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Special Issue Article

Organic agricultural practice enhances arbuscular mycorrhizal symbiosis in correspondence to soil warming and altered precipitation patterns

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Summary

Climate and agricultural practice interact to influence both crop production and soil microbes in agroecosystems. Here, we carried out a unique experiment in Central Germany to simultaneously investigate the effects of climates (ambient climate *vs*. future climate expected in 50–70 years), agricultural practices (conventional *vs*. organic farming), and their interaction on arbuscular mycorrhizal fungi (AMF) inside wheat (*Triticum aestivum* L.) roots. AMF communities were characterized using Illumina sequencing of 18S rRNA gene amplicons. We showed that climatic conditions and agricultural practices significantly altered total AMF community composition. Conventional farming significantly affected the AMF community and caused a decline in AMF richness. Factors shaping AMF community composition and richness at family level differed greatly among Glomeraceae, Gigasporaceae and Diversisporaceae. An interactive impact of climate and agricultural practices was detected in the community composition of Diversisporaceae. Organic farming mitigated the negative effect of future climate and promoted total AMF and Gigasporaceae richness. AMF richness was significantly linked with nutrient content of wheat grains under both agricultural practices.

Introduction

Agriculture depends greatly on climatic conditions; therefore, climate change in terms of increasing temperature and altered precipitation patterns introduces uncertainties into the global food production and threatens biodiversity in agroecosystems (Parry *et al*., 2004; Harley, 2011; Malhi *et al*., 2020). In turn, agricultural practice strongly affects climate, triggering societal demand for more sustainable and environmentally friendly methods. Organic farming is an alternative to conventional agriculture that contributes to climate change mitigation by reducing N_2O, CH_4 and CO_2 emissions from soils (Mondelaers *et al*., 2009) and promoting biodiversity (Bengtsson *et al*., 2005; Hole *et al*., 2005).

Arbuscular mycorrhizal association is the most ancient symbiosis between the roots of up to 80% of terrestrial vascular plants and fungi of subphylum Glomeromycotina (Smith and Read, 2008; Spatafora *et al*., 2016). Arbuscular mycorrhizal fungi (AMF) are an important component of agroecosystems. They do not only enhance plant resistance towards biotic and abiotic stressors, promote plant health and crop productivity (Al-Karaki *et al*., 2004; Kempel *et al*., 2010; Mäder *et al*., 2011; Zhang *et al*., 2019), but also contribute to enhanced ecosystem performance and

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sustainability (Thirkell *et al*., 2017; Rillig *et al*., 2019; Field *et al*., 2020). AMF have a key role in maintaining soil structure and function (Jeffries *et al*., 2003; Chen *et al*., 2018). Through their extra-radical mycelium and production of the glomalin protein, AMF increase water-stable soil aggregates and reduce soil erosion (Rillig, 2004; Mardhiah *et al*., 2016). They influence the soil carbon dynamics as 4%–20% of plant photoassimilates are allocated to the AMF (Bago *et al*., 2000). In addition, they contribute to further nutrient cycles, mainly of phosphorus (Karandashov *et al*., 2004) and nitrogen (Hodge and Storer, 2014). Therefore, studies focusing on how climate change would influence AMF communities in agroecosystems are crucial for predicting plant responses as well as ecosystem functions and services.

Climate change comprises a variety of elements, such as elevated atmospheric carbon dioxide concentrations (eCO_2), warming and altered precipitation patterns. These factors can affect AMF directly, or indirectly through their host plants (Cotton, 2018), or alter the interaction between AMF and the plants. A meta-analysis study showed that AMF have been promoted by elevated eCO_2 (Treseder, 2004). On the other hand, warming and variable precipitation were found to have more wavering impacts on AMF than eCO_2 (Bennett and Classen, 2020). However, no consistent trends can explain the direction of the detected impacts. For instance, although soil warming has been found to have positive (Rillig *et al*., 2002; Hu *et al*., 2015; Wheeler *et al*., 2017), neutral (Rudgers *et al*., 2014) and negative (Gao *et al*., 2016; Wilson *et al*., 2016) impacts on root colonization rate, it increased (Kim *et al*., 2015) or did not affect (Gao *et al*., 2016) spore density. Similarly, AMF community composition has been observed to be altered (Yang *et al*., 2013) or unaffected (Kim *et al*., 2015; Gao *et al*., 2016) by warming. Impact of altered rainfall patterns on AMF is less studied; however, AMF communities were found to resist rainfall reduction and drought stress in some ecosystems (Furze *et al*., 2017; Maitra *et al*., 2019), but were altered due to increased precipitation in others (Gao *et al*., 2016). Warming and altered precipitation patterns as elements of climate change do not occur in isolation, to the best of our knowledge. Nevertheless, the combined and interactive effects of both factors on AMF communities have been poorly studied.

Agriculturally-used land is known to be less rich in AMF communities compared to natural land (Gosling *et al*., 2006; Öpik *et al*., 2006). Agricultural practices in terms of intensity of soil management, crop rotation systems, fertilizers amendment and pesticide application significantly influence AMF abundance and community composition (Oehl *et al*., 2003; Oehl *et al*., 2004; Verbruggen *et al*., 2010; Peyret-Guzzon *et al*., 2016; Banerjee *et al*., 2019; Aldrich-Wolfe *et al*., 2020). However, experimental evidence indicates that organic farming, compared to conventional farming systems, is less detrimental to AMF (Gosling *et al*., 2006). Moreover, Verbruggen *et al*. (2010) found that a shift from conventional to organic farming corresponded to a change in AMF community composition, which resembled that in moderately used grasslands. In general, low-input organic agriculture enhances AMF populations (Oehl *et al*., 2004; Verbruggen *et al*., 2010). Nevertheless, the influence of the various agricultural regimes on each specific arbuscular mycorrhizal taxa is only investigated to a lesser extent. Clearly, the interactive influence of climate changes and agricultural regimes on the molecular richness and community composition of AMF is so far scarcely studied.

Wheat (*Triticum aestivum* L.) is a major cereal plant grown under diverse climatic conditions (Marris, 2008). The positive contribution of cultured AMF towards wheat growth, quality and yield is well studied (Treseder, 2013; Lehmann and Rillig, 2015; Watts-Williams and Gilbert, 2019). However, the contribution of naturally occurring AM fungal communities in agroecosystems to growth-related traits (in terms of nutrient concentrations and grain quality) is not yet well understood. For instance, García de León *et al*. (2020) reported varied responses of different wheat cultivars to AMF inoculum originated from organically managed fields. On the other hand, Gottshall *et al*. (2017) found a positive effect of organic field inoculum on wheat growth.

The present study took advantage of a field infrastructure, the Global Change Experimental Facility (GCEF), established in Germany. This facility has been designed to investigate the consequences of a predicted future climate scenario on ecosystem processes under different land-use types on large field plots in comparison with ambient climate (Schädler *et al*., 2019). Here, we aimed to evaluate the impact of future climate and agricultural practices (conventional *vs*. organic farming), as well as their combined effects on total AMF and individual predominant mycorrhizal families. In addition, we aimed to evaluate the relationship between molecular richness of indigenous root AMF and wheat yield parameters. Accordingly, we investigated the dynamics of mycorrhizal richness and community composition in wheat roots across different development stages of the plant, including the beginning of stem elongation (rosette), inflorescence emergence (heading) and ripening. We hypothesized that AMF richness and community composition will be shaped by climatic conditions, agricultural practices, and their interactions in complex manners. Specifically, we expected that (i) the future climate scenario will alter AMF richness and community composition, (ii) organic farming will maintain the AMF richness and community composition under future climate scenario as compared with the current climate, (iii) AMF richness will positively correlate with wheat yield and

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nutrient concentrations only in organically managed farms, where plant nutrition is highly dependent on AMF.

Results

AM fungal identities

A total of 192 ASVs were assigned to Glomeromycotina and matched 33 virtual taxa (VT) from the MaarjAM database. They belonged to three orders (Glomerales: 94 ASVs, Diversisporales: 63 ASVs, and Archaeosporales: 12 ASVs), plus 23 that were unclassifiable glomeromycetous ASVs. The classified ASVs belonged to seven families (Ambisporaceae, Archaeosporaceae, Diversisporaceae, Gigasporaceae, Pacisporaceae, Claroideoglomeraceae and Glomeraceae) and nine genera (*Ambispora*, *Archaeospora*, *Diversispora*, *Scutellospora*, *Pacispora*, *Claroideoglomus*, *Funneliformis*, *Rhizophagus* and *Septoglomus*). The most ASV-rich families were Glomeraceae, Diversisporaceae and Gigasporaceae, and their relative abundance accounted for ~ 60%, ~ 10% and ~ 9% of total sequences, respectively. The most frequently detected ASVs were classified as *Funneliformis* sp. (ASV2 and ASV3), *Funneliformis mosseae* (ASV4), *Rhizophagus intraradices* (ASV5) and *Archaeospora schenckii* (ASV8) (Fig. S1), and were detected in roots at all life stages of wheat under both climate regimes and both agricultural practices. Three genera were detected only in organic farming plots, namely, *Ambispora* (heading stage/future climate), *Pacispora* (ripening stage/future climate) and *Septoglomus* (rosette stage/ambient climate and in all growth stages/future climate).

Climate and soil factors influencing AMF community composition and richness

PERMANOVA and Spearman's rank correlation were carried out to examine the relative importance of each edaphic factor (Tables S1 and S2) for shaping AMF community composition and richness, respectively (Table S3). AMF communities significantly correlated with soil moisture (influenced by the climate regime), pH, mineral forms of N (NO_3 and NH_4) and plant-available P and K. In addition, significant correlations between soil stoichiometry (soil C/P and N/P ratio) and AMF community composition were detected. The factors shaping total and specific AMF family richness were total C, total N, NH_4, inorganic N, P, C/P ratio and pH. For instance, AMF ASV richness correlated inversely with total C, total N and C/P ratio. Gigasporaceae richness correlated inversely with NH_4, total inorganic N, C/N, and C/P ratio and positively with P and pH.

Impact of climate change, agriculture practices, plant growth stage and their interactions on arbuscular mycorrhizal community composition

PCoA analysis and PERMANOVA indicated that the overall AMF community composition differed between ambient and future climates, conventional and organic farming practices and plant growth stages (Table 1; Figs S2). Additionally, Glomeraceae, Diversisporaceae and Gigasporaceae were predominant with higher ASV richness and higher relative sequences abundances, followed by Archaeosporaceae and Claroideoglomeraceae, in both agricultural practices under both climates (Fig. S3). Two families (Ambisporaceae

Table 1. PERMANOVA (Bray–Curtis dissimilarity matrix, permutations = 999) tested the influence of climate regime, agricultural practice, plant growth stage and their interactions on arbuscular mycorrhizal community composition. Significant values are indicated in **bold**.

	AMF community		Glomeraceae		Gigasporaceae		Diversisporaceae	
Model	R^2	F.Model	R^2	F.Model	R^2	F.Model	R^2	F.Model
Climate regime	**0.04**	**2.60*****	**0.049**	**3.04****	0.03	1.11	0.03	1.32
Agricultural practice	**0.04**	**2.87****	**0.05**	**3.16****	0.03	1.36	0.02	1.17
Growth stage	**0.06**	**1.98****	0.05	1.60	0.05	1.03	0.03	0.70
Climate regime × Growth stage	0.02	0.90	0.02	0.84	0.04	0.73	0.04	0.85
Agricultural regime × Growth stage	0.02	0.92	0.03	1.16	0.08	1.48	0.03	0.76
Climate regime × Agricultural practice	0.02	1.44	0.01	0.82	0.02	0.77	**0.05**	**2.45****
Climate × Agricultural practice × Growth stage	0.02	0.69	0.01	0.52	0.09	1.62	0.03	0.73

	Ambient climate AMF community		Future climate AMF community	
	R^2	F.Model	R^2	F.Model
Agricultural practice	**0.06**	**2.08***	**0.07**	**2.22***
Growth stage	**0.10**	**1.68***	0.08	1.24
Agricultural practice × Growth stage	0.05	0.88	0.05	0.74

*$P < 0.05$;
**$P < 0.01$;
***$P < 0.001$.

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and Pacisporaceae) appeared to be restricted to organic farming under future climate, however only with low relative abundances (Fig. S3). Ambient climate AMF communities revealed significant differences between the two agricultural practices and between each plant growth stage. Similarly, the future climate community was significantly shaped by the agricultural practice, but did not change in response to the plant growth stages. A deeper look into the response of community composition of each AMF family to the tested experimental factors revealed that the Glomeraceae was shaped by climate regimes and agricultural practices (Table 1). The interactive impact of climate and agricultural practice was evident for community composition of Diversisporaceae, while Gigasporaceae showed resilience towards all tested factors.

Impact of climate change, agriculture practices, plant growth stage and their interactions on mycorrhizal ASV richness

Future climate alone neither had significant effect on the mycorrhizal ASV richness, nor within each of the three most frequently detected AMF families (Table 2). In contrast, AMF responded significantly to the different agricultural practices. Organic farming enhanced total AMF and Diversisporaceae richness in wheat roots (Table 2; Fig. 1A and D). In addition, a significant impact of interaction between climate and agricultural practice was observed for total AMF and Gigasporaceae; we found that organic farming increased the mycorrhizal ASV richness under the future climate regime. During different growth stages of wheat, AMF richness within the roots changed. In general, higher AMF richness was detected during the ripening stage after fruit development. However, the dynamics of individual AMF families within plant roots differed. For instance, the stage of stem elongation (rosette) was characterized by higher Glomeraceae and lower Gigasporaceae richness (Fig. 1B and C). By the beginning of wheat head emergence, this pattern was inversed.

Correlation between AMF molecular richness colonizing wheat roots and yield traits

We performed correlation analyses to explore possible links between the richness of total communities and specific families of the root-colonizing AMF and wheat production criteria (grain, straw dry mass and straw/ grain ratio, Fig. S4 and Table S4). Contrary to our expectations, wheat yield variables correlated positively with mycorrhizal richness under the nutrient-rich conventional farming system (Fig. 2). For instance, grain and straw dry mass correlated positively with the richness of family Glomeraceae (ρ = 0.69–0.82, P = 0.014–0.028), while straw/grain ratio correlated negatively with richness in Gigasporaceae. In contrast, under organic farming, grain yield correlated negatively with total AMF richness at the heading stage (ρ = −0.63, P = 0.049), while straw/grain ratio correlated positively with Gigasporaceae.

Correlation between AMF molecular richness colonizing wheat roots and nutrient concentrations of wheat grains

Spearman's rank correlation analyses were performed to elucidate possible links between the richness of

Table 2. Results of split-split-plot ANOVA summarizing the impacts of climate regime, agricultural practice, plant growth stage and their interactions on richness of total AMF community and the dominating families in wheat roots. Degree of freedom (DF). Significant effects are indicated in **bold** font.

	Total AMF richness			Gigasporaceae			Glomeraceae			Diversisporaceae		
Factors	DF	*F*-value	*P*-value	DF	*F*-value	*P*-value	DF	*F*-value	*P*-value	DF	*F*-value	*P*-value
Climate regime	1	0.09	0.768	1	0.19	0.679	1	0.78	0.426	1	0.57	0.491
Agricultural practice	1	**7.72**	**0.023***	1	1.21	0.302	1	2.04	0.191	1	**7.14**	**0.028***
Climate regime × Agricultural practice	1	**7.72**	**0.023***	1	**5.45**	**0.047***	1	0.20	0.665	1	0.79	0.399
Growth stages	2	**11.52**	**0.0001*****	2	**7.15**	**0.002****	2	**8.62**	**0.001****	2	0.81	0.453
Growth stage × Climate regime	2	1.74	0.190	2	1.93	0.160	2	0.22	0.798	2	0.11	0.890
Growth stage × Agricultural practice	2	0.14	0.867	2	1.15	0.329	2	0.05	0.943	2	0.08	0.916
Growth stage × Climate regime × Agricultural practice	2	0.85	0.434	2	**3.32**	**0.048***	2	1.03	0.365	2	0.37	0.689

*P < 0.05;
**P < 0.01;
***P < 0.001.

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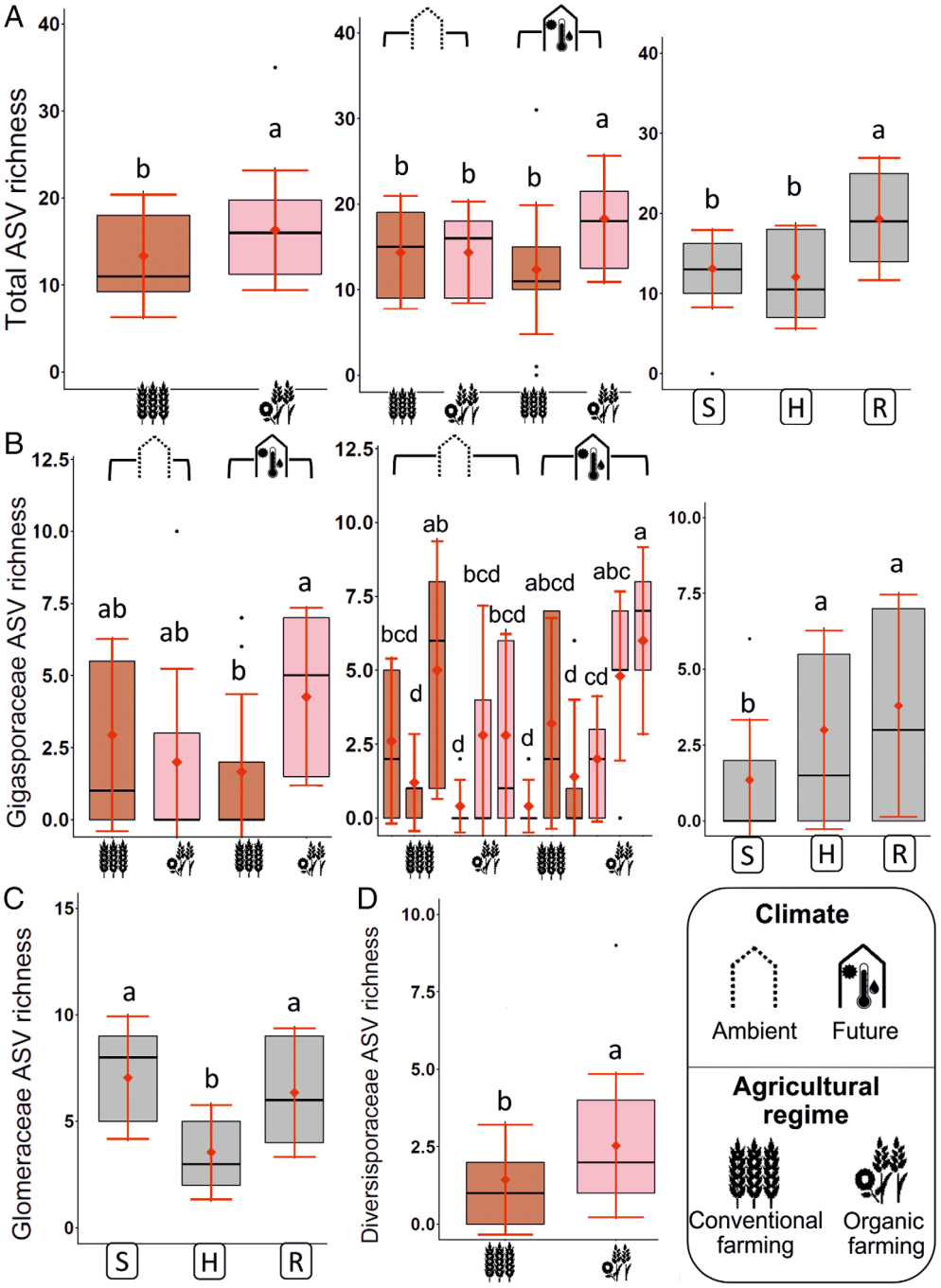

Fig 1. ASV richness of (A) Total AMF, (B) Gigasporaceae, (C) Glomeraceae and (D) Diversisporaceae within wheat roots in conventional and organic farming systems under ambient and future climate regimes. Plant growth stages; S = rosette, H = heading, R = ripening. Different lowercase letters indicate significant differences according to Fisher's Least Significant Difference. Error bars represent standard deviation, ♦ represents mean values.

total communities and specific families of the root-colonizing AMF and nutrient concentrations of wheat grains (C, N, P, K, Mg, Ca, S, Na, Mn and Fe) under both agricultural practices (Tables S5 and S6). Under conventional farming, we found C, N and Fe concentrations of the grains to be negatively correlated, but P, K, Mg and Mn positively correlated with AMF richness (Fig. 3). On the other hand, under organic farming, P, K, S, Na and Mn correlated positively with AMF richness.

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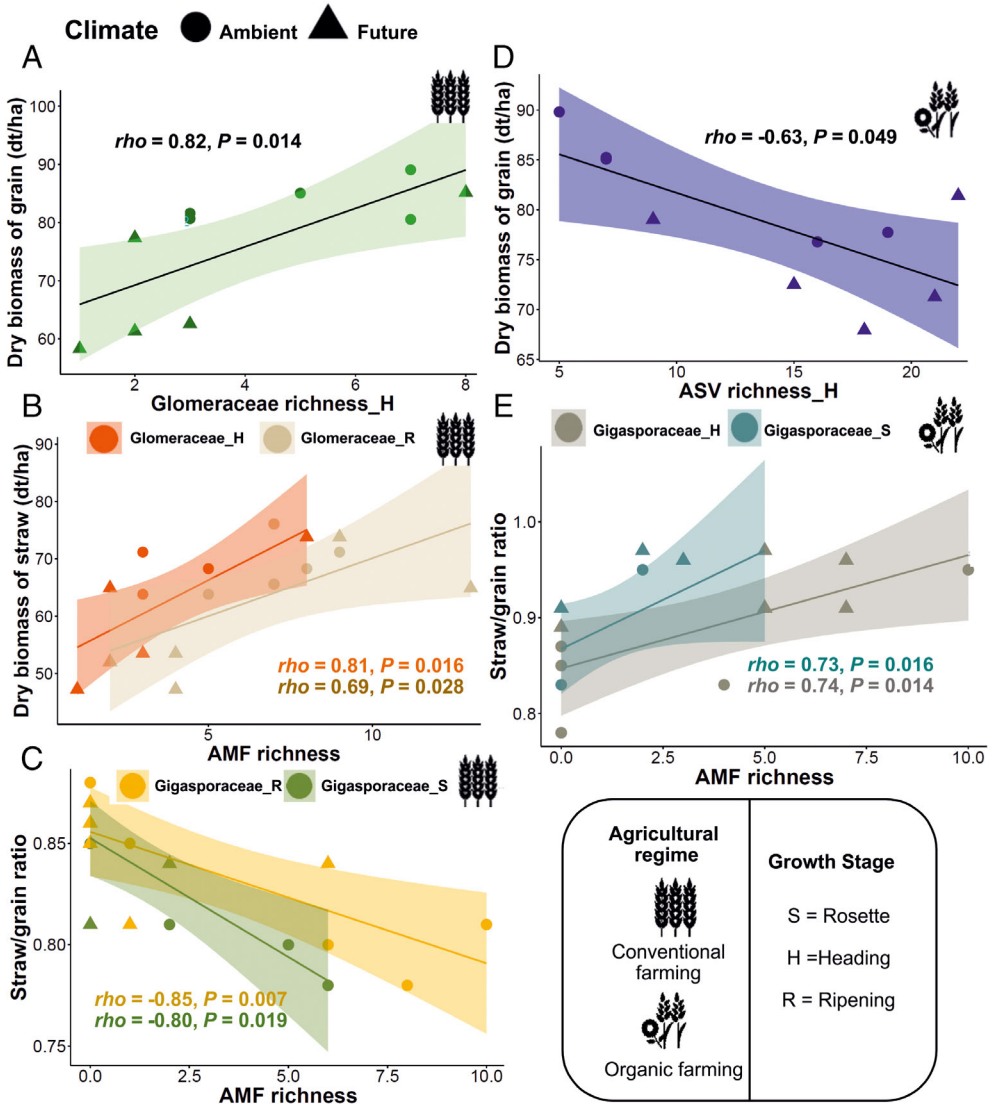

Fig 2. Spearman's rank correlations between AMF richness and yield in (A–C) conventional and (D, E) organic farming plots. Plant growth stages; S = rosette, H = heading, R = ripening.

Discussion

Future climate shapes AMF community composition but not AMF richness

Climate manipulation at GCEF has started 1 year before our experiment. The future climate scenario included altering of precipitation patterns as well as an average increase in daily mean temperature by 0.55°C (Schädler *et al*., 2019). This was accompanied by a stronger increase in minimum temperatures (1.14°C in average). Additionally, a longer frost-free period on the future climate plots was detected (Schädler *et al*., 2019), which influenced plant growth and accordingly the associated microbiomes. Moreover, precipitation was increased in spring and reduced during summer (before harvest on July), which means that the plant and associated microbes were influenced by both excess precipitation and drought stress. Therefore, the AMF communities were influenced by several climate factors that affected them directly or indirectly by influencing the host plant physiological processes. Although we sampled a successional AMF community that differed according to the sampling time, our analyses revealed strong correlation between soil moisture content and AMF communities during plant growth stages. One year of the realistic future scenario that manipulated both temperature and precipitation was enough to detect significant changes in soil organisms and soil functions by previous studies in the same platform (Yin *et al*., 2019; Yin *et al*., 2020). In our study, we found that future climate significantly altered

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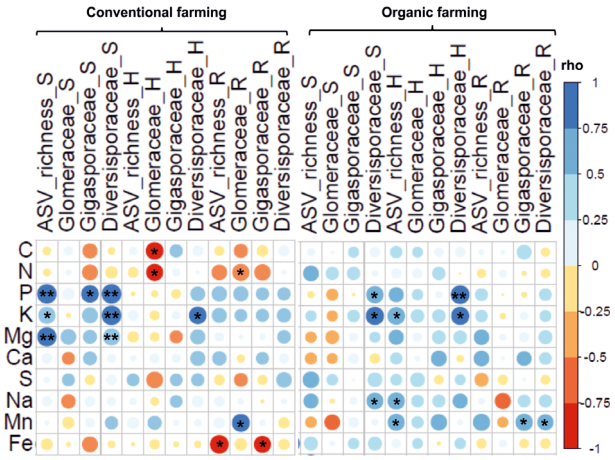

Fig 3. Spearman's rank correlations between AMF richness and nutrient concentrations of wheat grain under conventional and organic farming practices. Significant correlations are indicated in **bold**. (*P < 0.05, **P < 0.01). Plant growth stages; S = rosette, H = heading, R = ripening.

the total AMF and Glomeraceae community, but not AMF richness. Increased temperature and precipitation were found to increase C allocation to the root zone, while drought reduces C flow (Gorissen *et al*., 2004), which potentially alters the root microbial composition. Bennett and Classen (2020) in their meta-analysis of field studies summarized the effect of warming on AMF, with 38%, 57% and 5% of the studies showing positive, neutral and negative effect, respectively, on AMF richness, biomass and/or root colonization, while AMF community composition was altered in 44% of the studies. The variations in climatic conditions and land-uses play a crucial role in determining the impact of warming and altered precipitation patterns on AMF (Heinemeyer *et al*., 2004; Yang *et al*., 2013; Gao *et al*., 2016; Maitra *et al*., 2019); therefore, it is hard to generalize the influence of climate change on AMF behaviour.

Agricultural practices alter both community composition and richness of AMF colonizing wheat roots

Our results supported our second hypothesis and revealed that the agricultural practices significantly shaped total AMF and Glomeraceae community. Organic farming was found to significantly enhance total AMF and Diversisporaceae richness. Our findings bear resemblance to many studies performed on AMF under various agricultural management systems. Using traditional morphological identification, AMF communities were found to be shaped by the farming system, management intensity as well as fertilization, and AMF species richness and spore densities, diversities and abundance were higher under organic farming as compared to the conventional farming strategy (Oehl *et al*., 2004; Säle *et al*., 2015). Using high-throughput sequencing techniques, AMF community composition has been found to differ between organic and conventionally farming systems, with AMF abundance reported to be higher in soil and roots in organic farming systems (Banerjee *et al*., 2019; Aldrich-Wolfe *et al*., 2020).

In the present study, multiple interacting factors may have shaped the AMF community composition. During our field experiment (2015), water-soluble fertilizers (N and MgO), additives (21% N), fungicides (epoxiconazole and fluxapyroxad) as well as a herbicide (bentazon), were applied only to the conventionally managed field plots. Our results showed that the decline in AMF richness was related to the high concentrations of soil C and N in conventional farming system. Additionally, we observed that soil factors such as P, K, NO_3 and NH_4 as well as soil C/P and N/P ratios shaped total AMF community. This could be explained by a trade-off between P, N and C in the mycorrhizal symbiosis (de Mazancourt and Schwartz, 2010; Johnson, 2010). According to the 'trade balance model' (Johnson, 2010), under high concentration of available soil P and N, AMF colonization and richness are suppressed due to a reduced C allocation to the symbiont (Gosling *et al*., 2013; Aldrich-Wolfe *et al*., 2020). Conversely, AMF richness may be high when the minerals they provide to plants are scarce as in low-input organic farming systems (Alloush and Clark, 2007; Werner and Kiers, 2015).

Another factor that probably led to lower AMF richness in conventionally managed plots was the application of azole fungicides as well as other pesticides. Azole fungicides have been found to decrease hyphal biomass and activity, thereby reducing root colonization (Kjøller and Rosendahl, 2000; Calonne *et al*., 2012; Ye *et al*., 2012; Riedo *et al*., 2021). In addition, application of different crop rotation systems to the organically and conventionally managed plots could have affected the wheat-mycorrhizal colonization. In our study, the crop rotation of the organic farming system consisted of cultivating AMF-host broad bean in the season before the winter wheat. Such a system can maintain a large population of soil resident AMF (Isobe *et al*., 2015), thereby enhancing AMF colonization in the subsequent wheat cultivation. In contrast, the previous cultivation of winter rapeseed (Brassicaceae), which is non-AMF host plant (Cosme *et al*., 2018), in our conventional agriculture scenario may have lowered AMF colonization of the next wheat crop, as cultivation of non- AMF host plants decreases soil indigenous AMF and reduces fungal colonization of succeeding crops (Karasawa and Takebe, 2011).

Interactive impact of future climate scenario and agricultural practices on AMF

Diversisporaceae community structure responded differently to the agricultural practices under different climate

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treatments. At a global scale, Diversisporaceae is reported as an indicator of disturbed habitats (Moora *et al*., 2014). Other studies have shown that Diversisporaceae, over other taxa, was significantly influenced by soil re-cultivation following open-cast mining (Roy *et al*., 2017) or by altered precipitation and relative air humidity (Sun *et al*., 2013; Xiang *et al*., 2016), suggesting that those taxa are more sensitive to anthropogenic and climatic factors. In compliance with the second hypothesis, we recorded that the organic agricultural practice significantly enhanced total AMF richness under future climate over all other treatments, suggesting that organic farming not only helps to mitigate the impact of climate changes, but also enhanced AMF richness. It is noteworthy that Gigasporaceae richness increased in organic farming under future climate. Members of Gigasporaceae have robust, densely aggregated extra-radical mycelia that extend a greater distance from the root (Maherali and Klironomos, 2007). Therefore, Gigasporaceae primarily contributes in improving nutrient uptake (Hart and Reader, 2002), thereby suggesting that application of organic farming under future climate could secure mycorrhizal taxa associated with promoting plant nutrient status.

Correlation between AMF molecular richness and wheat yield and grain nutrient concentrations

In contrast to our third hypothesis, AMF richness correlated positively with wheat yield as well as P, K and Mg contents of wheat grains in the conventionally managed plots. The conventionally farmed plots were heavily fertilized but not with P. Moreover, wheat plants benefit from the most 'helpful' symbionts even in the nutrient rich agricultural system. These reasons may explain the unexpected positive correlation observed in our study. Baltruschat *et al*. (2019) were able to identify beneficial AMF from Chernozem soil even at highest input fertilization levels, which supports our findings. In addition, AMF richness inversely correlated with essential macronutrients (C, N and S) and micronutrients (Fe) in wheat grains. Our results suggest that increasing AMF richness leads to a shift in allocation of C, N and other elements from host to fungal symbionts. In organic farming plots, we observed a negative correlation between AMF richness and wheat yield. High AMF richness is not required to benefit the plant as the host discriminates the 'more-cooperative' symbiont (Kiers *et al*., 2011) especially in low-input systems in which plants mainly benefit from AMF. This is consistent with lower AMF diversity observed in conditions where plant communities depend on this symbiosis (Johnson *et al*., 2004). This enhanced functionality of the symbiosis is further indicated by our observation that specific AMF taxa positively correlated with P, N, S, Na and Mn contents of wheat grains under organic agriculture system combined with future climate scenario.

Conclusions

In conclusion, AMF communities appear to be sensitive to climate changes, as after a short-term, but realistic manipulation of future climate, the AMF community composition and a sub-community of Glomeraceae taxa changed while the whole richness remained stable. Further, application of different agricultural practices altered both the total AMF and Glomeraceae community, whereby organic farming appeared to enhance total AMF and Diversisporaceae richness. Under the future climate scenario, organic farming enhanced total AMF and Gigasporaceae richness in comparison with conventional farming. Our results revealed a positive correlation between AMF richness and wheat nutrient contents not only in organic farming system but also under conventionally managed fields. We conclude that AMF should be considered as a key component of sustainable agriculture in the future to enhance the sustainability of agroecosystems. While our study was carried out with one winter wheat variety (Glaucus) and therefore could not assess interactions of abiotic stresses, AMF and host genetics, future studies should address the interplay of wheat genetic diversity and AMF responses to future climate changes.

Experimental procedures

Study site and experimental design

The study was conducted within the Global Change Experimental Facility (GCEF) that is settled at the field research station of the Helmholtz Centre for Environmental Research in Bad Lauchstädt, Saxony-Anhalt, Germany (51°22′60 N, 11°50′60 E, 118 m a.s.l.). The area is characterized by a sub-continental climate and prevailing west winds. During the study period (2015), the mean temperature was 10.7°C with an annual rainfall of 400 mm. The soil of the study field is Haplic Chernozem, characterized by high content of organic carbon and a high water-holding capacity (Altermann *et al*., 2005). GCEF consists of 50 field plots (400 m^2 each) (Fig. S5), the two halves of which are subjected to ambient and future climate scenario, respectively (Schädler *et al*., 2019). Our experiment was performed on the conventional as well as organic farming plots subjected to both ambient and future climates. The plots were arranged in a split-plot design with climate regime (ambient *vs*. future) as the main plot factor (10 plots for each climate) and agricultural practice (conventional *vs*. organic farming) as the subplot factor (5 plots for each type and climate scenario).

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Manipulated future climate, agricultural practices and sampling times

The future climate regime is a consensus scenario across three models (COSMO-CLM (Rockel *et al*., 2008), REMO (Jacob and Podzun, 1997) and RCAO (Döscher *et al*., 2002)) of climate change in Central Germany for the time between 2070 and 2100. The resulting scenario includes manipulation of both temperature and precipitation. For this, future climate plots (Fig. S6) were equipped with mobile shelters and side panels, as well as an irrigation system; the roofs were controlled by a rain sensor. The shelters and panels automatically close from sunset to sunrise and increase the mean daily temperatures by ~ 0.55°C. This is accompanied by an increase in minimum temperatures (up to 1.14°C in average) with longer frost-free periods and an increase in growing degree-days by 5.2%. Owing to continuously adjusting irrigation or roof closing, precipitation is reduced by ~ 20% in summer and increased by ~ 10% in spring and autumn. (Schädler *et al*., 2019).

The conventional farming system was characterized by a regional crop rotation consisting of winter wheat, winter barley and winter rapeseed with application of fungicides, pesticides, additives and mineral fertilizers (Table S7). The organic farming system included a mechanical control of weeds with application of organic fertilization based on legumes and rock phosphate (Schädler *et al*., 2019). In 2014, a year prior to our experiment, conventional farming plots were cultivated with winter rapeseed while broad bean was grown in organic farming plots.

In 2015, three sampling campaigns were conducted at three growth stages (Lancashire *et al*., 1991; Hack *et al*., 1992) (rosette growth, late booting/early heading and ripening) of winter wheat (*Triticum aestivum* L.) 'Glaucus variety' from May to July. Detailed information regarding the growth parameters of winter wheat at each sampling time is provided in Table S7. From each GCEF plot, three healthy individuals of winter wheat were collected, the shoot systems were removed, and the roots were shaken to remove bulk soil and the rhizosphere. Roots were rinsed with sterile saline solution (0.5% NaCl) to remove adhering soil particles. Roots of all three plants per plot were composited to one bulk sample for further analyses.

DNA extraction and amplification, Illumina library preparation and MiSeq sequencing

Fine roots were homogenized and 0.1 g of the ground material was used for DNA extraction using a DNeasy Plant Mini kit (QIAGEN-MO BIO, Carlsbad, California, USA) according to the manufacturer's instructions. Genomic DNA was amplified using nested polymerase chain reaction (PCR). The first reaction was performed with GlomerWT0 (Wubet *et al*., 2006) and Glomer1536 (Wubet *et al*., 2006; Morgan and Egerton-Warburton, 2017) primer pair. The second reaction was performed using NS31 (Simon *et al*., 1992; Morgan and Egerton-Warburton, 2017) and AML2 (Lee *et al*., 2008) primers. All PCRs were conducted using the proofreading Kapa HiFi polymerase (2X KAPA HiFi HotStart ReadyMix, Kapa Biosystems, Boston, MA, USA) (Data S1). The PCR product was purified using Agencourt AMPure® XP beads (Beckman Coulter Inc., Indianapolis, IN, USA). Indexing of the purified amplicons was done using the Nextera index kit (Illumina, San Diego, CA, USA). Finally, the amplicon libraries were quantified by PicoGreen assays (Molecular Probes, Eugene, OR, United States) and pooled to give equimolar representation of each. Illumina MiSeq sequencing was performed at the Department of Soil Ecology, UFZ – Helmholtz Centre for Environmental Research in Halle (Saale), Germany. The raw 18S rRNA gene amplicon sequences have been deposited in the Sequence Read Archive (SRA) operated by the National Center for Biotechnology Information (NCBI) under BioProject accession number: PRJNA678852.

Bioinformatics workflow

Sequences corresponding to the forward and reverse primers were trimmed from the demultiplexed raw reads using cutadapt (Martin, 2011) to produce 1,564,752 reads from 60 samples. Paired-end sequences were quality-trimmed, filtered for chimeras and merged using the DADA2 package (Callahan *et al*., 2016) by the dadasnake pipeline (Weißbecker *et al*., 2020). Briefly, sequences were trimmed in order to include only bases with quality scores of at least 20 with maximum expected error score of 2 for forward and reverse reads, and minimum length of 200 and 100 nucleotides for forward and reverse reads, respectively. Merging was carried out with zero mismatch and a minimum overlap of 12 nucleotides. We obtained 7,61,935 high-quality reads clustered into 192 amplicon sequence variants (ASVs), after chimera removal. The taxonomic identification of each ASV was performed by aligning it against the AMF virtual taxa (VT) from the MaarjAM database (Opik *et al*., 2010) using BLAST (Altschul *et al*., 1990) to match 33 VT (Table S8). A total of 5,48,913 of sequences assigned to Glomeromycotean fungi were retrieved from all samples with a maximum of 15,057 and a minimum of 1676 reads per sample. For normalization, the dataset was rarefied to the minimum number of reads per sample using the function 'rrarefy' from the vegan package (Oksanen *et al*., 2019) of the R software (R-Development-Core-Team, 2019).

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Determination of soil physicochemical properties

Soil physicochemical properties were determined from each field plot at each sampling time point. Gravimetric soil moisture contents were determined using automated moisture analysers (Kern DBS60-3, Kern & Sohn, Balingen, Germany). pH was measured using InLab Expert Pro-ISM pH electrode (Mettler-Toledo, Gießen, Germany). Total organic carbon (TOC) and nitrogen (TN) contents were determined by dry combustion using Vario EL III C/H/N analyser (Elementar, Hanau, Germany). Since the carbonate concentration of Chernozem soil is negligible (Altermann *et al*., 2005), measured TC concentrations were considered to additionally represent TOC content. Hot water-extractable carbon (HWC) and nitrogen (HWN) were determined according to Schulz (2002). Soil mineral N was extracted from fresh soil and measured using flow injection analysis (FlAstar 5000, Foss GmbH, Rellingen, Germany). Plant-available P and K were extracted from fresh soil and were quantified colorimetrically (Murphy and Riley, 1962).

Measure of wheat yield and grain nutrient concentrations

Wheat was harvested on 30 July 2015, using 'Wintersteiger' plot combine. Yields (86% dry matter content of grain and straw) were determined separately for grain and straw from 9 $\times$ 1.5 m harvest subplots and converted into decitonnes per hectare (dt/ha). Mars 6 microwave closed system (CEM GmbH) was used for acid digestion of dried and finely milled wheat grains. Analyses of diluted acid extracts were carried out using an inductively-coupled plasma optical emission spectrometer (Thermo Scientific™ iCAP™ 7400 ICP-OES Duo) to determine P, K, Mg, Ca, S, Na, Mn and Fe. Total N and C concentrations were measured with an elemental analyser (Vario EL cube, Elementar Analysesysteme GmbH).

Statistical analyses

Statistical analyses were performed using the R software (R-Development-Core-Team, 2019) and PAST program v. 2.17c (Hammer *et al*., 2001). Due to the low number of VT representing each AMF family, we used the ASV richness as a proxy for AMF richness during our analyses. The observed richness of total ASVs and that of the major families (Glomeraceae, Gigasporaceae and Diversisporaceae) were calculated for each sample using the 'diversity' function on PAST. To test the impact of the experimental factors on mycorrhizal ASV richness, we applied split-split-plot ANOVA test analysis, using the function 'ssp.plot' from the agricolae R package (de Mendiburu, 2019). The impact of climate (two levels) was analysed at the main-plot level, the impact of agriculture practice (two levels) and its interaction with climate at the sub-plot level, and the impact of plant growth stage (three levels) and its interactions with the other two factors at the sub-sub-plot level. Based on split-split-plot ANOVA results, the least significant difference (LSD) test was applied, using the function 'LSD.test', to show differences of each variable between treatments. Analysis of arbuscular mycorrhizal community structure based on Bray–Curtis distances (permutations = 999) across the experimental factors (climate, agriculture practice and plant growth stage) was tested by permutational multivariate analysis of variance (PERMANOVA). The following model was applied: 'ASVs abundances ~ climate regime* agricultural practice * plant growth stage' using the function 'Adonis2' from the vegan R package (Oksanen *et al*., 2019). To visualize the variation in AMF communities, principal coordinate analysis (PCoA) was performed using 'cmdscale' (vegan). Each edaphic variable was fitted onto the ordination space using 'envfit' (vegan), and the significance of each correlation was tested based on 999 permutations (Bray–Curtis dissimilarity distance) by PERMANOVA. Same test was applied to evaluate the impacts of our experimental treatments on each individual AMF family. Data normality was checked by Jarque–Bera test (Jarque, 2011). Spearman's rank correlation analysis was performed to calculate the correlation between AMF richness and plant growth variables, and between AMF richness and wheat grain nutrient concentrations. Benjamini–Hochberg FDR multiple test correction was applied. The correlation analysis was visualized using the function 'ggscatter' from the ggpubr R package (Kassambara, 2018).

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Conflict of interest

The authors declare that they have no competing interests.

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Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Appendix S1. Supporting Information.

Table S7. Phenological observations of winter wheat carried out with the BBCH (Biologische Bundesanstalt, Bundessortenamt and CHemical Industry) centesimal scale showing various growth stages during the experimental period.

Table S8. Virtual Taxa (VT) assignments from MaarjAM detected from the whole wheat samples.

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