



Review

Effects of Pesticides on the Arbuscular Mycorrhizal Symbiosis

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Abstract: Substantial amounts of pesticides, used in agricultural production to control pests, diseases, and weeds, and thereby attain high product quantities and quality, can severely affect the ecosystem and human health. The amounts of pesticides used depend on the specifics of the current production system but also exhibit large effects of past practices. Pesticides do not act only on the target organisms but also on organisms for which the chemicals were not specifically formulated, constituting hazardous molecules for humans and the environment. Pesticides, therefore, also influence soil microbial communities including organisms that engage in mutualistic plant symbioses that play a crucial role in its mineral nutrition, such as arbuscular mycorrhizal fungi. In this review, we summarize the current knowledge on the effects of synthetic and natural ('green') pesticides (fungicides, herbicides, and insecticides) on arbuscular mycorrhizal symbiosis. We deal with both the direct effects (spore germination and extraradical and intraradical growth of the mycelium) and indirect effects on the agroecosystem level. Such indirect effects include effects through the spread of herbicide-resistant crops and weeds to neighboring ecosystems, thereby modifying the mycorrhizal inoculum potential and altering the plant–plant interactions. We also briefly discuss the possibility that mycorrhizal plants can be used to enhance the phytoremediation of organic pesticides.

Keywords: pesticides; fungicides; nematicides; plant symbioses; arbuscular mycorrhizas; bioindicators; agroecosystems; genetic modified crops; weeds; land management



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1. Introduction

Massive amounts of pesticides are used in agricultural production systems to control pests, diseases, and weeds, and thereby attain high product quantity and quality. The amount of pesticides used and, hence, the presence of pesticides in food, for example, is associated with the farming system used for their production, being higher in conventional > integrated pest management > organic systems [1]. However, it is not just the actual agricultural production system that matters but also what has been described as the ghost of conventional agriculture past [2]. Thus, past and current conventional agricultural practices (with high levels of pesticides) show adverse effects on soil microbiota, which conflicts with the use of beneficial soil organisms such as arbuscular mycorrhizal fungi (AMF) [3]. Such adverse effects are not only due to the direct effects of these pesticides on soil life but also because the agricultural systems in which pesticide use is regularly applied reshape the soil ecosystem by selecting for different crops and weeds through the development of pesticide resistance [4]. Equally, more sustainable agricultural practices that include cover crops for weed suppression, and thereby reduce the need for pesticides, can impact communities of AMF [5]. The main classes of pesticides are fungicides, nematicides, insecticides, and herbicides. Their use can severely affect ecosystem health due to nontarget effects on AMF [6,7]. Studies that examined pesticide effects on the mycorrhizal symbiosis indicated that they could stimulate, damage, or have no impact on AMF. Pesticides can

equally affect plant growth and nodulation by rhizobia at different stages of plant growth, being dependent on pesticide type, plant species, and their compatibility [8].

Arbuscular mycorrhizal (AM) symbioses are ubiquitous between certain root-inhabiting fungi of the Glomeromycotina, and the vast majority of terrestrial plants, including the large majority of crops. AM symbioses occur in most natural ecosystems and are also a prominent part of agroecosystems. They provide essential ecosystem services such as soil fertility regulation and provisioning of plant products (food, fodder, wood, and firewood) [9–12]. In the last years (2000–2023), an increasing number of peer-reviewed journal papers regarding the interaction of AMF and pesticides have been published (Table 1). In this review, we focus on the direct and indirect impacts of both synthetic and natural (or ‘green’) pesticides on arbuscular mycorrhizas, following earlier reviews [8,9,13,14]. We address both ‘classical’ pesticides and novel, natural (‘green’) pesticides [15], evaluate the effects of genetically modified plants with biocidal action (Bt crops) [16] or chitinase overexpression, and the indirect effects of pesticides on AMF through changes that these pesticides effect on plants, weeds, and other soil biota; for instance after the use of genetically modified crops that harbor genes for herbicide resistance [17]. Systematic reviews on AMF and pesticides are not only needed to summarize existing data but especially to improve current hypotheses, for instance on hormetic effects induced by low doses of pesticides [18], and direct future research, for instance towards indirect fungicide addition to soils through the application of antifungal medicines in wastewater [19]. We compile here, based on selected papers included in the SCOPUS DATABASE, significant reports on the topic. Further development of standardized protocols to assess the toxicity effects of pesticides on AMF is also discussed [20,21].

Table 1. Journal articles, published between 2000 and 2023, dealing with AMF and pesticides, based on a Scopus search, 25 April 2023.

Key Words	Number of Journal Articles
Mycorrhiza * + pesticide *	315
AMF + pesticide *	232
AMF + fungicide *	226
AMF + herbicide *	122
AMF + insecticide *	42
AMF + nematocide *	24
Mycorrhiza * + nanopesticide *	2

* = AND related words.

2. Synthetic Pesticides

More than approximately 10,000 species of fungi, bacteria, and viruses cause plant diseases. Several of these are of major economic importance and are controlled mainly by spraying crops with a vast amount of synthetic chemical pesticides. Next to these microbes, several animal groups (nematodes and arthropods) are major pests in crop production, and nematocides and insecticides are regularly applied as well. Crop yield could be further reduced by weeds for which herbicides are used. An alternative would be to manage AMF in agroecosystems as there are many reports that AMF makes a major contribution to pathogen and pest protection and can also reduce weeds. This topic will not be further discussed, and we refer to the pertinent reviews that discuss this topic [22–28].

Whereas the specific modes of action of pesticides differ, their effects on AMF can be summarized in Figure 1. Impacts of pesticides, whether negative, neutral, or positive, can be expressed through spore germination, extraradical growth towards and subsequent colonization of roots, and intraradical growth of AMF. Impacts can often be assessed through changes in the P uptake of the mycorrhizal plant. As different species of AMF differ in their sensitivity, pesticide application can shift competitive relations between species, hence resulting in shifts in AMF communities. Changes in AMF communities can also be caused by changes in other microbiota.

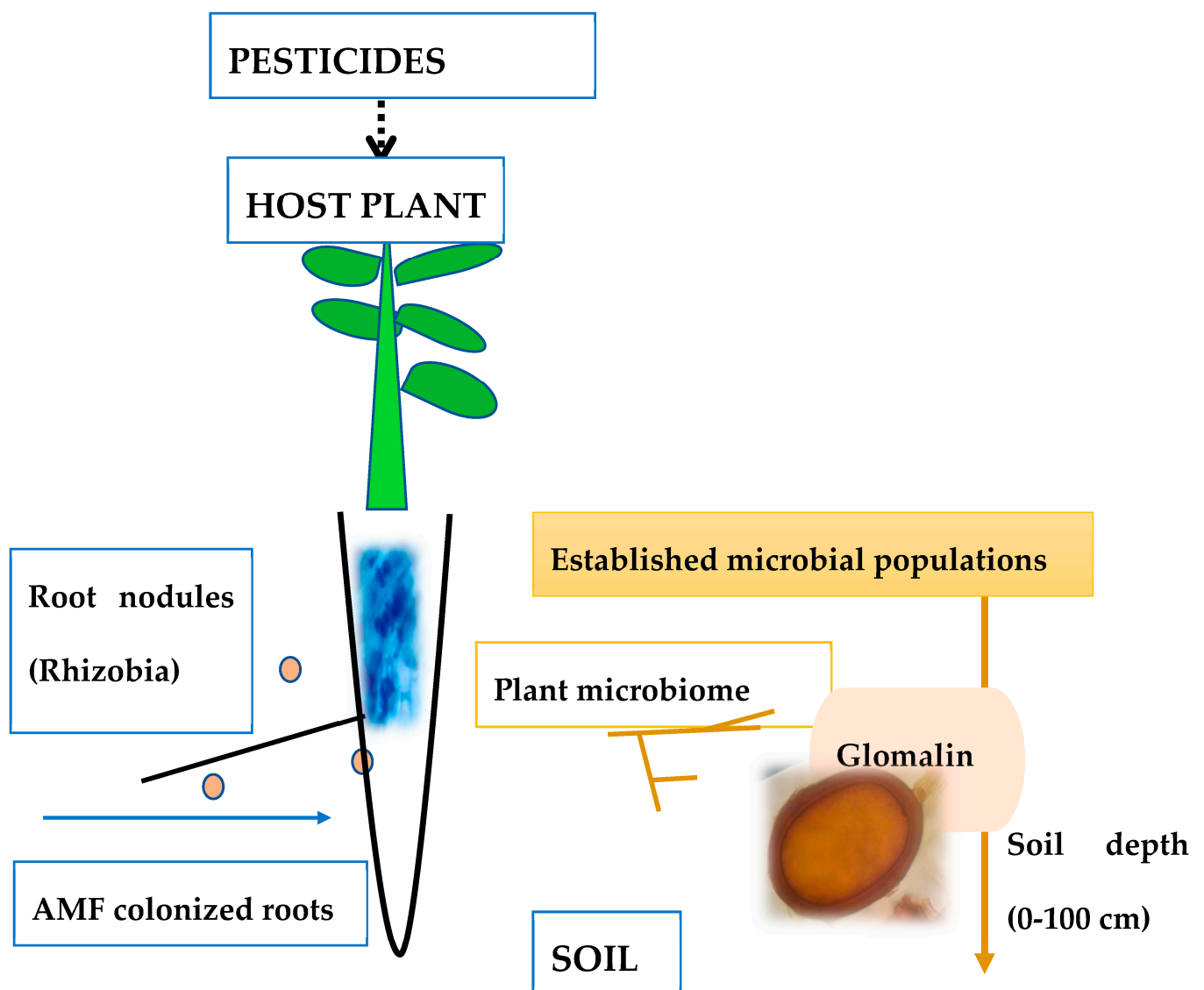


Figure 1. Arbuscular mycorrhizal fungal symbiosis as affected by pesticides, through either direct or indirect interactions. The different plant–soil compartments are indicated. AMF spores (dots and image).

2.1. Fungicides

It comes as no surprise that AMF could be negatively affected by fungicides. Some fungicides target specific groups of fungi (e.g., Ascomycota, to which most fungal pathogens belong) and, for that reason, there is a differential sensitivity of AMF to fungicides, which then explains why negative, neutral, and positive effects of fungicides have been reported. However, some fungicides such as thiazoles (benomyl and carbendazim) have a strong negative effect on Glomeromycota, the fungal phylum to which AMF belongs. For that reason, benomyl has even been used to suppress AMF activity in the field [29–32]. Results are not always very consistent. Marshall et al. [33] noted that benomyl application in a field experiment reduced root colonization but did not affect AMF biomass as assessed through its specific NLFA marker. Pedersen and Sylvia [34] showed that benomyl reduced AMF colonization under greenhouse conditions but not under field conditions, and attributed this to groundcover prevention of penetration to the soil surface, or to the timing of application relative to AMF development. Benomyl might reduce the diversity and abundance of saprotrophic soil fungi as well, negatively impacting decomposition and nutrient mineralization. It has since been prohibited. In 2008, a new fungicide: Topsin

M (or topsin) was reported as an alternative fungicide for use in ecological research that involves AMF suppression [35].

The effects of fungicides furthermore depend on the dose applied and the interactions of the fungicide with the soil matrix (its adsorption to organic matter or its solubility in the soil solution). Low doses of certain fungicides may actually even have a beneficial effect. Such positive effects of intrinsically toxic compounds, when applied at low doses, have been described by the term hormesis. However, mechanistic explanations for hormesis have rarely been tested. Hormesis by AMF was described by Jakobsen et al. [18]. The authors studied low doses of carbendazim and mancozeb applied to pea (*Pisum sativum*) plants in association with three different AMF species (*Claroideoglomus claroideum*, *Funneliformis mosseae*, and *F. caledonium*). Both fungicides generated unimodal response curves, where low doses were stimulated and high doses were suppressed for fractional root colonization and hyphal phosphorus (P) uptake. In contrast, the length of the extraradical mycelium did not respond to or decreased with increasing doses of the fungicides. Their study was the first to report hormesis in response to fungicides in AMF and contrasts with two earlier studies that reported linear (negative) responses to increasing doses [36,37]. It is currently unknown what caused the differences in the response curves, as these studies were executed with different fungicides, test plants, and AMF. The agronomically relevant conclusion from this study [18] is that extrapolation of toxicity from one dose only, based on the assumption of linear responses to a stressor, is likely not warranted. The study did not show strong differences in the responses by the three different AMF species, similar to an earlier greenhouse study by Kling and Jakobsen [37] with *C. claroideum*, *Rhizophagus intraradices*, and *R. inovermaius*, also in association with pea. In that latter study, there were only marked interspecific differences in the production of succinate dehydrogenase and P transport after the application of propiconazole and carbendazim. Other studies reported marked differences between AMF species. Carrenho et al. [38] reported changes in AMF diversity as influenced by fungicide treatments on citrus plants in São Paulo state, Brazil. *Gigaspora ramisporophora*, *Cetranspora gilmorei*, and *Glomus macrocarpum* were less sensitive to fosetyl and metalaxyl than other species in their study. Fungal species-specific effects of fungicides, (benomyl, pentachloronitrobenzene, and captan) were observed in colonized pea roots with three different AMF species, *Claroideoglomus etunicatum*, *F. mosseae*, and *Gigaspora rosea* [39].

Positive effects from fungicide application could either result from a direct positive effect on the fungus, as in [18] where γ -irradiated soil was used, hence in the absence of competition of saprotrophic and biotrophic microbiota, or from increased competitive ability due to control of pathogens or supply of nutrients, as in many field studies. The wide variation in AMF responses to fungicides has prompted research into underlying mechanisms. Jin et al. [40] noted that systemic fungicides had a significant negative impact, whereas contact fungicides had only minimal effects. These results could not be confirmed in a later study [41] where two systemic fungicides had significantly different impacts on AMF.

Most research on systemic fungicides (carbendazim and/or copper-based agents, such as copper-hydroxide), presented negative effects on AMF [42]. Other fungicides such as metalaxyl, and biological agents, can stimulate root colonization by *Glomus* spp. [43]. An analysis of 25 fungicides on leek (*Allium porrum*) demonstrated that those containing prochloraz, mancozeb, iprodione, and tetramethylthiuram disulphide, as well as fenarimole and miclobutanil, can eliminate or inhibit mycorrhizal colonization differently from fungicides containing chinazol, copper oxychloride, propamocarb or fosetyl aluminium, ciprodinyl + fludioxonil, fenhexamide, dimetomorph + folpet, and azoxystrobin [44]. In a greenhouse experiment in Brazil, Campos et al. [45] proposed to use AMF as bioindicators to select less harmful fungicides to control diseases in the common bean (*Phaseolus vulgaris*), which is important in the Brazilian diet. Their study suggested the choice of the following pesticides: azoxystrobin, tebuconazol + trifloxystrobin, and trifloxystrobin because these did not reduce the benefits of AMF root colonization.

Recently, Sallach et al. [19] noted an emerging issue of fungicides that are used in human medicine. These antifungal compounds, such as azoles, can end up in wastewater; if such water resources are used for irrigation, these fungicides can enter agricultural production systems. They observed reduced P uptake by mycorrhizal wheat (*Triticum aestivum*) in soils that were contaminated by wastewater containing these antifungal compounds. Considering the large and increasing number of pharmaceuticals with antifungal properties that end up in the environment, this issue demands more dedicated studies.

2.2. Herbicides

Herbicides are designed to eradicate agricultural weeds. As many crops are now genetically altered for herbicide resistance, the ecological impact of such GM crops and their associated practices demands special discussion, because herbicide applications with GM crops could be different from that with non-GM plants in terms of timing and/or number of applications. Herbicide effects on soil biota have received little attention as most of the efforts so far have focused on aboveground management [46]. Since AMFs are obligate autotrophs, it is evident that the effect of herbicides, as directly mediated by the host plant on AMF, is negative. Sublethal doses may not kill the plant but reduce photosynthetic rates to the extent that this symbiosis is impaired. Such cases will not be discussed here.

In this review, we are mostly concerned with indirect effects. Indirect effects occur if an herbicide-resistant plant, whose photosynthesis is not impaired, still shows an impact of the herbicide treatment on AMF; if some unwanted plants (weeds) are eliminated with herbicides but not the desired crop, it still suffers from the herbicide application; if the herbicide enters the soil ecosystem, it has a direct impact on AMF. A special case is the use of EPSPS (5-enolpyruvyl-shikimate-3-phosphate synthase) transgenic plants that are resistant against glyphosate. Fields in which glyphosate-resistant crops are sown can be sprayed with the herbicide more frequently or in higher doses. The effects of this application on AMF can be tested. The question is also relevant whether the insertion of that gene for glyphosate resistance in plants impairs (or improves) the molecular dialogue between plants and AMF and thereby impairs the establishment of a functional AMF symbiosis, and whether the increased application of glyphosate to fields with such GM crops can have an impact on AMF.

Commonly used herbicides are glyphosate, oxyfluorfen, and paraquat. More than half of the studies published so far examined the effects of glyphosate on arbuscular mycorrhiza. The herbicide oxyfluorfen was reported to have either negative or neutral effects on mycorrhiza. Baumgartner et al. [47] tested the impacts of weed control and cover crop treatments on AMF in a California vineyard. They found that differences in colonization among weed-control treatments may be due to differences in AMF species composition among dominant weed species rather than the herbicides themselves. A study of the influence of different management practices (including oxyfluorfen application) on AMF species composition in a semiarid Mediterranean olive orchard found that the addition of herbicides resulted in the lowest AMF diversity [48], though the impacts on mycorrhizal colonization and plant growth were unclear. Another study found that the combination of sulfentrazone, oxyfluorfen, and isoxaflutole reduced root AMF colonization and the potential solubilization of inorganic phosphate in clay soils cultivated with *Eucalyptus* spp. [49]. Oxyfluorfen appears to affect AMF differently depending on the species of plant and fungus, soil type, and timing of application. Paraquat application also showed variable results for potentially similar reasons. A long-term study of the effects of different management practices (including no-till with phenmedipham and paraquat application) on citrus orchards in Wuhan, China, found the lowest overall spore numbers in plots with herbicide applied, though there was significant variation between the different types of orchards [50,51]. Ramos-Zapata et al. [52] found the lowest AMF colonization for herbicide treatment in a long-term cover crop and weed-control experiment. Paraquat application resulted in weed communities dominated by resistant species such as *Parthenium hysterophoro-*

rus. Another study found that chemical control of weeds with paraquat and glyphosate prior to sowing enhanced early AMF colonization for wheat roots. However, the type of herbicide had no effect on wheat AMF colonization [53]. Sulfentrazone was reported to have a strong negative effect (a reduction of about 50%) on mycorrhizal colonization of soybean (*Glycine max*) by Vieira et al. [54]. Karpouzas et al. [55] evaluated the effects of nicosulfuron (a new low-dose, high-potency herbicide of the sulfonylureas group of herbicides) on the abundance and diversity of AMF in pot and field experiments. This herbicide inhibits the acetolactate synthase in plants and microbes. Their results showed a reduction in AMF colonization and richness only when repeatedly applied at dose rates $\times 100$ higher than the recommended dose. They observed that some AMFs (such as *C. etunicatum*) were not affected by the herbicide. Extraradical mycelium length decreased by the application of the herbicides dicamba and glufosinolate. In addition, a decrease in spore production was observed with the application of dicamba [56].

The most commonly used herbicide is currently glyphosate (commercially known as RoundUp). Glyphosate is applied both directly to fields (and from which it can drift to neighboring fields) and to crops. Its use is likely to increase now that genetically modified crops (maize, soybean, cotton, canola) that have entered the market contain a gene that makes such plants insensitive to glyphosate. The consequences could be increased use of glyphosate as a form of weed management, especially under no-tillage or conservation agriculture [17]. This has already resulted in glyphosate resistance in weeds, with 48 weed species having already been recorded as possessing glyphosate resistance [4].

Glyphosate has been considered a relatively beneficial foliar-acting herbicide as it is supposedly rapidly degraded in soil and has low toxicity to vertebrates [57,58]. However, a report by the International Agency for Research on Cancer [59] classified glyphosate as potentially carcinogenic to humans. That suggestion was opposed by other agencies. While glyphosate effects on soil biota have been widely studied, no consistent pattern with regard to its effects on AMF has been observed, such as reducing spore production and root colonization [14]. Studies by Zaller et al. with a more complex design involving both AMF and earthworms, showed significant negative effects of glyphosate on root colonization, suggesting that further trophic interactions do matter for risk assessment [60]. This effect only occurred in longer-term studies, as two weeks after foliar application of glyphosate there were only minor effects [61].

Reis et al. [62] studied the application of glyphosate (in single or sequential applications; partly in combination with other herbicides: endosulfan and tebuconazole) on mycorrhizal colonization in soybeans. They observed no glyphosate effects on root colonization, both when the other pesticides were applied or not. In contrast, the combination of endosulfan and tebuconazole significantly increased root colonization. Leaf P levels were not significantly affected by glyphosate, by the combination of endosulfan and tebuconazole, and by the combination of the three pesticides. Nodulation and leaf N concentration were equally unaffected by the glyphosate treatments. Shen et al. [63] investigated wheat-based production systems in the Canadian prairie for two years. They noted that glyphosate changed the species composition of AMF in continuous durum wheat during one of two years, with *F. mosseae* increasing and another *Glomus* species decreasing under the influence of glyphosate. Total species richness (which was very low in these fields, <2 species on average) was not affected by glyphosate. Root colonization was also unaffected by glyphosate. They also noted that tillage reduced the effects of glyphosate on the soil microbial community somewhat, likely due to increased glyphosate adsorption to soil.

Wilkes et al. [64] and Druille et al. [65] investigated the impact of glyphosate on the spore viability of AMF and root colonization of grassland plants located in the Flooding Pampa region in Argentina. Spore viability in the control soils was 6–8 times higher than in the glyphosate-treated soils (at doses equal to or lower than the recommended dose). As a consequence of lower spore viability, root colonization of *Lolium multiflorum* was also reduced after glyphosate treatments. Arbuscular colonization was significantly lower,

whereas there was no significant effect on vesicular colonization, suggesting a reduction in the functionality of the symbiosis [65].

Savin et al. [66] studied the effect of glyphosate application on GM (glyphosate-resistant) maize (*Zea mays*), cotton (*Gossypium hirsutum*), and soybean. In nonpasteurized soils, glyphosate did not change fractional root colonization of the three plant species compared to the control. In pasteurized soils, effects were plant-species specific: no effect on soybean, a weak positive effect on cotton, and a negative effect on maize. Differences in root colonization did not translate into differences in plant biomass or shoot P mass fractions. The difference between pasteurized and nonpasteurized soils may suggest substantial resilience of the mycorrhizal inoculum in the field, with some (small) increases in risks for glyphosate effects on AMF if agricultural practices bring mycorrhizal inoculum potential to low levels.

More detailed studies are available for these individual transgenic crops. For maize, Hart et al. [67] demonstrated that neither crop (glyphosate-resistant maize or wildtype) nor treatment (with or without glyphosate) had a negative impact on fungal communities (including, almost certainly, mycorrhizal fungal communities, although this was not investigated separately). For cotton, Knox et al. [68] demonstrated no effect of GM crops, compared to glyphosate-sensitive cotton, with regard to AM colonization, indicating that the GM trait itself did not impact the mycorrhizal symbiosis. In addition, when this resistance was stacked upon GM cotton that produced the Bt toxin, no negative effect was noted. The effect of a glyphosate addition was not tested, however. Maly et al. [69] were the first to study the effect of glyphosate on mycorrhizal GM soybeans in Brazil. They noted a negative effect of glyphosate on spore germination of three species of AMF, with *C. etunicatum* being the most sensitive, followed by *Dentiscutata heterogama* and *Gigaspora margarita*. The physiological basis for differential sensitivity was not investigated. Growth of the germinated spores on agar followed the same pattern. Despite this sensitivity, soil application of glyphosate did not reduce mycorrhizal root colonization of soybean. In a study in North America with six genetically modified soybean cultivars with glyphosate resistance, Powell et al. [70] noted variation in mycorrhizal root colonization between cultivars but no significant effect of transgenic plants. They did not compare GM and non-GM plants but only studied the impact of glyphosate on GM soybean. They noted no impact of glyphosate on total mycorrhizal colonization or arbuscular colonization by *R. intraradices*, regardless of glyphosate dose or time elapsed since application. Their results are similar to those of an earlier study by Mujica et al. [71] who found increased shoot dry mass of AM soybean treated with low doses of herbicides when grown together with *Sorghum halepense*, but not when grown alone, additionally suggesting nutrient transfer from weeds to soybean mediated by AMF. These results suggest a lack of direct negative effects of glyphosate on the arbuscular mycorrhizal symbiosis. Consistent with this suggestion, P uptake was also not changed under the influence of glyphosate. Finally, the authors noted that there was a positive interaction between AMF and rhizobia in enhancing the performance of GM soybean in the presence of glyphosate.

Watrud et al. [17] studied the impact of glyphosate drift on constructed roadside plant communities. They hypothesized that transgenic canola (*Brassica napus*) would increase due to glyphosate drift and that this effect would cascade into lower inoculum levels of AMF and subsequent lower colonization of mycorrhizal legumes such as crimson clover (*Trifolium incarnatum*). They concluded that glyphosate drift indeed results in lower root colonization of crimson clover by AMF (from 44% to 14%) and lower biomass (a reduction of around 50%) of the clover, and suggested that glyphosate drift can result in changes in plant communities (with weedy *Brassica* species that have the resistance gene to glyphosate introgressed from canola) resulting in increasing dominance of nonmycorrhizal *Brassica* species to the detriment of mycorrhizal plants. They also suggested that the effects observed were not due to a direct toxic effect of glyphosate on AMF but the result of the increase in the nonmycorrhizal *Brassica* species that reduced mycorrhizal inoculum levels as Brassicaceae are not hosts to AMF [72,73].

It is important to dwell on more agroecosystemic effects of the glyphosate resistance of crops. Roundup-ready crops may be subjected to more intensive application of glyphosate for weed control, especially in the context of conservation or no-tillage agriculture [74–76]. It, therefore, demands scrutiny of how such changes in agricultural practices could impact AMF communities. Overuse has already led to the evolution of herbicide resistance of surrounding weeds, with 48 weeds currently being glyphosate-resistant [4]. The evolution of glyphosate resistance in weeds could lead to lowered mycorrhizal inoculum potential. From the list compiled by Baek et al. [4] species (17%) are nonmycorrhizal and several other species, which form arbuscular mycorrhiza, are often poorly colonized, and could, therefore, equally reduce mycorrhizal inoculum potential.

Glyphosate is decomposed and during decomposition releases P; thus, it may serve as a P source for some microorganisms. However, whether this nutrient release might be related to some effects or whether quantities are too low is unknown [77].

On the internet, there are compilations about the compatibility between herbicides and AMF [78]. The site states that glyphosate is compatible and oxyfluorfen incompatible, whereas the effects of paraquat and simazine are variable. A study by Baumgartner et al. [47] compared different modes of action of herbicides. They concluded that pre-emergence treatments (oxyfluorfen and simazine) resulted in an increase in nonmycorrhizal weeds, especially *Cyperus esculentus*, whereas postemergence treatments (glyphosate) resulted in an increase in mycorrhizal weeds (*Sonchus oleraceus* and *Conyza canadensis*). The increase in mycorrhizal weeds did not result in impacts on the AMF community on the roots of the grapevine (*Vitis vinifera*) [47]. These results may either indicate the insensitivity of the AMF to the herbicides or indicate that the AMF species of weeds and grapevines were different and that a lack of mycorrhizal connections between weeds and grapevines explains lack of herbicide treatment effects despite changing the weed community towards mycorrhizal or nonmycorrhizal weeds. Cover crops in the dormant season did not equally mediate any effect on the AMF fungal assemblage or root colonization of the grapevine. Recent reports also compared the effects of different doses of two types of herbicides, alachlor (soil-acting herbicide) and glyphosate on *F. mosseae* associated with the peanut (*Arachis hypogaea*) [79]. They found that plant growth was significantly reduced with alachlor but was unaffected by glyphosate. Moreover, they observed increased P influx into roots and increased P concentration in shoots after glyphosate treatment, consistent with suggestions that glyphosate might add P to the soil system.

Finally, we refer to a curious (and potentially ecologically relevant) result of a study by Schwab et al. [79], who noted that simazine application on *Chenopodium quinoa*, generally considered a nonmycorrhizal plant, induced the plant to form arbuscular mycorrhizas. They observed functional arbuscules, vesicles, and spores in the cortex of roots, in spite of the reduced plant growth. Whereas mycorrhiza formation in some species of the Chenopodiaceae and Brassicaceae has been observed, the mycorrhizal symbiosis is almost certainly not functional as no arbuscules are formed or they are not present in all growth stages [73]. Unfortunately, the data collected until now do not allow for evaluating the implications of the hypothesis of induction of plants by herbicides to form arbuscular mycorrhiza.

The AMF sensitivity to chemical pesticides in field conditions is weakly understood, and only recently explored in ecotoxicology protocols [20], which evaluated the effects of different concentrations of glyphosate and diuron + paraquat on the germination of spores of *Gigaspora albida* and *Rhizophagus clarus* in tropical artificial soils.

2.3. Insecticides and Nematicides

As Table 1 indicates, studies on the impacts of insecticides and nematicides on AMF lag far behind those on the impacts of fungicides and herbicides. Earlier reviews concluded that insecticides and nematicides showed no negative or fairly beneficial effects on AMF [13,28]. However, here, as in the case of fungicides, differential effects of systemic and contact insecticides were reported [80,81]. The insecticide/acaricide ‘Phoxim’ was found to inhibit AM colonization in carrot (*Daucus carota*) but not in green onion (*Allium*

fistulosum) [50,51]. The nematicide aldicarb did not affect mycorrhizal colonization on potato (*Solanum tuberosum*) [82].

Nowadays, neonicotinoid insecticides are the most used group worldwide, due to their wide spectrum of action on countless pests of different crops. Their ecosystem effects have been reviewed elsewhere. Neonicotinoids are widely used in different cultures. Their very significant negative effects on the diversity of insects (including negative implications for ecosystem services such as pollination) have attracted wide attention [83,84]. Studies on the impacts of neonicotinoids on AMF are in their infancy. Malfatti et al. [84] tested two neonicotinoids, imidacloprid and thiamethoxam, on the spore germination of two species of AMF, *R. clarus* and *G. albida*. Spore germination was significantly reduced by both neonicotinoids in a dose-dependent manner. The study concluded that reduced spore germination might ultimately impact the functioning of AM symbiosis and therefore recommended further studies.

2.4. Interactions between Pesticides

Almost all studies on the impact of pesticides on AMF addressed single pesticide effects in isolation. Combinations of pesticides have only been seldom investigated and, therefore, the potential for additive or interactive (positively or negatively synergistic) cannot yet be properly evaluated. We found only four studies where combinations of pesticides were tested [62,85]. In the study by Menge et al. [85] Sudan grass (*Sorghum bicolor*) seedlings received a combination of three pesticides (one nematicide and two fungicides). The nematicide and one of the fungicides resulted in higher root colonization than the untreated control, whereas the other fungicide resulted in a very significant decline in root colonization. The combination of the three pesticides resulted in equally low colonization as that of the toxic fungicide. Parvathi et al. [86] tested one fungicide and three insecticides on mycorrhizal colonization by *F. mosseae* in groundnut. The fungicide (benomyl) had a strong negative effect on root colonization, whereas the effect of the insecticides was variable. A combination of two insecticides, both of which had minor effects, resulted in a strong decrease in colonization, providing evidence for negative synergistic effects. In contrast to those findings, Reis et al. [63], who tested a combination of a fungicide, an insecticide, and an herbicide, showed that the combination increased mycorrhizal colonization compared to the herbicide-only treatment. A mechanistic explanation was not provided for this effect. In France, Rivera-Becerril et al. [87] assessed the ecotoxicological impact of a cocktail of three commonly used agricultural pesticides (two fungicides and one insecticide) on the abundance and composition of the AMF community in vineyards and arable soils. They noted a limited negative effect on AMF abundance but shifts in species composition. As they did not assess the effects of each pesticide separately, the issue of possible synergistic effects could not be addressed. Clearly, further studies are desirable to test the effects of cocktails of pesticides, more so as many soils, there were previously under conventional agricultural management and may harbor a large number of pesticide residues [2]. Combinations of fungicides have been used in the study by Edlinger et al. [88], however, the paper did not allow evaluation of which pesticides have been used. Their study, with cropland soils from 150 sites across a gradient across Europe of 3,000 km, showed that AMF-driven P uptake was reduced by 43% with repeated applications of fungicides.

3. Biological ('Green') Pesticides [89]

In cases where pest or pathogen damage exceeds acceptable or tolerable levels, organic farmers have to take recourse to pesticides of biological origin. It is often assumed that such pesticides can be quickly degraded in the soil matrix and that therefore their effects are of short duration, at least much shorter than those of synthetic pesticides. Consequently, biological pesticides are considered low risk for the environment [90,91]. Azadirachtin acts mainly as an antifeedant and/or insect growth controller at low concentrations (0.05–5 ppm) and a contact poison at concentrations greater than 50 ppm [90]. Fungicidal properties

at all these concentrations have been reported as well [90]. However, their impacts on mycorrhizal fungi have been rarely studied.

Ipsilantis et al. [15] evaluated the effects of four biological pesticides (spinosad, pyrethrum, azadirachtin, and terpenes) on AMF and compared those with a control of carbendazim, a synthetic fungicide (a conversion product of benomyl), with well-known strong negative impacts on AMF. They assessed the impacts of these pesticides on root colonization by AMF, both in pot and field experiments. They also assessed impacts on the composition of the AMF assemblage and on the plant performance of pepper (*Capsicum annuum*). Plant growth was reduced in the presence of carbendazim and azadirachtin but not by the other biological pesticides. Mycorrhizal colonization in pots was completely reduced by carbendazim (see above) and significantly reduced by spinosad and pyrethrum. In the field experiment, the effects were completely different, however. No pesticide (including carbendazim) reduced root colonization, whereas spinosad, pyrethrum, and terpenes increased root colonization. These differences between pot and field experiments are unexplained but raise questions about the design of experiments aimed at assessing the effects of biopesticides on mycorrhizal symbioses. Assessment of the AMF assemblages showed some effects of the pesticides, but no consistent pattern that linked fungal species composition, root colonization, and plant performance was established. The authors concluded that three out of four biological pesticides, applied at realistic doses, seem to have no negative impact on AMF and that their use is therefore compatible with management that tries to conserve soil biological diversity in organic systems. However, azadirachtin seemed to have negative effects on plant performance, root colonization in the field, and the composition of the species assemblage, and these effects were likely even more persistent than those of carbendazim. As azadirachtin, a naturally occurring phytochemical from the neem tree (*Azadirachta indica*) is the most common aspirant to substitute some synthetic chemicals for the control of insect pests [92,93], the issue of toxicity of neem extracts to AMF needs to be addressed.

Earlier studies had indicated only minor, short-term negative effects of azadirachtin on AMF [94,95]. Neem extracts (azadirachtin in acetone or methanol) were toxic but the toxicity effects were short lasting and significantly less than those of several pesticides. The lower toxicity for azadirachtin in ethanol and propanol suggests that the specific way of applying these biopesticides does count. The IC_{50} values were around 200–500 times lower than for glyphosate, and 8000–40,000 lower than for benomyl, well-known for its strong potential to suppress AMF.

4. Nanopesticides and AMF

Nanopesticides have been defined as nanostructures (with a diameter of up to 200 nm) that carry pesticides [96,97]. Due to their very small size, these nanopesticides, which could be herbicides, fungicides, insecticides, etc., allow better contact with the pest organism. Its stability permits the slow release of the pesticide to improve pest-control management. Nanopesticides combined with smart delivery systems that blend with soil particles can decrease the advance of resistant weeds. Targeted use of nanoherbicides is potentially useful in effective weed control programs but could also exhibit risks, similar to other risks on nanoparticles for AMF [98].

Only a few studies have been published on nanopesticides and AMF (Table 1). Simonin et al. [99] investigated the effects of the $Cu(OH)_2$ nanopesticide Kocide 3000 in a field experiment under three levels of mineral fertilization, thereby simulating both conventional and low-input agriculture. They reported no negative effects on AMF, nor on N_2 -fixing rhizobia. They also reported reduced soil enzyme activities, especially in the treatment that mimicked low-input agriculture. They concluded that the use of this Kocide nanoparticle had no negative effects on soil microbiota (nor on plant production) under high-input, conventional agriculture. However, in the context of low-input agriculture, for which this nanoparticle is approved, applications might have some unintended negative effects, notable for enzymes involved in P cycling. Such outcomes are consistent with observations

that nanoparticles of TiO₂ negatively impacted AMF [100]; and with a suggestion that nanoparticles could be a threat to mycorrhizal and rhizobial symbioses [101]. There is a clear need for more ecotoxicological and biosafety studies on the interactions between nanoagrochemicals, including nanopesticides, and soil biota.

5. Mycorrhiza and Genetically Modified Crops

Miller [102] was the first author to raise the issue of whether genetically modified (GM) crops (especially when their modification relates to traits that confer resistance to pesticides such as glyphosate; or to traits that allow plants to constitutively express biocides such as the fungicidal chitinases or the insecticidal Cry proteins) could generate ecological effects. Several authors [103–105] have provided reviews of this topic, and for that reason, only a small part of these studies is summarized here, viz., where the GM plants directly express the production of an insecticide (Bt crops) or fungicide (chitinase overproducers). The effect of GM crops that are glyphosate resistant has been discussed above in the section on herbicides. Justification for our restriction to those two classes can be found in the fact that a majority of all GM crops, in terms of area covered, are either Bt, glyphosate-resistant, or both.

5.1. Bt Crops

Many GM crops around the globe contain the gene for the *cry* 1AB endotoxin produced by the bacterium *Bacillus thuringiensis* (Bt). This toxin disturbs insect performance. Due to the biological (i.e., nonsynthetic) nature of the product, the toxin, and hence the plants that constitutively produce it, are considered environmentally friendly. One possible pathway through which Bt plants could show hampered mycorrhizal development or functioning is through the insertion of the Bt gene at places where it affects mycorrhiza-induced gene expression [106]. However, such effects have not been noted.

A review of the impact of Bt-plants (maize (*Zea mays*), cotton (*Gossypium* spp.), and other species) showed several instances of negative impacts on the AM symbiosis, suggesting that those effects can sometimes occur, even though most studies did not report significant changes. Mechanisms underlying reduced root colonization are currently unknown (Table 2). From this majority of studies without significant effects, several authors have suggested that the cultivation of Bt crops does not pose risks for AMF.

For maize, Castaldini et al. [107] showed negative impacts of Bt Corn on early events of the mycorrhizal establishment (the formation of functional entry points that subsequently develop arbuscules) and in root colonization (decrease of ~50% compared with nontransgenic plants). They did not find an effect of plant residues of GM maize on germination ability and hyphal growth of the mycelium of *F. mosseae*. Tan et al. [108] compared Bt and non-Bt maize and observed differences in AMF assemblages but also observed that these effects were smaller than differences between different non-Bt maize genotypes. Root colonization was also not different between Bt- and non-Bt maize, in agreement with most other studies. One problem with these studies should be finally noted. The extent to which the Cry gene was expressed in roots did not correlate with the degree of effects, so it remains impossible to establish a causal relation (rather than a coincidental correlation) between the gene and its impact on mycorrhizal fungi. Cheeke et al. [109] noted that Bt maize had lower levels of mycorrhizal colonization (specifically arbuscular colonization; there were no differences for hyphal, vesicular, or total colonization) compared to non-GM parental lines, suggesting a specific negative effect on symbiotic properties due to the decline in the ratio between arbuscules and vesicles, a ratio considered indicative for mycorrhizal benefit [110]. However, when the soil was pregrown with Bt maize or parental maize, the colonization of subsequently grown soybean remained similar. As this study used field inoculum (rather than commercial inoculum in more controlled experiments), the authors suggested that this outcome might be of higher ecological relevance compared to earlier studies. For cotton, Knox et al. [111] demonstrated that GM cotton, possessing both the gene for the Bt toxin and for glyphosate resistance, did not perform more poorly than GM

cotton which was only glyphosate resistant. Unfortunately, no comparison was made with non-GM variants of the species. There is a need to further test genetically modified plants, onto which different genes have been stacked after genetic modification, for the impact on soil microbial communities and especially the AM symbiosis.

Table 2. Effects on the arbuscular mycorrhizal symbiosis in Bt-plants.

Plant Species	Greenhouse/Field [†]	AMF Parameter Assessed	Effect	Reference
Aubergine	Sandwiched root system	Root colonization by <i>F. mosseae</i>	n.s.	[112]
	Sandwich system	Early stages of AMF life cycle		
Cotton	Field	Root colonization	n.s.	[111]
		Germination ability		
Cotton	Field	AMF communities	n.s.	[113]
Cotton	Sandwich system	Mycorrhizal colonization	negative	[114]
Cotton	Sandwich system	Mycorrhizal colonization	negative	[115]
Maize	Pot/greenhouse	AMF carry-over effects on soybean	n.s.	[110]
Maize	Field	Root colonization	n.s.	[116]
		Spore abundance		
Maize	Microcosms	Hyphal growth of presymbiotic mycelium of <i>F. mosseae</i>	negative	[103]
		Colonization by indigenous fungal propagules		
Maize	Field	AMF communities	n.s.	[117]
Maize	Field	AMF communities	n.s.	[118]
Maize	Field	AMF communities	n.s.	[119]
Soybean	Greenhouse	Root colonization	n.s.	[120]

[†] Growing conditions; n.s. = nonsignificant effect. MI50 = mycorrhizal infectivity of soils; negative = decreased fractional root colonization.

5.2. Chitinase Overexpression

A final type of GM crops that could impact AMF symbioses are those that constitutively overexpress chitinases. Chitinases break down the cell walls of all fungi (but the cell walls of *Phytophthora* and *Pythium* contain cellulose, as these organisms do not belong to the true Fungi). Chitinolytic activity through plant roots could, therefore, reduce fungal pathogen pressure in the rhizosphere. At that same time, they could have a negative impact on arbuscular mycorrhizal fungi. Only a few studies have been published in this regard [121–123]. The general outcome of these studies was that chitinase overexpressing plants did not have a negative impact on AMF.

6. Conclusions

In this review, the effect of substantial amounts of pesticides used in agricultural production (to control pests, diseases, weeds, etc.) to attain high product quality was discussed with regard to the AMF symbioses. In spite of the fact that various types of soil microorganisms are affected by pesticides, few reports on AMF and pesticides have been published. Many of these looked at relatively short-term effects under controlled conditions, and with the pesticides most often in isolation. However, in conventional management, more pesticides might be used simultaneously, necessitating research towards additive or even interactive effects of pesticides on AMF. Our knowledge of effects in the longer term under ecologically more meaningful conditions has equally been lagging behind. Many studies on pesticide effects investigated the direct effects of the pesticide on the abundance and species composition of AMF communities. However, it is also becoming clear that indirect effects should not be neglected. A clear example was provided by Lekberg et al. [124]. The authors studied the effect of the herbicide picloram on the invasive weed *Centaurea stoebe* (spotted knapweed). In greenhouse experiments, the herbicide killed spotted knapweed and reduced AMF, whereas it had no effect on the survival of *Elymus trachycaulis* (slender wheatgrass) nor on AMF. While these results suggest that the herbicide

could be effective in controlling the exotic weed and restoring the original prairie vegetation, field experiments indicated otherwise. In the field, picloram still killed spotted knapweed but it was then replaced by bulbous bluegrass (*Poa bulbosa*). As the latter plant is a much poorer host for AMF than spotted knapweed, a reduction in mycorrhizal inoculum potential resulted. This reduction in AMF inoculum then changed the vegetation composition in ways that could hamper restoration efforts. It might be hypothesized that a similar effect could occur with glyphosate resistance as several of the weeds listed as glyphosate resistant [4] seem relatively poor mycorrhizal hosts. The study by Watrud et al. [57] provides a further instance of the importance of indirect effects. In fact, such studies remind us of the double role that mycorrhizal weeds play in agroecosystems; they could boost common mycorrhizal networks but they could equally gain competitive dominance through their integration in such networks [125].

Another topic that deserves more attention in future research is the possibility that soils with an active AMF community are more effective in degrading organic pollutants. This ability of AMF, or rather AMF-associated hyphosphere and rhizosphere bacteria, has been demonstrated for several organic pollutants [126,127] and it is likely that it also extends to the degradation of organic pesticides. White et al. [128] noted that inoculation with AMF improved the remediation potential of zucchini (*Cucurbita pepo*) in soils spiked with (dichlorodiphenyldichloroethane (DDE), a primary metabolite of the insecticide dichlorodiphenyltrichloroethane (DDT). Therefore, pesticide toxicity might be alleviated by AMF either through enhanced degradation or through increased plant uptake and subsequent removal.

The large variation in response of AMF to various pesticides, as a function of their chemical nature, dose [18], soil conditions, timing of measurement, and plant and AMF species and communities investigated makes generalizations difficult. It is therefore understandable that there are pleas for standardization of tests to better assess risks. Such tests could be targeted at the direct effects of the mycorrhizal fungus, such as spore germination [20,84]. Usually conducted under standardized conditions, are extremely important. However, we should not forget these indirect risks under field conditions that cannot be captured by such standardized tests. Further developments in this field are necessary before AMF can be evaluated in a regulatory framework for the assessment of toxicities of synthetic and natural pesticides to AMF.

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