se desenvolvendo desde então, com crescente contribuição especialmente aos sistemas de produção agrícola. Contudo, na área ambiental os estudos se iniciaram muito tempo depois, mas demonstraram igual importância, especialmente para os programas de restauração vegetal e de conservação de germoplasma. Nesta revisão são apresentadas informações acerca do conhecimento em patologia de sementes de espécies não domesticadas de ecossistemas tropicais e são discutidos os benefícios e as lacunas desses estudos.

Termos de indexação: sementes florestais, doenças transmitidas por sementes, espécies selvagens.

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INTRODUCTION

In 2020, environmental issues dominated the top five global risks of highest probability, as identified by the World Economic Forum, particularly the loss of biodiversity, failure to mitigate and adapt to climate change and extreme weather conditions. In 2021, problems related to the environment continued to prevail among the main global risks of greatest concern (World Economic Forum, 2021).

Human actions have significantly altered the earth's surface over the years. Changes in land use and climate increasingly threaten biodiversity (Newbold et al., 2015; IPBES, 2019). Protecting plants in their natural environment is the most effective method for the conservation of species, but with the frequent environmental changes and degradation in land use, conserving plants away from these threats is necessary. In this context, building seed banks is crucial to preserve a wide diversity of plant germplasm for immediate and future use, without impacting the wild population (Breman et al., 2021).

Ecological restoration is one of the main solutions to prevent the loss of species and increase the ability of native species to adapt to environmental changes (Barral et al., 2015; Crouzeilles et al., 2016), once an increase in diversity is generally interpreted as an indication that ecosystem resilience is recovering (Holt-Giménez, 2002; Swift et al., 2004). For this, it is essential that the seedlings intended for this process come from native seeds of the plant formation in question, where there is genetic variability (Santos-Junior and Barbosa, 2006). In this context, knowledge about the sanitary quality of these seeds is extremely important to avoid the introduction and dissemination of disease-causing phytopathogens. However, the lack of investment in research and development in this area has neglected the importance of the pathology of seeds of native species. This article demonstrates the critical role of pathogens in structuring plant communities and maintaining their diversity, as well as their performance in disturbed areas. The introduction of invasive exotic pathogens into natural and agricultural ecosystems and the importance of studying these microorganisms also in native seeds are as well discussed.

STRATEGIES OF FUNGI IN SEEDS

There are three ways by which fungi can infect or colonize seeds: (i) while they are still attached to the parent plant, during fruit development, (ii) inside the soil, after dispersal, and (iii) by animal vectors (Somrithipol et al., 2002; Gallery et al., 2007). In addition, they can occur in three different ways in the host, being classified as: (i) endophytic – living inside the seeds without causing apparent damage, (ii) saprophytic – decomposing the organic matter, and (iii) pathogenic – causing damage to the seed (Figure 1).

Some endophytic fungi can become opportunistic and behave like pathogenic fungi, while others can behave as saprophytes, and this greatly depends on different environmental factors (Fukasawa et al., 2012; Udayanga et al., 2013; Jeewon et al., 2017, 2018). The result of the interaction of the endophyte with its host varies from mutualism to antagonism and, therefore, this interaction is referred to as “continuum” (Schulz and Boyle, 2005). A change from mutualism to antagonism can occur under environmental pressure and the interaction can become saprobic when the host begins senescence (Rashmi et al., 2019).

Some of the functions of endophytes that have been attributed to them as mutualists include several benefits to the host plant, such as stress tolerance, growth promotion and disease resistance (Hyde and Soytong, 2008; Das and Varma, 2009; Dudeja et al., 2012; Nair and Padmavathy, 2014; Gouda et al., 2016; Bilal et al., 2018). In addition, some fungi may be potential sources of bioactive compounds (Gupta et al., 2020). Shen et al. (2014), for instance, identified several endophytic fungi in seeds of moso bamboo (*Phyllostachys edulis*) with antimicrobial activity against bacteria.

Saprophytic fungi are the main contributors to nutrient decomposition and cycling processes (Somrithipol et al., 2002; Fukasawa et al., 2012), because they secrete enzymes, degrading the lignocellulose present in the woods and leaves (Fukasawa et al., 2012). Saprophytic fungi can also become opportunistic and behave like pathogens, when seeds are damaged, for instance (Gure et al., 2005).

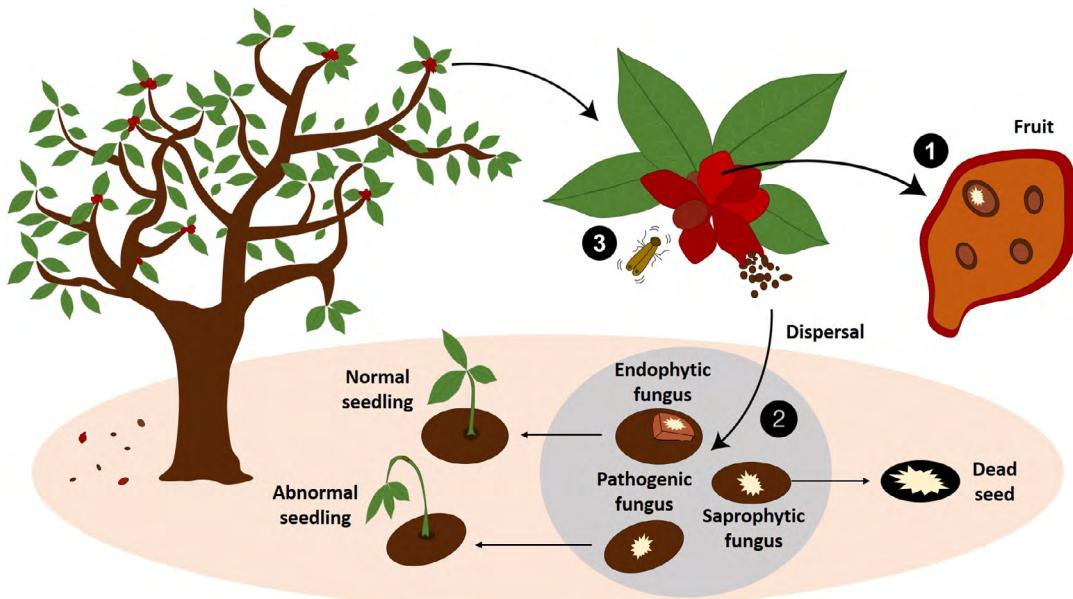


Figure 1. Mechanisms and sources of inoculum of fungi in seeds. Seeds acquire their microbiota (1) while they are still attached to the parent plant, during fruit development, (2) in the soil, after the dispersal of the seeds, and (3) by animal vectors, which may occur in an endophytic manner, without causing damage to the seed, in a saprophytic manner, absorbing nutrients from dead organic matter and/or decomposition, and in a pathogenic manner, causing damage to the seed.

Pathogenic fungi infect seeds and destroy internal tissues, endosperm, and embryo, causing reductions in storage time, vigor and germination of seeds and seedlings (Cram and Fraedrich, 2010).

Thus, it is difficult to predict what types of damage are caused by seed-borne fungi. Some fungi start the infection process in the field, while others infect only under storage conditions. They can be saprophytic or even beneficial because they compete with other potentially pathogenic species. Some, however, are consistently associated with reduced germination and vigor levels, as well as a short storage period (Amza, 2018).

One of the major problems related to the conservation of native seeds aimed at the restoration of ecosystems is precisely their storage. Seeds of many species begin to deteriorate rapidly, becoming susceptible to fungal growth, which compromises their storage for prolonged periods, making it impossible to use these seeds in the future.

SANITARY QUALITY OF NATIVE FOREST SEEDS

The demand for seeds of native species results from the need for conservation of tropical forests, since they are essential in ecosystem restoration and conservation programs (Carvalho et al., 2006; Bernardi et al., 2020). To obtain high quality seedlings, the seeds must have good genetic, physical, physiological, and phytosanitary characteristics. This last attribute causes concern, because the seed can move over great distances and can become a disseminating agent, especially of fungi, in places where there is no occurrence of diseases (Schultz et al., 2015). In addition, the sanitary quality of seeds is one of the most important factors that affect the development of forest crops, as microorganisms can cause deterioration in seeds, as well as subsequent lesions and abnormalities in seedlings, which later compromises the establishment of forest stands (Piveta et al., 2010).

Most native forest species are propagated sexually and, therefore, the sanitary quality of their seeds is of great importance for the production of healthy seedlings (Resende et al., 2008), because pathogenic microorganisms can deteriorate them and cause lesions in seedlings. The greatest damage to seeds is caused by fungi during the

germination and storage phase (Piveta et al., 2010; Amza, 2018). Evaluation of these fungi provides information on the main problems that can occur in seeds, such as loss of viability resulting in low longevity of stored seeds, reduction of germination due to losses caused by deterioration and, consequently, the formation of abnormal seedlings or their failure (Machado, 2000; Botelho et al., 2008; Barrocas and Machado, 2010; Asdal et al., 2019; Almeida et al., 2021).

Generally, in the harvest of seeds of native forest species, some fruits are already open, causing part of their seeds to receive contamination via rains, winds, and insects (Santos et al., 2011). The presence of tall trees, characteristic of tropical forests, causes seed harvesting to be more easily performed from fruits or seeds fallen on the soil, where they may be colonized by various microorganisms (Vechiato and Parisi, 2013; Lazarotto et al., 2013; Amza, 2018). In addition, the cyclicity that certain forest species have regarding their production and supply of seeds makes sanitary analysis indispensable to know the agents, causes and consequences arising from contamination by microorganisms (Castellani et al., 1996; Oliveira et al., 2012). Seeds can also carry microorganisms or pathogens from all taxa, so their identification is essential for disease control (Barrocas and Machado, 2010; Chowdhury et al., 2015; Mancini et al., 2016).

In this context, quarantine is the most efficient, economical, and sustainable form of pest control, being of fundamental importance in germplasm exchange procedures (Mendes et al., 2016). Developing quarantine programs requires information about the pathogens transmitted by the seeds, such as the ability to detect their presence, the type of inoculum, their location in the seeds and control methods. With this information, the risks associated with the import of seeds of certain species can be assessed more accurately (Galli et al., 2008). Several quarantine pathogens have already been intercepted for a wide range of crops from different countries. This emphasizes the need for phytosanitary surveillance during the quarantine process of imported plant genetic resources to prevent the entry of exotic or more virulent pathogens (Mendes et al., 2016; Singh et al., 2018). However, knowledge about seed-borne pathogens and the development of disease prevention and control practices have been limited for native species.

Another important factor to be considered is the survey of phytopathogens present in native adult species, which helps in understanding the factors related to seed infection, in addition to filling the existing gap related to information about native species, as will be presented below. These surveys should be periodic, before these organisms become endemic and cause significant damage to plants (Batista et al., 2007).

Thus, searching for materials free of phytopathogens is essential for the establishment of forest plantations, especially in areas not yet infested. When there are no native seeds with good sanitary quality, in sufficient quantity, an alternative is the treatment of these seeds (Santos et al., 2011). Currently, alternative methods to chemical treatment have been studied to reduce environmental risks due to its indiscriminate use. In addition, there is no record of chemicals for the treatment of native forest seeds, causing this practice to be considered illegal according to the legislation.

The results of forest seed health obtained in research developed with seed treatment, involving physical methods (Oliveira et al., 2011; Lazarotto et al., 2013; Françoso and Barbedo, 2014; Hennipman et al., 2017), biological methods (Fantinel et al., 2015; Martín-García et al., 2017; Silva et al., 2018) and more recently the use of plant extracts (Choudhury et al., 2018; Dourado et al., 2020; Lima et al., 2020; Almeida et al., 2021; Andrade et al., 2021), have shown some advances in pathogen control. However, studies that seek to increase the storage period, especially of species intolerant to desiccation, despite important advances, have not yet achieved substantial gains, obtaining an extension for a few months or, exceptionally, years (Barbedo, 2018).

Thus, studying seed health and control alternatives, especially in relation to fungi, may provide greater knowledge about the production system of native forest seeds and their storage for future use. Today, there are no methodologies to formalize the activities of commercialization and quality control of the seeds of these species, mainly due to the lack of knowledge of some biological aspects of most of them. Thus, investment in research and development is the key to transforming these ideas into actions to promote environmental protection.

FUNGI ASSOCIATED WITH SEEDS OF NATIVE FOREST SPECIES OF TROPICAL ECOSYSTEMS

There are few studies carried out with groups of fungi present in native seeds, when compared to other plant substrates and their domesticated commercial representatives (Somrithipol et al., 2002; Dighton and White, 2017; Rashmi et al., 2019; Perera et al., 2020). Previous research has focused mainly on post-harvest fungi, as they are primarily responsible for economic losses of edible grains and fruits (Tang et al., 2003; Neergaard, 2017).

Seeds of domesticated species are different from seeds of wild species in many characteristics, such as size, nutrient contents, and chemical defenses. This differentiation between populations is expected due to genetic changes that occur in the evolutionary process of domestication (Hernández-Terán et al., 2017). In addition, the development of diseases of domesticated species occurs during transport and storage, unlike what occurs in nature (Tang et al., 2003).

Interest in studies addressing the health of native seeds has grown in recent years. Table 1 presents the list of fungi identified in seeds of native forest species of tropical ecosystems in the last decade. During this period, 130 species of fungi have been identified in 50 plant species, totaling 380 occurrences (Figure 2). The reported fungi belong to 80 genera of three different phyla: Ascomycota (92%), Basidiomycota (5%) and Zygomycota (3%). The dominant genera include: *Penicillium*, *Fusarium*, *Aspergillus*, *Cladosporium*, *Alternaria*, *Rhizopus*, *Pestalotiopsis*, *Colletotrichum*, *Trichoderma*, *Phoma* and *Phomopsis* (Figures 3 and 4), and *Fusarium*, *Aspergillus*, *Diaporthe*, *Penicillium*, *Colletotrichum* and *Phomopsis* were the genera that had the greatest diversity of species of tropical ecosystems (Figures 5 and 6). Some of the relevant studies of this survey will be detailed below.

Françoso and Barbedo (2016), evaluating the effect of thermal and osmotic treatments on the control of fungi associated with *Eugenia brasiliensis* and *E. pyriformis* seeds, native to the Atlantic Forest (Wilson, 2011), verified the presence of *Penicillium* sp., *Fusarium* sp., *Pestalotiopsis* sp., *Phoma* sp., *Phomopsis* sp., *Cladosporium* sp., *Fusarium* sp., *Colletotrichum* sp. and *Botrytis* sp. fungi, the last three of which are found only in *E. pyriformis*. The results showed a drastic reduction in incidence for most fungi found, proving the efficacy of the treatments used in these species.

Carmo et al. (2017), when researching fungi associated with the seeds of six species native to the Atlantic Forest, reported the presence of saprophytic and potentially pathogenic fungi of the genera *Alternaria* sp., *Aspergillus* sp., *Botrytis* sp., *Chaetomium* sp., *Cladosporium* sp., *Colletotrichum* sp., *Epicoccum* sp., *Fusarium* sp., *Gliocladium* sp., *Penicillium* sp., *Pestalotiopsis* sp., *Phoma* sp., *Phomopsis* sp., *Rhizopus* sp., *Torula* sp., *Trichoderma* sp. and *Trichothecium* sp. The results showed the diversity of the microflora present in native forest seeds, demonstrating the importance of preventive methods so that these phytopathogens are not transmitted and cause damage to seedlings originating from these seeds.

Oliveira et al. (2017), working with the forest species *Crataeva tapia* and *Ziziphus joazeiro*, native to Brazil, with the last occurrence in the Brazilian Cerrado (Lima, 2015; Alves et al., 2017; Pinto and Santos, 2020), verified the presence of *Aspergillus*, *Fusarium*, *Rhizopus*, *Rhizoctonia* and *Trichoderma*, with *Aspergillus* and *Fusarium* being the most frequent in *C. tapia*. In the seeds of *Z. joazeiro*, the authors observed contamination by *Aspergillus* sp., *Fusarium* sp., *Rhizoctonia solani* and *Rhizopus* sp., and *Aspergillus* sp. was the genus that occurred most frequently. Since fungi of the genus *Fusarium* sp. are generally reported as one of the main responsible for damping-off in forest species (Lazarotto et al., 2010; Fantinel et al., 2013), their presence in the seeds becomes a problem, as well as *Aspergillus* spp., which are fungi responsible for damaging seeds under storage conditions, which can cause deterioration and death of the embryo, or subsequently infect the seedling (Machado, 2012).

Parisi et al. (2016) carried out a series of experiments to analyze the effects of fungicides and hydration levels on the suppression of fungi in seeds (embryos) of *Inga vera*, a species native to tropical regions (Pennington, 1997). The fungicide treatment reduced the incidence of the most common fungi (*Acremonium curvulum* and *Phomopsis diachenii*) and extended the lifespan of embryos that did not undergo the drying process, which is a great advantage for the studied species for showing a highly recalcitrant behavior, maintaining its viability only for a few days under natural conditions (Bilia et al., 2003).

Table 1. Fungi identified in seeds of native forest species of tropical ecosystems, in the bibliographic survey conducted in the period from 2012 to 2022.

| Botanical family Host | Country | Fungi found | References |
|---------------------------------------|---------|---|----------------------------|
| Anacardiaceae | | | |
| <i>Lithraea brasiliensis</i> | BR | <i>Alternaria</i> sp., <i>Aspergillus</i> sp., <i>Cladosporium</i> sp., <i>Fusarium</i> sp., <i>Pestalotiopsis</i> sp., <i>Penicillium</i> sp., <i>Phoma</i> sp., <i>Phomopsis</i> sp., <i>Trichoderma</i> sp. | Vechiato and Parisi (2013) |
| <i>Myracrodroon urundeava</i> | BR | <i>Alternaria</i> sp., <i>Aspergillus</i> sp., <i>Cladosporium</i> sp., <i>Curvularia</i> sp., <i>Epicoccum</i> sp., <i>Exserohilum</i> sp., <i>Fusarium</i> sp., <i>Macrophomina</i> sp., <i>Pestalotiopsis</i> sp., <i>Penicillium</i> sp., <i>Phoma</i> sp., <i>Trichoderma</i> sp. | Vechiato and Parisi (2013) |
| <i>Astronium graveolens</i> | BR | <i>Alternaria</i> sp., <i>Aspergillus</i> sp., <i>Aspergillus niger</i> , <i>Botrytis</i> sp., <i>Cladosporium</i> sp., <i>Colletotrichum</i> sp., <i>Cylindrocladium</i> sp., <i>Fusarium</i> sp., <i>Mucor</i> sp., <i>Penicillium</i> sp., <i>Rhizoctonia</i> sp., <i>Rhizopus</i> sp., <i>Stemphylium</i> sp., <i>Trichoderma</i> sp. | Bernardi et al. (2020) |
| <i>Schinopsis brasiliensis</i> | BR | <i>Aspergillus flavus</i> , <i>Aspergillus glaucous</i> , <i>Aspergillus niger</i> , <i>Curvularia</i> sp. | Andrade et al. (2021) |
| Annonaceae | | | |
| <i>Annona muricata</i> | BR | <i>Fusarium</i> sp., <i>Lasiodiplodia theobroma</i> , <i>Penicilium</i> sp., <i>Rhizopus</i> sp. | Santos et al. (2020) |
| Apiaceae | | | |
| <i>Heracleum sphondylium</i> | FR | <i>Diaporthe angelicae</i> , <i>Diaporthe subordinaria</i> | Gomes et al. (2013) |
| Apocynaceae | | | |
| <i>Aspidosperma polyneuron</i> | BR | <i>Fusarium solani</i> , <i>Fusarium oxysporum</i> , <i>Fusarium verticillioides</i> , <i>Fusarium equiseti</i> , <i>Fusarium fujikuroi</i> , <i>Fusarium pseudocircinatum</i> , <i>Fusarium subglutinans</i> | Mazarotto et al. (2020) |
| Arecaceae | | | |
| <i>Archontophoenix cunninghamiana</i> | AU | <i>Penicillium coccotrypicola</i> | Crous et al. (2014) |
| <i>Euterpe globosa</i> | US | <i>Xylaria palmicola</i> | Ju et al. (2018) |
| Asteraceae | | | |
| <i>Cosmos</i> | NL | <i>Colletotrichum cosmi</i> | Damm et al. (2012) |
| <i>Silybum marianum</i> | US | <i>Alternaria eichhorniae</i> , <i>Diaporthe cotoneastri</i> | Raja et al. (2015) |

Continues...

Table 1. Continuation

| Botanical family Host | Country | Fungi found | References |
|------------------------------|---------|---|---|
| Bignoniaceae | | | |
| <i>Tabebuia impetiginosa</i> | BR | <i>Alternaria</i> sp., <i>Aspergillus</i> sp., <i>Botrytis</i> sp., <i>Cladosporium</i> sp., <i>Colletotrichum</i> sp., <i>Curvularia</i> sp., <i>Epicoccum</i> sp., <i>Exserohilum</i> sp., <i>Fusarium</i> sp., <i>Macrophomina</i> sp., <i>Nigrospora</i> sp., <i>Penicillium</i> sp., <i>Pestalotiopsis</i> sp., <i>Phoma</i> sp., <i>Rhizopus</i> sp., <i>Stemphylium</i> sp., <i>Trichoderma</i> sp. | Vechiato and Parisi (2013) |
| Boraginaceae | | | |
| <i>Cordia trichotoma</i> | BR | <i>Alternaria</i> sp., <i>Aspergillus</i> sp., <i>Aspergillus niger</i> , <i>Bipolaris</i> sp., <i>Botrytis</i> sp., <i>Chaetomium</i> sp., <i>Cladosporium</i> sp., <i>Colletotrichum</i> sp., <i>Cylindrocladium</i> sp., <i>Fusarium</i> sp., <i>Penicillium</i> sp., <i>Rhizoctonia</i> sp., <i>Rhizopus</i> sp., <i>Stemphylium</i> sp., <i>Verticillium</i> sp. | Bernardi et al. (2020) |
| Brassicaceae | | | |
| <i>Arabidopsis thaliana</i> | DE | <i>Aureobasidium</i> sp., <i>Coniothyrium</i> sp., <i>Gaeumannomyces graminis</i> , <i>Microdochium</i> sp., <i>Phoma</i> sp., <i>Phomopsis</i> sp., <i>Pleurocytospora lycii</i> , <i>Torula herbarum</i> | Junker et al. (2012) |
| Capparidaceae | | | |
| <i>Crataeva tapia</i> | BR | <i>Aspergillus</i> sp., <i>Aspergillus niger</i> , <i>Fusarium</i> sp., <i>Rhizoctonia</i> sp., <i>Rhizopus</i> sp., <i>Trichoderma</i> sp. | Oliveira et al. (2017) |
| Dipterocarpaceae | | | |
| <i>Shorea obtusa</i> | TH | <i>Pestalotiopsis shoreae</i> | Song et al. (2014) |
| Fabaceae | | | |
| <i>Acacia mangium</i> | BR | <i>Alternaria</i> sp., <i>Aspergillus</i> sp., <i>Cladosporium</i> sp., <i>Colletotrichum</i> sp., <i>Fusarium</i> sp. | Vechiato and Parisi (2013) |
| <i>Bauhinia forficata</i> | BR | <i>Alternaria</i> sp., <i>Ascotricha chartarum</i> , <i>Aspergillus niger</i> , <i>Aspergillus ochraceus</i> , <i>Bipolaris</i> sp., <i>Botrytis</i> sp., <i>Chaetomium</i> sp., <i>Cladosporium</i> sp., <i>Colletotrichum</i> sp., <i>Cylindrocladium</i> sp., <i>Fusarium</i> sp., <i>Gibberella</i> sp., <i>Penicillium</i> sp., <i>Penicillium aurantiogriseum</i> , <i>Penicillium corylophilum</i> , <i>Penicillium glabrum</i> , <i>Pestalotia</i> sp., <i>Phomopsis</i> sp., <i>Pithomyces atro-olivaceus</i> , <i>Rhizoctonia</i> sp., <i>Rhizopus</i> sp., <i>Stemphylium</i> sp., <i>Verticillium</i> sp. | Bernardi et al. (2020); Bezerra et al. (2015) |
| <i>Dalbergia nigra</i> | BR | <i>Aspergillus</i> sp., <i>Cladosporium</i> sp., <i>Epicoccum</i> sp., <i>Macrophomina</i> sp., <i>Penicillium</i> sp., <i>Phomopsis</i> sp., <i>Trichoderma</i> sp. | Vechiato and Parisi (2013) |

Continues...

Table 1. Continuation

| Botanical family Host | Country | Fungi found | References |
|-------------------------------|---------|--|--|
| Fabaceae | | | |
| <i>Dalbergia sissoo</i> | IN | <i>Alternaria alternata</i> , <i>Aspergillus candidus</i> , <i>Aspergillus flavus</i> , <i>Aspergillus niger</i> , <i>Aspergillus phoenicis</i> , <i>Aspergillus sydowii</i> , <i>Aspergillus tamarii</i> , <i>Aspergillus terreus</i> , <i>Curvularia lunata</i> , <i>Fusarium moniliforme</i> , <i>Fusarium oxysporum</i> , <i>Geotrichum</i> sp., <i>Helminthosporium</i> sp., <i>Neocosmospora solani</i> , <i>Penicillium citrinum</i> , <i>Penicillium glabrum</i> , <i>Rhizopus nigricans</i> , <i>Trichothecium roseum</i> , <i>Trichoderma viride</i> , <i>Vuilleminia comedens</i> | Kumar (2014); Naz et al. (2015) |
| <i>Erythrina falcata</i> | BR | <i>Alternaria</i> sp., <i>Aspergillus</i> sp., <i>Chaetomium</i> sp., <i>Cladosporium</i> sp., <i>Fusarium</i> sp., <i>Penicillium</i> sp., <i>Pestalotiopsis</i> sp. | Carmo et al. (2017) |
| <i>Inga vera</i> | BR | <i>Acremonium curvulum</i> , <i>Aspergillus</i> sp., <i>Cladosporium</i> sp., <i>Colletotrichum gloeosporioides</i> , <i>Fusarium oxysporum</i> , <i>Penicillium</i> sp., <i>Pestalotiopsis</i> sp., <i>Phoma</i> sp., <i>Phomopsis diachenii</i> | Parisi et al. (2016) |
| <i>Leucaena leucocephala</i> | BR | <i>Aspergillus</i> sp., <i>Botrytis</i> sp., <i>Cladosporium</i> sp., <i>Colletotrichum</i> sp., <i>Nigrospora</i> sp., <i>Penicillium</i> sp. | Vechiato and Parisi (2013) |
| <i>Lonchocarpus</i> | BR | <i>Aspergillus</i> sp., <i>Cladosporium</i> sp., <i>Fusarium</i> sp., <i>Penicillium</i> sp., <i>Rhizopus</i> sp., <i>Trichoderma</i> sp. | Carmo et al. (2017) |
| <i>Machaerium villosum</i> | BR | <i>Cladosporium</i> sp., <i>Fusarium</i> sp., <i>Penicillium</i> sp. | Vechiato and Parisi (2013) |
| <i>Piptadenia gonoacantha</i> | BR | <i>Cladosporium</i> sp., <i>Colletotrichum</i> sp., <i>Fusarium</i> sp., <i>Penicillium</i> sp., <i>Pestalotiopsis</i> sp., <i>Phomopsis</i> sp., <i>Rhizopus</i> sp. | Carmo et al. (2017) |
| Lauraceae | | | |
| <i>Chlorocardium rodiei</i> | GY | <i>Xylaria karyophthora</i> | Husbands et al. (2018) |
| Malvaceae | | | |
| <i>Apeiba tibourbou</i> | BR | <i>Alternaria</i> sp., <i>Exserohilum</i> sp., <i>Fusarium</i> sp., <i>Penicillium</i> sp., <i>Phoma</i> sp., <i>Stemphylium</i> sp., <i>Trichoderma</i> sp. | Vechiato and Parisi (2013) |
| <i>Luehea divaricata</i> | BR | <i>Alternaria</i> sp., <i>Aspergillus</i> sp., <i>Chaetomium</i> sp., <i>Cladosporium</i> sp., <i>Epicoccum</i> sp., <i>Fusarium</i> sp., <i>Penicillium</i> sp., <i>Pestalotia</i> sp., <i>Pestalotiopsis</i> sp., <i>Phoma</i> sp., <i>Rhizopus</i> sp., <i>Torula</i> sp., <i>Trichothecium</i> sp. | Carmo et al. (2017); Quevedo et al. (2020) |
| Meliaceae | | | |
| <i>Cedrela fissilis</i> | BR | <i>Aspergillus</i> sp., <i>Cladosporium</i> sp., <i>Macrophomina</i> sp., <i>Penicillium</i> sp., <i>Rhizopus</i> sp. | Vechiato and Parisi (2013) |
| <i>Dysoxylum malabaricum</i> | IN | <i>Penicilliopsis indica</i> | Priya and Nagveni (2012) |

Continues...

Table 1. Continuation

| Botanical family Host | Country | Fungi found | References |
|------------------------------|---------|---|--|
| Musaceae | | | |
| <i>Musa</i> | VN/MY | <i>Aspergillus</i> sp., <i>Fusarium</i> sp., <i>Lasiodiplodia</i> sp. | Hill et al. (2021) |
| Myrtaceae | | | |
| <i>Acca sellowiana</i> | BR | <i>Alternaria</i> sp., <i>Aspergillus</i> sp., <i>Aspergillus flavus</i> , <i>Aspergillus niger</i> , <i>Colletotrichum gloeosporioides</i> , <i>Curvularia</i> sp., <i>Epicoccum</i> sp., <i>Fusarium</i> sp., <i>Penicillium</i> sp., <i>Phomopsis</i> sp., <i>Trichoderma</i> sp. | Fantinel et al. (2017); Saldanha et al. (2020) |
| <i>Eucalyptus citriodora</i> | BR | <i>Aspergillus</i> sp., <i>Cladosporium</i> sp., <i>Fusarium</i> sp., <i>Nigrospora</i> sp., <i>Penicillium</i> sp. | Vechiato and Parisi (2013) |
| <i>Eucalyptus grandis</i> | ZA | <i>Alternaria</i> sp., <i>Austropleospora keteleeriae</i> , <i>Bipolaris</i> sp., <i>Botryosphaeria</i> sp., <i>Cercospora</i> sp., <i>Cladosporium</i> sp., <i>Cochliobolus</i> sp., <i>Colletotrichum</i> sp., <i>Curreya</i> sp., <i>Curvularia</i> sp., <i>Davidiella</i> sp., <i>Diaporthe</i> sp., <i>Exophiala</i> sp., <i>Fusarium</i> sp., <i>Hormonema</i> sp., <i>Lasiodiplodia</i> sp., <i>Macrophomina</i> sp., <i>Mycosphaerella</i> sp., <i>Neofusicoccum eucalyptorum</i> , <i>Neonectria</i> sp., <i>Nigrospora</i> sp., <i>Penicillium</i> sp., <i>Pestalotiopsis</i> sp., <i>Phoma</i> sp., <i>Pleosporales</i> sp., <i>Sporobolomyces</i> sp., <i>Sydiowia</i> sp., <i>Teratosphaeria zuluensis</i> , <i>Trichosporon</i> sp., <i>Umbelopsis</i> sp., <i>Valsa</i> sp. | Jimu et al. (2016) |
| <i>Eugenia brasiliensis</i> | BR | <i>Botrytis</i> sp., <i>Cladosporium</i> sp., <i>Fusarium</i> sp., <i>Penicillium</i> sp., <i>Pestalotiopsis</i> sp., <i>Phoma</i> sp., <i>Phomopsis</i> sp. | Françoso and Barbedo (2014); Françoso and Barbedo (2016) |
| <i>Eugenia dysenterica</i> | BR | <i>Alternaria</i> sp., <i>Aspergillus</i> sp., <i>Aspergillus niger</i> , <i>Cladosporium</i> sp., <i>Curvularia</i> sp., <i>Fusarium</i> sp., <i>Penicillium</i> sp., <i>Rhizopus</i> sp. | Bruschet et al. (2022) |
| <i>Eugenia pyriformis</i> | BR | <i>Botrytis</i> sp., <i>Cladosporium</i> sp., <i>Colletotrichum</i> sp., <i>Fusarium</i> sp., <i>Penicillium</i> sp., <i>Pestalotiopsis</i> sp., <i>Phoma</i> sp., <i>Phomopsis</i> sp. | Françoso and Barbedo (2016) |
| <i>Eugenia uniflora</i> | BR | <i>Botrytis</i> sp., <i>Cladosporium</i> sp., <i>Fusarium</i> sp., <i>Penicillium</i> sp., <i>Pestalotiopsis</i> sp. | Françoso and Barbedo (2014) |
| <i>Psidium cattleyanum</i> | BR | <i>Aspergillus</i> sp., <i>Chaetomium</i> sp., <i>Cladosporium</i> sp., <i>Fusarium</i> sp., <i>Gliocladium</i> sp., <i>Penicillium</i> sp., <i>Pestalotiopsis</i> sp., <i>Rhizopus</i> sp., <i>Trichoderma</i> sp. | Carmo et al. (2017) |
| Onagraceae | | | |
| <i>Clarkia hybrida</i> | DK | <i>Colletotrichum godetiae</i> | Damm et al. (2012) |
| Pinaceae | | | |
| <i>Pinnus elliottii</i> | BR | <i>Aspergillus</i> sp., <i>Cladosporium</i> sp., <i>Nigrospora</i> sp., <i>Penicillium</i> sp. | Vechiato and Parisi (2013) |
| <i>Pinnus taeda</i> | BR | <i>Aspergillus</i> sp., <i>Cladosporium</i> sp., <i>Colletotrichum</i> sp., <i>Penicillium</i> sp., <i>Rhizopus</i> sp. | Vechiato and Parisi (2013) |

Continues...

Table 1. Continuation

| Botanical family Host | Country | Fungi found | References |
|-----------------------------|---------|--|------------------------|
| Plantaginaceae | | | |
| <i>Plantago lanceolata</i> | NZ | <i>Diaporthe subordinaria</i> | Gomes et al. (2013) |
| Poaceae | | | |
| <i>Phyllostachys edulis</i> | CN | <i>Alternaria</i> sp., <i>Arthrinium</i> sp., <i>Aureobasidium</i> sp., <i>Cladosporium</i> sp., <i>Colletotrichum</i> sp., <i>Curvularia</i> sp., <i>Fusarium</i> sp., <i>Leptosphaerulina</i> sp., <i>Microdochium</i> sp., <i>Penicillium</i> sp., <i>Pestalotiopsis</i> sp., <i>Phoma</i> sp., <i>Sebacina</i> sp., <i>Shiraia</i> sp., <i>Simplicillium</i> sp., <i>Umbelopsis</i> sp., <i>Xylaria</i> sp. | Shen et al. (2014) |
| <i>Poa annua</i> | US | <i>Epicoccum poae</i> | Chen et al. (2017) |
| Rhamnaceae | | | |
| <i>Ziziphus joazeiro</i> | BR | <i>Aspergillus</i> sp., <i>Aspergillus niger</i> , <i>Fusarium</i> sp., <i>Rhizoctonia</i> sp., <i>Rhizopus</i> sp. | Oliveira et al. (2017) |
| Sapindaceae | | | |
| <i>Dodonea viscosa</i> | BR | <i>Alternaria</i> sp., <i>Aspergillus</i> sp., <i>Botrytis</i> sp., <i>Chaetomium</i> sp., <i>Cladosporium</i> sp., <i>Penicillium</i> sp., <i>Rhizopus</i> sp. | Carmo et al. (2017) |
| <i>Magona pubescens</i> | BR | <i>Aspergillus</i> sp., <i>Aspergillus niger</i> , <i>Fusarium</i> sp., <i>Penicillium</i> sp., <i>Periconia</i> sp., <i>Trichoderma</i> sp., | Bruschet et al. (2022) |
| <i>Paullinia cupana</i> | BR | <i>Diaporthe hongkongensis</i> , <i>Diaporthe melonis</i> , <i>Diaporthe phaseolorum</i> , <i>Diaporthe terebinthifolii</i> , <i>Fomitopsis meliae</i> , <i>Fusarium oxysporum</i> , <i>Fusarium polyphialidicum</i> , <i>Gibberella zae</i> , <i>Glomerella acutata</i> , <i>Mariannaea campitospora</i> , <i>Mycoleptodiscus terrestris</i> , <i>Nectria rigidiuscula</i> , <i>Nigrograna mackinnonii</i> , <i>Paraphaeosphaeria arecacearum</i> , <i>Periconia macrospinosa</i> , <i>Pestalotiopsis microspora</i> , <i>Peyronellaea pinodella</i> , <i>Phomopsis asparagi</i> , <i>Phomopsis lagerstroemiae</i> , <i>Pochonia boninensis</i> , <i>Trichoderma harzianum</i> , <i>Xylogone ganodermophthora</i> | Azevedo et al. (2018) |

*AU = Australia; BR = Brazil; CN = China; DE = Germany; DK = Denmark; FR = France; GY = Guyana; MY = Malaysia; IN = India; NL = Netherlands; NZ = New Zealand; TH = Thailand; US = United States; VN = Vietnam; ZA = South Africa.

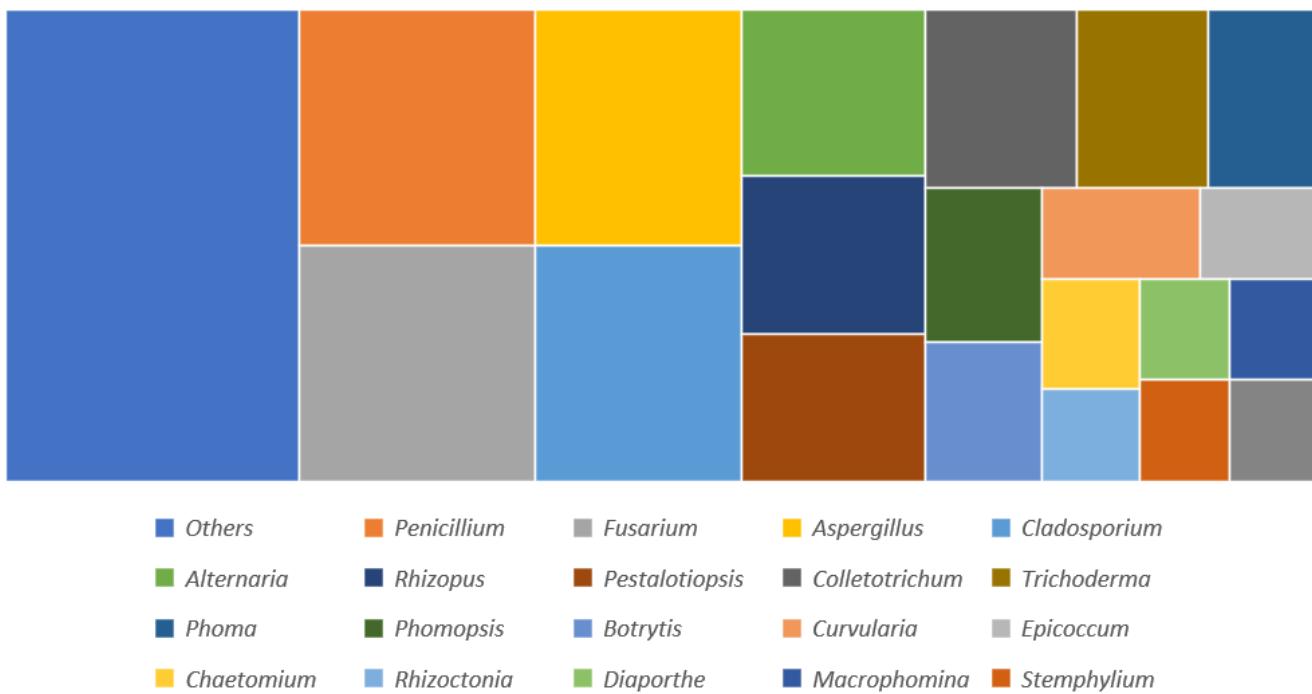


Figure 2. Frequency (%) of each genus of fungus relative to all fungal genera found in the bibliographic survey conducted in the period from 2012 to 2022.

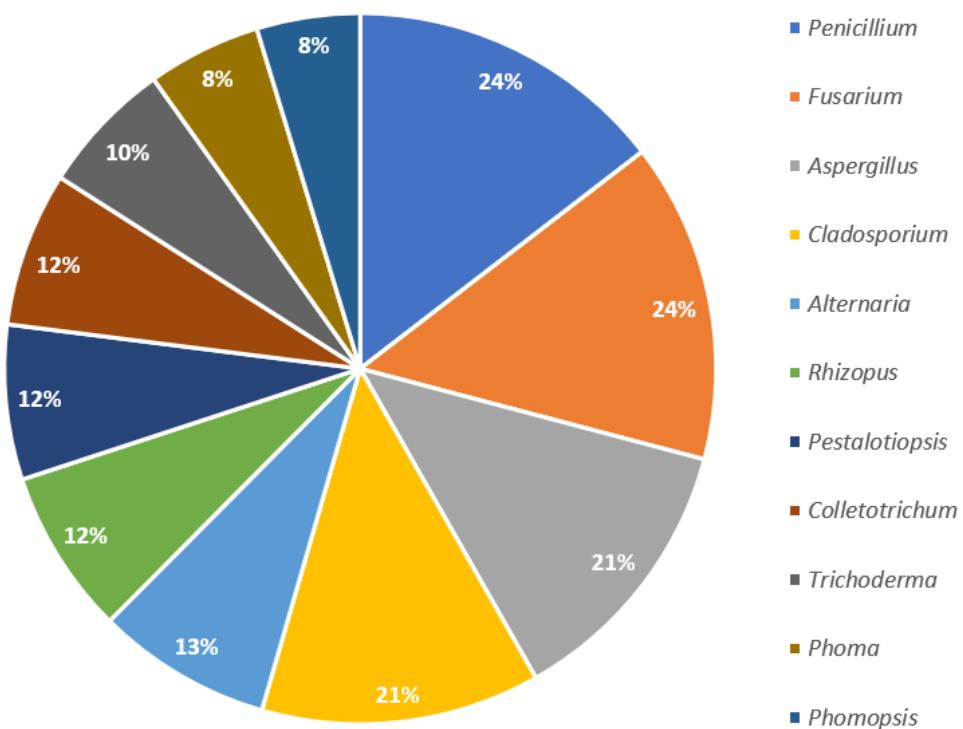


Figure 3. Frequency (%) of each genus of fungus relative to the main fungal genera found in the bibliographic survey conducted in the period from 2012 to 2022.

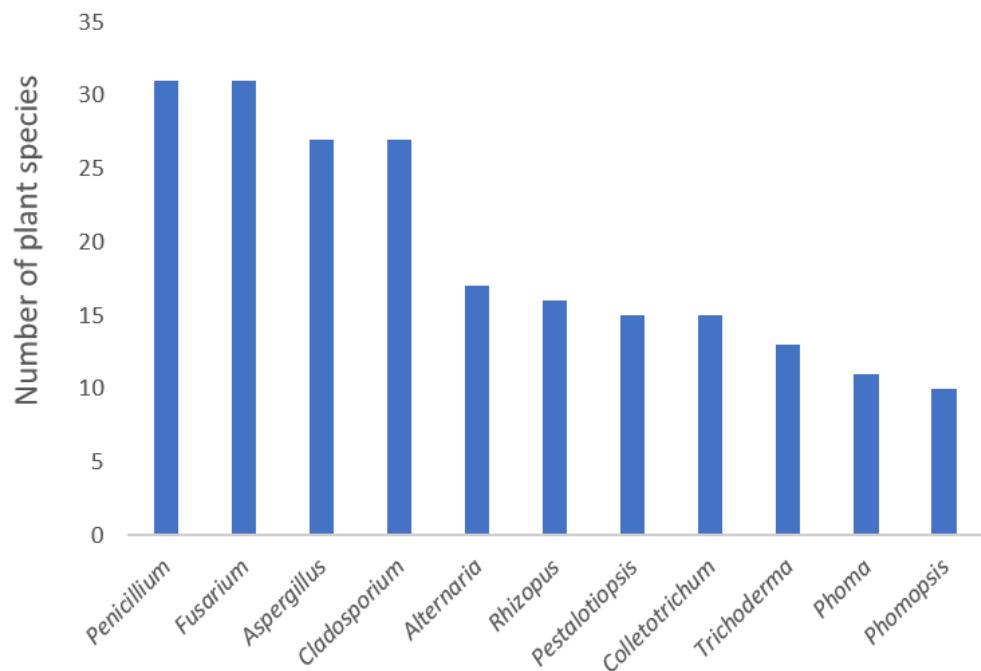


Figure 4. Number of plant species in which each genus of fungus was found, in the bibliographic survey conducted in the period from 2012 to 2022.

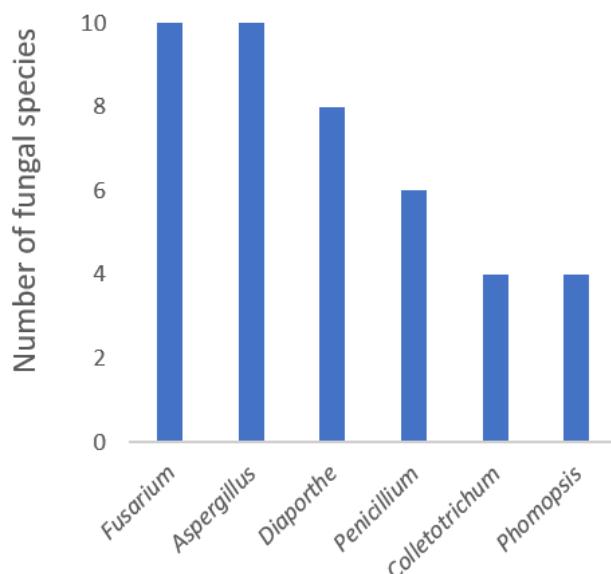


Figure 5. Number of fungal species reported for each genus of fungus, in the bibliographic survey conducted in the period from 2012 to 2022.

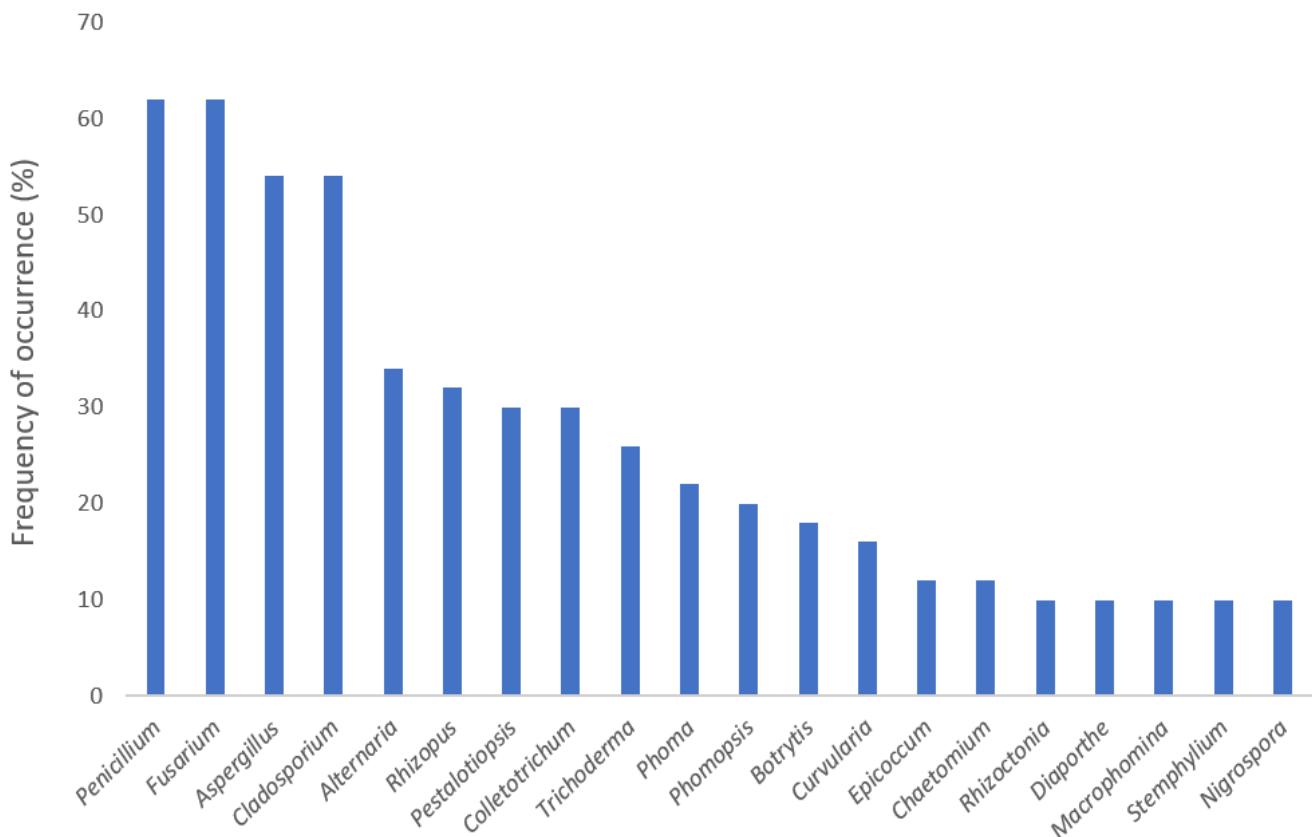


Figure 6. Frequency of occurrence (%) of each genus of fungus in the plant species, in the bibliographic survey conducted from 2012 to 2022.

A study developed by Mazarotto et al. (2020), with samples of seeds of *Aspidosperma polyneuron*, an important tropical tree native to South America (Woodson, 1951), allowed the identification of a diverse group of *Fusarium* sp. species. Morphological and phylogenetic analyses revealed the following fungi: *F. solani*, *F. oxysporum*, *F. verticillioides*, *F. equiseti*, *F. fujikuroi*, *F. pseudocircinatum* and *F. subglutinans*. All species identified have pathogenic potential, representing a risk to the native plant in the future, since new organisms can be accidentally introduced into the native ecosystem and lead to the emergence of diseases (Herron et al., 2015).

In sanitary analyzes carried out by Bernardi et al. (2020), with samples of seeds of *Astronium graveolens*, *Bauhinia forficata* and *Cordia trichotoma*, species native to the Americas (Fonseca Vaz, 1979; Pena-Chocarro et al., 2010; Villaseñor, 2016), the fungus with the highest incidence for the different detection methods tested was *Fusarium* sp. Commonly found in forest seeds, most species of *Fusarium* sp. are responsible for causing damping-off in plantlets and seedlings (Lazarotto et al., 2010; Fantinel et al., 2013), which demonstrates the importance of pathogenicity tests to verify the transmission and severity of these fungi in plants (Benetti et al., 2010).

Andrade et al. (2021), analyzing the microflora associated with stored seeds of *Schinopsis brasiliensis*, a species native to South America (Mogni et al., 2017), found a high incidence of fungi of the genus *Aspergillus* (*A. alutaceous*, *A. candidus*, *A. flavus*, *A. glaucous* and *A. niger*). These are considered storage fungi that damage the seeds and, depending on the period and conditions of conservation, the damage can be intensified, rendering stored seeds useless (Cherobini et al., 2008; Machado, 2012; Santos et al., 2016).

In the study carried out by Quevedo et al. (2020), it was possible to evaluate the sanitary quality of stored seeds of *Luehea divaricata*, a species native to the Americas (Acevedo-Rodríguez and Strong, 2012), and the transmission of fungi associated with seeds to seedlings in different lots. In the health test, the fungi *Fusarium* sp., *Alternaria* sp.,

Aspergillus sp., *Penicillium* sp., *Rhizopus* sp., *Cladosporium* sp., *Pestalotia* sp. and *Epicoccum* sp. were identified; *Rhizopus* and *Cladosporium* had the highest incidence percentages, and the genus *Fusarium* was transmitted via seed. *Rhizopus* sp. is considered a storage fungus and can cause seed rot, and *Cladosporium* sp. is a pathogenic fungus that can reduce the germinating power of seeds. *Fusarium* sp. is known to be a fungus capable of being transmitted from seed to seedling, causing the rot of cotyledons and the malformation of the root system, as observed by Quevedo et al. (2020). These results highlight the importance of knowing the microflora present in the seeds, so that it is possible to store these seeds correctly and use treatments to eradicate the fungi present in the seed lot in order to obtain good quality seedlings.

Saldanha et al. (2020), working with *Acca sellowiana* seeds from different origins, a species native to the South American region (Belsham and Orlovich, 2003), identified the fungi *Penicillium* sp., *Aspergillus* sp. and *Trichoderma* sp. in all lots analyzed. The health test showed that, although the same fungal genera were found in the analyzed lots, the origin had an influence on the incidence of fungi associated with *A. sellowiana* seeds. In the study carried out by Fantinel et al. (2017), aiming to determine the sanitary quality of seeds of the same species and also of different origins, it was possible to identify the following fungi: *Aspergillus niger*, *Aspergillus flavus*, *Penicillium* sp., *Colletotrichum gloeosporioides*, *Fusarium* sp., *Curvularia* sp., *Alternaria* sp., *Trichoderma* sp., *Epicoccum* sp. and *Phomopsis* sp. In this case, the fungi differed not only in incidence, but also at species level, for the origins analyzed.

Hill et al. (2021) evaluated the diversity of endophytic fungi in seeds of six species of wild banana (*Musa* sp.), native to tropical and subtropical Asia to the western Pacific regions (Govaerts and Häkkinen, 2006), which were stored at Millennium Seed Bank. *Lasiodiplodia*, *Fusarium* and *Aspergillus* were the most common genera, and the most abundant species belonged to the genus *Fusarium* sp., known to cause *Fusarium* wilt, a disease that threatened banana plantations (Dita et al., 2018). Since the vast majority of commercial banana plantations are clones of a single cultivar, Cavendish, the crop is highly susceptible to disease (Ordonez et al., 2015). However, it has been reported that endophytic fungi of *Fusarium* sp. can act by promoting the germination and growth of seedlings of other crops (Bayman and Otero, 2006; Tamura et al., 2008). When analyzing the results found in their study, the authors concluded that stored wild banana seeds are a valuable conservation resource and that there is an invisible fungal dimension that has been previously neglected in seed banking, since almost 200 species of fungi were found in only six species of wild banana. This could have implications for seed collection and storage procedures, causing collections such as Millennium Seed Bank to be a novel source of potentially useful fungal strains. In fact, some fungi may produce a set of secondary metabolites, providing an opportunity for the discovery of new relevant bioactive compounds (Gupta et al., 2020).

Although there are examples of mutual endophytes that act by benefiting the host plant, others are considered latent or saprophytic pathogens (Promputtha et al., 2010; Delaye et al., 2013; Nelson et al., 2020). There is uncertainty regarding endophytes that inhabit stored seeds, as to whether they are beneficial, or even essential, to the host plant or if they are potentially harmful. Considering that many endophytes are known to be related to the success of germination and establishment of seedlings (Li et al., 2017; Shearin et al., 2018; Leroy et al., 2019), little attention has been paid to the microbiota associated with the seeds stored in these collections.

Thus, the phytopathogens of the domesticated host may differ from those of its native representative, both at the species level and in terms of incidence and severity, hence the importance of studying fungi that inhabit native seeds. Knowledge about fungal diversity and its morphological and molecular identification will lead to a better evaluation of the implications associated with the transport and storage of these seeds. Although originally designed for the conservation of plant genetic diversity, seed banks may play an equally important role in the conservation of seed microbiota. Thus, creating databases on the microbiota present in native seeds is paramount to safeguard plant resources.

FINAL CONSIDERATIONS

The environmental issue has become increasingly frequent on the agenda of various global forums. Conserving tropical forests has become one of the greatest challenges of this century. With the increasing growth of human population, native forest areas are increasingly being deforested, mainly for the purpose of urbanization and food production through the agricultural sector, which has drastically reduced biodiversity.

Seeds of native forest species from tropical regions are the basic input in ecological restoration and ecosystem conservation programs since they have high genetic variability. Although the productivity of native species has remained basically at the same level in the last 50 years, the interest in using them for restoration purposes has grown in the last five years. One of the biggest challenges to achieve this goal has been the quality and quantity of seeds available, as well as their conservation for future use. It is known that seed is an efficient means of introducing plant pathogens into a new area. Since many seeds begin to deteriorate rapidly during storage, becoming susceptible to the growth of various microorganisms, especially fungi, studying the pathology of seeds of native forest species of tropical regions has never been more important.

As can be seen, the diversity of fungi existing in seeds of native species of tropical ecosystems is immense. The concept that fungi are microorganisms harmful to plant health is outdated. They can have an ecological relationship ranging from mutualism, through commensalism, to parasitism. Strong evidence has been presented that these microorganisms play a critical role in structuring plant communities and maintaining their diversity. In this context, investing in research and development in this area is fundamental to enhance techniques on production aspects, such as seed origin and quality, pathogen control and methods of storage for prolonged periods. Ignoring this information for native species generates a delay in science, and this type of investment could promote and accelerate the restoration of degraded areas, having the same positive effect as for the currently domesticated species.

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