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RESEARCH ARTICLE

Impact of plant breeding on the responsiveness of maize and wheat varieties to an arbuscular mycorrhizal fungal symbiont

Ido Rog[1,2] | **Marco Malinowski**[1,2] | **Dylan Baumann**[1,2] |
Raphaël Boussageon[1,2] | **Stefanie Lutz**[1,2] | **Marcel G. A. van der Heijden**[1,2]

[1]Department of Plant and Microbial Biology, University of Zurich, Zurich, Switzerland

[2]Plant-Soil Interactions, Division Agroecology and Environment, Agroscope, Zurich, Switzerland

Correspondence
Ido Rog, Department of Plant and Microbial Biology, University of Zurich, Zollikerstrasse 107, 8008 Zurich, Switzerland.
Email: ido.rog@uzh.ch

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Societal Impact Statement

Field inoculation with arbuscular mycorrhizal fungi (AMF) offers a promising route to improve sustainable agriculture and food production, yet results are often variable. We investigated the mycorrhizal growth response of maize and wheat varieties recommended for farmers and found substantial variation under greenhouse conditions. The mycorrhizal growth response varied from +7% to −12% for maize and from +6% to −25% for wheat and varied by breeding company. Selecting suitable varieties is crucial to fully harness AMF benefits. Field trials under diverse climatic and biotic conditions are required to support AMF application to ultimately promote sustainable agriculture and food security.

Summary

- Arbuscular mycorrhizal fungi (AMF) enhance plant nutrient uptake and can reduce reliance on external inputs. Yet, it is unresolved whether plant breeding influences the ability to benefit from AMF and whether certain modern varieties benefit more from AMF associations compared to older varieties.
- We tested 15 maize (*Zea mays*) and 15 wheat (*Triticum aestivum*) varieties recommended for farmers, as well as three older wheat cultivars under greenhouse conditions. The plants were inoculated with an AMF (*Rhizoglomus irregulare*), and effects on mycorrhizal root colonization and mycorrhizal growth response (MGR) were assessed. To explore whether genetic background influences AMF responsiveness, we assessed whether response patterns varied across breeding companies and differed when comparing modern and old plant varieties.
- For maize, most modern varieties showed positive or neutral MGR, ranging from +7% to −12%. In contrast, the majority of modern wheat varieties exhibited neutral or negative responses, with MGR ranging from +6% to −25%. Crucially, modern varieties did not respond uniformly; maize varieties from the same breeder tended to cluster together in terms of MGR, suggesting a strong influence of genetic background. Three old wheat varieties generally showed more positive responsiveness than modern ones, but variation remained within both groups.

- Our study demonstrates that modern crop varieties differ markedly in their responsiveness to AMF, and that genetic background is a key determinant. These findings suggest that breeding programs and variety testing should integrate beneficial microbial interactions as selection criteria. Such an approach would maximize crop benefits from soil microorganisms and advance sustainable agriculture.

KEYWORDS
breeding, genetic variation, mycorrhizal fungi, plant–soil interaction, soil ecological engineering, sustainable agriculture

1 | INTRODUCTION

New plant varieties are often bred under nutrient-rich conditions, producing cultivars that benefit less from associations with beneficial microorganisms that support nutrient uptake (Nerva et al., 2022). Nevertheless, soil microorganisms play a central role in biogeochemical cycles, shaping nutrient availability and influencing both plant nutrition and resilience against biotic and abiotic stresses (Bender & van der Heijden, 2015). Among these beneficial microorganisms, arbuscular mycorrhizal fungi (AMF) form symbiotic associations with most crop species and are particularly important for plant nutrition. AMF acquire and transfer soil nutrients to their hosts in exchange for photosynthates (Martin & van der Heijden, 2024). Their extensive mycelium explores large soil volumes beyond the root zone, granting plants access to nutrients located far from the roots, thereby enhancing plant growth (Allen, 2007). Despite considerable efforts by scientists and biotech companies to improve plant–AMF interactions through AMF and other biostimulant inoculations, results in the field remain inconsistent (Boussageon et al., 2023; Hoeksema et al., 2010; Lekberg & Koide, 2005; Lutz et al., 2023). A key reason for these variable outcomes is the diverse response among plant species and varieties (Zhang et al., 2019). Older crop varieties frequently exhibit a higher mycorrhizal growth response (MGR) than modern cultivars (Hetrick et al., 1993; Koide et al., 1988; Lehmann et al., 2012). Yet relatively little attention has been given to breeding programs that deliberately select for traits enhancing beneficial microbial associations—whether with native soil microbes or inoculated strains.

Most terrestrial plants, including major crops such as maize, rice, wheat, and potatoes, form beneficial associations with AMF. Although this symbiotic interaction has existed since plants first transitioned from aquatic to terrestrial environments, the mechanisms underlying its initiation and function are still not fully understood (Field & Pressel, 2018). Recent studies have identified several genomic regions and root traits that contribute to a high MGR (Lehnert et al., 2017; Thirkell et al., 2022). Root morphology and anatomy are critical in facilitating and sustaining AMF symbiosis. For instance, species with thick, sparsely branched root systems often exhibit higher colonization rates and greater AMF abundance (Bardgett et al., 2014; Bergmann et al., 2020). Traits such as root order and, in particular, the presence of root hairs also strongly influence AMF establishment (Wang et al., 2025; Wen et al., 2019). Root exudates, especially strigolactones, attract AMF hyphae from the rhizosphere to the root surface (Akiyama et al., 2005; Bouwmeester et al., 2007). Variation in strigolactone biosynthesis has considerable potential to enhance AMF colonization (Chesterfield et al., 2020). Additional molecular players, referred to as microbiome-associated genes, including phosphorus transporters and symbiosis receptor kinases, regulate these processes at the cellular level (Cernava, 2024). These morphological and molecular traits represent promising targets for breeding programs aimed at strengthening crop–AMF associations.

Breeding plant genotypes that respond well to AMF is not the only requirement. The abundance of AMF in the soil is also essential for a beneficial association. AMF are present in most healthy soils, and AMF richness constitutes one of the main predictors for primary productivity in grasslands (Romero et al., 2024). However, in intensively fertilized and heavily managed agricultural soils, AMF abundance and diversity are often reduced (Verbruggen et al., 2012, 2013). Furthermore, the widespread use of pesticides can diminish AMF nutrient uptake capacity and limit their potential to improve nutrient use efficiency (Edlinger et al., 2022). Therefore, enriching soils with beneficial AMF—through targeted inoculation—must be paired with the selection of responsive plant genotypes and suitable agricultural management to maximize the likelihood of establishing a beneficial and stable symbiosis.

Not all AMF products currently available on the market deliver consistent agronomic benefits. Recent studies found that most commercial formulations lack viable propagules and fail to reliably promote AMF colonization or plant growth (Boussageon et al., 2025; Koziol et al., 2024; Salomon et al., 2022). The composition of the existing soil microbial community and soil characteristics also play a major role in inoculation success (Aguilar-Trigueros & Frew, 2026; Frew, 2021). Positive effects are more likely in soils with lower health status (Rog et al., 2025), where native AMF communities are less abundant (Bender et al., 2019). The strain *Rhizoglomus irregulare* SAF22 has shown strong potential for broad agricultural use due to its adaptability to a wide range of soil types and conditions (Lutz et al., 2023). Nonetheless, further research is needed to understand the compatibility between specific AMF strains and biotic and abiotic factors to achieve consistent results under field conditions. Such integrated approaches can strengthen natural processes and contribute to the development of sustainable agricultural systems, reducing the need for chemical fertilizers and pesticides.

Mycorrhizal symbioses are bilaterally controlled, with both the plant and the fungus capable of enforcing cooperation. It has been proposed that the most cooperative AMF fungal symbionts transfer more nutrients to host roots when they receive more carbon in return (Kiers et al., 2011). This highlights the importance of considering plant–AMF interaction traits in breeding programs specifically for maize and wheat (Pellegrino et al., 2015; Zhang et al., 2016). Incorporating AMF into modern agricultural practices holds great promise for advancing sustainable farming (with yield increases of up to 17% in wheat and 13% in maize) (Zhang et al., 2016), yet several challenges remain. A central open question is why crop varieties display highly diverse responses to AMF and whether certain varieties are especially well-suited to these symbioses, making them preferable for sustainable agriculture and AMF inoculation strategies. In this study, we evaluated MGR and AMF root colonization in two of the world's most widely cultivated crops, maize and wheat, focusing on recent varieties recommended to farmers. We hypothesized that MGR would vary widely among varieties, reflecting strong genetic influences despite decades of breeding without direct selection for traits promoting microbial associations. Moreover, we expected varieties from the same breeder (e.g., from the same company) to cluster within similar MGR ranges due to shared genetic backgrounds. Lastly, we hypothesized that, because breeding under high-input conditions selects against AMF responsiveness, the older varieties will benefit more. Understanding the influence of variety on MGR could help guide farmers in selecting cultivars with high AMF responsiveness and encourage breeders to integrate AMF compatibility as a formal target in future breeding programs.

2 | MATERIALS AND METHODS

2.1 | Maize and wheat variety selection

A total of 15 maize varieties (*Zea maize*) were selected from the list of the most currently recommended seed varieties for farmers in Switzerland in 2023 (Published by Agroscope every year) (Table S1). The varieties are all recommended for silage use and some as well for grain production (both referred to as *elite* varieties). They are produced by four different breeder companies: Pioneer, Limagrain, Syngenta CH, and KWS Saat AG. The variety LG 302222 is not present in the recommended list anymore and was selected for comparison with previous field trials (Bender et al., 2019; Lutz et al., 2023). The varieties *LG 31280* and *KWS Haiko* were only included in the list of recommended varieties in 2022 but not in 2023 and are included in the experiment to better represent the different breeding companies. The different seed varieties received from the breeders were not coated. Variety LG 30222 is an exception and was received from the breeder coated with a bird repellent (Korit), which was removed during the seed sterilization treatment (explained in detail in the *Experimental design* section). A total of 18 wheat varieties were selected for this experiment. The experiment incorporates 10 wheat varieties from the recommended Agroscope list in 2023 (Published by Agroscope every year); five additional varieties from Germany, Austria, and France (referred to as *elite* varieties); and three older varieties from before the Green Revolution in the 1950s (Table S1). The older variety *Plantahof* originated from the agricultural school and research station Plantahof in Graubünden and *Mont-Calme 268* originated from the research station at Mont-Calme, near Lausanne. The recommended varieties are categorized into four yield groups: Top, I, II, feed taken from the farmer recommendation list published every year by Agroscope.

2.2 | Experimental design and growth conditions

Eight replicates of each variety were grown in a controlled greenhouse environment (Agroscope, Reckenholz, Zürich), maize during May and June 2023 and wheat during July and August 2024. Plants were grown under long-day conditions (16/8 h photoperiod, additional light from sodium-vapor greenhouse lights) and 22/17°C day/night temperature. Seeds of the different varieties were surface sterilized by 70% EtOH and 5% bleach-Tween solution. To avoid bias and ensure optimal growth conditions, average-sized seedlings were selected after 1 week for further growth. Soil was kept in the range of 15%–20% relative water content during the entire growth stage. Pots were organized in a randomized block design rotated once a week both within the block and location of blocks in the greenhouse (Figure S1).

2.3 | Substrate and AMF inoculum

Soil from a site near Agroscope Reckenholz was sieved with a 5-mm mesh before it was mixed with quartz sand (Capito, Landi) at a 1:1 volume ratio, sterilized (using autoclave, 121°C, 90 min) and left to rest for 1 month. Soil nutrient content analysis performed by the soil analytics laboratory at Agroscope revealed the following parameters for the substrate: calcium (6.85 cmol+/kg), soil organic carbon (3.795%), potassium (0.18 cmol+/kg), magnesium (0.42 cmol+/kg), sodium (0.05 cmol+/kg), and pH = 7.08. AMF inoculum of *Rhizoglomus irregulare strain SAF22* (soil and root fragments), produced by Plant–Soil Interactioncs group at Agroscope, was used in a total volume of 5% (the AMF inoculum contains single species but several OTUs described in detail in (Lutz et al., 2023)). No fertilizer was applied. Because the two plant species have different growth rates and sizes, we used 3-L pots for maize and 1.5-L pots for wheat (Figure S1).

2.4 | MGR calculation

The plants were harvested 60 days after sowing. For plant biomass quantification, the aboveground part of the plants was harvested and dried for 48 h at 60°C. For the belowground biomass part, the entire root system was collected from the substrate, washed, cut into 1.5-cm pieces, and mixed, and subsamples for DNA extraction were taken and frozen for further analysis. The rest of the root system was dried, and dry mass was determined. The overall dry biomass of all treatments was used to calculate the MGR for each variety following the formulas by Köhl et al. (2016) (Figure S2 and Figure S3). The dry biomass of each AMF-treated plant was compared with the mean dry biomass of the respective control treatment.

2.5 | DNA extraction and AMF colonization analysis

Freeze-dried roots (VirTis, BenchTopK, USA, New York) were ground with glass beads using a FastPrep-24 5G (MP Biomedicals, USA, Irvine). From each sample, DNA was extracted using 20–30 mg of roots with the NucleoSpin 96 Plant II DNA kit (Macherey-Nagel). DNA concentration was quantified with PicoGreen staining on a Fluorescence Spectrometer (Cary Eclipse Varian, Agilent Technologies, Inc.) and diluted to 1 ng/μL across all samples using a pipet robot (PIPETMAX 268, Gilson). The abundance of the small nuclear ribosomal subunit (SSU) of AMF sequences was determined by qPCR absolute quantification for each sample. Amplifications were performed using HOT FIREPol® EvaGreen® qPCR Mix Plus and the Bio-Rad CFX Maestro 2.2 thermocycler (CFX Opus 384, Bio-Rad Laboratories, Inc., USA, Hercules). Triplicates of the samples were pipetted onto a 384-well plate, each consisting of 5 μL of DNA (1 ng/μL) and 5 μL of a PCR mix (2-μL Eva Green 5x HOT FIRE Pol, 2-μL ddH_2O, and two primers). For maize, the primers *AMG1F* and *AM1* were used to amplify the *18S rRNA*. These primers are specific to the phylum Glomeromycota and have been validated as suitable for detecting a broad diversity of AMF taxa (Bodenhausen et al., 2021). Due to nonspecific amplification in wheat plants, we used 22KS-F (Bender et al., 2019) and Alk-R (Alkan et al., 2006) primers. Quantitative RT-PCR was performed in a 384-well plate with the following PCR cycling conditions: 95°C for 12 min; 40 cycles of 95°C for 15 s, 62°C for 30 s, and 72°C for 20 s. Primer specificity was further verified by melting curve analysis at the end of each qPCR run (65°C–95°C, 0.5°C increments), ensuring amplification of a single product. Standard curves were generated using tenfold serial dilutions (1.39×10^{-3} to 1.39×10^{-9} ng DNA μL^{-1}). Each qPCR plate included a complete standard series and no-template controls to monitor potential contamination. Amplification efficiency and coefficient of determination ($R^2 > 0.98$) confirmed reliable and consistent quantification. Each biological sample was analyzed in triplicates, and mean values were used for further analyses. Raw fluorescence data were processed with LinRegPCR v2016.0 to determine the threshold cycle (Ct) and reaction efficiencies. Copy numbers per ng of DNA were calculated from the standard curve and normalized across samples (Bender et al., 2019). Non detects or failed technical replicates were excluded if PCR efficiency deviation is larger than 0.2 and cycle number is larger than 2. To verify the low AMF colonization of wheat, four representative varieties from the MGR range were selected and assessed using the microscopy method described by McGonigle et al. (1990). Roots were stained with ink-vinegar after incubation in 10% KOH for 20 min at 80°C. Using 200x magnification, AMF structures (arbuscules, hyphae, and vesicles) were quantified for 100 root intersections.

2.6 | Statistical analysis

Data were analyzed and visualized using R (Team, 2018) and the interfaces R Studio (RStudio Team, 2019) and Jamovi (The jamovi project, 2023). Impacts of AMF inoculation and colonization were investigated on MGR, quality, and breeding company. During the harvest, three wheat plants (*Alpval* Control and two *Plantahof* Control) died, and for one maize plant (P9610), the belowground part is missing. A one-way ANOVA was conducted to test for significant differences among maize and wheat varieties (fixed effect). Model assumptions were evaluated using Levene's test for homogeneity of variances and the Shapiro–Wilk test for normality of residuals. Post hoc comparisons were performed with Tukey's adjustment, and specific contrasts were applied to assess differences in MGR. To examine the effect of Breeder on MGR, we fitted a nested linear mixed-effects model (LMM), with breeder included as a fixed effect, variety as a random effect, and block included as an additional random effect. Residual normality was assessed using the Shapiro–Wilk test. Effect sizes, confidence intervals, and model specifications are provided in the supplementary tables. For the AMF colonization model, however, the normality assumption was not met. Finally, Pearson's correlation test was used to evaluate the relationship between MGR and AMF colonization.

3 | RESULTS

3.1 | Large range of MGR in maize and wheat varieties

The 15 maize varieties showed significant variation in MGR in response to AMF inoculation (ANOVA, $F_{[14,104]} = 2.47$, $p = 0.0047$) (Figure 1). Mean MGR values ranged from +7.1% to −11.6%. Four varieties—*LG31245*, *P8834*, *P9363*, and *SY Amfora*—exhibited significantly positive or negative MGR values compared with the overall mean (ANOVA contrast, $p < 0.05$; Figure 1, Table S2). Among the 15 wheat varieties, we also detected significant differences (ANOVA, $F_{[14,105]} = 2.00$, $p = 0.024$) (Figure 1, Table S2). Only one winter wheat variety showed positive MGR values, while the remaining 14 winter wheat varieties displayed either no effect or a significant negative effect. Wheat MGR responses spanned a broader range, from +5.8% to −25.6%. Overall, both maize and wheat displayed a wide range of MGR responses; maize varieties generally showed more positive effects than wheat.

3.2 | Varieties from the same breeder cluster together on the MGR scale

Varieties from the same breeding companies tended to cluster together on the MGR scale. In maize varieties, the breeding company significantly explained 16% of the variation in MGR (LMM, Fixed effect: breeder, random [nested] effect: variety), $F_{(4,10.1)} = 5.05$, $p = 0.017$ (Figure 1, Table S3). For wheat, the breeding company had a weak effect on MGR, accounting for 10.6% of the variation (LMM,

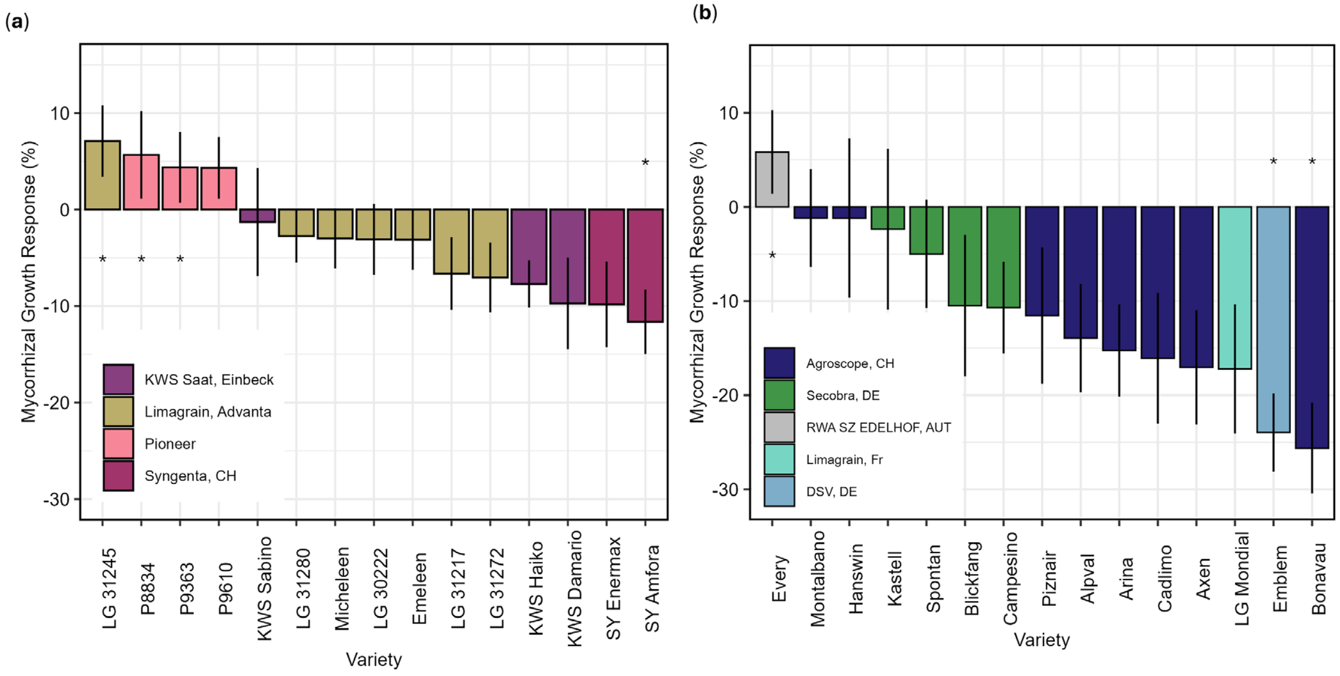

FIGURE 1 Large range of mycorrhizal growth response in elite varieties of maize and wheat. Range of mycorrhizal growth responses (MGR) among 15 maize (a) and 15 wheat (b) elite varieties recommended for farmers. Colors represent the different plant breeding companies. Bars represent mean mycorrhizal growth response (MGR), with standard errors (SE) indicated by black lines. Significant differences of individual varieties are indicated (* = $p < 0.05$). MGR is calculated according to Köhl et al. (2016) ($n = 8$).

breeder, $F_{[4,10]} = 2.74$, $p = 0.089$, Figure 1, Table S4). In both maize and wheat varieties, other parameters such as seed quality and yield category could not explain the MGR variation (maize, LMM, $F_{(2,11.9)} = 0.54$, $p = 0.596$; wheat, LMM $F_{(4,10)} = 0.256$, $p = 0.899$). These results indicate that, even after many years of breeding, MGR is influenced by the plant's genetic background and can explain part of the variation in MGR.

3.3 | AMF root colonization of maize and wheat varieties

All varieties of maize and wheat were successfully colonized in the AMF inoculation treatments (Figure 2, Figure S4). In maize, the mean absolute copy numbers of AMF sequences per root sample ranged from 467 to 2451, with no significant differences among breeding companies and varieties (LMM, $F_{[4,227]} = 1.57$, $p = 0.184$). In wheat, colonization levels were from 8 to 520, with no significant differences among varieties (LMM, $F_{[4,10.3]} = 0.104$, $p = 0.979$) (Figure 2). As wheat colonization was very low, qPCR results were verified by microscopy. Root colonization levels of four representative varieties, from the MGR range, ranged from 16% to 27% and showed no significant differences in AMF structure (arbuscules, hyphae, and vesicles) between the selected varieties (Figure S5). Overall, all tested varieties were colonized by AMF; maize varieties showed high colonization, and wheat varieties showed low colonization.

3.4 | AMF root colonization is related to MGR

Analyzing the correlation between AMF colonization levels and MGR helps to clarify the functional role of AMF across crop varieties. In maize, we observed no correlation between colonization and MGR ($R = 0.04$, $p = 0.03$) (Figure 3). In wheat, which generally exhibited lower colonization and MGR values, the correlation was weak ($R = 0.32$, $p = 0.00051$) (Figure 3). Overall, both crops showed weak correlations between colonization and MGR, suggesting that factors beyond colonization intensity also influence plant growth responses to AMF.

3.5 | Old wheat varieties benefit more from AMF association

All maize and wheat varieties tested in this experiment can host AMF, but not all benefit equally from the association. To explore potential differences across breeding history, we compared three older wheat varieties with 15 modern varieties. Interestingly, older varieties exhibited significantly higher MGR than modern ones (ANOVA, $F_{[1,142]} = 3.98$, $p = 0.048$; Figure 4). However, no significant differences were detected in AMF colonization levels (ANOVA, $F_{[1,125]} = 1.44$, $p = 0.233$; Figure 4). Thus, while older and modern varieties differ in their growth response to AMF, these differences are not explained by colonization intensity alone.

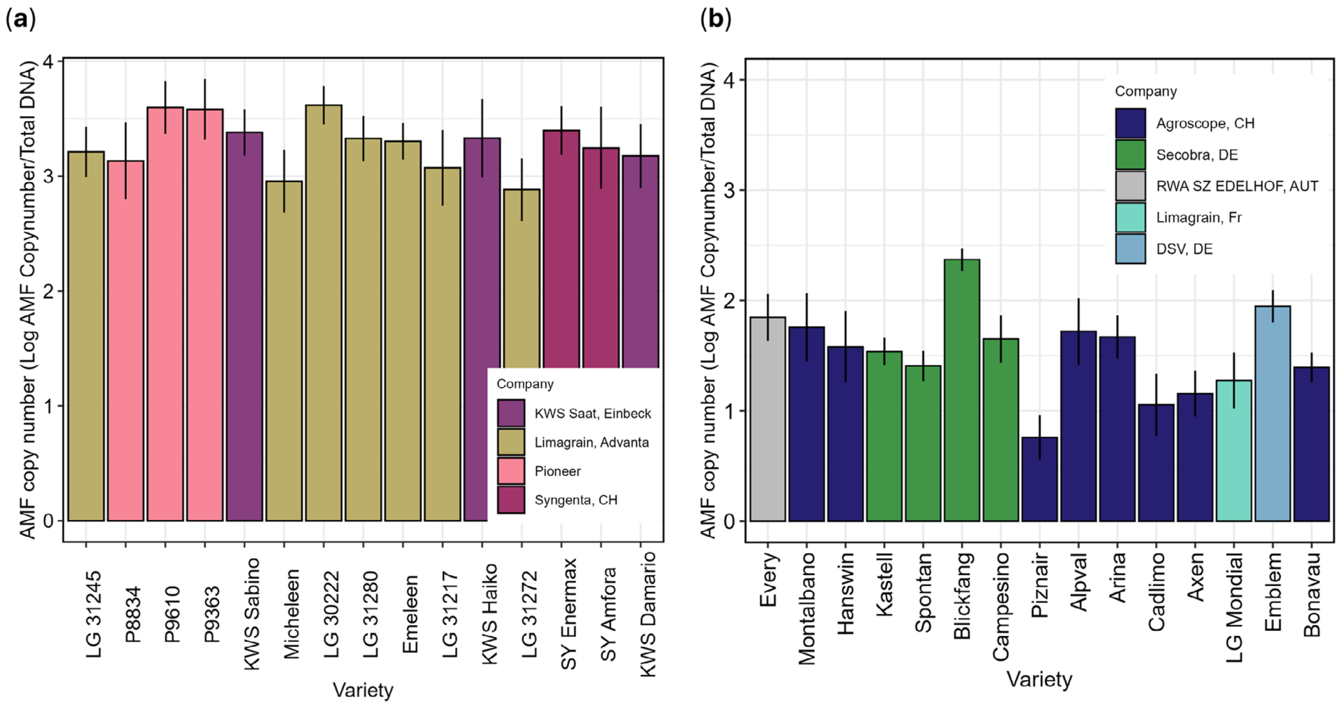

FIGURE 2 Arbuscular mycorrhizal fungi (AMF) colonization of elite varieties of maize and wheat. AMF root colonization of 15 maize (a) and 15 wheat (b) measured by quantitative polymerase chain reaction (qPCR). Root colonization rates of inoculated plants varied among elite varieties. Colonization of control plants was very low or negligible (Figure S4). Root colonization is shown as the log-transformed absolute AMF copy number per total deoxyribonucleic acid (DNA). Bars represent mean values, with standard errors (SE) indicated by black lines ($n = 8$). Varieties are colored according to breeding company and ordered by mycorrhizal growth responses values shown in Figure 1.

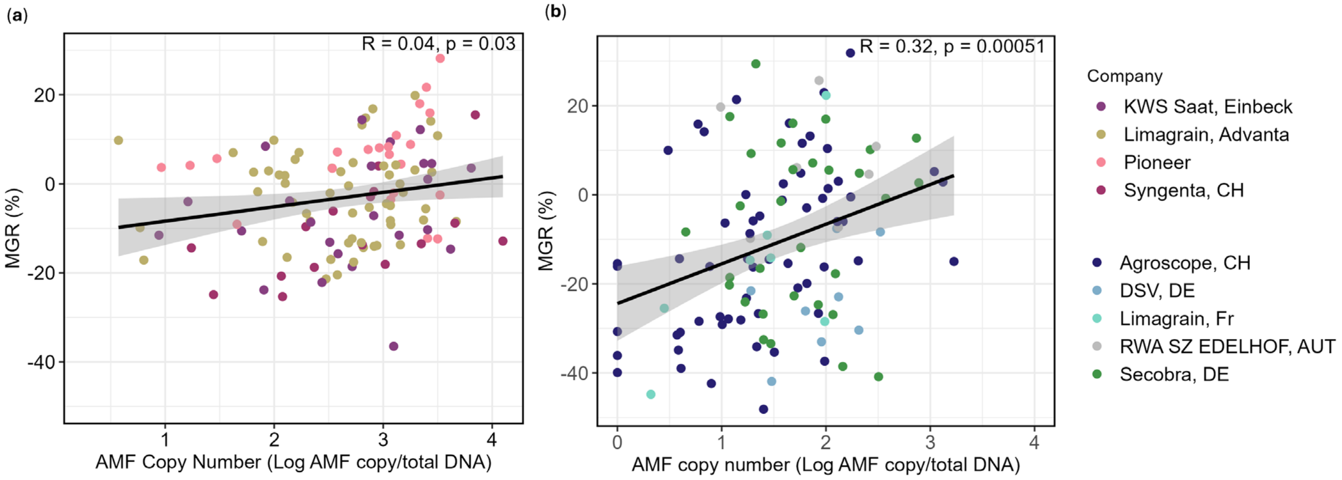

FIGURE 3 Mycorrhizal growth response (MGR) and the relation to arbuscular mycorrhizal fungi (AMF) root colonization. Positive correlation between MGR and AMF colonization rate in maize (a) and wheat (b). Colonization is shown as absolute AMF copy numbers (log transformed) from root samples. Individual replicates are colored by breeding company. The correlation is calculated on the replicate-level, statistical values are presented in the figure ($n = 8$ per variety), gray areas are 95% confidence interval.

4 | DISCUSSION

Field inoculation with AMF is a promising approach to promote sustainable agriculture. However, field inoculation outcomes are often inconsistent, ranging from strong positive effects to, in some cases, negative impacts (Lutz et al., 2023). In this study, we investigated the influence of plant genotypes, specifically that of elite, modern varieties, on MGR variation. Using maize and wheat cultivars recommended for farmers, inoculated with a single AMF species under greenhouse conditions, we observed substantial variation in MGR. Varieties from the same breeding company tended to cluster within similar MGR ranges (Figure 1). In both plant species, we observed

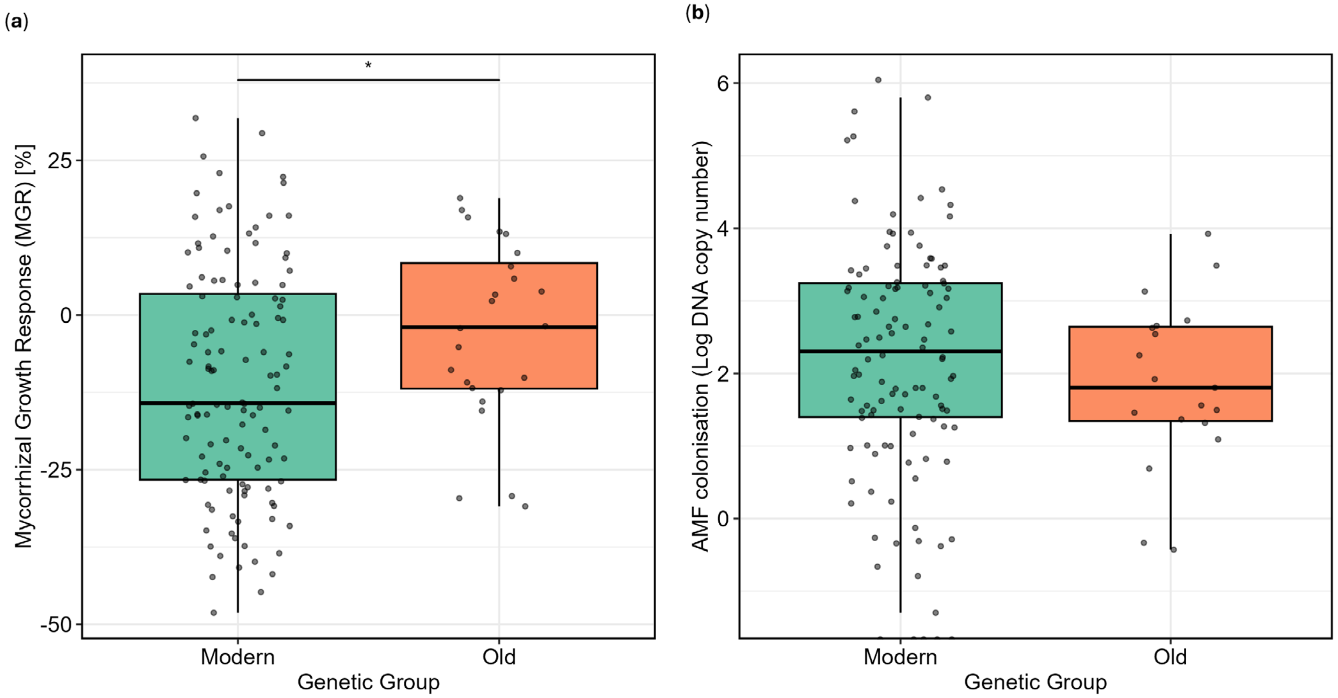

FIGURE 4 Old varieties have a higher mycorrhizal growth response (MGR), but not a higher level of arbuscular mycorrhizal fungi (AMF) colonization. Old wheat varieties show higher MGR (a) but not higher AMF colonization (b) compared to modern varieties. MGR is calculated according to Köhl et al. (2016), and AMF colonization is measured using quantitative polymerase chain reaction (qPCR). 15 modern varieties, compared to three old varieties ($n = 8$) ($* = p < 0.05$).

weak correlations between AMF abundance in roots and MGR (Figure 3). Interestingly, old wheat varieties respond better in terms of MGR compared to modern varieties (Figure 4). These findings highlight the critical role of functional compatibility between AMF and specific plant genotypes. The selection of suitable varieties is essential to fully realize the potential of AMF for enhancing sustainable agriculture, soil health, and yield.

4.1 | Effect of breeding on MGR

Breeding programs generally focus on yield, yield quality, and disease resistance, and have generally not prioritized traits that influence symbiosis with AMF. This potentially results in crop varieties that derive fewer benefits from these interactions. All varieties were colonized by AMF, and the observed range of MGR, from $+7.1\%$ to -11.6% in maize and from $+5.8\%$ to -25.6% in wheat (Figure 1), indicates that modern breeding lines still retain some root traits necessary for attracting, establishing, and maintaining AMF associations and the capability of doing so is not completely lost despite intensive breeding. The clustering of varieties from the same breeder within similar MGR ranges confirms a strong genetic influence on plant–AMF relationships (Figure 1). Comparisons between old and modern wheat varieties reveal significant differences, with three older varieties showing higher MGR than 15 modern varieties (Figure 4). While this pattern is based on small number of varieties, it is supported by studies showing that older varieties of maize, wheat, and rice (bred before 1900) often exhibit stronger yield responses to AMF inoculation than modern varieties (bred after 1950) (Zhang et al., 2019). In contrast, other research has reported no significant differences between older and modern varieties across cereals, vegetables, and legumes (Hetrick et al., 1993; Koide et al., 1988; Lehmann et al., 2012). A possible explanation is that breeding methods led to reduced AMF dependence as a response to increased use of mineral fertilizer (Lehmann et al., 2012; Martín-Robles et al., 2018). Interestingly, cultivars from organic systems show higher MGR than those bred for conventional agriculture (Garcia de Leon et al., 2020). These findings underscore both the complexity of plant–AMF interactions and the challenge of drawing broad conclusions from individual studies. In the long term, to fully harness the potential of AMF in sustainable agriculture, future breeding programs might integrate interaction traits and functional compatibility into new sustainable varieties.

Even within the same species, different varieties display morphological and genetic variation that can influence the MGR. Key plant traits, such as the exudation of fungal attraction signals, the allelic variations of mycorrhizal inducible-transporters, and the regulation of carbon allocation to fungal symbionts, are critical for initiating and sustaining AMF association (Berger & Gutjahr, 2021). Modern breeding practices, which often prioritize yield stability and nutrient uptake efficiency, may inadvertently select against traits that enhance AMF benefits (Kumar et al., 2024). In this study, we observed weak correlations between MGR and AMF root colonization (Figure 3) as shown by others (Bender et al., 2019; Lutz et al., 2023; Thirkell et al., 2022). To fully exploit AMF benefits, a deeper understanding of the molecular characteristics of the mycorrhizal association—such as the roles of phosphorus transporters, carbohydrate transporters, and lipid transporters—is needed (Frew, 2025; Sawers et al., 2017). Future breeding programs should actively select for mycorrhizal responsiveness and identify specific quantitative trait loci (QTL) associated with MGR (Chen et al., 2026; Martín-Robles et al., 2018; Thirkell et al., 2022). Other factors, such as plant epigenetics and epistasis, add complexity to breeding programs and selection of the phenotypic traits (Burch et al., 2024; Zanetti et al., 2024). Such insights will be essential for breeding varieties that maintain or enhance traits supporting beneficial AMF associations.

One of the key traits that has changed through decades of breeding is the level of polyploidy, together with extensive hybridization—both factors that can influence MGR. Wheat evolution involved multiple rounds of hybridization, allopolyploidization, and domestication, with each genomic change potentially affecting AMF associations through the presence and expression of specific QTLs (Lehnert et al., 2017). While this study compared plants at the same ploidy level (Figure 4), comparisons among diploid, tetraploid, and hexaploid wheats have shown that specific genomes contribute significantly to AMF associations (Kapulnik & Kushnir, 1991). In contrast, maize was domesticated through a single event, but its subsequent introduction into Europe created two major germplasm pools, each adapting to diverse environmental niches—a process likely underlying the wide variability in AMF responsiveness observed today (Matsuoka et al., 2002). Modern maize breeding has relied heavily on hybrids to boost yield, but this has sometimes reduced AMF associations. Hybrids typically show lower colonization rates than inbred lines, likely due to selection for rapid early growth and high nutrient uptake efficiency (Sangabriel-Conde et al., 2015). This suggests that AMF may enhance growth only up to a certain threshold; once plants approach their maximal size, further AMF contributions to biomass accumulation become limited (Rog et al., 2025). Instead, their role may shift toward other functions, such as mediating interactions with soil microbes, including pathogens. Screening ancient or traditional varieties that have undergone less intensive breeding, and testing them under field conditions, will be essential for assessing the full protective and functional potential of AMF.

4.2 | Maize is a more promising candidate for AMF inoculation

Maize plants generally exhibit higher MGR than wheat, largely due to differences in root architecture and morphology (Han et al., 2023). Ramírez-Flores et al. (2020) emphasize the importance of distinguishing between two components of the symbiosis: dependence (the ability of a variety to perform without AMF) and benefit (the degree to which a plant gains from the association), and a potential trade-off between host dependence and benefit is suggested. Consistently, maize displayed both high MGR and high AMF colonization (Figure 1; Figure 2). Maize roots typically have thick, deep roots with shorter root hairs, whereas wheat roots possess finer, longer root hairs and a more extensive network of fine roots. This morphology makes maize more dependent on AMF for fine-scale nutrient uptake, while wheat can access nutrients more independently, although it still benefits from the symbiosis (Frew, 2025). Root diameter also plays a role: maize roots, particularly the cortex cells, are thicker than those of wheat, providing more space for fungal colonization (Smith & Smith, 2011). The negative MGR observed in wheat in our study (Figure 1) may be attributable to the specific AMF strain used, which is a highly aggressive colonizer. Previous research has shown that aggressive AMF strains can negatively affect plant growth under low-phosphorus conditions by reducing sucrose availability (Graham & Abbott, 2000). Although direct comparisons of maize and wheat under identical conditions remain limited, our results support numerous studies indicating that maize is generally more responsive to mycorrhizal associations.

4.3 | Only one AMF species was tested

In healthy soils, plants are typically associated with multiple AMF species, whereas in this study, we tested only a single AMF strain across different plant varieties. Wheat and maize show variation in root colonization by native mycorrhizal communities at different scales (Ujvári et al., 2023; Veršulienė et al., 2024). The AMF strain, SAF22, has been tested with multiple plant species and field sites, providing up to 40% MGR but also negative under field conditions (Lutz et al., 2023). In our study, SAF22 increased growth by up to 7% but also caused reductions down to −25% (Figure 1; Figure 2). Studies indicate that multiple AMF strains often act synergistically across a wider range of conditions, enhancing plant responsiveness. Nevertheless, in fields with low native AMF abundance, SAF22 can still produce high MGR (Bender et al., 2019), while in other fields, it was suggested to function as a protector against pathogens (Branco et al., 2022). Different AMF species and strain compositions significantly affect plant growth and MGR (Deja-Sikora et al., 2023; Koziol et al., 2024). Further experiments are needed to determine whether the observed MGR range is specific to SAF22 or generalizable across other AMF strains.

4.4 | Short growth in sterilized soil might not reflect MGR under field conditions

Testing MGR under controlled environments may not fully reflect outcomes under field conditions. The relatively short growth duration of 60 days likely contributed to lower and inconsistent responses (Cheeke et al., 2019). Since maize and wheat did not reach flowering, grain yield and quality could not be assessed. Both experiments were conducted in uniform, sterile substrates, eliminating native microbial communities. However, indicators of the soil microbiome are strong predictors of MGR variability (Lutz et al., 2023), and the absence of a native microbiome likely limited both AMF colonization and functionality (Compant et al., 2025; Delgado-Baquerizo et al., 2025). Additionally, the use of homogeneous, sterile substrates reduces the applicability of findings to field conditions, where microbial diversity and soil structure play a critical role in shaping AMF dynamics. Despite these limitations, the observed variation in MGR among plant varieties under sterile, controlled conditions provides compelling evidence for the role of plant genotype in influencing mycorrhizal interactions. Field trials using multiple AMF strains under diverse biotic and abiotic conditions are required before making further recommendations for agronomic application. The maize variety LG30222 had an average MGR among the 15 varieties and a large range under field trials with the same mycorrhizal inoculation product (−12% to +40%; (Lutz et al., 2023)). Using one of the varieties from the high MGR range might cause even higher MGRs under field inoculation. This underscores the potential for incorporating such traits into breeding programs, which should ultimately be validated under field conditions.

5 | CONCLUSIONS

Despite decades of breeding, we observed a link between plant genetics and MGR. Among maize and wheat varieties recommended for farmers, MGR varied widely and tended to cluster by breeder. Field trials testing the plant varieties under natural conditions are required to provide recommendations for variety selection. We propose incorporating AMF interaction traits into breeding trials and recommended variety lists to encourage farmers to enhance plant–microbe associations through management practices or field inoculation. Strengthening these beneficial associations can improve soil health, support sustainable agriculture, and increase crop yield.

AUTHOR CONTRIBUTIONS

Design of the research: Ido Rog and Marcel G. A. van der Heijden. *Funding acquisition*: Ido Rog, Stefanie Lutz, and Marcel G. A. van der Heijden. *Performance of the research*: Ido Rog, Marco Malinowski, and Dylan Baumann. *Data analysis, collection, and interpretation*: Ido Rog, Marco Malinowski, and Dylan Baumann. *Writing the manuscript*: Ido Rog, Marco Malinowski, and Dylan Baumann. *Editing the manuscript*: Ido Rog, Marco Malinowski, Dylan Baumann, Raphaël Boussageon, Stefanie Lutz, and Marcel G. A. van der Heijden.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

All data and scripts are available on Zenodo, 10.5281/zenodo.19556622.

ORCID

Ido Rog https://orcid.org/0000-0002-9120-3617
Raphaël Boussageon https://orcid.org/0000-0002-5858-8105
Stefanie Lutz https://orcid.org/0000-0002-3845-0862
Marcel G. A. van der Heijden https://orcid.org/0000-0001-7040-1924

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SUPPORTING INFORMATION

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