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BRIEF REPORT

Water availability alters the community structure of arbuscular mycorrhizal fungi and determines plant mycorrhizal benefit

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Societal Impact Statement

The world faces major changes in rainfall patterns and water availability, posing a significant threat to plant productions systems and food security. The arbuscular mycorrhizal (AM) fungi associate with most major crops and can support plant nutrient and water uptake. Here, AM fungi were shown to mitigate the negative effects of low water availability on sorghum growth and phosphorus uptake, an effect that was associated with shifts in the fungal community structure. To realise the potential of AM fungi in sustainable agriculture requires more examination of their interactions with edaphic stresses in crop systems.

KEYWORDS
arbuscular mycorrhiza, community structure, fungal community, sorghum, sustainable agriculture, water availability

1 | INTRODUCTION

Global precipitation patterns are predicted to change, with many regions facing more frequent and prolonged droughts (Pörtner et al., 2022). These shifts in rainfall will have substantial effects on agriculture, rural livelihoods and food security. A scarcity of water for crops can result in stunted growth, diminished yields and even crop failure in severe circumstances (Lobell et al., 2015). Additionally, soil water availability influences the accessibility to essential plant nutrients, particularly phosphorus (Suriyagoda et al., 2014). Periods of drought that last for several years are a common occurrence in various parts of the world, such as Australia (Kiem et al., 2016). Hence, for agriculture, water availability poses a major challenge to preserving crop productivity in the future, and it is urgent to explore methods for optimising water use and soil resource utilisation while preserving soil ecosystems. Most crop species associate with arbuscular mycorrhizal (AM) fungi, which colonise their root systems, along with the soil environment, where they facilitate plant uptake of nutrients and water (Kakouridis et al., 2022). Additionally, AM fungi play key roles in various ecosystem processes and can enhance the ability for plants to tolerate a variety of biotic and abiotic stresses (Powell & Rillig, 2018). Given these benefits, the continued exploration of the AM symbiosis for the progression of sustainable agriculture is both logical and necessary (Thirkell et al., 2017), particularly as we attempt to improve crop nutrition and stress tolerance while maintaining soil ecosystems.

Substantial research has been invested in exploring the influence of AM fungi on plant–water relations, uncovering their potential to modify plant growth, stomatal conductance, phytohormone levels and other plant-related responses (Augé, 2001; Begum et al., 2019). Plants will often exhibit a proportional increase in biomass allocation towards roots when soil water (and nutrient) availability is limiting, which can facilitate the exploration of greater soil volume (Aroca & Ruiz-Lozano, 2012). In contrast, the AM symbiosis typically reduces plant root:shoot ratios, presumably as plants have improved access to belowground resources. However, the outcomes of these interactions are variable, with some studies indicating positive outcomes, whereas others exhibit either no effects or negative impacts in comparison to control groups (Cheng et al., 2021; Martin & Stutz, 1994; Schellenbaum et al., 1999; Veresoglou et al., 2012). Moreover, the effect of AM fungi on plant responses to water scarcity is contingent not only on the plant host species but also on the AM fungal taxon identity (Grümberg et al., 2015). For instance, taxa belonging to the

Gigasporaceae tend to allocate more of their growth towards extraradical hyphae, potentially leading to greater nutrient and water uptake benefits for their hosts (Maherali & Klironomos, 2007). However, our ability to assign functional characteristics, such as plant tolerance to drought, to particular AM fungal taxa is limited by a lack of empirical data (Marro et al., 2022; Weber et al., 2019).

Most glasshouse studies on crops have used single AM fungal species or a small number of cosmopolitan taxa (Augé, 2001; Cheng et al., 2021). Although these studies hold significance, plants interact with multiple AM fungi simultaneously in a dynamic way, shaped by environmental filtering and competition among fungi (Vályi et al., 2016). Yet comparatively few studies have evaluated how different water availabilities impact fungal diversity and composition, with even fewer focussing on the diversity of root-colonising fungal communities. Research that has examined fungal community responses in plant roots has found that both flooding and reduced water availability can reduce fungal diversity (Deepika & Kothamasi, 2015). Given that AM fungi are functionally diverse, changes to the taxonomic diversity, composition and community structure of these root-colonising communities will have direct influence on plant outcomes.

Here, this study explored the effects of decreased water availability on AM fungal communities colonising the roots of sorghum, as well as the corresponding plant growth and nutrient responses. It was hypothesised that (i) reduced water availability would decrease plant growth and phosphorus concentration but increase root:shoot ratios; (ii) AM fungi would promote plant growth and phosphorus concentrations and reduce root:shoot ratios and that these effects would be stronger under low water availability; (iii) reduced water availability would decrease AM fungal colonisation and species richness and alter community structure.

2 | MATERIALS AND METHODS

2.1 | Experimental set-up

A factorial pot experiment was conducted to explore the impacts of watering regime on the community structure of root-colonising AM fungi in sorghum (*Sorghum bicolor* L. Moench cv. 'MR Taurus') and the concomitant impacts on plant growth and nutrient responses to the fungi. Forty plants (40 biological replicates) were grown either with or without AM fungi under one of two watering regimes of 'low' and 'high' water availability, thus there were 10 replicates per treatment combination. Plants were grown from seed that were surface sterilised using 10% sodium hypochlorite solution before being germinated in Petri dishes for 6 days at which point individual seedlings were transplanted into 3.7 L pots. These pots contained an autoclaved 40:60 sand/soil mixture (Table S1). The experiment was conducted in a glasshouse chamber subject to natural sunlight with 20°C:28°C day:night temperatures (± 4°C).

Plants to be grown with AM fungi were inoculated with 150 g of sieved and dried field soil inoculum which was taken from arable field in Queensland, Australia (−27.432°, 152.349°) known to harbour a diverse AM fungal community (Ng et al., 2023). Plants without AM fungi were inoculated with the same inoculum, autoclaved. All pots received 200 ml microbial filtrate from washed soil inoculum filtered through a 38 μm sieve to standardize the non-AM fungal microbial community (Koide & Li, 1989). Plants were watered ad libitum for the first 3 weeks to allow establishment. At this stage, water treatments were applied where half of the pots under the 'no AM fungi' treatment and half 'with AM fungi' were subjected to low water availability, whereas the remainder were subject to high water availability. To achieve these treatments, soil water holding capacity was determined prior to initiation of the experiment using the gravimetric method (Schmugge et al., 1980) where the weight of oven dried soil is subtracted from saturated soil weight. Target weight for pots was calculated as pot + dry soil weight + water weight at maximum soil water holding capacity multiplied by either 80% (high water) or 50% (low water).

After a further 11 weeks of growth, plants were removed from their respective pots, and roots and aboveground tissues were separated. Roots were washed and a 1 g subsample of fresh roots were taken from each plant for mycorrhizal fungal colonisation assessment. Remaining plant tissue was oven dried at 35°C, then weighed. Aboveground plant tissue was ground to powder for subsequent chemical analyses, and homogenized dried root samples were taken for downstream molecular analyses.

The process of confirming root colonisation by AM fungi and the lack of colonisation in the control group involved taking 1–2 g of root samples, treating them with 10% potassium hydroxide at 80°C in a water bath for 15 min, then stained with 5% ink vinegar (Vierheilig et al., 1998) using Quink ink (Parker© Nantes, France) at 80°C for 10 min, after which roots were rinsed with acidified tap water (2% acetic acid). Roots were then stored in lactoglycerol for 24 h, after which colonisation could be assessed. To score colonisation, roots were mounted on glass slides with glycerine and examined for AM fungal colonisation using the intersect method (McGonigle et al., 1990), assessing 100 intersects per replicate. Only hyphae that had a clear connection to AM fungal structures (such as arbuscules, vesicles or spores) were counted to conservatively quantify colonisation (Figure S1).

2.2 | Chemical, molecular and bioinformatic analyses

To determine the tissue carbon and nitrogen content, the dried and ground material was subjected to the high temperature combustion method using a LECO analyser. In this process, the sample is placed in a combustion tube and exposed to oxygen, and the gases produced are analysed using a thermal conductivity cell. Plant phosphorus was assessed using inductively coupled plasma (ICP) spectroscopy after the dried plant material was digested with hydrogen peroxide and nitric acid, following the procedure described by Rayment and Lyons (2011).

DNA was extracted from 70 mg of the dried root samples using a DNeasy Powersoil Pro kit (Qiagen, GmBH, Hilden, Germany) according to the manufacturer's instructions, with the modification that dried root material cut into fragments is added to extraction tubes. Sequencing was processed through the Western Sydney University's Next-Generation Sequencing Facility's (Richmond, NSW, Australia) liquid handling pipeline. The DNA was purified using the Agencourt AMPure XP Beads (Beckman Coulter), followed by a quality assessment using the Qunat-iT™ PicoGreen fluorescence-based analysis (ThermoFisher Scientific, North Ryde, NSW, Australia). The purified DNA then underwent amplification using polymerase chain reaction (PCR) targeting the small-subunit (SSU) ribosomal RNA gene using AM fungal-specific primers: WANDA (Dumbrell et al., 2011) and AML2 (Lee et al., 2008). Briefly, PCR reactions consisted of 5 μL Q5® High-Fidelity DNA Polymerase 2× master mix (New England Biolabs, Notting Hill, Victoria, Australia), 0.2 μL of 10 μM forward and reverse primer with 2 μL of DNA, total volume of the reaction was 10 μL. PCR reactions were as described in Caporaso et al. (2018). The amplified PCR product then underwent a short second PCR to attach the Illumina Nextera XT v2 index set (Illumina Australia, Melbourne, Australia), as per manufacturer's instructions (https://support.illumina.com). Each reaction consisted of 3.8 μL of Q5® High-Fidelity DNA Polymerase 2x master mix (NEB), 1.5 μL of each index (Illumina) and 2.3 μL of PCR product, total reaction volume was 7.6 μL. The amplicons were then diluted and again assessed using the Qunat-iT ™ PicoGreen (ThermoFisher Scientific) assay and normalised library pools were constructed using the Eppendorf epMotion. The libraries were cleaned-up and prepared for sequencing following the Illumina MiSeq protocol. Sequencing was performed on the Illumina MiSeq platform using the Illumina MiSeq reagent kit v3 2 × 300 bps paired-end chemistry as per manufacturer's instructions.

Bioinformatic data analysis and processing was conducted using the graphical downstream analysis tool (gDAT) for analysing rDNA sequences (Vasar et al., 2021). Raw reads (2 × 702,339 reads in total) were demultiplexed and cleaned using a series of bioinformatic steps

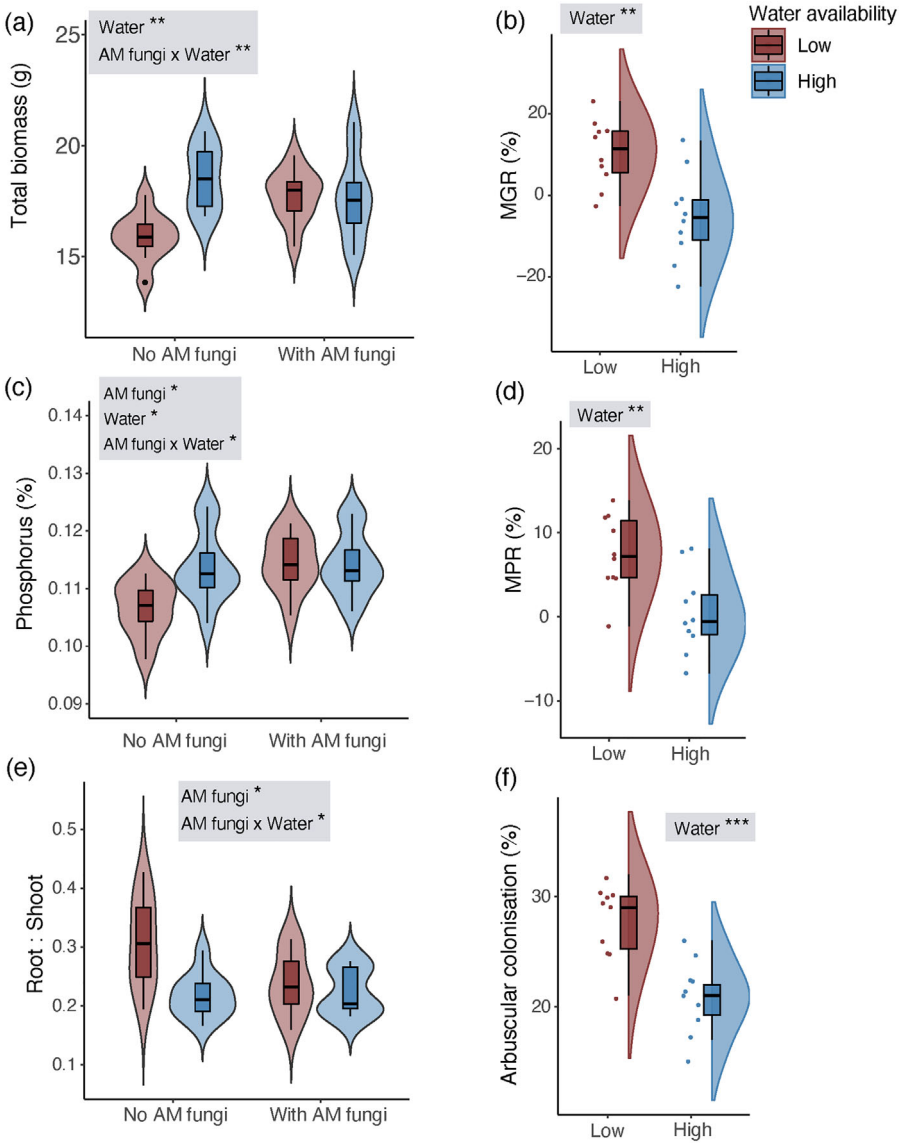

FIGURE 1 Violin and raincloud plots showing the effects of watering treatment on plants (*Sorghum bicolor*) with and without arbuscular mycorrhizal (AM) fungi on the (a) total biomass (g), (c) phosphorus concentration, and (e) root:shoot ratio. The effects of watering treatment on plant (b) mycorrhizal growth responses (MGR), (d) mycorrhizal phosphorus response (MPR), and (f) arbuscular colonisation of roots are also shown. The width of the violin represent data densities whereas the boxplots embedded within represent the median, 25% and 75% quantiles. Significant effects of the water treatment, AM fungi treatment, and their interaction are indicated. *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

(see Vasar et al., 2017, 2021). In short, reads were demultiplexed by checking double barcodes, allowing one mismatch for both reads. Reads were retained if they carried the correct primer sequences (WANDA and AML2; allowing one mismatch for each) and had an average quality of at least 30, and orphan reads were removed (leaving 2 × 572,164 cleaned reads). Putative chimeric sequences (2200 reads; 0.4% of cleaned reads) were identified and removed using vsearch v2.15.0 (Rognes et al., 2016) with the default parameters in reference database mode against the Maarj*AM* database (v.2019; Öpik et al., 2010). Cleaned and chimera-free sequences were assigned to virtual taxa (VT) using BLAST+ (v2.7.1; Camacho et al. (2009) referencing the Maarj*AM* database (v.2019; Öpik et al., 2010) with at least 97% identity and 95% alignment thresholds.

2.3 | Statistical analyses

All analyses were carried out using R statistical interface v4.0.5 and RStudio v2022.07.2.

To explore the effects of AM fungi on plant responses to two water treatments, 'high' and 'low' water availability on plant response variables, simple linear models were fitted exploring the factors AM fungi and water, and their interaction using the *lm* function and then *Anova* from the package 'car' (Fox & Weisberg, 2011). This approach was used to assess plant biomass, root:shoot ratio, phosphorus and nitrogen concentrations, C:N, and N:P responses to the water and AM fungal treatments. The effect of the water treatments on the mycorrhizal growth response (MGR) and mycorrhizal phosphorus response (MPR) of plants, along with the fungal colonisation of plant roots, AM fungal VT richness and community evenness (Pielou), were also analysed using simple linear models using *lm* and *Anova*.

To counteract bias from differences in sequencing depth, samples were rarefied to the minimum number of sequences per sample by means of the *rarefy_even_depth* function from the R package 'Phyloseq' (McMurdie & Holmes, 2013), prior to statistical analyses. Dissimilarity in community structure and composition of root-colonising AM fungi was analysed using principle coordinate analysis (PCoA, package 'Phyloseq'; McMurdie & Holmes, 2013) based on Bray–Curtis dissimilarity, and network analysis using *make_network* in 'Phyloseq' based on Jaccard distances with maximum distance between samples set at the default 0.4. The effects of the water treatments on these community metrics were analysed using permutational multivariate ANOVA (perMANOVA) using *adonis* from the 'vegan' package (Oksanen et al., 2015).

3 | RESULTS AND DISCUSSION

Understanding how root-colonising AM fungal communities respond to water availability and their capacity to support plant productivity

	AM fungi		Water		AM fungi × Water	
	$F_{1, 36}$	*P*	$F_{1, 36}$	*P*	$F_{1, 36}$	*P*
Biomass	1.097	0.302	**16.499**	**0.007**	**9.373**	**0.004**
Root:shoot	3.614	0.065	**9.7832**	**0.003**	**5.259**	**0.027**
Phosphorus concentration	**6.335**	**0.016**	**4.158**	**0.048**	**4.988**	**0.031**
Nitrogen concentration	0.097	0.758	0.048	0.828	2.317	0.137
C:N	0.305	0.584	0.000	0.98	1.881	0.179
N:P	2.189	0.148	0.516	0.477	0.182	0.672
			$F_{1, 18}$	*P*		
MGR			**13.409**	**0.002**		
MPR			**11.422**	**0.003**		
Total colonisation			2.989	0.1		
Arbuscular colonisation			**21.457**	**<0.001**		
Vesicular colonisation			0.391	0.539		
			$F_{1, 18}$	*P*		
VT richness			0.9	0.355		
Pielou			3.011	0.099		
Bray–Curtis distance[a]			**6.976**	**0.003**		
Jaccard distance[a]			**4.523**	**0.002**		

TABLE 1 Model results for the main effects of arbuscular mycorrhizal (AM) fungal treatments (with or without AM fungi) and water treatments (low or high water availability), and their interaction on plant response variables of biomass, root:shoot ratio, phosphorus (P) and nitrogen (N) concentrations, C:N ratio, and N:P ratio.

Note: Also shown are the model results examining the main effects of the water treatments on the mycorrhizal growth response (MGR), mycorrhizal phosphorus response (MPR), the total, arbuscular and vesicular fungal colonisation, AM fungal virtual taxon (VT) richness, Pielou's evenness, Bray–Curtis dissimilarity and Jaccard dissimilarity between communities. Significant impacts ($P < 0.05$) are indicated in bold.

[a]PERMANOVA.

is crucial for our ability to effectively manage AM fungi in a changing environment. Here, plant growth and phosphorus concentration were significantly reduced when grown under limited water availability, compared with the high water treatment (Figure 1a,c; Table 1). This effect, however, was only observed in the plants grown without AM fungi. Furthermore, although the fungi promoted plant biomass and phosphorus, this effect was only evident under the low water treatment. These context specific outcomes were also reflected in the mycorrhizal growth and phosphorus responses, where plants acquired growth and phosphorus benefits from the AM symbiosis when water was limited, but evidently not under the high water treatment (Figure 1b,d; Table 1). Thus, the AM fungal-derived benefits for the crop were dependent on soil water status. Although these results support the first and second hypotheses, in part, it was anticipated that AM fungi would also augment plant growth and nutrient uptake under the high water conditions, albeit to a lesser extent. In this case, plants with access to sufficient water garnered no significant biomass or phosphorus benefits from AM fungi.

It is possible that the plants with high water availability had more of their soil resource requirements fulfilled; thus, there was limited additional benefits to be garnered from the AM symbiosis. Indeed, plants with AM fungi or with abundant water availability had low root:shoot ratios, whereas contrastingly, plants from the low water treatment without AM fungi had the highest root:shoot ratio across all treatments (Figure 1e, Table 1). This would suggest that in the absence of fungal symbionts, plants made a greater investment in belowground biomass to meet their water and nutrient requirements (Shipley & Meziane, 2002). Under limited water conditions, plants often exhibit reductions in both nitrogen and phosphorus concentrations (He & Dijkstra, 2014). In this case, despite their overall reduced growth and nutrient concentration, the N:P ratios of non-AM fungal plants under low water conditions (Figure S2a) indicate that phosphorus was not the limiting factor for growth (Koerselman & Meuleman, 1996). This suggests that the plants employed effective strategies to meet their water and phosphorus needs, either through investment in root biomass or via the AM symbiosis. Furthermore, although total colonisation was unaffected by water status

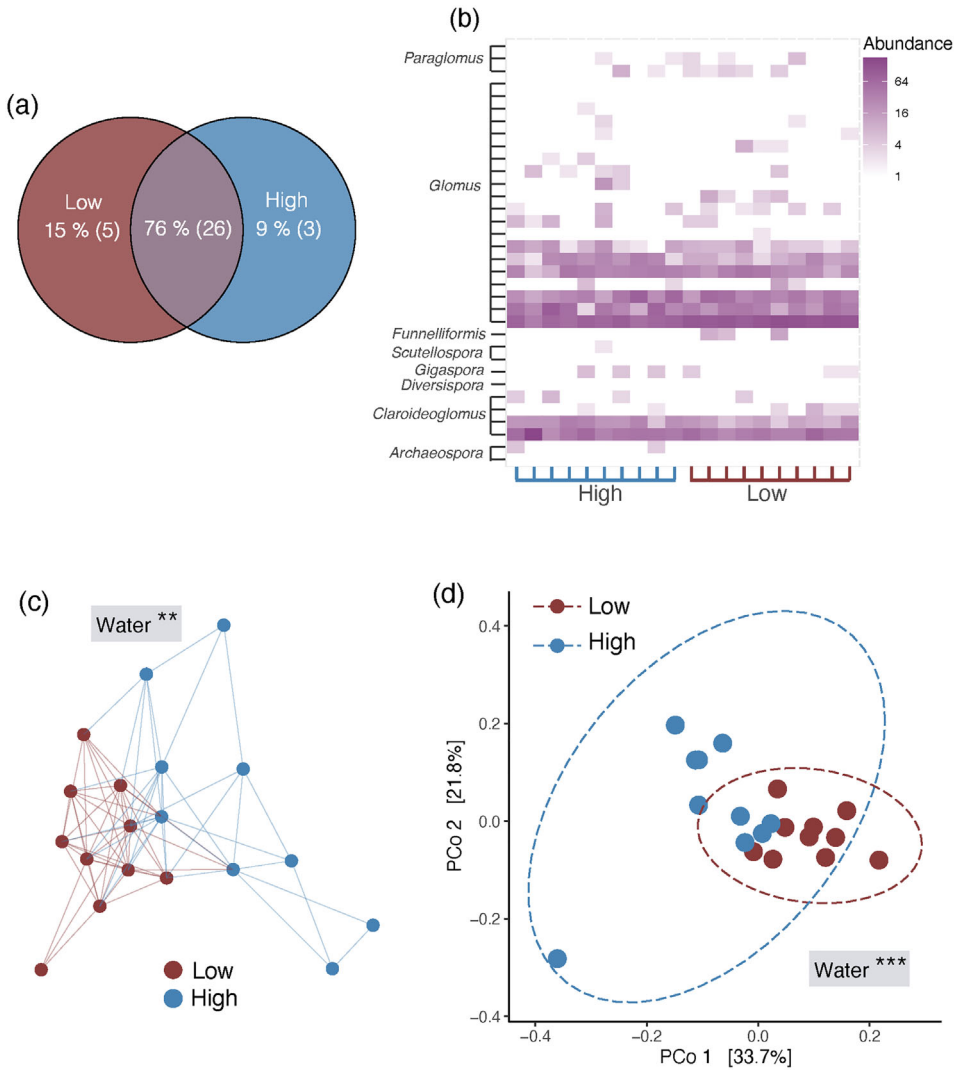

FIGURE 2 Plots presenting the effects of the water treatments (low and high water availability) on the arbuscular mycorrhizal (AM) fungi colonising the roots of *Sorghum bicolor*. (a) Venn diagram showing the number of arbuscular mycorrhizal (AM) fungal taxa unique and shared between plants under the low or high water treatments, (b) heatmap showing the abundance of virtual taxa (VT) within AM fungal genera across root samples from the high and low water treatments. (c) Network analysis of samples based on Jaccard dissimilarity and (d) principal coordinates analysis (PCoA) of Bray–Curtis dissimilarity comparing the structure of root-colonising AM fungal communities under the low or high water treatments. Significant effects of the water treatment are indicated. $^{**}P < 0.01$, $^{***}P < 0.001$.

(Figure S2b), the higher proportion of arbuscules in root of plants under low water treatment (Figure 1f; Table 1) indicates more active resource exchange between plant and fungi, which further suggests plant investment in the AM symbiosis was augmented under these conditions.

It was hypothesised that the low water treatment would reduce AM fungal VT richness, as reported in a previous work (Deepika & Kothamasi, 2015). Here, this was not observed, where AM fungal richness was similar under low and high water (Figure S2c). Furthermore, the majority of fungal taxa (76%) were found across both water treatments (Figure 2a,b; Table 1), whereas 15% and 9% were taxa unique to the low and high water treatments, respectively. Despite that fungal species richness was similar between treatments, the overall community composition and structure did differ significantly (Figure 2c,d; Table 1), supporting the hypothesis that reduced water availability would alter AM fungal community structure. Both communities harboured high proportions of *Claroideoglomus* and *Glomus* taxa, and although certain taxa were clearly dominant across all samples, there was variability in the presence and abundance of individual VT within these genera (Figure 2b; Table S2). The shifts in fungal community structure along with the increase in arbuscules under low water conditions are likely to be associated with the positive growth and phosphorus responses to AM fungi that were observed (Figure 1b,d; Table 1). This highlights that although changes in species richness is often a primary consideration when predicting functional outcomes of the AM symbiosis for crops, complex variation in community structure can also have functional significance for host plants, although this is less well-studied (Chagnon et al., 2012). Thus, there is a need for further exploration into the impact of soil water status on root-colonising AM fungal communities, as well as a deeper understanding of the relative importance of diversity and community assembly in these complex symbiotic interactions.

This study demonstrated how soil water status can significantly alter the community structure of root-colonising AM fungi and determine mycorrhizal growth and phosphorus benefit for sorghum. Effectively harnessing the potential of the AM symbiosis in agriculture requires a comprehensive understanding of the ways in which natural AM fungal communities adapt to environmental variations and the consequential impact on plant growth and productivity.

AUTHOR CONTRIBUTIONS

Adam Frew designed the study, collected and analysed the data, and wrote the manuscript.

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CONFLICT OF INTEREST STATEMENT

The author confirms there are no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available from the FigShare repository at doi: 10.6084/m9.figshare.22029062. Raw DNA sequencing data are available under the NCBI accession number PRJNA932042.

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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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