Glomeromycota Associations with Bamboos (Bambusoideae) Worldwide: A Qualitative Systematic Review of a Promising Symbiosis

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Abstract

Background. Around the world, bamboos are ecologically, economically, and culturally important plants, particularly in tropical regions of Asia, America, and Africa. The association of this plant group with arbuscular mycorrhizal fungi belonging to the phylum Glomeromycota is still a poorly studied field, which limits understanding of the reported ecological and physiological benefits for the plant, fungus, soil, and ecosystems under this symbiosis relationship.

Methods. Through a qualitative systematic review following the PRISMA framework for the collection, synthesis, and reporting of evidence, this paper presents a compilation of the research conducted on the biology and ecology of the symbiotic relationship between Glomeromycota and Bambusoideae from around the world. This review is based on academic databases enriched with documents retrieved using different online databases and the Google Scholar search engine.

Results. The literature search yielded over 6000 publications, from which 18 studies were included in the present review after a process of selection and validation. The information gathered from the publications included over 25 bamboo species and nine Glomeromycota genera from eight families, distributed across five countries on two continents.

Conclusion. This review presents the current state of knowledge regarding the symbiosis between Glomeromycota and Bambusoideae~~,~~ while reflecting on the challenges and scarcity of research on this promising association found across the world.

Subjects. Mycology, Plant Science

Keywords. Glomeromycota, Arbuscular Mycorrhizal Fungi, Bambusoideae, Bamboo, Symbiosis

Introduction

Bamboos belong to the subfamily Bambusoideae within the Poaceae family (commonly known as grasses) (Clark et al., 2015) and tend to be evergreen plants that flower at prolonged intervals, after which some species die (Banik, 2015). They are a highly versatile group of fast-growing plants for which more than 4000 traditional uses and 1500 commercial applications have been reported (Hsiung, 1988) and are currently used as fuel, building material, raw material for the paper industry, and even as a resource for creating artisanal crafts (Singh et al., 2020). These reasons, along with the resistance properties of their fibers, have earned them the nickname "vegetable steel" (Amada et al., 1997).

Furthermore, due to their phenotypic plasticity, bamboo plants are extensively cultivated in numerous regions around the world — in 2007, 36.8 million hectares were counted across temperate, tropical, and subtropical regions (Lobovikov et al., 2007). Most cultivation areas are concentrated in Asia, America, and Africa (Bystriakova et al., 2004), coinciding with the areas of the world that most utilize these plants (de Moura et al., 2019), as well as where their centers of diversity are found. According to Soreng et al. (2022), there are around 136 genera and 1698 species of bamboo distributed in the aforementioned zones, with tropical Asia considered the center of bamboo diversity, harboring around 53 genera and 550 species (Bystriakova et al., 2003).

Plants do not exist as isolated entities but as complex communities where their organs and tissues constitute diverse niches for microorganisms (Kothe & Turnau, 2018). One of the central themes surrounding the organisms associated with plants ~~are~~ is the interactions (not always beneficial) generated with fungi, for which those established with the phylum Glomeromycota stand out (Gehring & Johnson, 2017). This phylum comprises a monophyletic clade of fungi whose members (~~with the exception of~~except for the species *Geosiphon pyriformis* (Kütz). F. West.) are all obligate mutualistic symbionts of plants, better known as arbuscular mycorrhizal fungi or AMF (Smith & Read, 2008).

These fungal symbionts, which include over 350 described and accepted morphological species, establish associations with the roots of the vast majority of terrestrial plants around the world. According to recent estimates, this value surpasses 60% or even 80% of plant species on the planet (Heijden et al., 2015; Smith & Read, 2008; Prasad et al., 2017; Brundrett & Tedersoo, 2018), with the exceptions being a few plant families that do not exhibit any type of association, such as Amaranthaceae, Brassicaceae, Chenopodiaceae, Caryophyllaceae, Juncaceae, Cyperaceae, and Polygonaceae (Brundrett, 2009).

Once they colonize the roots of the host plant, AMF ~~have the ability to~~can develop extensive extraradical networks of mycelium that grow three-dimensionally in the soil matrix and specialize in capturing mineral nutrients and water. These nutrients and water are subsequently transported and translocated to the interior of the plant symbiont in exchange for an energy reward for the AMF in the form of carbohydrates, which are produced through photosynthesis (Smith & Read, 2008).

Of all the microorganisms present in soils, Glomeromycota fungi are fundamental to the maintenance and functionality of numerous ecosystem processes. Their symbiotic establishment is related to the development and growth of the plants with which they associate, the maintenance of plant diversity, nutrient cycling, phosphorus solubilization, the facilitation of water and nutrient capture, and soil aggregation, among other ecosystem contributions (Marulanda et al., 2003; Silva-Flores et al., 2019; Heijden et al., 2015).

The objective of this systematic review is to provide a summary of the current state of qualitative knowledge reported in the global scientific literature regarding the symbiosis between Glomeromycota fungi and bamboo plants of the Bambusoideae subfamily with which they associate worldwide. This group of plants, once considered the "wood of the poor," is now recognized as "green gold" and presents particularly promising perspectives for environmental issues and a rapidly growing market (Sandhu et al., 2017). Thus, requires the development of strategies to propagate bamboo species quickly and economically, and the stimulation of their growth and development can be achieved through the use of beneficial microorganisms such as AMF (Zamora-Chacón et al., 2019; de Moura et al., 2019).

Materials & Methods

The present study utilizes a literature search and review process that is summarized in the PRISMA (Preferred Reporting Items for Systematic Reviews and Meta-Analyses) flowchart, adapted from Page et al. (2021) and Moher et al. (2009). This flowchart follows a clear separation of the stages of identification, screening, eligibility, and inclusion (Fig. 1). An updated PRISMA checklist (Page et al., 2021) with a guide specific to this review is presented in the supplementary material (Table S1).

Search strategies and inclusion criteria

To gather relevant literature on the symbiotic association between Glomeromycota and bamboo plants (Bambusoideae) worldwide, academic and bibliographic databases including Scopus, Web of Science, Wiley Online Library, Taylor and Francis Online, Elsevier Science Direct, and Springer Link, as well as the search engine Google Scholar, were utilized. Documents published up until the search date of February 2023 were recovered using the following search equation with keywords and Boolean operators: (Glomeromycota OR "arbuscular mycorrhizal fungi" OR arbuscular OR mycorrhiza OR AMF) AND (Bambusoideae OR Bamboo) AND (Association OR symbiosis).

The search was conducted and assessed by both authors using both English and Spanish terms, without imposing language restrictions or applying time restrictions in terms of the date of publication to avoid potential bias. This initial search resulted in over 6300 publications, from which scientific articles published in peer-reviewed and indexed journals were selected, while books, book chapters, and reviews were excluded. The reference lists of the selected literature and articles were used to find additional articles, resulting in a total of 18 scientific articles included in the final review (*Fig. 1*).

Data extraction, compilation, and exclusion criteria

The following information related to the focal association was extracted from the compiled selected articles: (1) the country where the study was conducted, (2) the compartment used to perform the taxonomic identification of Glomeromycota specimens, whether it was the soil associated with bamboo plants, bamboo roots, or both; (3) the taxonomic genus of the bamboo host of the AMF, (4) the species (and, if known, variety) of bamboo hosting the AMF; (5) the family, (6) genus, and (7) species (if identified) of the Glomeromycota fungi associated with bamboo, as well as (8) the type of identification used to determine the taxonomic categories of the AMF found, whether it was morphological or molecular (i.e. based on phylogenetic markers).

From these documents, secondary information related to the symbiosis established between Glomeromycota and Bambusoideae was also extracted and discussed, particularly information that referred to the effects of the establishment of symbiosis between these groups of fungi and plants. As such, out of the total number of publications found and selected, those that did not explicitly state the taxonomic identity (at any level) of the plant and its associated arbuscular mycorrhizal fungus, beyond the generic classifications of "bamboos" and "Glomeromycota," were excluded from the meta-synthesis, as well as publications classified as "grey literature".

Lastly, while the taxonomic information extracted from the mentioned documents was not modified, it was verified according to the latest updates in the mycological databases Index Fungorum (http://www.indexfungorum.org/) and MycoBank (http://www.mycobank.org/) for the Glomeromycota fungi, and according to the freely accessible book "World Checklist of Bamboos and Rattans" for the bamboo plants (Vorontsova et al., 2016).

Figure 1. Workflow displaying the search, selection, and eligibility criteria applied to the literature, adapted from the PRISMA 2020 guidelines for reporting new systematic reviews (Page et al., 2021).

RESULTS

Worldwide studies on AMF-bamboo association

In the field of mycorrhizal symbiosis established between Glomeromycota and Bambusoideae, most studies have been carried out in Asia, particularly in India (Bhattacharya et al., 2002; Debnath et al., 2015; Jamaluddin & Turvedi, 1997; S. Das et al., 2021; P. Das & Kayang, 2010; Jha et al., 2011; Parkash et al., 2019; Babu & Reddy, 2010; Ravikumar et al., 1997; Verma & Arya, 1998; Muthukumar & Udaiyan, 2006; Singh et al., 2020) and China (Guo et al., 2023; Xing et al., 2021; Qin, et al., 2017a; Qin, et al., 2017b; Jin et al., 2022; M. Zhang et al., 2022; X. Zhang et al., 2019; Weixin et al., 2013). There are also some studies from Indonesia (Mansir et al., 2021; Kramadibrata et al., 2007; Kramadibrata, 2011) and one each from Sri Lanka and Japan (Mafaziya et al., 2019; Fukuchi et al., 2011). However, from the Americas, only one report has been published by an indexed journal, a study carried out in Brazil (de Moura et al., 2019), while no studies were reported from other continents or areas where bamboo~~s~~ may establish and develop. Nevertheless, not all the studies mentioned were included in the review for the reasons previously described, leading to a reduced number of publications presented in *Fig. 2*, which summarizes how many publications were carried out in each country. The Bambusoideae taxa reported from each country and where the presence of the association with Glomeromycota has been described are presented in *Table 1*, and the taxonomic groups of Glomeromycota reported in the selected studies from each country are presented in *Table 2*.

Figure 2. Map showing the number of studies from each country that include symbiotic associations between Glomeromycota and bamboo~~s~~ and identify both symbionts at least to the taxonomic level of the family.

Table 1. Countries from which bamboo genera and/or species associated with Glomeromycota have been reported. 1 (Jamaluddin & Turvedi, 1997), 2 (Jha et al., 2011), 3 (Mafaziya et al., 2019), 4 (Parkash et al., 2019), 5 (Kramadibrata, 2011), 6 (Weixin et al., 2013), 7 (P. Das & Kayang, 2010), 8 (deMoura et al., 2019), 9 (Kramadibrata et al., 2007), 10 (Husein et al., 2022), 11 (Verma & Arya, 1998), 12 (Ravikumar et al., 1997), 13 (Muthukumar & Udaiyan, 2006), 14 (Bhattacharya et al., 2002), 15 (Babu & Reddy, 2010), 16 (Mansir et al., 2021), 17 (Qin, et al., 2017a), 18 (Qin, et al., 2017b).

Table 2. Countries from which Glomeromycota families and/or genera associated with bamboo (Bambusoideae) have been reported, along with the specific reference of the report of each fungal taxa. *Ni* (Not identified)

Categorization and description of the general framework of the studies

In the studies, some of the most common approaches involve analyzing rhizospheric and non-rhizospheric soils in search of AMF spores, from which a morphological evaluation is carried out that in most cases results in genus-level resolution, with some being able to identify further to species level. A considerably smaller percentage of studies were found to apply molecular approaches. These use BLAST and specific fungal sequence databases to search for genetic resemblances with previously described and reported species. Other studies that include an analysis of the host bamboo roots often calculate the percentage of mycorrhization or root colonization by AMF and relate it to edaphic or biotic variables of the bamboo. For example, through an analysis of rhizospheric soils from several species of bamboo and their microbial communities, Xing et al. (2021) found that at the phylum level, the relative abundance of Glomeromycota was higher in *Phyllostachys edulis* than in other species of bamboo such as *Phyllostachys sulphurea*, *Phyllostachys bambusoides*, *Sinobambusa tootsik* and *Sasa auricoma*. Meanwhile, Jamaluddin & Turvedi (1997) planted a bambusetum with thirteen different bamboo species corresponding to *Bambusa vulgaris* var. *vittata* and var. *striata*, *Bambusa nutans*, *Bambusa nana*, *Bambusa bambos*, *Bambusa arundinacea*, *Bambusa burmanica*, *Bambusa polymorpha*, *Cephalostachyum pergracile*, *Dendrocalamus asper*, *Dendrocalamus strictus*, *Dendrocalamus membranaceus* and *Melocanna baccifera*, and after a subsequent evaluation of their roots, reported that all of them established associations with AMF. Another study included *Bambusa bambos* from three different sampling sites, and all presented the presence of AMF in their rhizospheric soils (Mafaziya et al., 2019). Kramadibrata et al. (2007) studied soil samples from several species of bamboo in Java, Indonesia, and Kramadibrata (2011) described AMF from soils associated with eight species of bamboo on the island of Sumba, Indonesia. More recently, de Moura et al. (2019) characterized the AMF community associated with the bamboo species *Actinocladum verticillatum* and *Bambusa vulgaris* var. *vittata* in Brazil, which showed no significant differences in colonization rates, and Das & Kayang (2010) described that *Bambusa tulda* exhibits an Arum-type AMF colonization, while other bamboo species (*Dendrocalamus hookeri*, *Dendrocalamus hamiltonii*, and *Phyllostachys mannii*) present ~~a~~ Paris-type colonization.

Other cases include Fukuchi et al. (2011), who described how the Japanese bamboo species *Sasa senanensis* establishes arbuscular mycorrhizal associations with Glomeromycota; however, they did not report the fungal taxonomy. Debnath et al. (2015) evaluated the presence of AMF in the roots of several bamboo species from two sampling sites in India. The first sampling site included the species *Bambusa balcooa*, *B. tulda*, *B. bambos*, *B. cacherensis*, *B. tuldoides*, *Dendrocalamus hamiltonii*, *D. asper*, and *Oxytenanthera nigrociliata*, while the second contained only two species, *Bambusa vulgaris*, and *Bambusa polymorpha*. All species from both sites presented roots colonized by AMF. It has also been noted that the bamboo species *Dendrocalamus strictus* is moderately sensitive to AMF colonization, with the presence of such association being restricted to lateral roots, particularly those of the third and second order, respectively, but rarely in the first order roots (Bhattacharya et al., 2002).

Based on the aforementioned considerations and information available from each study, the primary factor in categorizing these studies was the type of tools used for the identification of Glomeromycota species or taxonomic groups associated with each bamboo species or group, whether through molecular tools, morphological tools, or both (an event that was not observed). The secondary categorization of these studies involved the compartment type used for such taxonomic identification, which could vary depending on the identification technique~~,~~ since molecular techniques are not restricted by the type of compartment (roots or soil), while morphological techniques can only explore spores extracted from the soil given that exact identification within the roots is practically impossible (Smith & Read, 2008). This categorization allows for an assessment of tools used and compartments analyzed per Bambusoideae species or groups, as shown in *Table 3*, where it is evident that the only compartment studied in all studies, regardless of the AMF identification technique, was soil. It is also apparent that the molecular identification of groups within Glomeromycota was only performed in two studies, both on the same bamboo species, *Phyllostachys edulis*.

AMF composition associated with bamboo~~s~~

In terms of the Glomeromycota diversity associated with bamboo species, only richness approximations, such as the number of reported species, and composition, such as the assignment of taxonomic identity to the group, were considered in the selected studies. Most studies taxonomically resolved the isolated morphological species from the soils associated with different bamboo species to the genus level, with some cases reaching a finer resolution to the species level. In some studies, although the presence of several morphological species within a given ~~genera~~ genus was recognized, the species was not reported, as in Mafaziya et al. (2019). *Table 3* summarizes the genera and families of Glomeromycota fungi identified in soils associated with every bamboo species reported (grouped by genus), as well as the type of identification and the compartment from which the specimens were obtained. *Figure 3* presents the bamboo genera and species associated with the Glomeromycota genera described in the selected documents, showing that *Glomus* and *Acaulospora* are the AMF genera associated with the most bamboo genera (eight each) and species (25 and 23, respectively). *Gigaspora* followed with associations with six genera and 14 bamboo species, while *Sclerocystis* and *Scutellospora* recorded five genera and 12 bamboo species each, and *Ambispora*, *Claroideoglomus*, and *Diversispora* associated with two genera and two bamboo species each. *Entrophospora* and an unidentified Glomeromycota genus were reported to associate with only one bamboo species within a single bamboo genus~~ each~~.

Table 3. Identification method and compartment type from which Glomeromycota have been reported in different bamboo species, as well as the fungal groups described for each bamboo at the genus and family levels. Ac (Acaulosporaceae), Am (Ambisporaceae), Ar (Archaeosporaceae), Cl (Claroideoglomeraceae), Di (Diversisporaceae), Gi (Gigasporaceae), Gl (Glomeraceae), Pa (Paraglomeraceae), *Aca* (*Acaulospora*), *Ent* (*Entrophospora*), Ni (Not identified), *Amb* (*Ambispora*), *Cla* (*Claroideoglomus*), *Div* (*Diversispora*), *Gig* (*Gigaspora*), *Scu* (*Scutellospora*), *Glo* (*Glomus*) and *Scl* (*Sclerocystis*); 1 (Jamaluddin & Turvedi, 1997), 2 (Jha et al., 2011), 3 (Mafaziya et al., 2019), 4 (Parkash et al., 2019), 5 (Kramadibrata, 2011), 6 (Weixin et al., 2013), 7 (P. Das & Kayang, 2010), 8 (deMoura et al., 2019), 9 (Kramadibrata et al., 2007), 10 (Husein et al., 2022), 11 (Verma & Arya, 1998), 12 (Ravikumar et al., 1997), 13 (Muthukumar & Udaiyan, 2006), 14 (Bhattacharya et al., 2002), 15 (Babu & Reddy, 2010), 16 (Mansir et al., 2021), 17 (Qin, et al., 2017a), 18 (Qin, et al., 2017b).

Figure 3. ~~Chord~~ The chord diagram of the bamboo~~s~~ was reported to associate with Glomeromycota. On the left, the genera of Bambusoideae (on top) and the Glomeromycota genera with which they have been reported to associate. On the right, the genera of Glomeromycota (bottom) and the species of bamboo with which they have been reported to associate (top). Aca (*Acaulospora*), Ent (*Entrophospora*), Ni (Not identified), Amb (*Ambispora*), Cla (*Claroideoglomus*), Div (*Diversispora*), Gig (*Gigaspora*), Scu (*Scutellospora*), Glo (*Glomus*) and Scl (*Sclerocystis*). Bamboo genera: Phyll (*Phyllostachys*), Acti (*Actinocladum*), Bamb (*Bambusa*), Ceph (*Cephalostachyum*), Dend (*Dendrocalamus*), Dino (*Dinochloa*), Giga (*Gigantochloa*), Melo (*Melocanna*), Nast (*Nastus*), Schy (*Schizostachyum*). Bamboo species: A_ve (*Actinocladum verticillatum*), B_ar (*Bambusa arundinacea*), B_ba (*Bambusa bambos*),

B_bl (*Bambusa blumeana*), B_bu (*Bambusa burmanica*), B_gr (*Bambusa grandis*), B_na (*Bambusa nana*), B_nu (*Bambusa nutans*), B_pa (*Bambusa pallida*), B_pe (*Bambusa pervariabilis*), B_po (*Bambusa polymorpha*), B_sp (*Bambusa sp.*), B_tu (*Bambusa tulda*), B_vu (*Bambusa vulgaris*), C_pe (*Cephalostachyum pergracile*), D_as (*Dendrocalamus asper*), D_ha (*Dendrocalamus hamiltonii*), D_ho (*Dendrocalamus hookeri*), D_me (*Dendrocalamus membranaceus*), D_st (*Dendrocalamus strictus*), D_sp (*Dinochloa sp.*), G_ap (*Gigantochloa apus*), G_at (*Gigantochloa atter*), G_ma (*Gigantochloa manggong*), M_ba (*Melocanna baccifera*), N_re (*Nastus reholttumianus*), P_ed (*Phyllostachys edulis*), P_ma (*Phyllostachys mannii*), S_br (*Schizostachyum brachycladum*), S_li (*Schizostachyum lima*), S_zo (*Schizostachyum zollingeri*).

Discussion

In addition to the collection and extraction of information related to the symbiotic association between Glomeromycota fungal taxa and Bambusoideae plants (which are described and gathered in the results), discoveries and descriptions of the relationships between symbionts in this association were also identified within the framework of this review from both the selected articles and those that were not necessarily included in the first part of this document. The central results of this review are summarized and discussed below, as well as the reported effects derived from the establishment of such arbuscular mycorrhizal symbiosis between fungi and bamboo~~s~~ from around the world.

AMF assemblages in soils associated with bamboo~~s~~

Based on the information compiled in *Table 3*, there are specific systems, such as those subject to high-impact management, where the composition of the AMF assemblage associated with *Phyllostachys edulis* was dominated by the Glomeraceae family in terms of abundance in sequence numbers (Qin et al., 2017a). However, the same study found that such management did not significantly affect the fungal family, which is consistent with the assertion that Glomeraceae is a disturbance-tolerant group. Acaulosporaceae, on the other hand, is not considered as such, and therefore it can be concluded that under these conditions, *P. edulis* is not an ideal host for Acaulosporaceae (Chagnon et al., 2013; Qin et al., 2017a).

Regarding systems derived from plantations, Jamaluddin & Turvedi (1997) reported the presence of five AMF genera (*Glomus*, *Gigaspora*, *Acaulospora*, *Scutellospora*, and *Sclerocystis*) in a bambusetum containing 13 bamboo species; however, despite mentioning some particular morphological species, they did not distinguish which bamboo sample was isolated. They also found that *Bambusa nana* presented the highest AMF colonization, followed by *Bambusa vulgaris* var. *vittata*, while the lowest colonization was obtained by *Bambusa bambos*, generating a gradient ranging from 80% to 33% in terms of mycorrhizal percentage (Jamaluddin & Turvedi, 1997).

Similarly, studies such as Parkash et al. (2019) confirmed that *Bambusa tulda*, *Bambusa pallida*, *Bambusa nutans*, and *Bambusa bambos* form mycorrhizal associations with AMF after quantifying the percentage of root colonization by these fungal symbionts, with values in all cases exceeding 70%. In specific, within the rhizosphere of *Bambusa bambos*, they identified five morphological species of the genus *Acaulospora* (*A. laevis*, *A. scrobiculata*, *A. lacunosa*, *A. mellea*, and *Acaulospora* sp.), seven belonging to *Glomus* (*G. clavisporum*, *G. reticulatum*, *G. macrocarpum*, *G. claroideum*, *G. pansihalos*, *G. geosporum*), two in the genus *Gigaspora* (*G. gigantea* and *Gigaspora* sp.), and one *Entrophospora* sp. In the rhizosphere of *B. tulda*, they identified a total of four morphological species: *Acaulospora foveata*, *Glomus clavisporum*, *G. albidum*, and *Scutellospora* sp. Meanwhile, in *Bambusa pallida*, they reported eight morphological species, two *Acaulospora* (*A. laevis* and *Acaulospora* sp.) and six *Glomus* (*G. macrocarpum*, *G. monosporum*, *G. geosporum*, *G. epigaeum*, *G. fasciculatum*, and *Glomus* sp.); and in *Bambusa nutans*, they only recorded one species: *Glomus epigaeum*. Jha et al. (2011) found six species of Glomeromycota (*Acaulospora scrobiculata*, *Glomus aggregatum*, *G. arborense*, *G. diaphanum*, *G. intraradices*, and *G. invermayanum*) in the rhizospheric soil of *Dendrocalamus strictus*. Mansir et al. (2021) described the presence of three genera inside the roots of *Gigantochloa atter*, specifically *Glomus*, *Gigaspora*, and *Acaulospora*. In the rhizosphere of *Bambusa* sp., Husein et al. (2022) identified the presence of spores ~~pertaining to~~of the genera *Glomus*, *Gigasporaceae*, and *Acaulospora*, with several morphological species each, but their specific identities were not able to be determined. Additionally, in a study on populations of *Bambusa bambos*, Mafaziya et al. (2019) found 14 AMF morphotypes associated with the rhizospheric soil of the genera *Glomus*, *Scutellospora*, *Gigaspora*, and *Acaulospora*, with *Glomus* being the dominant genus and *Acaulospora* the least represented in terms of abundance.

Kramadibrata et al. (2007) found that *Acaulospora foveata* and *A. scrobiculata* associated with *Dendrocalamus asper* and *Gigantochloa apus*, while *Acaulospora tuberculata* established associations with *Bambusa vulgaris*, *Dendrocalamus asper*, *Schizostachyum zollingeri*, *Gigantochloa manggong*, and *Gigantochloa apus*. In addition, *Glomus etunicatum* was associated with *Bambusa vulgaris*, *Dendrocalamus asper*, *Gigantochloa manggong*, and *Gigantochloa apus*; while *Glomus fuegianum* associated with *B. vulgaris*, *D. asper*, and *Schizostachyum zollingeri*. *Glomus* cf. *formosanum* and *Glomus geosporum* were associated with *D. asper* and *G. apus*. *Glomus mosseae* established associations with *S. zollingeri* and *G. apus*, and finally, *Scutellospora calospora* was associated with *G. manggong*. From the island of Sumba, Indonesia, Kramadibrata (2011) reported that *Acaulospora foveata* associated with *Bambusa blumeana*, *Dinochloa* sp., and *Nastus reholttumianus*, while *Acaulospora scrobiculata* associated with *Bambusa blumeana*, *Schizostachyum brachycladum* (green variety), and *Nastus reholttumianus*. *Acaulospora tuberculata* was found with *Gigantochloa atter*, *Schizostachyum brachycladum* (yellow variety), and *Schizostachyum lima*. Furthermore, *Glomus etunicatum* was associated with *Gigantochloa atter*, and finally, *Glomus rubiforme* with *Gigantochloa atter*.

In other studies, inoculants were prepared with isolated AMF identified as *Glomus rosea*, *G. magnicaule*, *G. etunicatum*, *G. heterogama*, *G. maculosum*, *G. multicaule*, *Scutellospora nigra*, and *S. heterogama* for application to bamboo. Babu and Reddy (2010) applied the inoculants to *Dendrocalamus strictus* and confirmed fungal colonization. Ravikumar et al.

(1997) worked with independent inoculations and all possible combinations of *Glomus aggregatum*, *G. fasciculatum*, and *G. mosseae* on *Dendrocalamus strictus*. Under all circumstances, their roots were colonized with a colonization percentage ranging from 30% to 60%. This finding is similar to that of Verma and Arya (1998), in which five morphological species were isolated, including *Acaulospora scrobiculata*, *Glomus intraradices*, *G. aggregatum*, *G. mosseae*, and *Scutellospora heterogama*, from the rhizosphere of *Dendrocalamus asper* ~~in order~~ to develop two inoculants: one with the first species (I1) and the other with the remaining four (I2). Furthermore, they tested another inoculant (I3) from isolated teak spores, which contained *Acaulospora scrobiculata*, *A. delicata*, *Gigaspora* sp., *G. ramisporophora*, *Glomus intraradices*, *G. geosporum*, *G. mosseae*, *G. etunicatum*, and *Scutellospora pellucida*. These fungi established symbiotic associations with the bamboo species, which was confirmed by quantifying the percentage of colonization within the roots of *D. asper*. The statistical analyses showed that the maximum percentage of colonization was found in I3, followed by I1 and I2, respectively (Verma & Arya, 1998). In 2002, *Dendrocalamus strictus* was inoculated with three species of AMF, namely *Glomus mosseae*, *G. fasciculatum*, and *Gigaspora margarita* (Bhattacharya et al., 2002). Later, in 2011, Jha et al. (2011) inoculated *Bambusa bambos* and *Dendrocalamus strictus* with *Acaulospora scrobiculata*, *A. mellea*, *Glomus aggregatum*, *G. cerebriforme*, *G. arborense*, *G. diaphanum*, *G. intraradices*, *G. etunicatum*, *G. fasciculatum*, *G. hoi*, *G. occultum*, and *Glomus* sp., and all the fungi established an association with the roots of both bamboo species. Considering that the current veracity of the fungal identity of spores present in commercial bio-inoculants is compromised (Vahter et al., 2023), the fact that most of the studies mentioned resorted to the use of trap cultures or direct isolation of Glomeromycota species to be inoculated provides some certainty regarding the accuracy of their results. It was frequently observed that *Acaulospora* and *Glomus* were among the most commonly isolated strains or fungal genera inoculated to different bamboo species, as these AMF genera are commonly found worldwide in a wide range of natural ecosystems including those altered by humans, such as agricultural systems (Davison et al., 2015; Oehl et al., 2017).

Effects of Glomeromycota on host bamboo plants

On bamboo physiology and morphology

While the effects of symbiosis were not reported for all the bamboo species mentioned, some of them such as *Dendrocalamus strictus* were reported to significantly stabilize the upper layer of the soil due to the nature of their root system and enhance the leaf litter accumulation in response to associations with AMF (Ben-zhi et al., 2005). Furthermore, seedlings of *Dendrocalamus strictus* that were inoculated with *Glomus fasciculatum* and *G. mosseae* (simultaneously) reached the greatest internodal distance of all treatments, followed by bamboo seedlings inoculated only with *G. aggregatum* (Ravikumar et al., 1997). Another study found that *D. strictus* rhizomes reached their maximum length when the inoculation contained only the *G. aggregatum* isolate, followed by the combination of *G. aggregatum* and *G. mosseae* (Ravikumar et al., 1997). Total biomass production in *D. strictus* was also favored by mycorrhizal associations with Glomeromycota fungi, reaching maximum dry matter production when seedlings were inoculated with *G. aggregatum* and *G. fasciculatum* (Ravikumar et al., 1997).

In *Bambusa bambos* and *Dendrocalamus strictus*, phosphorus uptake, and shoot length increased significantly with all inoculated AMF (8 commercial formulations), except for *Glomus* sp. in *D. strictus* (Jha et al., 2011), indicating that effective AMF utilization can enhance productivity of these bamboo species in the region (Jha et al., 2011). Similarly, Bhattacharya et al. (2002) found that inoculating some AMF in *D. strictus* seedlings significantly promoted lateral branching (in number and length) of roots in this species, although no clarifications were made regarding the status of such fungi in the soil or even the percentage of mycorrhization, only reports of the morphological response of the seedling root system.

In terms of morphology, as mentioned above for species such as *D. strictus*, AMF inoculation causes differentiating effects on the structures of inoculated plants. For instance, inoculating *G. mosseae* and *G. intraradices* in Chenglu bamboo seedlings, a hybrid bamboo between *Bambusa pervariabilis* (as the female parent) and *B. grandis* (as the male parent), resulted in a significant increase in the number of shoots, diameter, and total leaf area of the inoculated plants compared to those not inoculated with AMF (Weixin et al. 2013).

On growth and nutrient uptake

In general, bamboo plants favor the establishment of mycorrhizal symbiosis given their fast growth which requires high nutrient requirements during the initial growth stages (Ravikumar et al., 1997). This explains the increase in the rhizosphere of several bamboo species after establishing a mycorrhizal symbiosis, a phenomenon that has specifically been described in *Bambusa balcooa*, *Bambusa vulgaris* var. *vittata* (known as green bamboo) and var. *striata* (known as yellow bamboo), *Bambusa nutans* and *Dendrocalamus asper* (Singh et al., 2020).

In *Dendrocalamus strictus* (a bamboo species with an extensive root and rhizome system), inoculation of AMF along with *Aspergillus tubingensis* (an Ascomycota fungus) showed a synergistic effect on bamboo growth, nutrient uptake (such as P, K, Ca, and Mg), and reduction in heavy metal translocation to the plant (Babu & Reddy, 2010). Similar effects have also been observed in other plants that establish associations with AMF (Chen et al., 2007; Chen et al., 2001). This is consistent with what Muthukumar & Udaiyan (2006) described, who performed a nursery experiment evaluating the effects of applying a *Glomus aggregatum* inoculum on promoting the growth of *D. strictus* plants in two different soil types (alfisol and vertisol). They found that root colonization percentages by *G. aggregatum* (reaching 55% and confirming the establishment of the association with this AMF species) were positively and significantly related to the dry weight of bamboo seedlings, and thus to the concentrations of N, P, and K in their tissues (roots, rhizome, and shoots) (Muthukumar & Udaiyan, 2006). In addition, Verma & Arya (1998) found that *Dendrocalamus asper* seedlings treated with AMF inocula extracted from their rhizospheric soil (2) and one associated with Teak were significantly taller than those that did not receive treatments, and they also presented higher concentrations of P in their shoots, which they describe as an effect resulting from AMF-mediated improvements in the efficiency of capturing available P in the soil. Even earlier, Ravikumar et al. (1997) also reported that AMF association with *Dendrocalamus strictus* seedlings improves their growth compared to a control not inoculated with AMF, emphasizing that inocula with *G. fasciculatum* and *G. aggregatum* (alone or in combination) are the best option (among those evaluated) for achieving the highest rates of growth and total dry matter production.

Another study also described how in *Bambusa bambos* and *Dendrocalamus strictus*, total dry weight and P uptake (an essential nutrient for plant growth) increased significantly in seven of the eight AMF inoculated plants (Jha et al., 2011). Additionally, the confirmed establishment of symbiotic associations between Chengdu bamboo (a hybrid) and AMF, specifically an inoculum of *Glomus intraradices* and *G. mosseae*, improved the uptake of P and K in inoculated plants, as well as their growth and biomass accumulation, making these AMF good candidates in efforts to increase the production of this hybrid bamboo (Weixin et al., 2013).

Effects of bamboo~~s~~ on AMF assemblages

Host plants are not passive actors during symbiosis, and AMF assemblages are not randomly distributed in patches of host plants but rather tend to associate with particular ecological groups (Davison et al., 2011). Considering this, Guo et al. (2023) described that the rhizospheric soil of bamboo, particularly *Phyllostachys edulis* and four of its forms (*P. edulis* f. *tao kiang*, *P. edulis* f. *luteosulcata*, *P. edulis* f. *pachyloen* and *P. edulis* f. *gracilis*) has more complex, longer, and interconnected fungal networks than those in non-rhizospheric soil, in addition to significant differences in diversity. However, at least for Glomeromycota, abundance appears to be higher in non-rhizospheric soil, suggesting that this is the original pool of species from which the plant root will establish associations with only some of the AMF available in the rhizosphere (Bledsoe et al., 2020, Fiore-Donno et al., 2022). This contrasts with the results of Husein et al. (2022), who showed that the rhizosphere of *Bambusa* sp. has more abundance and diversity of Glomeromycota spores than those of other plants, such as *Cichorium intybus* and *Pinus merkusii*, which, although not compared to the non-rhizospheric soil of these species, gives indications of a possible affinity of *Bambusa* for selecting AMF, or the preference of AMF to associate with this bamboo species.

On the other hand, bamboos classified as runners (with leptomorph rhizomes), such as those of the genus *Phyllostachys* that are known for invading and quickly replacing neighboring forest cover, tend to increase the biomass of their associated AMF. This significantly changes the fungal assemblages in the soil, contributing to the formation of aggregates and carbon storage in the system (Xu et al., 2020; Qin et al., 2017). Likewise, when comparing a forest of *Phyllostachys pubescens* with surrounding forests, Quin et al. (2017) found that in the former, both AMF spore density and root colonization rate were significantly higher than in the latter~~,~~ and that the former favored the presence of the Glomeraceae family but reduced that of the Acaulosporaceae and Archaeosporaceae families.

In considering the dominance of some plant species over others, Mafaziya et al. (2019) did not find perceptible changes in the AMF community structure in forest ecosystems after an increase in the dominance of *Bambusa bambos* in these systems. However, when they compared the soil of the forest patches adjacent to the populations of *Bambusa bambos*, these recorded a higher abundance of AMF spores. They ~~therefore~~, therefore, conclude that, at least under the conditions of the study, the fungal community shows high resistance to changes in soil surface coverage, as well as resilience to the influence generated by the dominance of a single plant species.

Additionally, Jin et al. (2022) found that when extensive management is carried out in bamboo forests, particularly those of *P. edulis* (forests regularly harvested without any management), the abundance of AMF increases substantially leading to an increase in AMF respiration rates and a significant change in carbon cycling within bamboo forest ecosystems produced by AMF.

Challenges ahead

Qin et al. (2017 a, b) and Jin et al. (2022) report molecular marker-based approaches to elucidate the composition of AMF assemblages in bamboo forest soils using primers described by Sato et al. (2005) that amplify part of the 18S region (AMV4.5NF and AMDGR). These sequences can then be compared to the MaarjAM database using BLAST (Öpik et al., 2010) to assign taxonomic identities to the Glomeromycota groups in the sample. With similar approaches, Zhang et al. (2022) amplified the ITS region with the ITS1F and ITS2R primers to evaluate the fungal community in the roots, soil, and aerial structures of *Phyllostachys edulis*, and Zhang et al. (2019) amplified the ITS2 region with the ITS3 and ITS4 primers to investigate the rhizospheric community structure of *P. edulis* at the phylum level, identifying sequences using BLAST in the UNITE database. In these studies, they were able to identify groups within the Glomeromycota phylum, but the internal transcribed spacer (ITS) was not proven to be an optimal candidate for barcoding arbuscular mycorrhizal fungi (AMF) because the region alone is exceptionally variable and does not adequately resolve species, especially among closely related taxa. Other primers targeting regions of the small subunit (18S) or large subunit (28S) tend to be biased as the primers only are effective in some taxonomic groups within the Glomeromycota community (Stockinger et al., 2010). In addition, although the specific primers proposed by Sato et al. (2005) are promising in terms of coverage and specificity, Van Geel et al. (2014) highlights that they are biased towards groups within the Glomeraceae family within Glomeromycota, even detecting groups in Basidiomycota and Chytridiomycota, but not detecting any members of the Ambisporaceae family and only a few of the Claroideoglomeraceae and Paraglomeraceae families in Glomeromycota. This situation generates difficulties when comparing the results of studies on AMF diversity and richness or composition, as there is little consistency regarding the target genes and primers used (Van Geel et al., 2014). While there is still no consensus region for AMF barcoding (Kolaříková et al., 2021), recent studies suggest that the ideal approach is to perform nested PCR approaches on different regions of the rRNA gene (Kolaříková et al., 2021). Tedersoo et al. (2022) also recommend that when performing taxonomic identification of a sequence using BLAST that may belong to Glomeromycota (if the selected primers allow it), the searches should preferably be made against the MaarjAM database, not UNITE, as the latter uses reads based on the ITS region, whose disadvantages have been previously mentioned.

Bamboo species such as *Phyllostachys edulis* have been described as promising in their roles of carbon sequestration through ~~its~~ their mycorrhizal associations. This could lead to increases in planted areas or facilitate their expansion in ecosystems through the application of Glomeromycota bio-inoculants. However, it is imperative to pay attention to the ecological risks this may also entail in terms of negative effects on plant diversity and other soil microorganisms in the colonized areas (Qin et al., 2017). This type of management reduces soil pH, facilitates the hyperaccumulation of available N, P, and K, and promotes soil aggregation loss and erosion, which leads to a significant reduction in AMF biomass as well as alterations in soil assemblage diversity (Xu et al., 2008; Shinohara & Otsuki, 2015; Qin et al., 2017a; Liu et al., 2011). This situation can be avoided by promoting responsible and sustainable use and management of the resource such as the intensive management strategies traditionally applied to this bamboo species.

As for publications addressing the establishment of these symbiotic associations, although some report evidence of AMF colonization in roots of species such as *Dendrocalamus strictus* (Das et al., 2021), they do not include any other evidence in terms of spore identification or genetic material extraction from any of the different compartments where they are found (soil and/or the root of the host plant). As a result, the information conveyed is poor or incomplete, at least within the framework of the objectives of this work.

In addition, in some cases, the term ‘bamboo’ is used in a very generic way or even as if constituting a taxonomic rank by itself. This has led to several studies maintaining an ambiguous discourse when discussing the potential of bamboo (in ecological or economic terms) or even of their associated AMF species (i.e. Toh et al., 2018; Patra et al., 2021; Priya et al., 2014; Mafaziya et al., 2019), resulting in a loss of informative value. Additionally, as reported ~~in~~ by Debnath et al. (2015), several AMF genera were isolated from different sampling sites (*Acaulospora*, *Ambispora*, *Diversispora*, *Funneliformis*, *Glomus*, *Paraglomus*, *Rhizophagus*, and *Sclerocystis*), but the associated bamboo species was not clarified, nor is it considered that they may be working with other species, which generates noise in the analyses. Rather, studies must clarify which species of bamboo is being referred to, since as evidenced throughout this document, the nature of the symbiosis, its effects, and the potentials of each species of bamboo are, to some degree, specific.

This review highlights the need to compile information and build knowledge around a wider range of bamboo species and the symbiotic interactions they form or can potentially form with AMF. It is surprising that in tropical America, a continent where this group of plants is so diverse and where such ecologically, economically, and culturally important groups exist such as the Guadua sub-tribe (specifically *Guadua angustifolia* Kunth in terms of their uses, applications, and distribution range) (Cruz-Armendáriz et al., 2023; Akinlabi et al., 2017; Clark et al., 2015), associations with AMF are so absent in the scientific literature, at least in publications from indexed and/or peer-reviewed journals. This phenomenon may be the result of the ease of producing "gray literature" in terms of speed and low cost, or even ~~to~~ the difficulties involved in submitting and publishing a scientific document, as research often remains in undergraduate and graduate theses, conference proceedings, research reports, memoranda, scientific society documents, bulletins, or websites (Corlett, 2010). This greatly hinders access to information and the construction of knowledge on environmental and social issues such as those exposed in this document. Therefore, the publication of studies focused on this association ~~are~~ is the first step~~s~~ to supporting efforts aimed to propagate bamboos using AMF in various regions of the world, as proposed by (de Moura et al., 2019). With adequate knowledge of mycorrhizal fungal diversity in the rhizosphere of bamboo species and molecular approaches for analyzing roots and soils, the development of mycorrhizal inoculation programs is guaranteed to make bamboo available as a sustainable resource (Das & Kayang, 2010).

Finally, it is important to note that although this document did not modify the names of the taxa assigned to Glomeromycota and Bambusoideae reported in the reviewed documents, taxonomic reorganizations and changes in names or categories have occurred in several cases (i.e. Błaszkowski et al., 2022), with some being assigned as synonyms of a more accepted name, for example. In some cases, even the reported names were fundamentally incorrect, not stemming from any synonymy confusion. Therefore, it is relevant to keep up to date with nomenclatural changes associated with the study groups being investigated to facilitate research and communication both within and outside the academic community. This can be done through specialized databases such as Index Fungorum (http://www.indexfungorum.org/), Species Fungorum (https://www.speciesfungorum.org/), and MycoBank (http://www.mycobank.org/) for Glomeromycota fungi, and literature such as the freely accessible book "World Checklist of Bamboos and Rattans" by (Vorontsova et al., 2016) for bamboos. The current status of the names of Glomeromycota fungi and Bambusoideae bamboos are summarized in *Tables 4* and *5*, respectively.

Table 4. Names of the Glomeromycota taxa mentioned in the text, and the current status of these names according to Index Fungorum, Species Fungorum, and MycoBank.

Table 5. Names of the Bambusoideae taxa mentioned in the text~~,~~ and the current status of these names according to Vorontsova et al. (2016).

Conclusions

This study presents the first systematic review of the current state of knowledge surrounding arbuscular mycorrhizal symbiosis established between plants and fungal taxa within Glomeromycota and Bambusoideae (respectively) worldwide. Asia, specifically India~~,~~ and China, stood out as the continent and countries with the most (and almost all) studies on the topic of review, while no other studies were reported from other continents, except for Brazil with a single publication. This review only considered currently published scientific literature, as the filtering and selection process filtered documents classified as gray literature, a particularly common publication trend in Latin America. As such, although there may be significant interests or efforts to study the symbiosis between AMF groups and bamboo species in Latin America, access to such information is limited.

The bamboo species that have been evaluated, described, or evidenced to establish mutualistic associations with arbuscular mycorrhizal fungi (31 species within 10 botanical families) associate with a considerable diversity of Glomeromycota genera and families (17 and eight, respectively, including groups marked as "Ni"). The identification of these groups ~~to~~ at the species level through the application of molecular markers using samples from the root compartment would contribute to a better understanding of and future perspectives ~~for~~ on this symbiotic association.

Based on the information compiled here, it is evident that the study of arbuscular mycorrhizal fungi in bamboo species around the world remains incipient and poorly explored, particularly ~~with respect to~~for the biology and ecology of mycorrhizal symbiosis in Bambusoideae. This is surprising considering the growing and robust evidence supporting the role of AMF in ~~the~~ mineral nutrition, water absorption or capture, and protection against biotic and abiotic stress factors in the majority of plants (Fall et al., 2022). As described by de Moura et al. (2019), understanding the dynamics of symbiosis between bamboo and its associated AMF is fundamental for developing management practices aimed at improving plant productivity and reducing production costs for bamboo species of interest. Considering the high ecological, ecosystemic, and cultural value of this plant group, this would expand the spectrum of possibilities in terms of the applicability of these species for ecological restoration and the fight against socio-environmental problems.

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ADDITIONAL INFORMATION AND DECLARATIONS

Competing Interests

The authors declare that they have no competing interests.

Author Contributions

- Juan José Sánchez-Matiz performed the search strategy, conceived and designed the experiments, performed the experiments, analyzed the data, prepared the figures, authored or reviewed drafts of the paper, and approved the final draft.
- Lucía Ana Díaz-Ariza performed the search strategy, conceived and designed the experiments, performed the experiments, analyzed the data, prepared the figures, authored or reviewed drafts of the paper, and approved the final draft.

Data Availability

The following information is supplied regarding data availability:

The PRISMA 2020 Checklist for systematic reviews is available in the Supplemental Files.

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