

Article

Effects of Variations in Soil Moisture and Phosphorus Concentrations on the Diversity of the Arbuscular Mycorrhizal Fungi Community in an Agricultural Ecosystem

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Abstract: In farmland ecosystems, phosphorus and water have crucial roles. To elucidate the effects of phosphorus concentration and water management on arbuscular mycorrhizal fungi (AMF), field experiments were conducted in a farmland ecosystem (China). We examined the effects of different treatments, including drought and normal phosphorus, normal water and normal phosphorus, drought and low phosphorus, and normal water and low phosphorus, on the AM fungal biomass, diversity, and community. Results showed great differences in the AMF under different water and phosphorus concentrations. When under a suitable drought treatment, the AMF became more abundant and more conducive to plant growth. The abundance of AMF varied with different phosphorus treatments, and the abundance of AMF in low-phosphorus treatments was higher, which is more suitable for plant growth. In conclusion, as water and phosphorus concentrations change, the community structure of AMF constantly changes. Only under the appropriate water and phosphorus concentration processing can AMF play its role well. Understanding the influence of different phosphorus concentrations and the moisture contents of AMF can play a role in the agricultural production of AMF, and it can also provide improved theoretical support.

Keywords: arbuscular mycorrhizal fungi (AMF); the moisture content; soil phosphorus content; agricultural ecosystem



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1. Introduction

North China, which has relatively little water, is the major producer of wheat and corn in China. As it is affected by the monsoon climate, seasonal drought occurs frequently, which seriously affects the sustainable development of regional agricultural production [1]. Irrigation and fertilization are the key factors affecting crop yield. For plants that are under water stress, the water and nutrients in the soil cannot be absorbed by the plant, thus affecting the growth and development of the plants [2]. Phosphorus plays an important role in plants at the whole cellular level, including biomolecular synthesis, membrane transport structure, and physiological metabolism [3]. Many studies have been conducted on the effects of phosphorus and water on crops [4]. However, the effects of phosphorus and irrigation on soil arbuscular mycorrhizal fungi (AMF) in farmland ecosystems are not clear.

Soil microorganisms are an important component of soil ecosystems and are also an important group in farmland ecosystems [5]. Soil microorganisms play an important role in the nitrogen and phosphorus cycles by directly affecting the soil nutrient content. AMF are widely found in various natural soil ecosystems and can form symbiotic relationships with most higher plants [6]. The interaction between AMF and crops in the field has also

been extensively studied. They are examples of some soil microorganisms that have been found to be most closely related to plants [7]. AMF can have mutually beneficial symbioses with most plants. Plants reproduce necessary carbohydrates for AM fungal growth, which are taken in exchange for water and nutrient transport through the root system to the host plant to ensure that the plant can grow normally [8]. They can also promote plants to absorb nutrients and can absorb trace elements, such as nitrogen and phosphorus, to increase soil fertility and crop yield [9]. Moreover, AMF can help plants reduce the dangers of drought stress [10]. However, the relationship of water and phosphorus concentrations in relation to the diversity of AMF in agroecosystems remains unclear.

Phosphorus has a vital role in the growth of plants; existing experiments show that a low-phosphorus environment can lead to changes in the shape and structure of crop growth and the root-to-shoot ratio [11]. A series of structural changes can increase the enzyme activity of crop roots under low-phosphorus stress; moreover, as the hydrolysis of phosphate in soil increases, more inorganic phosphorus is released for crop uptake [12]. In addition, crop symbiosis with AMF can increase the absorption of phosphorus. Numerous experiments have proven that phosphorus concentration can affect the formation and development of AMF symbionts, and it has a great effect on crop growth and development [13]. Many studies have shown that a substantial amount of phosphate fertilizer reduces the community diversity of AMF. Nevertheless, just the right amount of phosphate fertilizer can increase the diversity of the AMF community [14]. Currently, our experiments investigate the effect of phosphorus concentration on the abundance of AMF in agroecosystems. Through our study, we can understand which level of phosphorus concentration for AMF is more suitable for their existence. It can also provide a reference for crop fertilization and improve the utilization efficiency of phosphorus fertilizer.

Water content is one of the most important factors for plant growth, whereas drought is one of the most important factors limiting crop growth and yield [15]. According to incomplete statistics, a large proportion of crop loss is due to drought; thus, water stress has always been the focus of agricultural production [16]. Proper droughts promote the development of mycorrhizal external mycelia, which can help plants absorb water, and their importance increases as the soil moisture content decreases [17]. Many investigations have noted that the *Glomus* species in AMF are the dominant species in arid ecosystems; they can grow under water-scarce conditions and help plants absorb water [18]. Chengshen et al. showed that AMF can regulate plant morphology and physiological processes to improve plant drought resistance [19]. These studies concluded that AMF can reduce the damage of drought to plants and improve their drought resistance [20]. Plants under drought stress can make better use of water in the soil and reduce the harm caused by drought stress. However, relatively little is known about the water conditions under which AMF can survive. In this study, by comparing the agricultural system under drought treatment and normal irrigation, the AMF abundance changes were determined so as to provide effective water management measures.

In addition, water and phosphorus concentrations were controlled and monitored through human disturbance experiments. By controlling the changes in water and phosphorus concentrations, we explored the changes in the diversity of AMF communities in agroecosystems. We examined four different treatments and compared the effects of different levels of moisture and phosphorus on AMF. Our expectations were achieved through drought shed cultivation and the application of different phosphate fertilizers. When we clearly understand how AMF are affected by water and phosphorus, we can then use AMF in agricultural production and maximize their effectiveness by adjusting water and phosphorus concentrations.

2. Methods

2.1. Study Site

The north (i.e., the northeast, northwest, and north China) is the main agricultural area in China. Wheat maize rotation is the most important planting method in northern

China. The basic water source is rainwater in the northern regions, and irrigation water use is relatively small. The site selected for this study, i.e., the Experimental Field of Henan Agricultural University, is located in Yuan-yang County, Henan Province (34°45' N, 113°32' E). It is characterized by a temperate continental monsoon climate, with a mean annual temperature of 14.4 °C and a mean annual precipitation of 550 mm. The soil phosphorus content is between 10.3 and 12.6 mg/kg. The altitude is 64.40 m, and the soil type of the experimental field is fluvo-aquic soil [21].

2.2. Sample Collection and Experiment Method

In April 2019, we set up four test zones in Yuan-yang County, each measuring 10 m × 10 m. Four different treatments were conducted for each test zone, and each treatment was repeated three times. Treatments consisted of (i) drought + normal phosphorus (DNP), (ii) normal water + normal phosphorus (NNP), (iii) drought + low phosphorus (DLP), and (iv) normal water + low phosphorus (NLP). The local agricultural ecosystem needs to add water and phosphate fertilizer. The application of phosphate fertilizer and local farmland is consistent, and the main content of phosphate fertilizer is P₂O₅. Normal phosphorus processing is conducted at 50 kg/hm², and low phosphorus treatment is 20 kg/hm². Drought treatment was conducted to control the moisture content and soil moisture content in a drought shed at 10–20%. According to the soil moisture content that wheat growth needs, the soil moisture content control was set at 20–30%. During the period of moisture content control, soil moisture content was monitored every two weeks, and three soil samples were taken each time as duplicates. The monitoring period was two months. After five measurements of soil moisture content, all the results were within the preset range of the experiment. The obtained moisture contents were DLP: 12–17%; DNP: 13–16%; NNP: 22–29%; and NLP: 24–28% (the standard deviations of the four groups were 1.9%, 1.1%, 2.6%, and 1.4%, respectively). The water source was rainfall and irrigation. In addition to dry processing, other management measures were the same as the field management.

In June 2019, after the wheat matured, soil sampling was performed. Three soil cores from each area were randomly sampled and mixed as a composite sample. A total of 12 soil samples were collected. When sampling, the topsoil and litter should be removed first, and soil (approximately 0–10 cm) should be collected using a soil drill. The soil should be fully mixed to eliminate the effects of some special cases. After this, it was divided into two parts, then passed through a 2 mm sieve and packed in an ice box and transported to the laboratory. Fresh soil was then stored at –80 °C for microbial DNA extraction. Another part of the soil was used in the physical and chemical experiments.

Before the determination of soil physical and chemical properties, the soil was sieved through a screen mesh size of 80 (0.18 mm hole) soil samples for dry screening. The soil samples were screened for subsequent measurements. Soil moisture was determined by comparing the fresh soil sample and measuring the weight of the soil sample after drying. The weight difference was used to calculate the soil water content. The sodium bicarbonate extraction method was used to determine the soil effective phosphorus. The phosphorus content was calculated by measuring its absorbance via a UV spectrophotometer (SHIMADZU, Beijing, China). The content of nitrate nitrogen was determined by ultraviolet spectrophotometry (SHIMADZU, Beijing, China). The effective potassium content was determined by flame spectrophotometry (Flame spectrophotometer 6400A, Shjingmi, Shanghai, China). The measured soil basic nutrients are shown in Table 1. All the above experiments are consistent with the soil agricultural chemistry analysis method [22].

Table 1. Soil basic nutrients in the experimental area. Each group took three soil samples and the average value was calculated. All results were rounded to one significant figure (all values are the mean value \pm standard deviation).

The Soil Nutrient Content			
Group	The Effective Phosphorus (P) (mg/kg)	The Effective Potassium (K) (mg/kg)	The Nitrate Nitrogen (N) (mg/kg)
DLP	1.7 \pm 0.1	21.7 \pm 4.3	15.1 \pm 2.1
DNP	6.6 \pm 0.7	33.0 \pm 10.3	16.1 \pm 1.4
NNP	12.3 \pm 2.0	19.7 \pm 5.9	18.8 \pm 3.6
NLP	4.2 \pm 1.8	15.4 \pm 2.9	12.4 \pm 1.4

2.3. DNA Extraction, Gene Amplification, and Sequencing

The AMF communities were analyzed with high-throughput sequencing. The total DNA from 0.5 g of soil was extracted, following the manufacturer's instructions, with a Fast DNA[®] Spin Kit (MP Biomedical, Irvine, CA, USA). DNA quality and purity were evaluated using a NanoDrop spectrophotometer (Thermo Scientific, Waltham, MA, USA). The DNA was stored at -80 °C until use. The amplicon library was constructed on the basis of the work of Kozich et al. [23], with each primer consisting of a suitable Illumina adapter, an 8-nt index sequence, a 2-nt linker, and a gene-specific primer. For the fungal communities, PCR amplification was conducted with primers, namely AML1F:5'-ATCAACTTTTCGATGGTAGGATAGA-3' and AML2R:5'-GAACCCAAACACTTTGGTTTCC-3'. The selection of the 50 μ L reaction system had the following setup: 98 °C for 2 min, 98 °C for 15 s, 55 °C for 30 s, 72 °C for 30 s, 72 °C for 10 min, and then 30 cycles at 72 °C for 10 min [24]. The amplifications were gel-purified using an EZNA[®] Quick Gel Extraction Kit (Omega Bio-Tek, Norcross, GA, USA), and then quantified using a Genomic Isolation Kit (Trevigen Inc., Gaithersburg, MD, USA) [25]. UPARSE (version 9.2) was used to cluster the operational taxa (OTUS) with 97% similarity cutoff points and to identify and remove chimeric sequences. Finally, the qualified PCR products were used to construct a DNA library, which was sequenced on the Illumina HiSeq platform [26]. All the microbial sequences from this study were uploaded to the SRA (BioProject ID: PRJNA977104).

2.4. Data Analysis

On the basis of the high flux of AMF gene sequencing, the four AMF in the soil were analyzed under different habitats of species diversity. According to the different similarities, for all the sequence divisions, 97% was usually used as the threshold of OTUs for the statistical analysis of biological information. To obtain the taxonomic information corresponding to each OTU, a Bayesian algorithm was used to perform taxonomic analysis on the representative sequences of OTUs with a 97% similarity level [27], and the species composition of the communities of each sample was counted at each taxonomic level (family, genus, and species).

The composition of the soil AMF was analyzed using Bray–Curtis nonmetric multidimensional scaling (NMDS) [28]. On the basis of 999 permutations, the permutation multivariate ANOVA (PERMANOVA) method was used to explore the differences in samples from the different habitats. A *p* value of less than 0.05 indicated that the reliability of the test is high. NMDS was generated by using “metaMDS” in the “vegan” package [29]. The rarefaction curve is a method of randomly sampling sequences, and the number of sequences drawn is related to the number of species (such as OTUs) or the diversity index corresponding to them [30]. The rarefaction curves were conducted in the “vegan” package. A Venn plot and a chord diagram were implemented in R.4.1.0.

Co-occurrence network analysis was conducted to show the sample between the species and distribution. According to the species abundance between the different samples for analysis, a coexistence relationship between species and the environment can

be obtained. Network analysis was performed to test the specificity of AMF to different habitats. The four habitats included DNP, NNP, DLP, and NLP. A co-occurrence network was plotted using Gephi 0.9.2 [31].

Torus translation refers to determining whether a species is considerably related to the habitat by randomly calculating the distribution probability of species in different habitats. In this study, we selected four 10 × 10 plots and conducted four different treatments to analyze the spatial association (positive or negative correlation) between AMF and different habitats [32]. The advantage of this method is that it can exclude the spatial autocorrelation between habitat and species distribution, thus making the test more sensitive. The associations of all OTUs with four treatments (positive correlations, $p \leq 0.05$) were analyzed. All statistical analyses were conducted in the R environment [33].

The normalized stochasticity ratio (NST) index quantifies the ecological stochasticity under different conditions through a mathematical framework [34]; NST usually utilizes 50% as the boundary point for determining whether it is more deterministic (<50%) or more stochastic (>50%). The NST was tested with simulated communities by considering abiotic filtration, competition, and spatial scales. The entire process used the “ggpubR” package in R.

3. Results

3.1. Distribution Patterns of AMF in Different Habitats

Through the clustering operation analysis, a total of 57 OTUs were obtained. The obtained OTUs belonged to three families, three genera, and 19 species. The three families were Diversisporaceae, Glomeraceae, and Gigasporaceae, and the three genera were *Diversispora*, *Glomus*, and *Scutellospora*. The four habitats of the dominant families were Glomeraceae, and the dominant genus was *Glomus*.

The AMF communities had good richness in four different habitats (Figure 1a,c). The species abundance was relatively high in DNP, among which OTU34 and OTU41 were the most abundant; moreover, OTU21 accounted for the largest proportion in the four habitats (Figure 1a,c). More AMF OTUs were found in DNP (39) than in DLP (37), and more AMF OTUs were found in NLP (37) than in NNP (31). We also found more unique OTUs in the AMF community of DNP (17) than in that of NNP (9) (Figure 1b).

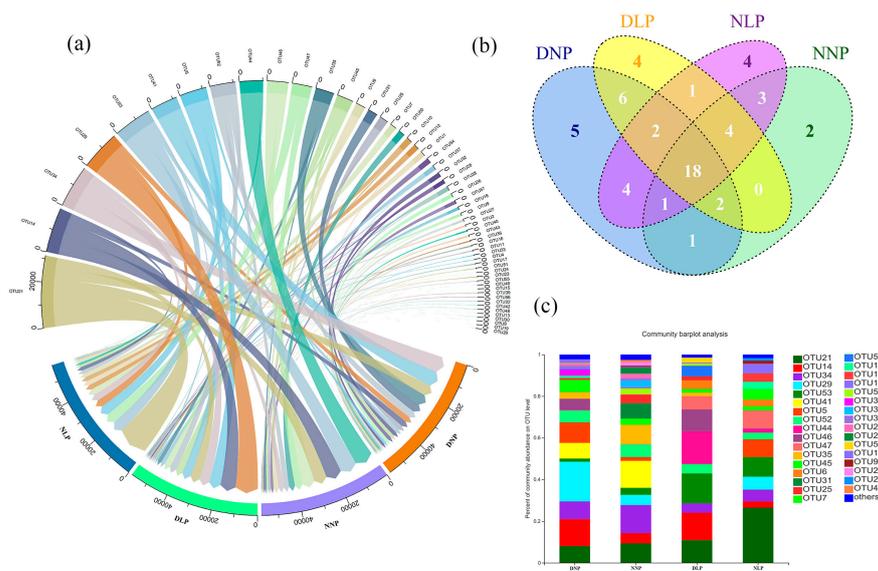


Figure 1. General description of different AMF communities. (a) Chord diagram showing the correlation between four habitats and OTUs, and the thickness of each strip indicates the number of OTU taxa in different habitats. (b) Venn diagram of shared and unique OTU numbers observed in different AMF communities. (c) The relative abundance of major OTUs in AMF communities in different soil samples.

3.2. Differences of AMF in Different Habitats

Conducting NMDS followed by PERMANOVA showed that the soil AMF communities in the four habitats were separated (Figure 2a). It also indicated that the AMF differed considerably in OTU composition between the different communities ($p < 0.05$). As the number of samples increased, the rarefaction curves of the AMF in each community in different habitats tended to be flat and reached saturation, indicating that the amount of sequenced data could cover almost all species (Figure 2b). The curve showed that the richness of soil microbial communities under drought treatment was higher in the DNP and DLP groups, whereas the richness of soil microbial communities under normal water treatment was lower in the NNP and NLP groups. These results indicated that the richness of AMF in soil increased under drought treatment.

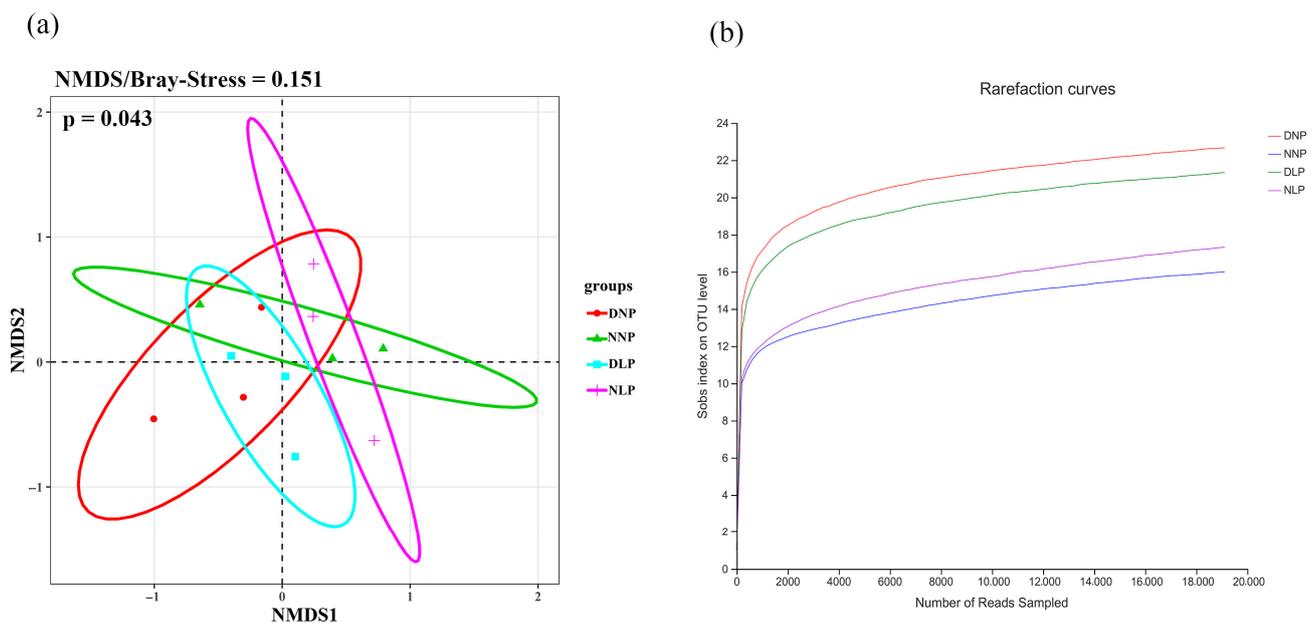


Figure 2. Differences in AMF in different habitats. (a) Nonmetric multidimensional scaling (NMDS) of AM community composition ($p < 0.05$, the reliability of the said inspection is higher). The points of different colors indicate different types of habitats. (b) Rarefaction curves of soil samples with different treatments.

3.3. Relevance of AMF and Different Habitats

The torus translation tests revealed that 77.2% (44/57) of the OTUs of the AMF were positively associated with the different habitats (Figure 3a). In the DNP, the positive correlation of AMF OTUs accounted for 28.1% (16/57), which was the largest of the four habitats. The positive correlation ratios of AMF OTUs under NNP and DLP were 15.8% (7/57); in the NLP, the positive correlation of AMF OTUs accounted for 17.5% (8/57). No AMF OTU was negatively correlated with the four habitats (Figure 3a).

Among the four different habitats, the NST indices of NLP were higher than 50%, which showed that the community assembly processes were stochastic. In addition, the NST values were lower than 50% in other habitats, thereby indicating that the community assembly processes are deterministic (Figure 4).

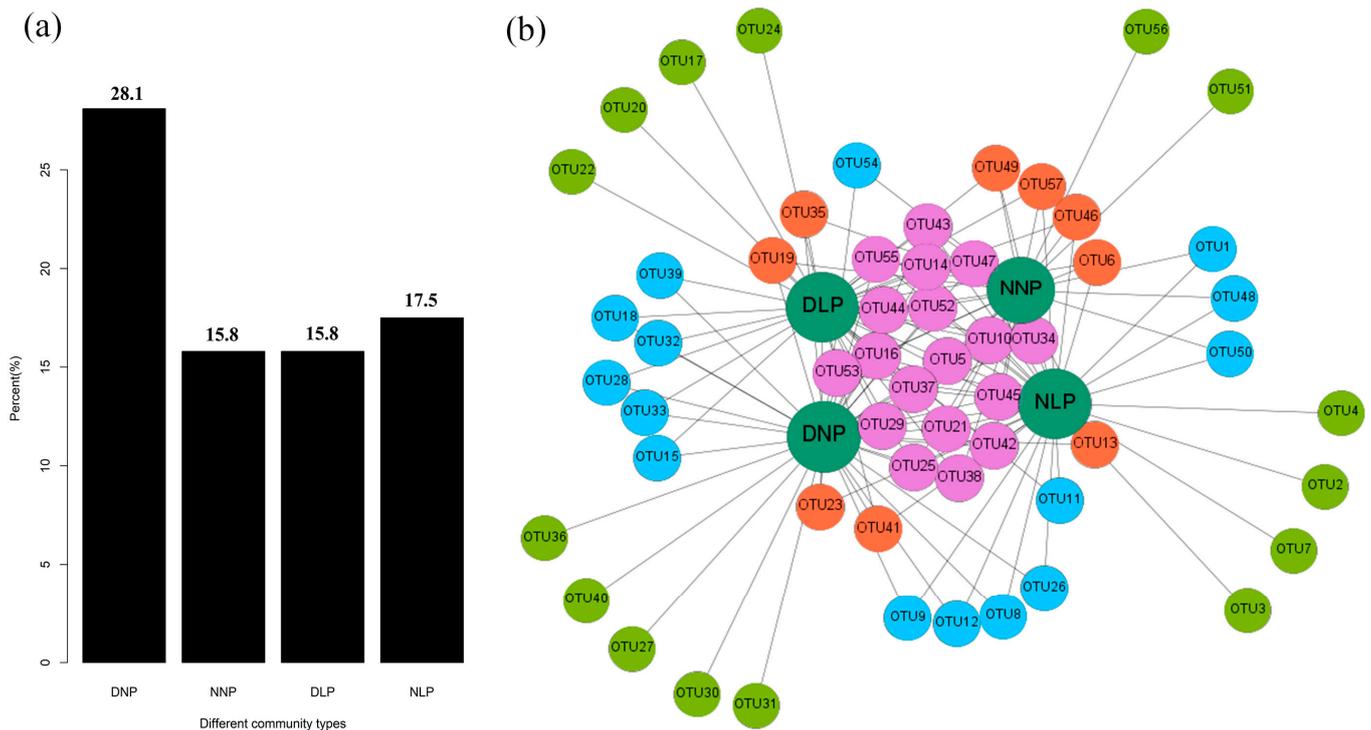


Figure 3. (a) Proportion of positively correlated OTUs in different habitats. (b) Co-occurrence network of the outcomes of AMF in the different habitats. The size of node indicates the richness of the OTUs in each microbial community.

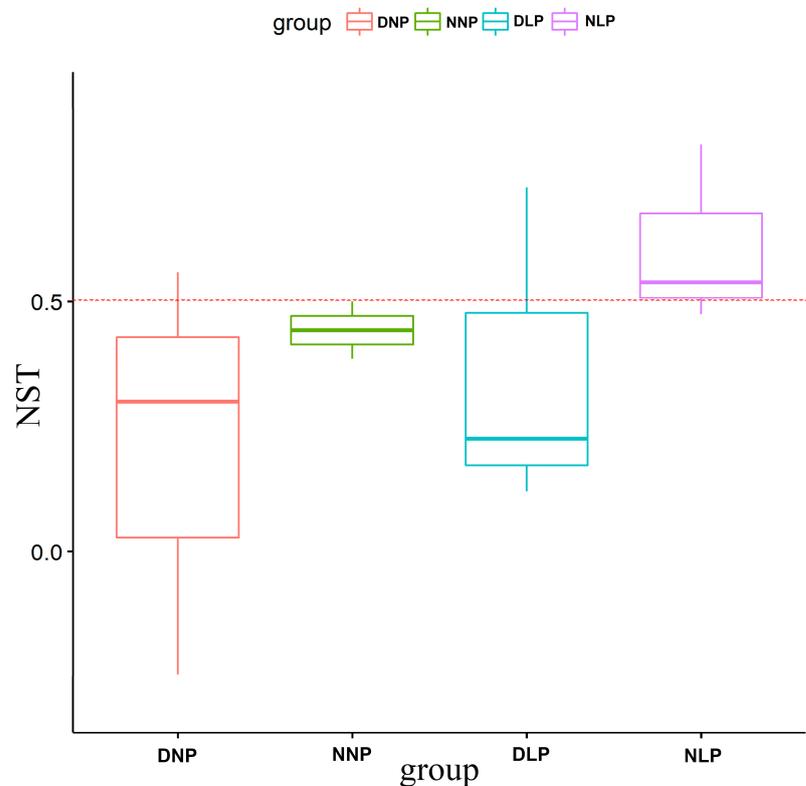


Figure 4. Normalized stochasticity (NST) ratios of AMF under different habitats. The box plots show the differences in the AMF. The NST values in different habitats are shown. An NST > 0.5 indicated that the assembly process of the AMF community was mainly stochastic, whereas an NST < 0.5 represents a deterministic assembly process. The dashed line represents the NST of 0.5.

4. Discussion

4.1. Relationship between AMF and Different Moisture Contents in Farmland Soil

Given that the worsening of global warming leads to increased drought intensity and frequency, continuous drought seriously influences the normal growth and physiology of plants. This study identified 57 AMF OTUs, which were divided into three families and three genera (including the *Glomus* genus, which is an absolute advantage). Several studies have demonstrated that, in agroecosystems, the dominant AMF community is *Glomus* [35]. The same conclusion was reached in other studies [36], probably because *Glomus* is more likely to survive. To establish the hyphal network and to help host plants resist bad environments, this finding could explain the advantage of the *Glomus* genus in dry environments.

Water is one of the indispensable factors for plant growth. In this study, to dry the two regions at the normal phosphorus concentration in the district, the drought treatment was observed to increase the richness of AMF (Figure 1a,b). The results suggested that the drought situation of AMF species diversity was remarkably higher than a normal water situation, which is consistent with other studies [37]. Some studies have also shown that in the early and midterm stages of drought, the structural change in the AMF community was not remarkable. Nevertheless, when reaching an extreme drought situation, the AMF hyphal infection rate and density were markedly reduced, and the community structure of soil AMF [38] was changed. This finding contradicts some of the studies mentioned above. This phenomenon may be due to different host plants, the duration of drought severity, or for other different reasons [39]. In DLP and NLP, no considerable changes were observed, and the abundant degree of AMF may be due to the low phosphorus treatment. Some studies have also confirmed that phosphorus addition can reduce the abundance of fungi [40].

The torus translation test showed that a total of 44 species and environmental factors had a positive correlation, and no species showed a negative correlation. In addition, we found that species prefer DNP, probably because the soil water content affected the species distribution (Figure 3a). Some studies have shown that [41], under certain drought conditions, AMF prefer to survive in drought environments, which are more conducive to the growth and development of host plants. Some studies have also found that, in the case of seasonal drought, the abundance of fungi is higher than that of bacteria and thus can adapt to the drought environment [42].

4.2. Effects of Phosphorus Application on AMF Diversity in Farmland Soil

Phosphorus is one of the important elements that are necessary for plant growth and development, accounting for more than 2% of the dry weight of plant cells; furthermore, it is indispensable in the process of plant metabolism [43]. The absorption of phosphorus by mycorrhizal plants is divided into two ways: direct absorption, which is direct absorption by the epidermal cells of the plant roots, and the other is absorbed by the formation of hyphae [44]. In this study, different phosphorus concentrations in NLP and NNP were treated. The results showed that AMF had a higher frequency in NLP than in NNP, suggesting a stronger effect of AMF under low-phosphorus conditions (Figure 1). Studies have found that AMF are present in most agricultural plants and are closely related to phosphorus in agricultural ecosystems, especially in low-phosphorus soil environments [45]. In soils with low-phosphorus content, the efficiency of phosphorus uptake by AMF decreased with increasing phosphorus concentration [46], which is consistent with our results. Some studies have also concluded that increasing phosphorus content inhibits the growth and development of mycorrhizae, resulting in poor plant growth and development [47]. Other studies may conclude that different levels of phosphorus have different effects on AMF [48]. When the phosphorus concentration is low, AMF have a symbiotic relationship with plants; when the phosphorus concentration is high, AMF can only become consumers, thus resulting in a parasitic relationship that directly affects the normal growth of plants.

Our experiments confirmed that drought increases the abundance of AMF, but the role of AMF in crop drought maximization remains uncertain. Phosphorus fertilizer is crucial to plant growth. Our study confirmed that the abundance of AMF can be increased under low-phosphorus conditions, which has beneficial effects on plant growth and development. If the phosphorus content is too high, it affects normal plant growth and development.

Microbial communities are formed by ecological process uncertainty and due to the randomness of ecological processes [49]. The deterministic process is determined by biological and nonbiological factors. The deterministic process is influenced by the fitness of the organism and determines the species composition and relative abundance. The stochastic process, including environmental filtering and competition between species and synergy, is unpredictable [50]. On the basis of the calculation of NST, we found that AMF is random in NLP, indicating that the influence of environmental factors in this habitat was uncertain. The other three habitats were deterministic (Figure 4). The results can facilitate an improved understanding of which AMF habitats occur as stochastic or deterministic processes.

In recent years, studies on the effects of phosphorus fertilizers on AMF have been widely conducted. The effects of high-concentration phosphorus fertilizers on AMF have been confirmed by many studies and have been widely recognized by researchers [51]. That is, a high phosphorus content in soil inhibits the development and functional expression of AMF. The lower the phosphorus content in the soil, the better the growth and development of AMF (this relationship is consistent with our results [52]). This finding can provide a reference for phosphate fertilizer application and is crucial for raising the output of farm crops.

5. Conclusions

Our study found that the abundance of AMF is affected by moisture content and phosphorus content. Moreover, a suitable drought treatment increases the abundance of AMF. Compared with normal phosphorus concentration, a lower phosphorus concentration increases the abundance of AMF, which is beneficial to plant growth and development. In agricultural production, we should consider the demand of the plant itself and select the appropriate water and phosphate fertilizer. Improving the utilization rate of water and fertilizer can ensure yield and benefit maximizations.

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