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Wheat varieties show consistent differences in root colonization by mycorrhiza across a European pedoclimatic gradient

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Abstract

Arbuscular mycorrhizal (AM) fungi form mutualistic relationships with the majority of land plants and are an important part of the soil microbial community in natural and agricultural ecosystems. These fungi promote water and nutrient acquisition by their host plant and regulate the allocation of photosynthetic carbon to soil. Both crop variety and environment affect naturally occurring mycorrhizal abundance in roots, but the relative importance of those factors for mycorrhization is largely unknown. In a field study covering a large pedoclimatic gradient across four European sites, we (i) compared the abundance of AM fungi in the roots of 10 modern winter wheat (*Triticum aestivum* L.) varieties, (ii) evaluated the relative importance of variety and site for the variability in root colonization by AM fungi and (iii) tested the relationship between mycorrhizal abundance and grain yield. Root colonization by arbuscules and hyphae ranged from 10% to 59% and 20% to 91%, respectively, across all samples and varied by 8% and 18%, respectively, among varieties when averaged across sites. Variance decomposition analysis revealed a 10 times higher importance of site than variety for AM fungal root colonization. Specifically, we found the highest mycorrhizal abundance on the site with the most arid conditions and the lowest on the sites with low soil pH and high nutrient availability. Despite the low variability in mycorrhizal abundance among varieties, there were significant differences in both arbuscular and hyphal root colonization. However, this did not translate into an increase in yield as no significant relationships between mycorrhizal abundance at flowering and grain

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yield were detected. The consistent differences between wheat varieties in root colonization by AM fungi across European field sites underline that genetic drivers of mycorrhization are to some extent independent of the site. This highlights the relevance of breeding practices to shape a wheat variety's capacity for mycorrhizal symbiosis across a range of environmental conditions.

KEYWORDS
AM fungi, arbuscules, EJP SOIL, environmental conditions, hyphae, variance decomposition

1 | INTRODUCTION

Arbuscular mycorrhizal (AM) fungi are an important component of the soil biota in most agroecosystems and colonize the roots of the host plants by forming a mutualistic symbiosis. Those fungi form internal structures, namely, arbuscules, vesicles and intra- and intercellular hyphae, before developing a complex, ramified extraradical hyphal network into the surrounding soil (Trouvelot et al., 2015). This association potentially allows plants to explore larger volumes of soil and to acquire additional water and nutrients (Kakouridis et al., 2022; Trinchera et al., 2021) compared with plants lacking this symbiosis. The presence of AM fungi has been shown to reduce soil nitrogen (N) and phosphorus (P) losses (Qiu et al., 2022) and to promote sustainable nutrient cycling (Bender et al., 2014; Bender et al., 2015). Further, as pathways of root carbon to the soil (Vidal et al., 2018) and agents of root carbon stabilization in the soil matrix (Frey, 2019), AM fungi are an important component of the global carbon cycle (Leake, 2007). Thus, they could be key drivers of soil organic carbon accrual (Sulman et al., 2019; Verbruggen et al., 2021).

The extent of AM fungal colonization of plant roots is driven by multiple environmental factors, such as temperature, precipitation, soil pH or nutrient availability (Bender et al., 2019; Martínez-García et al., 2017; Wang et al., 2021). In addition, genetic predisposition determines a plant's ability to form mycorrhizal associations and to benefit from this symbiosis (Hetrick et al., 1993; Hetrick et al., 1995; Lehnert et al., 2017; Lehnert et al., 2018; Tawaraya, 2003; Thirkell et al., 2022). For instance, mycorrhizal dependence (i.e., plant growth response in the presence of AM fungi) has been found for the ancestors of wheat carrying the D genome but not for those carrying the A or B genomes, resulting in differentiated responses of modern cultivars of the hexaploid ABD genome (Hetrick & Schwab, 1992). Only few studies have examined how host plant genetics and environment simultaneously influence AM fungal colonization (Gehring et al., 2006).

Wheat is one of the most important field crops in Europe and easily colonized by AM fungi, but its susceptibility and/or responsiveness to mycorrhiza is highly influenced by the genotype (Lehnert et al., 2017). Modern breeding programs might have altered mycorrhizal dependence of wheat—both consistently decreased and increased growth response to AM fungi has been found for cultivars released after the 1950s compared with older cultivars (Hetrick & Schwab, 1992). Some modern wheat varieties may have even lost the ability to form AM fungal associations (Zhang et al., 2019).

Most studies on the genotypic variability in mycorrhizal colonization of wheat have been carried out under controlled conditions or after inoculation with AM fungi (Klironomos et al., 2000; Munkvold et al., 2004). As those study settings are not representative for agricultural practice, they may lead to biased conclusions on mycorrhizal colonization of modern wheat varieties under field conditions. To assess the role of AM fungi in wheat production and soil carbon accrual, the influence of varieties under various environmental conditions on mycorrhizal abundance needs to be better understood. Therefore, the aims of this study were to (i) compare the abundance of AM fungi in wheat roots between different varieties and sites, (ii) evaluate the relative importance of variety and site for the variability in mycorrhizal root colonization and (iii) test the relationship between mycorrhizal abundance and grain yield.

Highlights

- Mycorrhizal root colonization differs between wheat varieties across four European sites.
- Site is 10 times more important than wheat variety for mycorrhizal root colonization.
- Grain yield is not significantly related to mycorrhizal root colonization.

2 | MATERIALS AND METHODS

The study was carried out on four sites that were established within the Horizon 2020 project INVITE and the

European Joint Program SOIL project MaxRoot-C: CH-Es (Eschikon/Switzerland), DE-Fr (Freising/Germany), ES-Le (Lleida/Spain) and LT-Do (Dotnuva/Lithuania). The sites were chosen to cover the pedoclimatic variability in winter wheat production areas across Europe (Table 1, see Data S1 for location and management information). On each site, the same 10 winter wheat (*Triticum aestivum* L.) varieties were cultivated in the field season 2021/2022 in a variety testing trial. The 10 varieties chosen for the present study had commercial relevance and differed strongly in yield expectation based on their adaptability to certain climate conditions: Altigo, Aurelius, Bernstein, Dagmar, Julie, Montalbano, MV Nador, Nogal, RGT Reform and Tenor. The variety testing trials included three field replicates per site (= 30 experimental plots) except for CH-Es, where the 10 varieties were included in a large-scale variety testing panel and were therefore replicated only twice (= 20 experimental plots).

Winter wheat root samples from the experimental sites were taken at the crop flowering stage (BBCH 63–65) from 0 to 15-cm soil depth from three individual plants per experimental plot, which were combined to one composite sample per plot. In CH-Es, one field replicate was sampled twice to obtain the same number of samples as for the other sites. The samples were immediately taken to the lab at ambient temperature, where the roots were carefully separated from the soil during a washing process. They were cut into about 1.5-cm segments and dyed with an ink-vinegar mix to enhance the detectability of mycorrhizal structures. Mycorrhizal colonization was determined by microscopy in 100 intersections per sample at a magnification of ×100 according to McGonigle et al. (1990). Arbuscular and vesicular abundance was expressed as percentage (counts per 100 intersections), while hyphal abundance was calculated as the percentage of non-negative intersections. In addition, grain yield (at 15% moisture content) for each experimental plot and soil properties for each site (Table 1) were determined at harvest time. The data were analysed by means of simple linear, generalized mixed effects models, variance decomposition and principal component analysis (Data S1).

3 | RESULTS AND DISCUSSION

In this field study with 10 commercially relevant winter wheat varieties on four European sites with contrasting site conditions, 20%–91%, 10%–59% and 0%–3% of root segments were colonized with hyphae, arbuscules and vesicles, respectively. In other field studies, mycorrhizal colonization was found to be 10%–18% in 10 spring wheat varieties across four site-years in Canada (Kirk et al., 2011), 10%–22% in six bread wheat varieties under two phosphorus fertilization rates in South Australia (Nahar et al., 2020) and 8%–55% in six durum wheat varieties across three Tunisian sites (Boudabbous et al., 2022). The low root colonization by vesicles can be explained by the fact that not all AM fungal species seem to be forming these structures (Cavagnaro et al., 2001).

The varieties and sites showed distinct statistical groupings in arbuscular and hyphal abundances (Figure 1). However, differences between varieties were more pronounced in hyphae than arbuscules while differences between sites were more pronounced in arbuscules than hyphae. The latter might be due to the close relationship between AM fungal species composition and the formation of specific mycorrhizal structures. For example, all AM fungal species form hyphae, but species can differ in number and morphology of arbuscules (Cavagnaro et al., 2001; Johnson, 1993). Although we have not determined species composition, we expect huge differences between sites based on findings from regional studies in England, Italy and Switzerland (Bender et al., 2019; Turrini et al., 2017; van der Gast et al., 2011), thus possibly explaining the pronounced differences in arbuscular colonization between sites in our study. By contrast, different varieties at one site are less prone to differences in AM fungal species composition than to differences in AM fungal abundance (Hannula et al., 2010; Londoño et al., 2020), which might explain the larger differences in hyphal than arbuscular colonization between varieties in our study (Figure 1).

Variety explained 7% and 5% of the variance in hyphal and arbuscular abundance, respectively, while site explained 69% and 51% (Figure 1), indicating that site was 10 times more important than variety for mycorrhizal abundance. Those findings corroborate the conclusion of Meyer et al. (2021), who found that soil and climate conditions affected mycorrhizal colonization more strongly than genotype groups of modern, genetically modified and landrace maize in an on-farm study in Brazil. To our knowledge, our study is the first study that examined how host plant genetics and environment simultaneously influence naturally occurring mycorrhizal abundance in roots of modern wheat varieties across an intracontinental pedoclimatic gradient.

The sites in our study were characterized by pronounced differences in climate (Table 1) with the highest temperature between emergence and flowering in ES-Le (8.4°C) and the lowest in LT-Do (3.5°C) and the highest precipitation between emergence and flowering in CH-Es (450 mm) and the lowest in ES-Le (102 mm). The particularly high AM fungal root colonization in ES-Le might have been a response to low water availability during crop growth by investment into the hyphal network to reduce plant water stress (Kakouridis et al., 2022; Vidican et al., 2020), whereas wet soil conditions in CH-Es and LT-Do might have reduced the growth of arbuscules and hyphae (García et al., 2008). Soil characteristics also varied among sites (Table 1), e.g., soil pH between 5.2 (CH-Es) and 7.5 (ES-Le) or available phosphorus between 13 mg kg^{-1} (LT-Do) and 47 mg kg^{-1} (CH-Es). Low soil pH and high phosphorus supply have been shown to impair root colonization by AM fungi (Bender et al., 2019; Wang et al., 1993), which might also explain the low values in mycorrhizal abundance in CH-Es in our study. The relative importance of individual climate or soil variables for mycorrhizal root colonization, however, cannot be discerned from our data set due to the low number of sites and only one data point per site for each climate or soil variable.

Despite the low variability in AM fungal abundance among varieties, we still found clear differences between the varieties in both arbuscular and hyphal root colonization (Figure 1). Genotype effects on mycorrhizal abundance in roots have mainly been attributed to differences between modern and old varieties or modern varieties and landraces (Boudabbous et al., 2022; Ellouze et al., 2016; Nahar et al., 2020), whereas modern varieties only seem to be less diverse (Hildermann et al., 2010; Vierheilig & Ocampo, 1991). One reason for this might be the genetic dissimilarity of the studied varieties. In a genome-wide association study with 94 wheat genotypes differing in both year of release (before 1945–2010) and origin (Americas, Asia, Europe and Oceania), Lehnert et al. (2017) found a large variation in root colonization among genotypes (24%–56%) and significant association to 30 genetic markers. Although our panel is composed of only 10 varieties, their breeding background seems to be sufficiently diverse to disclose genotypic differences in mycorrhizal abundance and genetic drivers seem to be site-independent to a certain extent.

We did not detect any relationship between mycorrhizal root colonization at flowering and grain yield at harvest as the slopes were not significantly different from zero, neither the coefficients of the main effects across all sites (hyphal colonization: 0.004, $p = 0.60$; arbuscular colonization: 0.003, $p = 0.79$) nor the coefficients for the individual sites (Figure 2). Although the site with the lowest grain yield displayed the highest mycorrhizal root colonization and vice versa (Figure 2), a causality cannot be derived based on our study design. Multiple overlaying drivers such as climate, soil and management conditions are responsible for yield formation and cannot be disentangled with four field sites. In a meta-analysis on yield response to mycorrhization, a significant positive effect in the field was only found for a vast number of inoculation experiments (Zhang et al., 2019). Studies on

TABLE 1 Climate and soil (0–0.15-m depth) properties of four European sites. Further information is provided in Data S1.

Site abbreviation	Climate[a]	MAT [°C]	MAP [mm]	Temperature emergence-flowering [°C]	Precipitation emergence-flowering [mm]	Soil type (WRB)	Texture	Clay content [%]	pH ($CaCl_2$) [−]	SOC [g kg^{-1}]	SIC [g kg^{-1}]	Total N [g kg^{-1}]	Olsen-P [mg kg^{-1}]
CH-Es	Cfb	9.2	1175	6.2	450	Gleyic Cambisol	Loam	18	5.2	14	0	1.4	47
DE-Fr	Dfb	9.8	960	5.2	339	Cambisol	Silt loam	20	6.6	13	0	1.2	40
ES-Le	Cfb	15.5	450	8.4	102	Calcisol	Loam	24	7.5	23	51	2.3	38
LT-Do	Dfb	7.8	705	3.5	388	Haplic Endocalcaric Endostagnic Anthraquic Luvisol	Sandy loam	13	6.8	11	0	0.9	13

Abbreviations: MAP, mean annual precipitation; MAT, mean annual temperature; SIC, soil inorganic carbon; SOC, soil organic carbon.

[a] Köppen-Geiger classification: Cfb, oceanic; Dfa, continental; Dfb, humid continental.

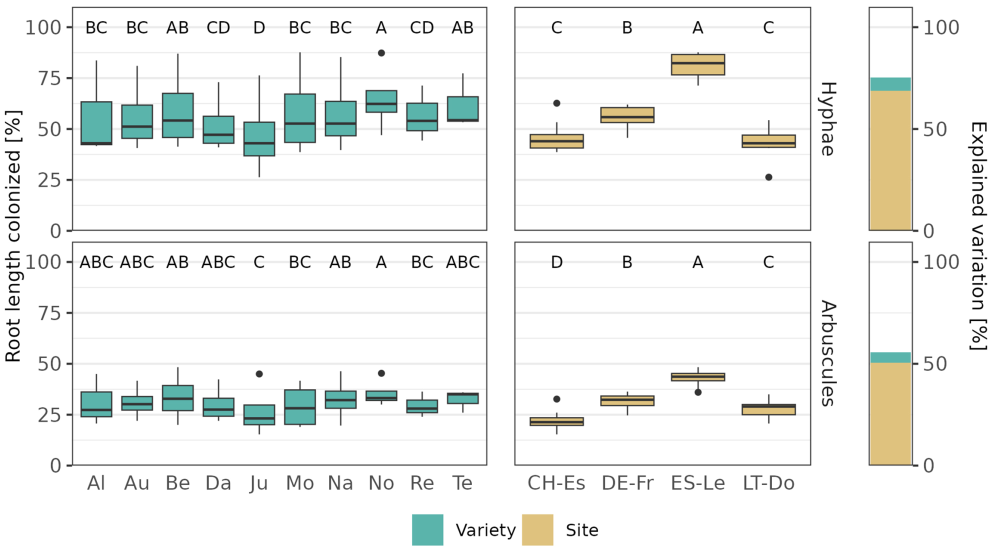

FIGURE 1 Hyphal and arbuscular abundance in roots of 10 winter wheat varieties grown at four European sites grouped by variety (left) or site (middle) and explained variation (LMG scores) in hyphal and arbuscular root colonization by variety and site (right). The boxplots are based on average values of three field replicates per variety: $N = 3$ or 4 sites per variety (left) and $n = 9$ or 10 varieties per site (middle). Al, Altigo; Au, Aurelius; Be, Bernstein; Da, Dagmar; Ju, Julie; Mo, Montalbano; Na, MV Nador; No, Nogal; Re, RGT Reform; Te, Tenor.

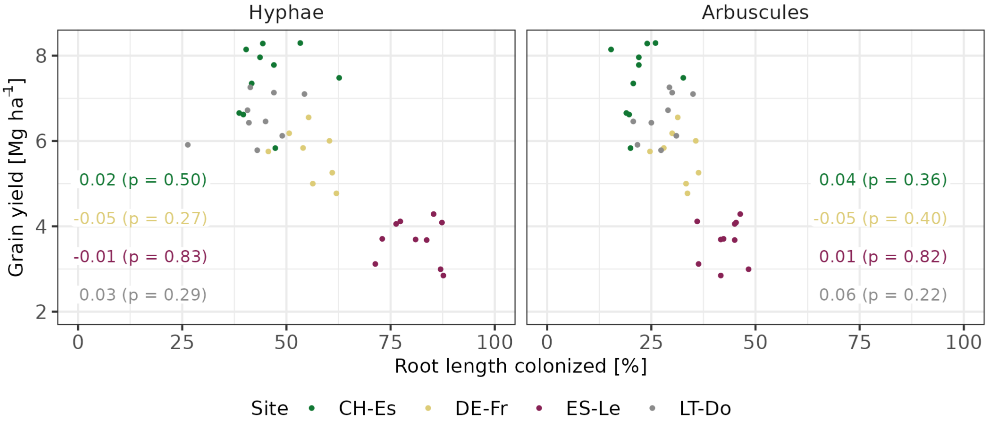

FIGURE 2 Relationship between hyphal and arbuscular root colonization at flowering and grain yield at harvest of 10 winter wheat varieties grown at four European sites. Points: average values of three field replicates per variety; numbers: coefficients of the slopes of simple linear models fitted to mycorrhizal abundance and yield per site; numbers in brackets: *p*-values.

yield response to naturally occurring mycorrhizal abundance of different varieties are comparably scarce (Ryan & Graham, 2018) and inconclusive, including positive effects when testing across old and modern varieties (Boudabbous et al., 2022) and no effects when testing only old or modern varieties (Kirk et al., 2011). In general, AM fungal colonization is considered to increase mineral nutrient uptake, disease resistance and drought tolerance of the host plants as well as to provide other ecosystem services, such as improving soil structure and closing nutrient cycles (Cavagnaro et al., 2015; Van der Heijden et al., 2015). Hence, increasing crop growth may not be the only benefit they can provide (Rillig et al., 2019). Moreover, genotypic differences in, e.g., morphological properties of the root system or crop physiology, may obscure benefits of mycorrhization for yield, which need to be studied in more detail in field experiments (Ryan & Graham, 2018).

4 | CONCLUSION

This study is the first to explore how both host plant genetics and the environment influence mycorrhizal root colonization within a variety × site network. It provides field-based evidence that winter wheat varieties can differ in their ability to form AM fungal associations across a wide environmental gradient. To gain a more profound understanding of the influence of soil properties and other environmental parameters, the pedoclimatic drivers need to be explored on a higher number of sites and in more detail in future studies. Even though the effect of site on mycorrhizal abundance was 10 times greater than the effect of variety, a 50% higher AM fungal root colonization between the least and the most mycorrhiza-forming variety was observed. Hence, genetic factors are substantial drivers of mycorrhizal abundance, underscoring the relevance of breeding practices to shape a wheat variety's capacity for mycorrhizal symbiosis. The lack of significant relationships between mycorrhizal abundance and yield in our study underscores the complex interplay of factors affecting crop performance beyond mycorrhizal colonization and emphasizes the need for continued research to fully understand the potential of mycorrhizal associations in agriculture.

AUTHOR CONTRIBUTIONS

Agnė Veršulienė: Data curation; investigation; funding acquisition; writing – original draft; resources. **Juliane Hirte:** Conceptualization; data curation; investigation; formal analysis; funding acquisition; visualization; project administration; resources; writing – original draft. **Federica Ciulla:** Data curation; investigation; writing – review and editing. **Moritz Camenzind:** Data curation; writing – review and editing. **Axel Don:** Conceptualization; funding acquisition; project administration; writing – review and editing; resources. **Fabien Durand-Maniclas:** Data curation; writing – review and editing. **Henrike Heinemann:** Data curation; writing – review and editing. **Juan M. Herrera:** Conceptualization; funding acquisition; project administration; resources; writing – review and editing. **Andreas Hund:** Data curation; writing – review and editing; resources. **Felix Seidel:** Data curation; funding acquisition; writing – review and editing. **Marta da Silva-Lopes:** Data curation; funding acquisition; resources; writing – review and editing. **Monika Toleikienė:** Data curation; funding acquisition; resources; writing – review and editing. **Margot Visse-Mansiaux:** Data curation; writing – review and editing. **Kang Yu:** Resources; writing – review and editing. **S. Franz Bender:** Conceptualization; methodology; validation; resources; writing – review and editing.

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CONFLICT OF INTEREST STATEMENT

All authors declare that they have no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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