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The use of arbuscular mycorrhizal inoculum in viticulture is not always positive: a systematic review

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Summary

For more than 70 years, the scientific literature has demonstrated that arbuscular mycorrhizal fungi (AMF) have positive effects on plant growth and stress tolerance. However, AMF have only been widely implemented in agricultural systems in the last decade. Recent reviews indicate AMF are key to the sustainability of viticulture. To explore the universality of the positive effects of AMF inoculation on grapevines, we created a database of the results from 30 publications that performed 169 experiments comparing the development of grapevine plants inoculated with AMF against control vines. We calculated inoculation dependence, as ID = ((mean of inoculated treatment – mean of control)/mean of inoculated treatment) * 100), to compare the effects of AM inoculation on the growth of grapevine plants between different experiments. In most studies, the experimental conditions differed significantly from commercial conditions, since 75% of the studies were conducted under greenhouse conditions and 71.8% of studies compared the growth of inoculated plants with plants growing in a sterilized substrate. High variability was observed in the ID of different response variables, between the various rootstocks tested, and between different species compositions of AMF inoculum, demonstrating that the effects of mycorrhizal inoculation in vineyard growth are highly context dependent. This study demonstrates further research is required to characterize the effects of AMF under field conditions. Moreover, this work indicates that specific trials are needed to determine the effect of particular mycorrhizal strains on individual rootstocks under specific growing conditions before the use of AMF can be recommended to vine-growers

Keywords

Arbuscular mycorrhizal fungi, inoculation dependence, rootstock, viticulture.

Introduction

In order to meet the future needs of the growing human population—and at the same time minimize negative environmental impacts—it is necessary to maintain food production using new agricultural techniques that promote sustainable systems. The ecological intensification of agriculture, sometimes also called sustainable intensification, has been suggested as a strategy to maintain or increase production in low-input agricultural systems (Bender *et al.*, 2016). Ecological intensification systems aim to emulate natural systems by promoting high production in a self-sufficient manner. The edaphic microbiome is a key element of agricultural productivity and thus appears to represent an important natural capital for ecological intensification systems (Bender *et al.*, 2016). The use of bio-based fertilizers (biofertilizers) is considered one of the most promising routes for ecological intensification (Cataldo *et al.*, 2022). Among the different types of biofertilizers available, the mycorrhizal-forming fungi are unique due to their universality and because, together with their associated bacteria, they can potentially be managed to protect crops against abiotic and biotic stresses (Srivastava *et al.*, 2017).

Mycorrhizae, in particular arbuscular mycorrhizae (AM), are fungal-root symbionts present in the soils of practically all terrestrial ecosystems and have established symbiotic relationships with more than 200,000 cultivated and uncultivated plants (Parniske, 2008). AM symbiosis is formed by Glomeromycotina fungi, which colonize the root biotroph and extend mycelium outside the root system, forming a complex net. AM fungi (AMF) play a key role in moving water and mineral nutrients from the soil into plants in exchange for photosynthetic products (Allen, 2011). In addition to these nutritional benefits, AMF also provide other positive effects to the plant. AMF may confer higher tolerance to abiotic stresses, such as water stress or salinity, and biotic stresses, such as root diseases caused by necrotrophic pathogens, herbivorous arthropods, or nematodes (Basu *et al.*, 2018).

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The economic importance of vine producon worldwide (Organisaon Internaonale de la Vigne et du Vin [Oiv]., 2022) and the impact of climate change (CC) on its quality and producvity impose an imperav e to develop alternav e methods of management to promote sustainability in vicultur e in future scenarios. The use of AMF in vicultur e can provide signic ant benets, as AMF have been shown to improve the resistance of grapevines to abioc stresses (Massa *et al.*, 2020; Nicolás *et al.*, 2015; Nogales *et al.*, 2021) and bioc stresses (Bruisson *et al.*, 2016; Hao *et al.*, 2012). Thus, various researchers have proposed the use of AMF-based bioferliz ers in vicultur e as a soluon to mig ate the impacts of CC and as a strategy to improve the environmental sustainability of the crop (Trouvelot *et al.*, 2015; Popescu, 2016; Aguilera *et al.*, 2022). Many AMF-based ferliz ers are currently available on the market and the number of companies producing mycorrhizal fungal inocula has increased in the last decade (Basiru *et al.*, 2020). However, there is sll a lack of informaon on relevant aspects related to the establishment of symbiosis, such as the e ecv eness of colonizaon depending on the mycorrhizal species, rootstock, and environmental condions (Hart *et al.*, 2018; Rillig *et al.*, 2016; Aguilera *et al.*, 2022).

Therefore, we systemac ally analyzed the results reported in published research studies that compared the development of grapevine plants inoculated with AMF versus control vines. The objecv es of this work were to provide an overview of the potenal posiv e e ects of AMF inoculaon in vicul ture and also to determine if the exisng informaon enables idenc aon of the most e ecv e species of mycorrhizal fungi to improve vicultur e and the rootstocks that benet most from inoculaon.

Material and Methods

To build a database, searches of the Google Scholar database were conducted for arcles published between 1980 and 2019. The following keywords were used: mycorrhiza*, inocul*, vineyard*, rootstock*. The Boolean truncaon character '*' was used to ensure that all variaons of each word (for example, mycorrhizae, mycorrhizas, and mycorrhizal) were included in the searches. The bibliographic references of the arcles retrieved were manually searched to nd other related publicaons.

We only selected arcles that compared the addion of a mycorrhizal inoculum with a control treatment in vine plants. We excluded arcles that only analyzed the natural mycorrhizal colonizaon, focused on analysis of the e ects of AMF on disease resistance, with no control treatment, with no growth measurements, or that did not specify important informaon such as the growth condions. We included studies with an independent control treatment (i.e., control plants grown in a sterile substrate or under natural condions). Finally, we idened and extracted data from 30 publicaons (Table S1).

From each study, we collected data on plant performance with and without mycorrhizal inoculaon considering the growth condions (greenhouse, outdoor condions, or eld); the rootstocks used in the experiment; the species of AMF used as inocula; the response variables measured; and the signic ance (or not) of the stas c al test applied. If the scienc name of the AMF changed over me, or has a synonym, the most recent name was used. *Glomus intraradices* was changed to *Rhizophagus intraradices* (N.C.Schenck & G.S.Sm.) C.Walker & A.Schüßler, *Glomus mosseae* to *Funneliformis mosseae* (T.H.Nicolson & Gerd. C.Walker & A.Schüssler), and *Dentiscutata heterogama* (T.H.Nicolson & Gerd.) Sieverd., F.A.Souza & Oehl to *Scutellospora heterogama* (T.H.Nicolson & Gerd.) C.Walker & F.E.Sanders.

The most frequently assessed habitual plant response variables were total dry and fresh biomass, shoot dry and fresh weight, root dry and fresh weight, total number of leaves, and total leaf area. We considered shoot length, total height, and plant height as the same growth variable. For some experiments, we calculated the total weight as the sum of shoot weight and root weight.

Most of the publicaons revised include several experiments. We included the data for all experiments that compared inoculated vines against non-inoculated vines under the same condions. To compare the performance of control and inoculated plants, we extracted the mean values for biomass, plant size and other growth measures. We calculated and expressed the degree of plant change associated with AMF inoculaon using inoculaon dependency (ID), which was calculated using the same method as mycorrhizal dependency (Plenche e *et al.*, 1983) as follows:

$$ID\ (\%) = 100\ (X_i - X_n)/X_i,$$

where X_i is the mean value of the response variable of the mycorrhizal-inoculated plant and X_n is the mean value of the same response variable for the non-mycorrhizal-inoculated plant. We described the resulng data graphically using the *ggplot2* (Wickham, 2016) and *car* (Fox and Weisberg 2023) packages of R version 4.2.0 (R Core Team 2022) with RStudio interface (RStudio Team 2020).

Results

We idened a total of 30 eligible publicaons reporng 169 experiments (tesng di erent mycorrhiza and rootstock combinaons or di erent substrate condions or plant ages) in which more than one response variable was measured. The studies included 25 di erent rootstocks and 14 trials of ungra ed or self-rooted grapevine culv ars. Only the two most common species of mycorrhiza used in inocula, *Rhizophagus irregularis* and *Funneliformis mosseae*, were studied on the same rootstock measuring the same variables in more than three di erent experiments. The number of replicates used in the analyzed experiments was very variable, ranging from 3 to 45, with an average of 10.64. Among the experiments included in this review, 15.38% were performed under eld condions, 76.92% in greenhouses, and 7.69% in pots in an outdoor area.

We detected very di erent responses of the vines to AMF inoculaon. In fact, the ID was negav e in 13.9% of the comparisons between control and inoculated vines. Moreover, very heterogeneous posiv e responses (ID from 0 to 92.8) were also reported. For 28.93% of the comparisons, we could not determine if the e ect of the inoculaon was stas c ally signic ant since the arcle did not report stas c al analysis or stas c al analysis was reported for the global e ect of the inoculaon, but not for comparisons within the same rootstock or the same AMF species. From the experiments that reported stas c al analysis, 42.51% reported inoculaon had a signic ant e ect whereas 57.48% indicated no signic ant di erences between the control and treatment.

Most of the experiments measured di erent response variables and reported posiv e e ects for AMF inoculaon; however, the dispersion of the data varied (Fig. 1). Although all mean ID values were posiv e, all variables had negav e ID values in some experiments: the total leaf area was the variable with a negav e ID in the largest number of experiments (28.75%) and the total dry weight had a negav e ID in the lowest number of experiments (3.5%; Fig. 1A).

Similarly, when we focused on the most invesg ated rootstocks, high variability in the ID was observed depending on the variable measured or the species of mycorrhiza applied. For example, AMF inoculaon had posiv e e ects on the number of leaves but led to a negav e mean value for shoot length in the 1103 P rootstock (Fig. 1B). Moreover, the mean increase in fresh weight a er inoculaon was greater than the mean increase in dry weight for the 1103 P rootstock (Fig. 1B).

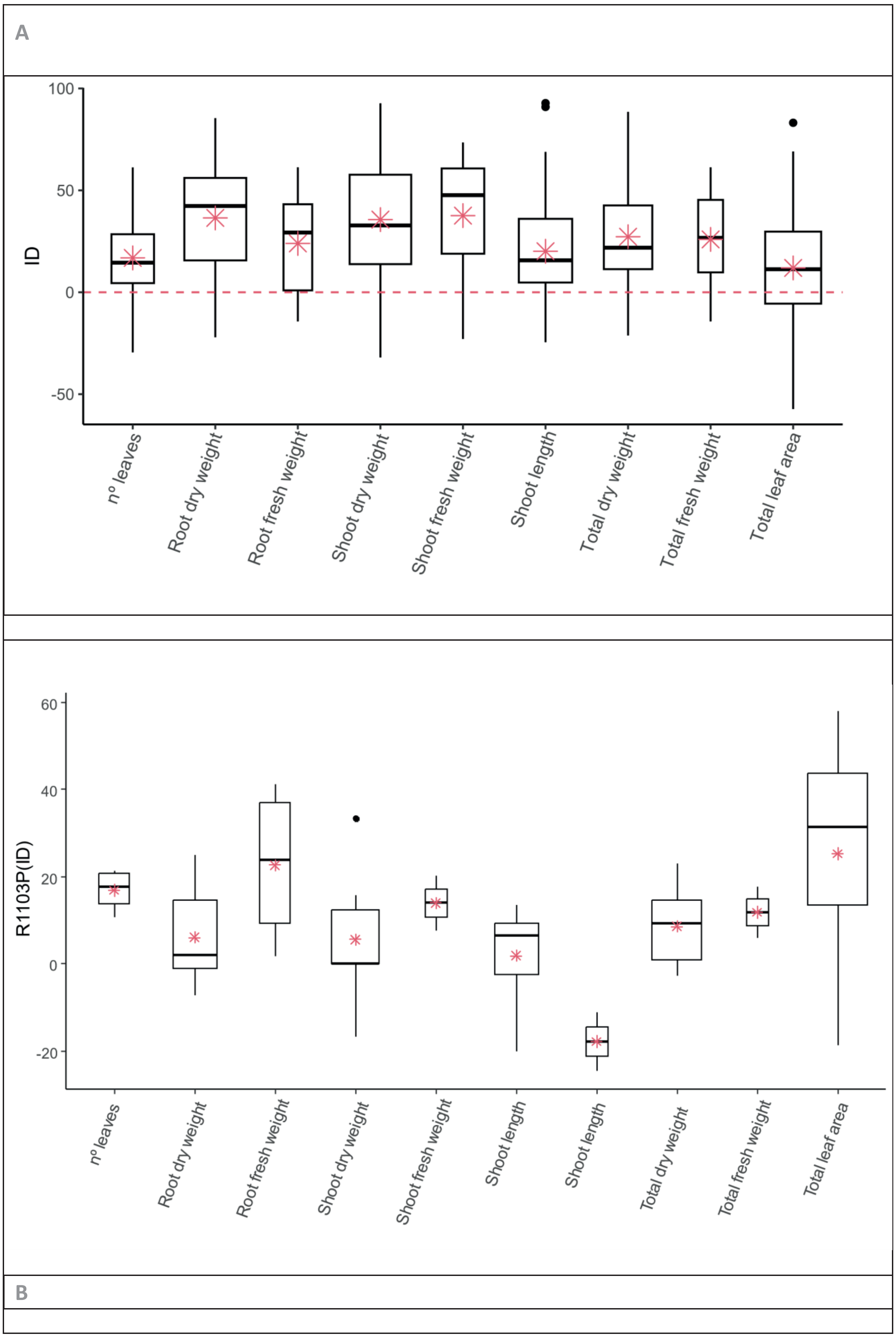

Figure 1. A. Degree of change in plant biomass, number of leaves (n), shoot length, and total leaf area change associated with inoculaon with arbuscular mycorrhiza fungi (AMF), expressed as inoculaon dependency (ID). B Degree of change in biomass associated with inocula on with arbuscular mycorrhiza fungi (AMF) expressed as inoculaon dependency (ID) for vines gra ed on '1103 Paulsen'. The boxes indicate the lower quar le and upper quarle, the whiskers indicate the minimum and maximum values. The width of the boxes is proporonal to the number of observaons for that variable. * Indicates the mean value, while the black line indicates the median.

In studies that only measured the shoot dry weight, variaons in ID were observed in several experiments conducted with the same rootstocks, such as 3309-C or FPS 93. AMF inoculaon had negav e e ects on the ID of plants gra ed on 110 Richter and 1103P rootstocks (Fig. 2), although the mean ID value was clearly posiv e for 110 R but close to 0 for 1103P. AMF inoculaon posiv ely increased the ID for other rootstocks, such as SO4 or 140 Rug, with a mean value close to 50%. Similarly, when we compared the rootstocks used in a single experiment, AMF inoculaon led to very di erent results for shoot dry weight ID between di erent rootstocks, ranging from 35.13% increments for 44-53 M to 3.58% for 99 Richter (Fig. 2A).

In the case of the Richter 110 rootstock, AMF inoculaon always posiv ely increased the ID for total dry weight when a sterile substrate was used as the control treatment. However, when the control was naturally mycorrhized, the ID of the AMF treatment was zero or even negav e (Fig. 2B). Several publicaons inoculated rootstock SO4 with di erent species of AMF or a mix of species, which resulted in very di erent ID values, with some negav e results for inocula prepared with *R. irregularis* and in some experiments that applied a mixture of species (Fig. 2C).

We collected data from 30 studies that examined 27 di erent species of AMF. In nine experiments, the authors mixed di erent species of mycorrhiza or used commercial inocula that contained a mixture of species. *Funneliformis mosseae* (previously named *Glomus mosseae*) and *Rhizophagus irregularis* (previously named *Glomus irregulare*) were the most frequently used, in 15.38% and 13.84% of the experiments, respecv ely. When all rootstocks and measured variables were considered together, di erences were observed in the ID values obtained (considering all measured variables) in the experiments with di erent AMF species (Fig. 3). The four species of *Acaulospora* used in various experiments led to very di erent results, from negav e e ects to close to 50% increments in growth compared to control plants. The most studied and most commonly used species in commercial inoculants, *F. mosseae* and *R. irregularis*, led to some negav e ID values, although the average ID values (considering all variables together) were posiv e and the majority of ID ranged between 0 and 50% of increments of growth.

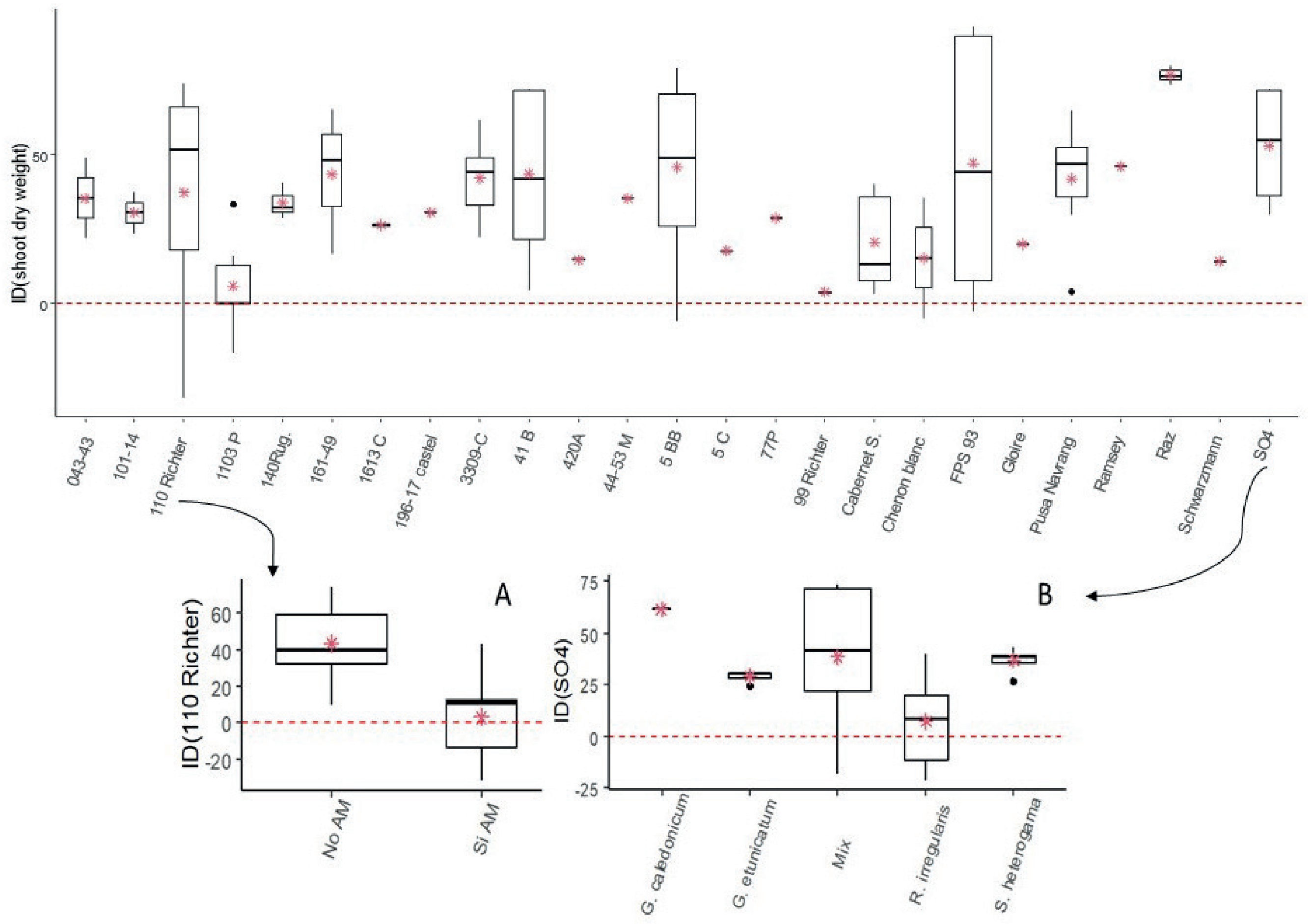

Fig. 2: A. Change in shoot dry weight of plants, expressed as inoculaon dependency (ID), associated with inoculaon with arbuscular mycorrhizal fungi (AMF) for di erent rootstocks. B. Change in total biomass, expressed as ID, of vines gra ed on Richter 110 in experiments where the control was not treated with AMF (No AM) or the control was naturally inoculated (Si AM). C. Change in total biomass, expressed as ID, of vines gra ed on SO4 inoculated with di erent species of AMF or a mixture of AMF species. The boxes indicate the lower and upper quarl es, the whiskers indicate the minimum and maximum values. The width of the boxes is proporonal to the number of observaons f or that variable, * indicates the mean value, while the black line indicates the median.

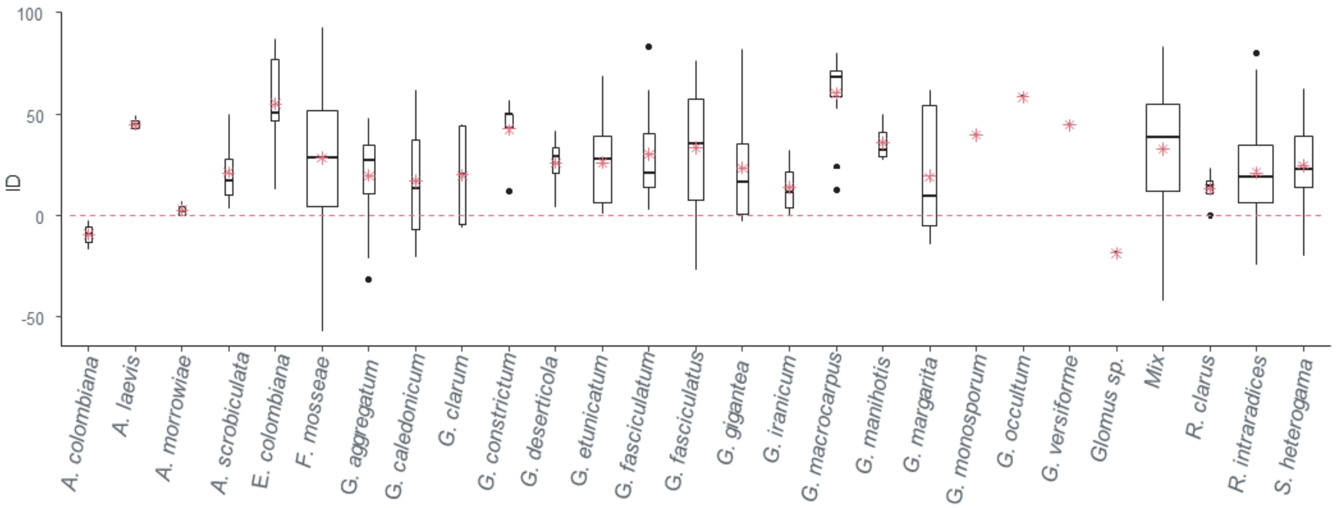

Fig. 3. Boxplot of the inoculum dependency (ID) for di erent studies considering the species of arbuscular mycorrhizal fungi (AMF) used in the experiments. The boxes indicate the lower and upper quarles, the whiskers indicate the minimum and maximum values. The width of the boxes is proporonal to the number of observaons for that variable, * indicates the mean value, while the black line indicates the median.

Several studies invesg ated the relaonship between the effect of AMF on plants and the percentage of colonizaon of the roots. However, the relaonship between the % colonizaon of the inoculated plants and the ID of the vines depended on the variable measured and was independent of the rootstock or the mycorrhiza species. For example, this relaonship was negav e for total leaf area and posiv e for shoot dry weight (Fig. 4A).

Finally, more recent publicaons t ended to report fewer posiv e e ects of AMF inoculaon; the mean ID value reported in each publicaon decreased over me (Spearman ρ = -0.55; P = 0.001; Fig. 4B).

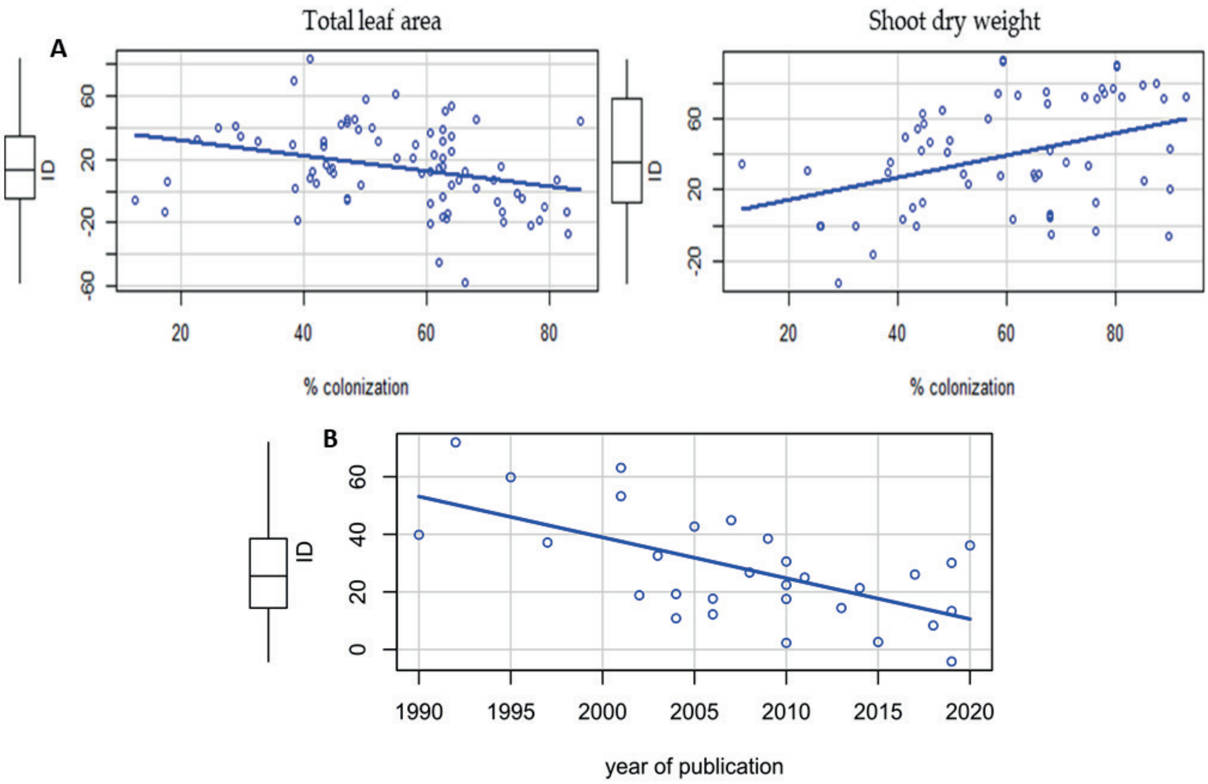

Fig. 4. A. Relaonship between the percentage of arbuscular mycorrhizal fungi (AMF) colonizaon of roots and the inoculum dependency (ID), with the linear t, considering all experiments that measured total leaf area (le) and shoot dry weight (right). B. Relaonship between the mean of all parameters measured of inoculum dependency (ID) value reported in each publicaon and the year of publicaon, with the linear t.

Discussion

Mycorrhizal efficiency must be assessed within a well-defined set of conditions, as it depends on the fungal inoculant, the plant genotype, and the environmental conditions, as well as the response variable considered. In fact, Sinclair *et al.* (2014) already concluded that it is necessary to identify the most suitable inocula for a given crop in a given environment. In the case of vine, positive results on the production and/or nutritional quality of the grape with specific species of mycorrhizal fungi with a specific plant grown under specific conditions (environmental, nutritional, etc.) should not be generally extrapolated (Torres *et al.*, 2018a; Goicoechea *et al.*, 2023). This review corroborates these ideas since results show that vines do not always benefit from inoculation with AMF and that the effects of mycorrhizae can be neutral or even negative, depending on the specific experimental conditions. The specific parameters examined as response variables are crucial, since not all parameters exhibited the same response to inoculation. Caglar and Bayram (2006) showed that AMF inoculation can be beneficial for plant nutrition, but also certain rootstock-AMF combinations can have a negative effect on specific parameters such as leaf area. Moreover, some inocula have greater effects on specific parameters than others (Ozdemir *et al.*, 2010). The strong variation in the response of different vine growth variables could result in different conclusions on the effects of inoculation, depending on the variables analyzed. Therefore, when assessing the advantages of using AMF in viticulture, it is very important to examine the response variables that are most relevant to crop development. This review did not analyze the variations in the ID of parameters related to harvest (such as yield or quality), since very few of the eligible studies evaluated the effects of inoculation on these parameters and growth at the same time. In some recent experiments carried out in commercial field settings, yield metrics including cluster number and weight were not different between control and infected plants (Rosa *et al.*, 2020; Thomsen *et al.*, 2021). Karoglan *et al.* (2021), found that only one of the two years of the study saw an improvement in yield after AMF inoculation, however, total flavonoids, total anthocyanins, and total polyphenols in berry skin increased in both experimental years. In the case of wine grape production, fruit quality could even be more important than yield. According to Velásquez *et al.* (2020), AMF inoculation was found to increase the concentration of volatile organic compounds, which are linked to better grape quality (Torres *et al.*, 2018b). Symbiotic wines can also have a higher amount of bioactive chemicals and better oxidative stability, which enhances their nutritional and nutraceutical value (Gabriele *et al.*, 2016). Additionally, it was demonstrated that mycorrhizal inoculation improve grape quality when plants are exposed to environmental challenges such as water deficit (Aguilera *et al.*, 2022; Torres *et al.*, 2021; Goicoechea *et al.*, 2023).

Different cultivars of the same crop are known to respond differently to the same AMF isolate (Bazghaleh *et al.*, 2018; Rohyadi *et al.*, 2017). In natural systems, the rootstock is an important factor that affects the species of AMF that colonize the roots (Moukarzel *et al.*, 2021). The high variability in the response of the same rootstock does not allow determining the rootstocks with the most positive response to AMF. Furthermore, comparisons between rootstocks studied in different experiments are difficult, since the study conditions and the inoculum used are very diverse. However, the same AMF can have varied effects on different rootstocks under the same conditions. For example, Belew *et al.* 2010 observed a significant difference in the growth responses of the 1613, Salt Creek, and St George rootstocks inoculated with the same AMF. Furthermore, the preference of the fungal species toward rootstocks can also affect mycorrhizal efficiency. *Glomus aggregatum*, for example, seemed to have a higher affinity for 161-49 Couderc than 196-17 castel (Aguin *et al.*, 2004).

As a result, wide dispersion of the results was observed for inoculation experiments that used the same species of mycorrhiza. For example, different effects were observed across experiments that used the same grapevine cultivar and the same AMF species but soil from different localization where the fungi were collected (Schreiner, 2007). Significant differences were also found between experiments in which various species of mycorrhiza or even several strains of the same species were compared (Biricolti *et al.*, 1997; Camprubí *et al.*, 2008). Moreover, our results confirm the variability in the response depends on the specific rootstock and mycorrhizal species combination. For instance, Aguin *et al.* (2004) reported that inoculation with *Glomus aggregatum* had a negative effect on R110 whereas Camprubi *et al.* (2009) found that *Glomus intraradices* (now *Rhizophagus intraradices*) had a positive effect on R110. This variability makes it difficult to determine the most suitable AMF inoculum for a given rootstock. Therefore, it is not appropriate to advise the use of a specific inoculum on a certain rootstock based on the positive effects of the inoculum on other rootstocks.

The responses of grapevines to AMF inoculation vary according to the experimental conditions. The differences in the growth of inoculated plants compared to control plants grown under sterile conditions or with spontaneous natural mycorrhization are remarkable (see Figure 2B). Most agricultural soils contain populations of local mycorrhizae that can establish symbiosis and have diverse effects on vines (Carbone *et al.*, 2021; Landi *et al.*, 2021; Schreiner *et al.*, 2007). This natural symbiosis may therefore reduce the advantage of foreign species. Under agricultural conditions, inoculation with AMF must provide an advantage for the vine beyond those provided by the spontaneously colonized native species, and such conclusions cannot be based on comparisons with sterile conditions. Moreover, the critical impact of the microbiome on vine development and the potential impact of inoculation on native microbial communities cannot be disregarded (Darriaut *et al.*, 2022). In fact, Cardinale *et al.* (2022) inoculated vine plants with a combination of AMF and Plant Growth Promoting Rhizobacteria (PGPR), which resulted in significantly higher survival and growth rates, as well as significantly higher accumulations of 18 elements but generate significant differences in the bacterial communities of the soil. Moukarzel *et al.* (2021) demonstrate that different AMF communities had different effects on the development and uptake of nutrients by grapevine rootstock. When present in equal abundance, competition between mycorrhizal species occurs, which leads to a reduction in the positive growth outcomes for vine plants (Moukarzel *et al.*, 2021).

Plants under biotic (presence of diseases) or abiotic stress conditions generally respond more positively to mycorrhizal inoculation than plants under standard conditions (Aguilera *et al.* 2022). As a result, an important factor to consider when deciding whether to inoculate mycorrhizal fungi is planting conditions. For example, in the case of vineyards, Cu levels in the soil are of great importance, since the application of copper products to combat pathogenic fungi has been common. High concentrations of Cu in the soil could decrease the beneficial effect of inoculation with AMF (Nogales *et al.*, 2019).

The growth conditions also determine the effectiveness of the application of AMF. The same type of AMF can have different levels of effectiveness when used under field or greenhouse conditions. Camprubi *et al.* (2008) found *Glomus intraradices* had a more positive effect on grapevines under greenhouse conditions than field conditions. The causes of these differences are still unclear but suggest poor establishment of the inoculum under field conditions, rather than weaker beneficial effects of the inoculum. In fact, Thomsen *et al.* (2021) reported that even with priority advantage and using different methodologies of inoculation, an introduced AMF strain did not establish in a commercial vineyard in Canada. However, Rosa *et al.* 2020 showed that an inoculated fungal strain could successfully establish and maintain symbiosis with grapevines under field conditions, but had no positive effects or even decreased vine performance.

The percentage of AMF colonization of roots is commonly used as an indicator of fungal abundance and inoculation success (e.g., Schreiner *et al.*, 2007 Ozdemir *et al.*, 2010). However, the relationship between the percentage of colonization and positive effects on the plant is more doubtful (Treseder, 2013). The analysis of the data collected in this literature review shows that the relationship between the percentage of colonization and the increase in growth depends on the variable analyzed and can be either positive or negative. Therefore, caution should be exercised when using % colonization as an indicator of inoculation success, as this parameter may indicate the presence of the fungus—but not necessarily a positive effect on the plant.

Our results also reported that the studies published more recently tended to report AMF inoculation had less positive effects. Temporary changes in the magnitude of the findings of published results in the scientific literature have been recognized as a general phenomenon in ecology and have been attributed to the late publication of non-significant results and contrary evidence (Jennions and Møller, 2002). There is general discourse in the scientific literature about the benefits of AMF and their usefulness in viticulture (Popescu, 2016.; Torres *et al.*, 2018b; Trouvelot *et al.*, 2015); critical voices that emphasize the possible neutral or negative effects of AMF and the difficulty of managing AMF in agricultural systems have only appeared in recent years (Hart *et al.*, 2018; Rillig *et al.*, 2016). The emergence of this viewpoint may have made it easier to publish results contrary to the dominant discourse of the positive role of AMF.

Conclusions

Although previous reviews promoted the use of arbuscular mycorrhizae in viticulture as a promising solution to improve plant performance, this review indicates that the effects of mycorrhizal inoculation on vine growth depend on multiple factors. This high dependence on multiple factors and the complexity of mycorrhiza-host rootstock modulated responses are evidenced by the neutral or even negative effects of AMF on growth parameters observed in different experiments. On the other hand, this review shows that a greater research effort is needed before being able to determine rootstocks with better response to AMF inoculation or the most effective AMF species. Furthermore, most of the existing studies were conducted under greenhouse conditions and did not consider parameters of commercial interest, such as the yield or grape quality. Therefore, the use of commercial inoculum under real field conditions may not have the expected beneficial effects. Thus, it is necessary to increase research efforts in real, specific environmental scenarios and to focus on parameters of commercial interest. In conclusion, before introducing AMF inoculum in viticulture, we suggest that it is important to identify the most appropriate mycorrhizal inoculum that provides benefits for a given rootstock or cultivar under actual, specific culture conditions. Moreover, environmental conditions such as water deficit, salinity or Cu levels and biotic factors such as presence of diseases and native microbial community of soils must be considered as important factors to determine the final effects of mycorrhizal symbiosis on vine plants. Finally, especially in grapevines, the pertinence or not of applying mycorrhizal inoculum cannot be concluded solely from their effect on vegetative growth parameters but also on quality factors.

Supplementary data to this article can be found online at: https://doi.org/10.5073/vitis.2023.62.183-192.

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Conflicts of interest

The authors declare that they do not have any conflicts of interest.

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