

## REVIEW

# Managing the functional diversity of arbuscular mycorrhizal fungi for the sustainable intensification of crop production

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**Societal Impact Statement**

The need to increase food production with reduced use of resources and environmental impact demands innovative rethinking and evolution of cropping systems. The essential changes required are consistent with sustaining arbuscular mycorrhiza, which, together with their associated microorganisms, could be managed to play an important role, especially in the protection of crops against abiotic and biotic stresses. Mycorrhiza should be included in agronomic decision processes, where chemical options to protect crops are limited or require the use of large applications. Defining rotational plant sequence or using cover crops and adopting reduced or no-till techniques are key components of a strategy for a consistent and predictable way of manipulating the native inoculum to capitalize on the manifold benefits potentially provided by arbuscular mycorrhizal fungi through their functional diversity.

**Summary**

Despite the wide range of benefits arbuscular mycorrhiza can confer, they are not usually considered in large-scale farming systems because the potential improvements in crop yields through the enhanced uptake of nutrients is a matter of debate and the advantages from the bio-protection afforded against biotic and abiotic stresses have not been adequately recognised. Research carried out by our group over the last 20 years has allowed the development of a strategy based on the intentional use of selected host plants (Developer plants), to develop an extensive extraradical mycelium which, when kept intact by the adoption of appropriate tillage techniques, acts as preferential source of inoculum for the following crop, leading to earlier and faster colonization by AM fungi. Depending on the particular host plant chosen as Developer, this strategy can also be used as a tool to manage AMF functional diversity. Using this approach, we have achieved effective protection against abiotic (Mn soil toxicity) and biotic (*Fusarium oxysporum* and *Magnaportheopsis maydis*) stresses in different crops. The strategy can easily be applied at field scale, both in low and high input cropping systems. It only requires small changes to the cropping system, such as employing no-till and altered crop rotation or cover crops, that are simple to adopt and can realistically be implemented at the field level. This represents an important

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breakthrough as it allows intentional and predictable manipulation of the native soil mycorrhizal population over a range of different soils and circumstances.

#### KEYWORDS

arbuscular mycorrhiza, biotic and abiotic stresses, conservation agriculture, crop management, functional diversity

## 1 | INTRODUCTION

In this review, we identify the essential issues facing agriculture and its practitioners. We show in a model system how the interests of a small group have come together to develop a practicable strategy addressing some of these issues by capturing the benefits available from improved functional diversity of the native AMF population. We further test the effectiveness of the method. Although formulating the strategy required work under controlled greenhouse conditions, we believe that testing of the agricultural system has to be completed in the field, and we have begun this process.

## 2 | SUSTAINABLE INTENSIFICATION OF AGRICULTURE AND THE SOIL

Agriculture and food producers are facing severe challenges in meeting the needs of the rapidly increasing population—expected to reach 9 billion within the next 30 years—that requires world food production to increase by 50%–70% under global climate change (FAO, 2009). Innovative rethinking of current cropping systems is required to meet this enhanced demand for food because the fundamental resources (land, soil, water and nutrients) needed to guarantee the required increases in production have limited availability (FAO, 2017; Goss et al., 2017). Furthermore, this enhanced production has to be achieved without environment degradation or critical depletion of the resources (FAO, 2017). These requirements characterise what FAO (2014) coined as sustainable intensification and described as looking at whole landscapes, territories and ecosystems to optimize resource utilization and management. Farmers must produce more from the same area of land using fewer inputs, which requires increased efficiency of production factors. The need is for farming systems that are more able to withstand the impacts of climate change, including an increased frequency of extreme events and emergence of new biotic stresses. In poorer countries, where increases in population and food demand are predicted to be greater, the challenge is both to reduce the gap between attainable yield and that typically realized and do so sustainably, even though access to inputs is limited. In wealthier countries, this yield gap is of less concern, but the challenge of protecting soils and maintaining yields, with reduced input, remains.

Some of the major threats to environmental sustainability are directly related to fundamental resource use in agriculture. Despite

improved efficiency in the energy requirement for N fertilizer production (Brentrup et al., 2016), the balance between economic benefits and environmental degradation from both its manufacture and use continues to concern (Alfian & Purwanto, 2019). Increasing the efficiency of use of nutrients, particularly N and P, is an important component of sustainable intensification. Worldwide, more than half of the N applied to cropland is lost to the wider environment, wasting the resource, threatening air, water and soil quality, reducing biodiversity and contributing to greenhouse gas emissions (Lassaletta et al., 2014). Phosphorus fertilizers rely on rock phosphate, which is a finite resource (Scholz et al., 2013), and although the estimated time to depletion of phosphate rock differs substantially between several studies (de Boer et al., 2019), in 2014, it was added onto the critical materials list of the European Commission (COM, 2014). Water quality and scarcity particularly in some regions of the world are also matters of great concern, aggravated by climate change. On average, depending on the climate and on the space and socio-economic and environmental conditions of the populations (Adeyemi et al., 2017; Pereira, 2017), agriculture accounts for 70% of global freshwater withdrawal (Gilbert, 2012) and irrigated agriculture represents 16% of the world cropped area but is expected to produce 44% of world food by 2050 (FAO, 2012).

In addition to the impacts of applying plant nutrients on soils, terrestrial and aquatic (both freshwater and marine) ecosystems, the use of herbicides and pesticides has affected the same systems but have also had toxic effects on humans and nonhuman biota. Although persistent organic chemicals have been phased out and replaced by more biodegradable pesticides, contamination by legacy residues and recent residues still impacts on the quality of human food, water and environment (Carvalho, 2017).

Soils of good quality make more efficient use of production inputs. Jenny (1941) identified that under a given climate and depending on the parent material, soil formation was a function of agronomic options, vegetation (including roots), the soil fauna and microbial activity. The aim has to be the optimisation of the quality of soil resources through manipulating these variables of soil formation. Some soil attributes, such as parent material and topography, cannot be changed by the adoption of appropriate agronomic management practices, but many others can be improved (Table 1). Key objectives identified for sustainable intensification are the enhancement of soil organic matter content and greater diversity of the soil microbiota. Mycorrhizal fungi are significant in this context (FAO, 2014).

**TABLE 1** Some examples of desirable improvements in soils, consistent with the sustainable intensification approach, and possible ways to attain them through agronomic practices.

| Improvements required to achieve sustainable intensification  | Impact  | Consequences  | Possible agronomic practices  |
|---|---|---|---|
| Increased soil organic matter (OM) content  | Increased soil structural stability<br>Greater cation exchange capacity     | Less soil loss from water and wind erosion<br>Enhanced nutrient availability and microbial diversity and activity | Leave crop residues at the soil surface<br>Include organic amendments |
| Reduction in excessive OM mineralization  | More controlled release of nutrients  | Better availability of N, P & K to plants, less loss by leaching  | Avoid inversion or intensive tillage                                  |
| Enhanced soil structure   | Different sized porosity and pore continuity within the soil profile        | Adequate balance of available water   | Adopt minimum or no-till, vary crop cycle length                      |
| Greater diversity of soil microbiota, including those involved in mutualistic symbiosis (Arbuscular mycorrhizal fungi, rhizobium) | Improved potential range of functionality for servicing soil and crop needs | Redundant and complimentary functionality<br>Greater resilience of ecosystems                                     | Work on crop sequence and avoid intensive tillage                     |

Note: FAO, 2014; Gan et al., 2020; Goss et al., 2017; Goss et al., 2019.

### 3 | ARBUSCULAR MYCORRHIZAL FUNGI—DIVERSITY AND FUNCTIONALITY

Arbuscular mycorrhiza (AM) is the oldest and most widespread mutualistic symbiosis between soil fungi and plants (Redecker et al., 2000; Wang & Qiu, 2006). Arbuscular mycorrhizal fungi (AMF) confer a wide variety of benefits to the host plant that can be summarised as.

- Facilitation of greater nutrient acquisition, particularly phosphorus and other slowly diffusing ions, by the extensive extra-radical mycelium (ERM) that significantly enlarges the soil volume exploited by plant roots (Harrison & Vanbuuren, 1995; Jansa et al., 2003). The ERM is also associated with water transport to roots (Püschel et al., 2020).
- Increased host plant vigour and growth under biotic (e.g. soil borne diseases) and abiotic stresses (e.g. metal toxicity), when well colonised (Brito et al., 2019).
- Altered regulation of host plant gene expression and hormone production (Cameron et al., 2013; Harrison, 1999; Poulsen et al., 2005).
- Indirect benefits, such as the enmeshing of soil particles to improve soil structural stability (Rillig & Mummey, 2006) and the provision of niche habitat by the ERM to other soil microbes, especially bacteria (Toljander et al., 2008), which may also provide growth promotion or bio-protection services.

Advances that have resulted from the new molecular tools developed over the last two decades (Öpik et al., 2013), together with recent developments in metagenomic analyses, have established that AMF diversity is greater than was formerly recognised from the description of spore morphological characters. Progress in metabolomics is providing ever more information about cellular processes in these fungi and of their functional capacity. These studies are mainly performed under very restricted experimental

environments with few tools available to permit greater understanding of functional diversity. Importantly, possibilities for integrating the roles and functionality of arbuscular mycorrhiza into agronomically effective practices is still in its infancy. It is considered that both less intensive cropping systems and selection of crop plant identity favour AMF biodiversity providing opportunity to improve mycorrhizal community function (Brito et al., 2012; Ciccolini et al., 2016).

In general, AM are not considered in the formulation of cropping systems. This position has been supported by Ryan and Graham (2018) and Ryan et al., (2019), who argue that farmers would not be justified in acting to manage AMF until the benefits of a prescriptive agronomic practice are established at the field scale. These authors focused on the lack of consistent evidence that the yield of cereal crops, mainly wheat (*Triticum aestivum*. L), colonized by AMF was greater than that of non-mycotrophic ones, even when the anticipated improvement in P acquisition occurred. Other potential benefits to crop production and quality from AMF: increased content of micronutrients in grain, improved soil structure and resilience, plant protection from herbivores and pathogens, greater resistance to soil acidity, toxic metals and metalloids, drought and salinity, were all acknowledged but not identified as contributing to a need for farmers to take into account in managing their enterprises. In response, Rillig et al., (2019) proposed that enhanced practices were necessary to establish agroecosystems that were more compatible with AM. This would enable farmers to take advantage of the services proffered by the soil biota. Both groups of authors agreed that better approaches were necessary to identify precisely the various roles played by AMF in agricultural systems, including how colonization of roots should be determined to evaluate AMF beneficial effects.

The source of AMF for investigating their contributions in different ecosystems, including how that might change with management practice, is an important issue (Rillig et al., 2019; Ryan & Graham, 2018). The manipulation of the native population, the application of an inoculum created from a native population or the production

of inoculum from laboratory cultures of AMF that readily sporulate have all been used. The efficacy of commercially available mycorrhizal inocula in agricultural systems remains controversial as inconsistent results in the field have been observed (Elliott et al., 2020; Gupta and Abbott, 2021). Although under some circumstances inocula give good results, often they cannot compete with the soil's native AMF communities or cannot survive standard agronomic practices (Berruti et al., 2016). Some commercial inoculum suppliers have undermined confidence by the imposition of high prices for material composed of only one or a few ubiquitous AMF species, which does not contain many viable propagules (Chen et al., 2018; Crossay et al., 2019). Some companies even recommend the application of inoculants in irrigation water. In this case, as propagules are not soluble, after arriving at the soil surface, they need to move through soil profile and find a suitable root to colonize, a very uncertain process. For many farmers, all these potential limitations have destroyed credibility in the use of AMF inoculation. Nevertheless, reliable commercial inoculum of proven effectiveness is available, and there are particular niches where it can certainly be usefully applied. These include greenhouse production systems or nurseries, where plants that have previously been inoculated and become mycorrhizal are better able to survive transplantation shock, golf courses and planting into extremely degraded soils, such as covering slopes after big engineering works. However, for larger scale field level use of AMF, farmers need to and should be able to count on native microbes. Inoculation with exotic AMF may have consequences for natural systems, particularly for fungal and plant communities. Hart et al., (2018) concluded that the current practice of AMF inoculation is at best a gamble and at worst an ecological threat. Every soil has its own resident AMF community, which is considered preferable to commercial inoculum (Frew, 2020). This resident community is usually quite diversified, certainly well adapted, definitely cheaper and more efficient than commercial inoculum. Furthermore, functional complementarity is described among AMF (Sikes et al., 2010) and a more diverse population expands the opportunity of beneficial outputs.

Preferential association between host plants and specific AMF genotypes is well-documented (Campos et al., 2018; Lekberg et al., 2013; McGonigle & Fitter, 1990; Öpik et al., 2009; Scheublin et al., 2004) as evidenced by differences between the consortia of fungal symbionts associated with particular plant genera grown in the same soil (Brígido et al., 2017). Current understanding indicates that the plant plays an important role in shaping the assemblage of AMF able to colonise its roots. For example, similar AMF communities have been found in the roots of *Hepatica nobilis* Mill., irrespective of sample location but providing these were under the same climatic conditions (Öpik et al., 2009). The AMF consortium in a root system of a plant is not necessarily the same from the beginning until the end of the plant cycle but can vary from just a few AMF species to some 30 different operational taxonomic units colonizing a single plant (Brígido et al., 2017). Furthermore, the same fungus can simultaneously colonise different plants, including those from different species, through its ERM in the soil (Jakobsen & Hammer, 2015; Walder et al., 2012). This is the basis of the common mycorrhizal

networks (CMN). Important agronomic advantages can be taken from this 'good promiscuity' between AMF and host plants, such as the transfer of nutrients between plants or the priming of plant defence mechanisms (Wipf et al., 2019).

A considerable functional diversity among AMF is well-recognised, not only in the extent and ability of their ERM to capture and transport nutrients from the soil to the host plant (Munkvold et al., 2004) but also in the degree of protection they can confer to the host plant against biotic and abiotic stresses (Brito et al., 2014; Lax et al., 2011; Thygesen et al., 2004). This means that a more diverse AMF community can provide a wider and more pertinent range of benefits to the host plants (Ellouze et al., 2014). It is ultimately site and plant specific, but both management of the diversity of AMF species and their functional traits in relation to the specific needs of the cropping system form the greatest challenge for a comprehensive integration of AMF into agronomic decision making.

Among AMF propagule types, ERM, when intact, is commonly the most infective providing greater AM colonization, as documented both in pot experiments and agricultural ecosystems (Goss et al., 2017). Intact ERM derives an earlier and faster AM colonization (Brito et al., 2019; Fairchild & Miller, 1988; Goss & de Varennes, 2002; Martins & Read, 1997). This is particularly important when crops are challenged by biotic or abiotic stresses existing in the soil at sowing, as the extent of AMF colonization when the host plant comes into contact with the stressor agent is directly related to the level of bio-protection achieved (Sikora et al., 2008) and a well-established AM is essential for an adequate protection (Garg & Chandel, 2010; Khaosaad et al., 2007; Nogales et al., 2009; Petit & Gubler, 2006; Rufyikiri et al., 2000). Consequently, colonization started by an intact ERM optimizes the potential benefits from AM to the host plant because it can capitalize on them sooner after exposure to stress. This earlier colonization is decisive for successful protection, as we will demonstrate below in some examples presented as case studies.

## 4 | A STRATEGY TO MANAGE AMF AND OVERCOME BIOTIC AND ABIOTIC STRESS

Conservation agriculture aims to make better use of agricultural resources through the integrated management of available soil, water and biological resources, combined with reduced external inputs (FAO, 2009). It contributes to environmental protection and to technical and economic or financial sustainable agricultural production and is based on three main pillars: (1) maintaining a permanent or semi-permanent organic cover on the soil, (2) a varied crop rotation and (3) the adoption of minimum tillage or no-till. It aims to enhance biodiversity and natural biological processes above and below the ground surface leading to improved and sustained crop production through increased water and nutrient use efficiency and protection from biotic and abiotic stresses.

The Mediterranean climate is characterized by a long, dry summer with irregular precipitation that is concentrated during

winter months. In such regions, soils commonly exhibit both physical and chemical limitations over extensive areas. The combination of weather and soil constraints determines the agronomic requirements in southern Europe and other Mediterranean regions of the world. Improvement in soil quality associated with the adoption of conservation agriculture has been the focus of research and extension activity at the University of Évora, Portugal, since the 1980s (Carvalho & Basch, 1995; Carvalho & Lourenço, 2014). These investigations addressed several components of conservation agriculture, including no-till systems and how to improve their performance, not only from a technological point of view but in relation to their impact on soil quality. The early studies reporting a more effective symbiosis when the soil was not disturbed, both in pot experiments (Jasper et al., 1989; Miller, 2000) and agricultural ecosystems (Kabir et al., 1997 a; McGonigle & Miller, 1996), together with an earlier and faster AMF colonization (Goss & de Varennes, 2002), inspired us to further explore the possible benefits of mycorrhizal symbiosis under no-till systems. Knowing that tools to fight biotic and abiotic stress in cropping systems are frequently non-existent, limited or expensive, or have serious environmental impacts, focussing on the role AMF might play in reducing or even controlling those stresses seemed to be a constructive option. Additionally, beyond the bioprotective effect granted by a well-established AMF colonization, the improved acquisition of relatively immobile plant nutrients generally associated with AMF (Ryan & Graham, 2018), and other benefits, such as protection from drought, would also be of particular relevance for Mediterranean cropping systems.

Following this theme, the research carried out by our group focused on a strategy for managing native AMF for bio-protection in cropping systems (Goss et al., 2017). The strategy was based on the intentional use of selected host plants (Developer plants) to develop an extensive ERM that, when kept intact by the adoption of appropriate tillage techniques, acts as preferential source for colonization of the following target plant and leads to earlier and more rapid colonization by AM fungi (Figure 1) to grant bio-protection. Depending on the host plant chosen as Developer, this strategy can also be used as an approach to manage AMF functional diversity. Using this approach, we have achieved effective protection against abiotic (Mn toxicity in soil) and biotic (*Fusarium oxysporum* and *Magnaportheopsis maydis*) stresses in different susceptible host plants. The strategy can easily be applied at the field scale, both in low- and high-input cropping systems. Typically, it only requires relatively small changes to the cropping system, such as employing some form of reduced tillage and crop rotations or cover crops that are easy to adopt and can realistically be implemented by farmers (Brito et al., 2019; Goss et al., 2017; Patanita et al., 2020).

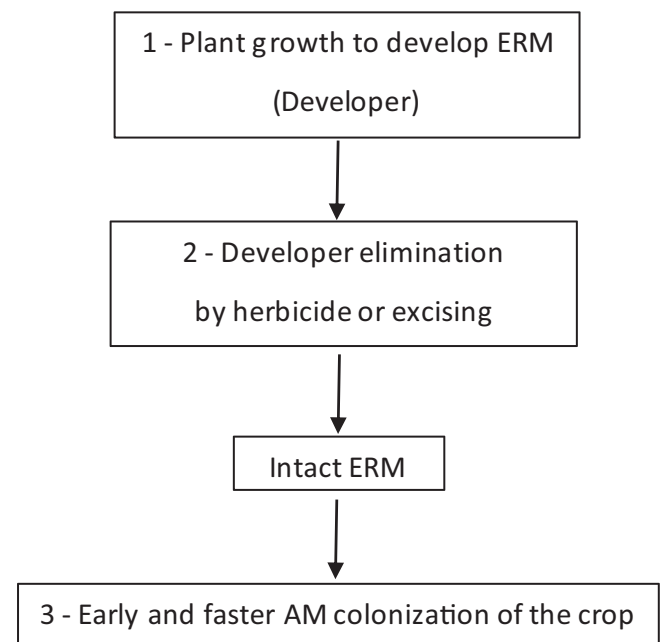
## 5 | EXPERIMENTAL WORK DEVELOPED TO ESTABLISH THE STRATEGY

The strategy adopted to manage AMF for bio-protection against biotic and abiotic stresses was first considered against metal toxicity

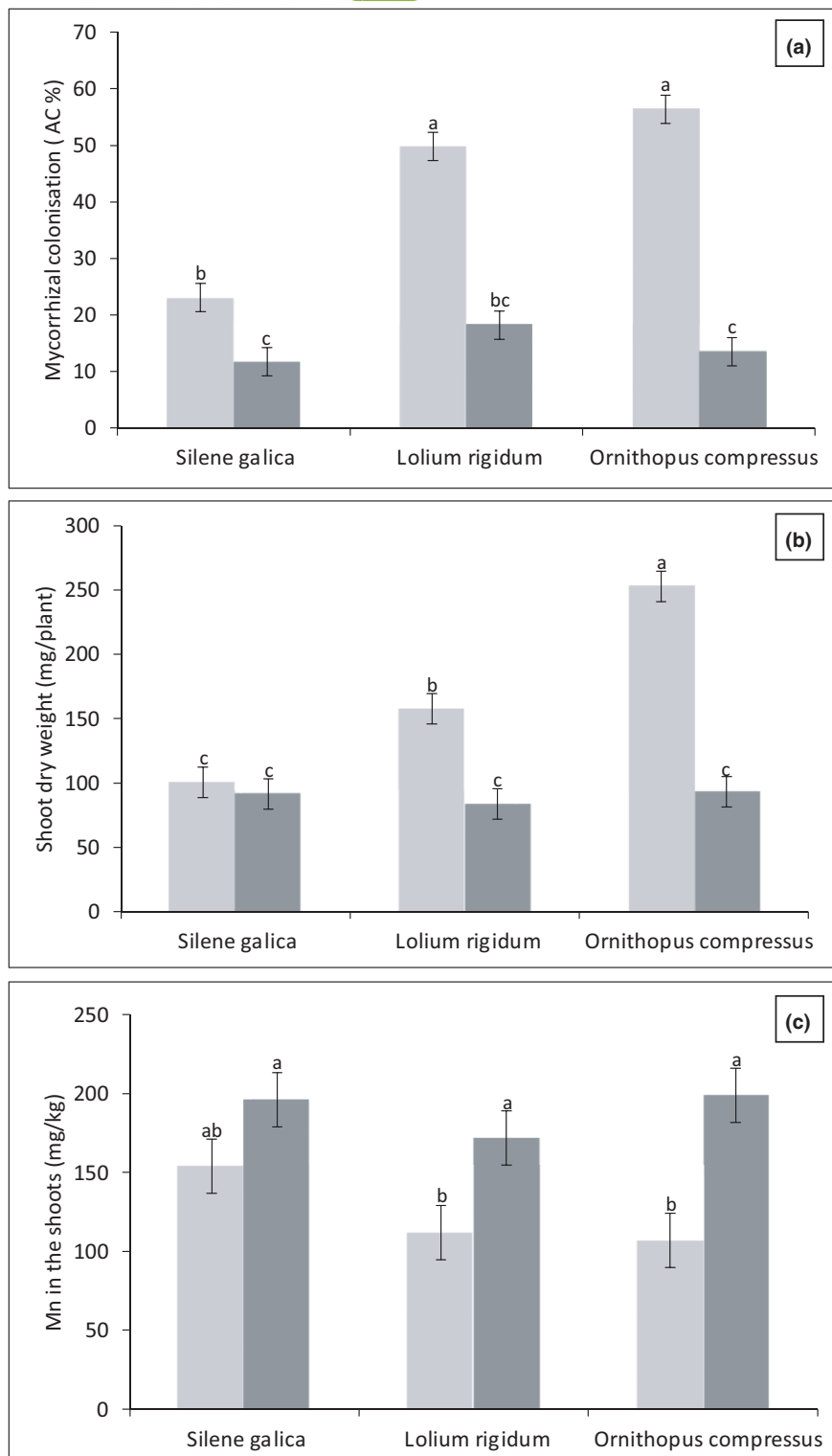
as we had already developed an agronomic approach to counter this stress (Goss & Carvalho, 1992). Fifty per cent of the world's potentially arable soil is acidic (Kochian et al., 2015), and manganese (Mn) toxicity is a severe problem in many acid soils, including those in the Mediterranean basin, where crop production can be greatly impaired. The toxic ions are continuously present in the soil, so a specific challenge relates to susceptible plants needing rapid protection after germination. Early colonization can also be required to initiate protection against biotic stress from soil-borne diseases. The responsible fungal or oomycete pathogens represent considerable threats to many cropping systems across the world, and there is a decreasing number of chemical tools considered acceptable for controlling them.

### 5.1 | Abiotic stress—Mn toxicity

Knowing that different host plants harbour different AMF populations, and to find some functional diversity among the soil native fungi, two Developer plants, *Ornithopus compressus* and *Lolium rigidum*, were chosen from the natural vegetation at sites where soil Mn toxicity was already known. A third plant species (*Silene gallica*), also from the native vegetation but non-mycorrhizal, was also included in the study as a negative control for the Developer plants. Another factor in the study was soil disturbance after the growth of Developer plants. The treatment with soil disturbance disrupted the ERM network created by the mycorrhiza and prevented it from effecting early AM colonization in the Mn susceptible test crop but



**FIGURE 1** An illustration of the strategy for the development of a network of ERM by a Developer plant (1), which after a few weeks is eliminated in such a way that ERM is kept intact (2) and will perform as a preferential AMF inoculum source of the crop, granting an earlier and faster AM colonization (3).



**FIGURE 2** The effect of Developer plant and soil disturbance on (a) mycorrhizal colonization of wheat determined as the percentage of root length with arbuscules (AC%); (b) shoot dry weight (mg/plant); and (c) manganese concentration (mg/kg) in shoots of wheat (*T. aestivum*) plants grown for 21 days after a non-mycorrhizal plant (*S. gallica*) or after two mycotrophic plants. Developers (*L. rigidum* and *O. compressus*), in disturbed soil (disrupted ERM) dark grey bars, and in undisturbed soil (intact ERM) light grey bars. Different letters indicate significant differences between treatments ( $p \leq 0.05$ ). A replicated experiment was carried out following the first, and the combined dataset was analysed using the different experiments as a factor (figure based on Brito et al., 2014).

guaranteed that all the other possible influences of the Developer plant on the soil were retained. The experiment was conducted in 8L pots, using a soil in which Mn toxicity had been previously identified. To mimic as faithfully as possible what could be reality in an open field, Developer plants were controlled after 7 weeks growth (stage 1 in Figure 1) with a synthetic herbicide (glyphosate) (stage 2 in Figure 1) and the test crop chosen for stage 3 (see Figure 1) was wheat, owing to its sensitivity to Mn (see Brito et al., 2014 for

details). To understand if the strategy under development was applicable at field level, it had to prove its efficacy in the same conditions as no-till operates in the field and that implies the use of synthetic herbicides.

After 21 days, wheat plants grown after mycotrophic Developers and where the ERM was kept intact, showed significantly ( $p < 0.05$ ) greater AMF colonization rates (Figure 2a). These plants also achieved greater shoot dry weight (Figure 2b) with a smaller Mn

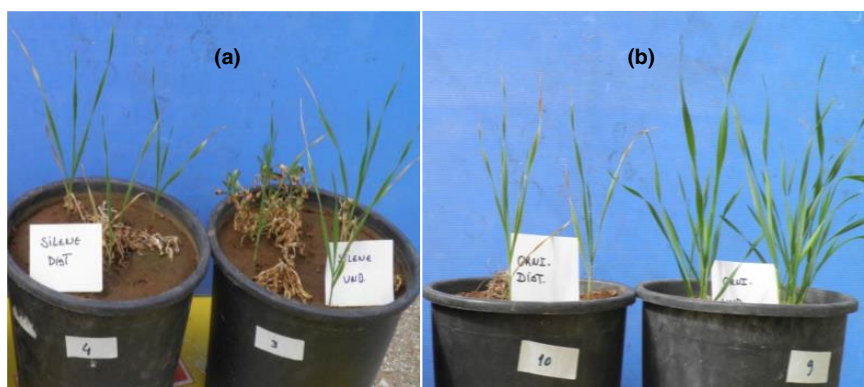
concentration in their shoots (Figure 2c). The effect on earlier AM colonisation on protection against Mn toxicity was clearly observed in these wheat test plants in comparison with those grown after the non-mycorrhizal Developer or in pots where the ERM had been disrupted after growth of the mycotrophic Developers. None of the wheat plants from the latter treatments were able to grow beyond the 4th-leaf stage, the period when utilization of seed reserves ceased. At this stage, the plant fully depends on the root system for nutrients acquisition and must deal with the soil Mn toxicity. The differences between treatments were overwhelming (Figure 3).

Importantly, when the ERM remained intact, wheat growth was obviously greater than in controls but not the same where following different mycotrophic Developers. Wheat dry weight was 2.7 times more after *O. compressus* and only 1.8 times more after *L. rigidum* (Figure 2b), and this result suggested that functional diversity between AMF could be influencing the extent to which the wheat was being protected against Mn, clearly influenced by the characteristics of the Developer. Pyrosequencing analysis confirmed this hypothesis. Each plant influences the choice of AMF in the assemblage colonizing its roots, and the choice is usually consistent at the family level of plant taxa (Hartmann et al., 2009; Scheublin et al., 2004). This level of selection is seen in the charts representing the AMF assemblages of *O. compressus*, *L. rigidum* and wheat when they are first planted in that soil (Figure 4 charts A, B and C). Both members of the Poaceae (*L. rigidum* and *T. aestivum*) align in their AMF consortium but differ from that of *O. compressus* (Fabaceae). The more surprising and original result was that when wheat was colonized by an intact ERM previously developed by a plant from a different family, its ability to control the AMF assemblage in its roots seemed to be reduced; certainly, the choice changed. As shown in chart D from Figure 4, when wheat comes after *O. compressus* and is primarily colonized by the intact ERM developed by the legume, its AMF assemblage is very similar to the one of *O. compressus* (Brigido et al., 2017). There is some evidence that the biochemical recognition dialogue between

AMF and the host plant, which leads to a functional mycorrhiza, does not follow the same pattern but depends on whether the inoculum source is based on spores or intact ERM, as the plant symbiotic program depends on some extent on the colonizing propagule type (Campos et al., 2018; David-Schwartz et al., 2001).

Our further studies on the causes and mechanisms underlying the functional diversity among these AMF were carried out using the experimental protocol described above. In general wheat roots were found to be sensitive to oxidative stress derived from excess soil Mn, that promoted Mn translocation and storage in shoot vacuoles (Faria et al., 2020). In wheat plants with greater AM colonization, more Mn accumulated in the apoplast and there was greater Mn-SOD isoform activity (Faria, Teixeira, et al., 2021). The activity of this enzyme, probably involved in AMF-mediated Mn stress mitigation, was also more evident in wheat grown after *O. compressus* than after *L. rigidum* (Faria, Pinto, et al., 2021). Interesting differences in gene expression by wheat depended on the particular AMF assemblage colonizing the roots, with the defense mechanism against Mn stress being activated differentially according to the preceding Developer. Whereas the assemblage developed by *O. compressus* activated processes in wheat related to cellular division and growth, but only a few related to stress, when *L. rigidum* was the Developer plant, it was mostly wheat genes related to oxidative stress, disease protection and metal binding that were induced. It suggested that the wheat genes activated following *L. rigidum* were less effective in protecting the plant from Mn toxicity than those activated after *O. compressus* (Campos, Patanita, et al., 2019).

The growth of contrasting Developer plants and disturbance of the soil also impacted soil biological activity in addition that of the AMF. Mycorrhizal fungi have a diverse bacterial population associated with their ERM (Bonfante & Anca, 2009; Ordoñez et al., 2016) that inevitably is impacted by the ERM disruption resulting from soil disturbance. Following the growth of *O. compressus* or *L. rigidum*, soil disturbance resulted in a decrease of P solubilizers and phosphatase



**FIGURE 3** The effect of Developer plant and soil disturbance on growth and presence of manganese (Mn) toxicity symptoms in wheat (*T. aestivum*). (a) Wheat grown after the non-mycorrhizal plant (*S. gallica*) showing similar growth and Mn toxicity symptoms in the leaves, irrespective of whether (Left) ERM was disrupted (Disturbed soil treatment) or (Right) ERM intact (Undisturbed soil treatment). (b) Wheat grown after a mycotrophic Developer plant (*O. compressus*) showing (Left) poorer growth and Mn toxicity symptoms in the leaves of plants from Disturbed soil treatment (ERM disrupted) compared with (Right) better growth and no symptoms of Mn toxicity in plants in Undisturbed soil treatment (ERM intact) and AM colonization occurred earlier.

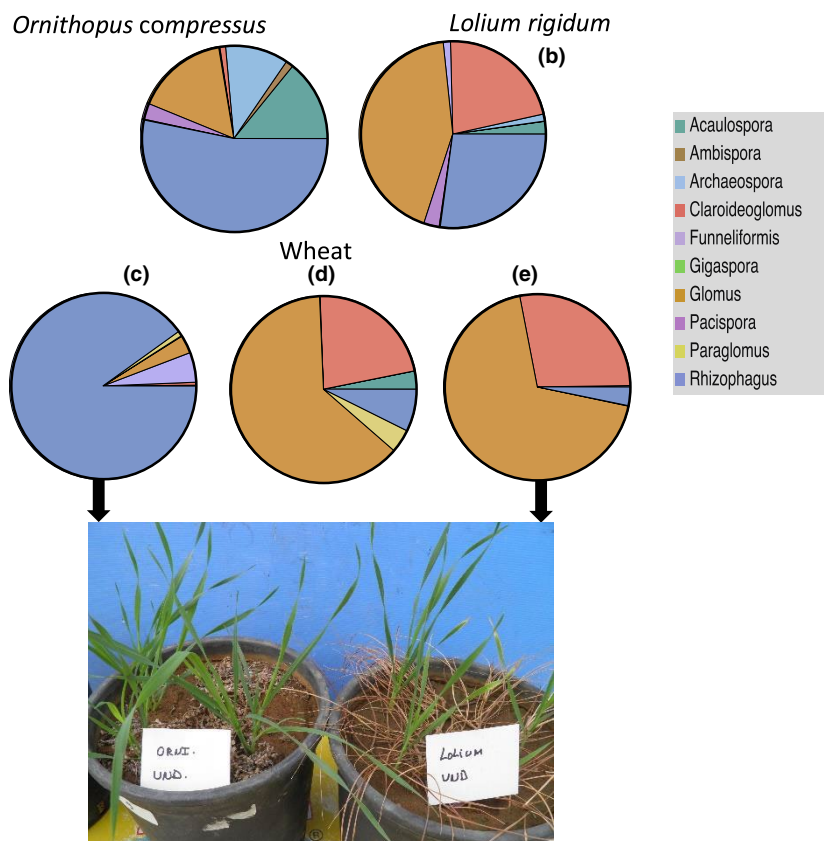
activity, whereas after the non-mycorrhizal plant (*S. gallica*) rhizosphere, P solubilizers did not change, and phosphatase activity increased after soil disturbance, indicating the different strategies for P acquisition for these plants. Soil disturbance particularly affected soil microbial respiration, microbial biomass carbon and the metabolic quotient (the ratio between soil basal respiration and microbial biomass carbon) after non-mycorrhizal plants and also promoted some microbial communities, such as ammonifiers or manganese oxidizers. Enzymatic activity and mineralization of organic matter after soil disturbance under non-mycorrhizal plants (*S. gallica*) were apparently slower than under mycotrophic plants (Conceição et al., 2021 submitted).

Important members of the soil microbiome include N-fixing symbiotic bacteria, globally referred to as Rhizobium. Also under conditions of Mn stress and using the same Developer plants, the strategy already described (Figure 1) was used to test the bioprotection of subterranean clover (*Trifolium subterraneum*). Mycorrhizal colonization 21 days after planting followed the same pattern as the one observed for wheat, and it was significantly greater in plants grown after mycotrophic Developers and where the ERM was kept intact and operated as the preferential inoculum source for AMF colonization of subterranean clover. These were also the plants where the Mn concentration in roots was the least and shoot dry weight the greatest (Figure 5). In these plants, the dry weight of nodules and N acquisition were enhanced, indicating an indirect protective effect of early AMF colonization on subterranean clover, not directly to the host plant but to the other member of the tripartite symbiosis, the rhizobia (Alho et al., 2015).

## 5.2 | Biotic stress—*Fusarium oxysporum* and *Magnaportheopsis maydis*

We have evaluated our strategy of using different Developer plants to create an intact ERM and permit the earlier development of mycorrhiza in a host crop susceptible to a known soil borne fungal infection. The same basic approach (Figure 1) was tested for bioprotection of a crop against biotic stress. However, modifications to the experimental protocol were required. In contrast to the selection process needed to identify suitable Developer plants to counter an abiotic stress, the main criterion for Developer plants for biotic stress was that they were tolerant of the prevailing stress. In the case of a biotic threat, the Developer plants cannot host the pathogen.

Under open field production, it is estimated that *Fusarium oxysporum* can cause yield losses in tomato (*Lycopersicon esculentum*) of 45%, with records of 100% loss for some crops; research on the pathogen has focused on the diverse strategies for its control (McGovern, 2015). We investigated the bio-protection of tomato by native AMF against *Fusarium oxysporum* f.sp. *radicis-lycopersici* using *L. rigidum* as Developer. These Developer plants were grown for 7 weeks in 8L pots with natural soil and its native AMF population. After the Developer was controlled by glyphosate, three pre-germinated tomato seedlings were planted per pot and conidia of *F. oxysporum* f.sp. *radicis-lycopersici* were inoculated onto the roots of each plant, using 1 ml per plant of a suspension with a concentration of 0,  $10^3$ ,  $10^6$ , or  $10^9$  conidia/ml. Nutrients were supplied according to normal fertilizer recommendations for tomato in the field and the plants were grown for 3 weeks.



**FIGURE 4** Taxonomic affiliation of the operational taxonomic units (OTU), colonizing *O. compressus* (Chart A), *L. rigidum* (Chart B) or wheat (Chart C). Chart D shows taxonomic affiliation of OTU in wheat grown after *O. compressus* and preferentially colonized by intact ERM. Chart E shows taxonomic affiliation of OTU in wheat grown after *L. rigidum* and preferentially colonized by intact ERM. The picture below charts D and E illustrates the growth of wheat after each Developer (based on van Tuinen et al., 2017).

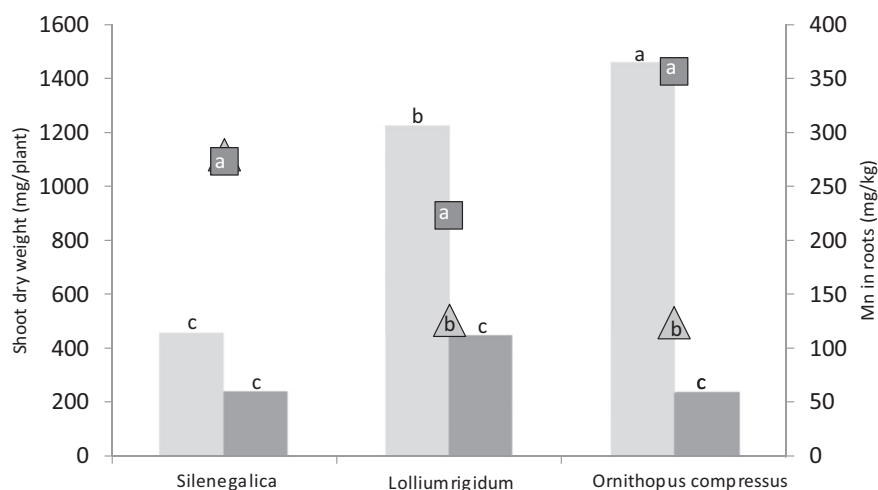


In this experimental protocol, the control treatment was to disturb the soil after the Developer plant growth, thereby disrupting the ERM and delaying AM colonization of the crop. The nature of the results was not surprising, but the effects far exceeded the expectations. When *F. oxysporum* was inoculated, arbuscular colonization was significantly greater in the tomato plants grown in undisturbed soil, where the ERM was kept intact and early colonization could be established. Incidence of disease was reduced in these plants, particularly for the  $10^6$  conidia/ml inoculation, the dose that more closely represents typical numbers in infested soil where the reduction was reduced by half, (Figure 6). The plant growth under the largest concentration of *F. oxysporum* inoculation ( $10^9$  conidia/ml) was greatly diminished when the ERM was disrupted (Figure 7a) compared with when the ERM was kept intact (Figure 7b). In this experiment, the growth of tomato in the absence of *F. oxysporum* inoculation was not affected by the AMF inoculum source, suggesting that other potential benefits from mycorrhiza formation were not evident under the tested circumstances, possibly due to the liberal applications of nutrients. But the results also indicate that the use of large amounts of fertilizer, particularly P, did not prevent the AMF colonization and protection against the pathogen.

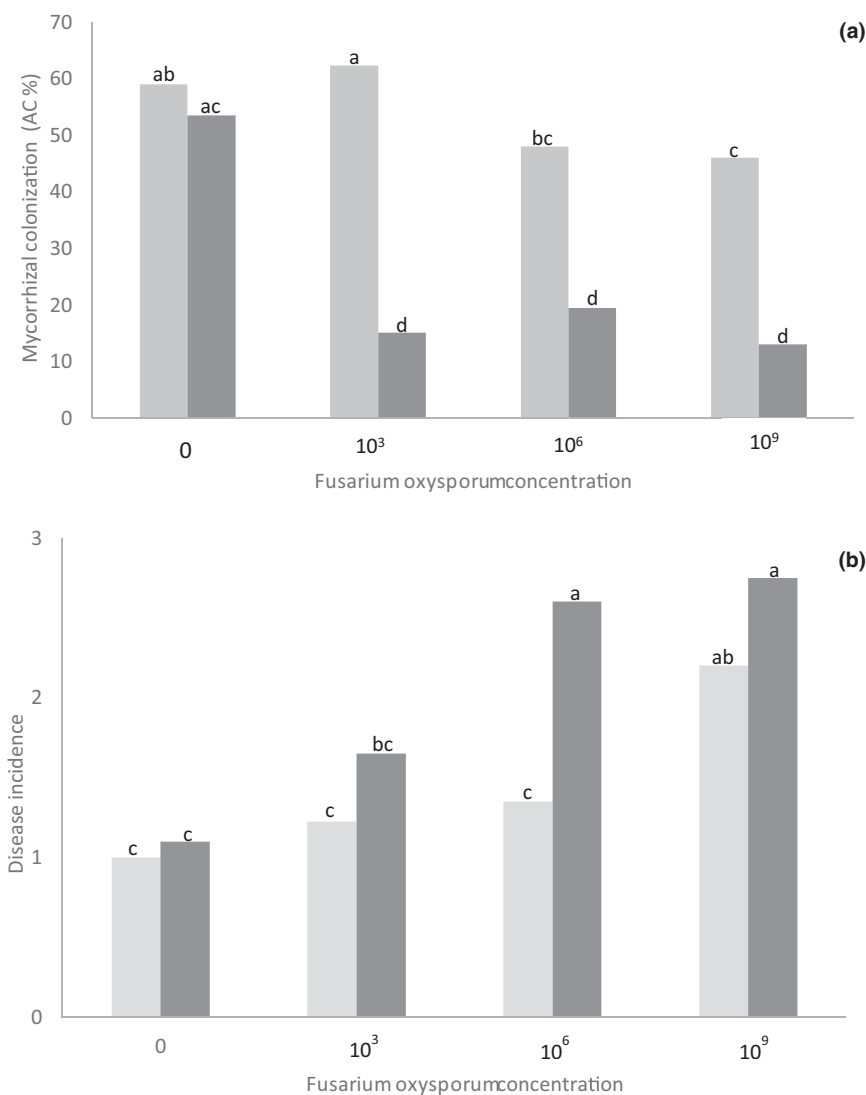
In a subsequent study with a similar protocol but including two Developer plants (*O. compressus* and *L. rigidum*), there was corroboration of the importance of the intact ERM for early AM colonization and its correlation with reduced incidence of disease and enhanced growth of tomato in the presence of *F. oxysporum*. However, this experiment allowed the comparison of outcomes resulting from different Developer plants. Although *L. rigidum* as ERM Developer gave rise to a greater AM colonization of tomato plants, the plants grown following *O. compressus* showed even less incidence of disease (Pinto, master thesis 2020, unpublished results). Although

these results should only be treated as preliminary, colonization rate seems to be only partially informative about the effectiveness of AMF. Similar indications have been observed in other experiments, where the response may be due to an increase of root growth and not a decrease in fungal development (Fan et al., 2019). Colonized root length density is a better assessment in these circumstances (Carvalho et al., 2015). According to earlier studies, AMF functional diversity associated with the plant sequence and the fact of having intact ERM as preferential inoculum source, may explain the differences observed in the tomato disease incidence.

The bioprotection strategy (Figure 1) was also tested in a field experiment for the protection of maize against the soil born fungus *Magnaportheopsis maydis* (same as *Cephalosporium maydis*). This organism has been affecting crops with increased incidence in many regions around the world. It has devastated crops and there are no chemical control measures available (Oerke, 2006). This experiment was carried out on two farms where *Magnaportheopsis maydis* has been causing important crop losses. In Mediterranean regions, maize is a spring crop, and therefore, the Developer plant role can be assumed by a cover crop grown over winter. In this case, *Lolium multiflorum* was used as cover crop and no-till or conventional tillage systems were employed. It should be emphasized that benefits of using cover crops or no-till systems go beyond the development of a mycorrhizal ERM, especially if continued over time (Sharma et al., 2018). In this study, the presence of *Magnaportheopsis maydis* in maize plants, assessed by qPCR (Campos, Nobre, et al., 2019), was significantly reduced only when the cover crop was grown in association with a no-till system. Also, significantly greater dry matter production and a 19% increase in grain production was observed in this combination of treatments. Again, results highlight the



**FIGURE 5** The effect of Developer plant species (*S. gallica*, *L. rigidum* and *O. compressus*) on shoot growth in subterranean clover (*Trifolium subterraneum*) and on the manganese concentration in root tissue, 42 days after planting. Histogram (Left axis): shoot dry weight (mg/plant) of subterranean clover following a non-mycorrhizal plant (*S. gallica*) and two mycotrophic plants. Dark grey bars are the Disturbed soil treatment (ERM disrupted after Developer growth); light grey bars are the Undisturbed soil treatment (ERM intact). Markers (Right axis): Squares denote manganese concentration in the roots (mg/kg) of the same plants from the Disturbed soil treatment (disrupted ERM); Triangles denote Undisturbed soil (intact ERM). On pairs of histogram bars or pairs of marks, different letters indicate significant differences between treatments ( $p \leq 0.05$ ) (figure based on Alho et al., 2015).



**FIGURE 6** (a) Mycorrhizal colonization determined as the percentage of root length with arbuscules (AC%) in tomato plants 16 days after inoculation with 0, 10<sup>3</sup>, 10<sup>6</sup> or 10<sup>9</sup> conidia of *Fusarium oxysporum* per plant at planting. (b) Disease incidence scored in the same plants and treatments, using visual assessment ranging from no visible symptoms (Score =1) to stem fully affected (Score =4). Dark grey bars are the Disturbed soil treatment (ERM disrupted); Light grey bars are the Undisturbed soil treatment (ERM intact). Different letters indicate significant differences between treatments ( $p \leq 0.05$ ) (figure based on Brito et al., 2019).



**FIGURE 7** Tomato growth after inoculation with 10<sup>9</sup> conidia of *F. oxysporum* at planting. Previous Developer plant for arbuscular mycorrhiza was *Lolium rigidum*. (a) Disturbed soil treatment, AMF inoculum source was spores and colonized root fragments. (b) Undisturbed soil treatment, the preferential inoculum source was intact ERM.

importance of an intact ERM and the early AMF colonization for the bio-protection of the crop (Patanita et al., 2020).

There are different mechanisms underlying the increased resistance or tolerance of mycorrhizal host plants to soil borne diseases that may be operating simultaneously and at multiple levels, as

generally described in the literature (Azcón-Aguilar & Barea, 1996). In addition to the damage compensation resulting from the improved plant nutrition, physical competition for infection sites and photosynthates, the priming of defence mechanisms, or changes in the microbial rhizosphere community (Cameron et al., 2013; Pozo et al., 2013) can be involved. The role of the CMN, that can be preserved only in no-till systems, is particularly important in the priming of defence mechanisms. The CMN enables the transmission of signals between pathogen-infected and healthy neighbouring plants, allowing the latter to be informed by afflicted neighbouring plants and to activate defence mechanisms before they are attacked themselves (Song et al., 2010).

## 6 | AGRONOMIC USE OF AMF AND ITS FUNCTIONAL DIVERSITY

The strategy described in this article to integrate the bio-protective and other beneficial roles of native AMF in cropping system is not too complicated for practical implementation and could have great

impact on the development of sustainable intensification of agricultural systems.

In practical terms, implementation of the strategy entails the beneficial management of the functional diversity of native AMF through the choice of the plant that precedes the crop, together with the use of reduced or no-till techniques to keep ERM intact and promote early AM colonization of the crop requiring protection. Even in high-input cropping systems, the general strategy has been shown to be effective (Goss et al., 2017) and therefore may also contribute to fertilizer use efficiency. Lekberg and Koide (2005) support the view that AMF diversity and abundance in agricultural soils could be improved by changing management practices which promote native AMF.

Adoption of different field operations and adjustments to their timing allowed our approach to be tested by a large-scale tomato producer in the southern region of Portugal (Brito et al., 2019). Here, the aim was to reduce production losses on land where *F. oxysporum* had greatly reduced crop performance in the previous year. Preparation of the land, which included deep tillage to remove the soil compaction caused during harvest, was usually carried out in spring before the next tomato crop was planted. This activity was brought forward and subsoiling was performed immediately after tomato harvest in September. Disk-harrowing followed to form planting beds before barley (*Hordeum vulgare*) was sown as a winter cover crop to act as the ERM Developer plant for native AMF. In the following Spring, barley was killed by glyphosate. Two weeks later, the planting beds were reformed using shallow disk-harrowing (10 cm), and tomato was then planted. As a result of the modified production system, plant mortality due to Fusarium wilt disease was significantly less and relative to a control area, where the standard practices were kept in place, tomato production increased by 20 ton/ha—a 20% increase in total fruit production (see Brito et al., 2019 for details). This example demonstrates the application of our strategy to address an agronomic problem, which allowed application of a biological solution for countering a damaging disease, when no chemical option was available. Furthermore, the liberal application of fertilizer did not prove a barrier to producing the protective effect through the mycorrhiza.

The choice of ERM Developer plant has to take account of several key aspects. The botanical family of the Developer determines the AMF assemblage and can facilitate the best AMF functional output appropriate to the prevailing stressors. ERM from AMF associated with one Developer plant may not be the best for enhancing the growth of the crop requiring protection, so it is important to identify possible positive and negative feed-back mechanisms that might contribute to the functional consequences (Beaver, 2002). For biotic stresses, the Developer plant cannot be a host of the pathogen that poses the threat and, for abiotic stresses, a wise approach is to choose a plant from the naturally occurring vegetation, as it most likely harbours AMF from the native population that enable it to cope with or alleviate the stress. When Developer plants are integrated in the framework of a rotation system, particularly under Mediterranean climate, it is important to ensure that intact ERM

remains infective after the hot and dry summer. This was confirmed for southern Portugal by Brito et al., (2011). Nevertheless, there are no previously established protocols, and, where possible, it is desirable first to undertake some small-scale experimental work before the choice of the Developer plant is made, thereby maximizing the impact.

Within cropping systems, there are a few options available to play the role of ERM developer plants. The possibilities include cover crops, the previous crop in a rotation or even the dominant weeds that germinate before the sensitive crop is planted. The use of systemic herbicide to eliminate the Developer plant (except in a crop rotation) is the most practical way of controlling it and simultaneously keep the ERM intact. The option of cutting the Developer plant, used in some of the pot experiments described, is not easily transferable to the field because natural regrowth could be competitive in the growth of the crop being protected. In our experience, if judiciously employed, with the appropriate timing and application rate per unit area of the active ingredient, the advantages of using herbicide in these circumstances supplant any possible inconvenience, as confirmed by Wilkes et al., (2020). We applied Glyphosate in our experiments as it is the most commonly used herbicide on arable farms and has been subject to considerable investigation of its effects on AMF. However, results have not been consistent and mainly focused on impacts on spore viability and AM colonization (Druille et al., 2016; Powell et al., 2009). Significantly, AMF can produce enzymes that may participate in the degradation of glyphosate (Wang et al., 2020).

Cover crops provide important ecosystems services in addition to their potential the role as ERM Developer plants. According to a multiple meta-analysis study performed Shackelford et al., (2019), soil in plots with cover crops contained 9% more organic matter and 41% more microbial biomass; and when legumes are included in the cover crop the associated cash crop yields were 16% greater.

As grain production is not the main objective in using cover crops, the seed and fertilizer costs are reduced. In intensive systems, such as tomato, the nutrients left in the soil after the main crop can meet the need of cover crops. Shackelford et al., (2019) have report 53% lower nitrate leaching in plots with non-legumes cover crops under Mediterranean conditions.

A tillage system compatible with the objective of ensuring the integrity of the ERM to allow earlier and faster AMF colonization of the crop, preferentially relies on no-till, but any kind of minimum or very shallow tillage (strip-tillage, ridge-till or reduced shallow cultivation) also appear to be acceptable, as all these limit disruption of ERM. No-tillage or reduced tillage systems involve many other gains. These systems are less demanding in terms of fuel energy and are associated with an increase of soil organic matter as mineralization processes are slower and can lead to reduced nutrient losses. Fertilizer use, particularly N, can therefore be lower and its costs in terms of manufacturing energy and environmental impacts can also be reduced (Carvalho & Lourenço, 2014). Under these soil management systems, soil physical properties are also preserved or ameliorated (Blanco-Canqui & Ruis, 2018), which can result in better water use efficiency, reduced soil losses by erosion and improved

soil trafficability. These improvements can increase the opportunities to be avoid delays in performing other field operations (sowing, application of fertilizer or other remedial treatments).

In conclusion, production practices could provide the means of both supporting and manipulating native soil microbes, such as AMF, in a consistent and predictable way over a range of different soils and conditions. Although further investigation and the evolution of agronomic systems are undoubtedly required, the approach can provide an important opportunity for combatting both biotic and abiotic stress. The specific bio-protection strategy proposed integrates no-till or other reduced tillage systems and the use of cover crops or crop rotations in addition to the protective and nutritional benefits potentially provided by early colonization of the crop by AMF. Moreover, it could be considered as a contribution to the reduction of environmental impacts through increases in water and energy use efficiency, the enhancement of biodiversity, the assuring of soil quality and by offsetting of concerns commonly associated with pesticides and fertilizer use. These goals also meet the conditions for sustainable intensification of agriculture, envisaged as one of the most promising possibilities for meeting the worldwide demand for increased food availability. The proposed strategy for the management of AMF in cropping systems aligns with these objectives and can contribute to a more effective use of the oldest mutualist symbiosis between fungi and plants.

## ACKNOWLEDGEMENTS

The work presented was financed by National Funds through FCT – Foundation for Science and Technology, in the frame of the project PTDC/AGR-PRO/111896/2009 and under the Project UIDB/05183/2020, also internal funding resulting from provision of external services by the Soil Microbiology Laboratory MED (Mediterranean Institute for Agriculture, Environment and Development). The data reported summarizes the work developed over a long period by a large dynamic team and the authors thank their co-authors in the several previous publications. We also acknowledge Filipa Santos and Manuel Figo for their technical assistance and Taiana Conceição and José Pinto for access to their unpublished results.

## AUTHOR CONTRIBUTIONS

All authors contributed for the design of the experiments mentioned, data analysis and interpretation. IB wrote the publication. All authors edited and approved the final manuscript.

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**How to cite this article:** Brito, I., Carvalho M., & Goss M. J. (2021). Managing the functional diversity of arbuscular mycorrhizal fungi for the sustainable intensification of crop production. *Plants, People, Planet*, 3(5), 491–505. <https://doi.org/10.1002/ppp3.10212>