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ORIGINAL PAPER

The effect of type and combination of fertilizers on eukaryotic microbiome of date palm rhizosphere

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Abstract

The date palm (*Phoenix dactylifera*) is an important cultivated crop in arid areas. Here, we studied the effect of plant genotype and type of fertilizers on the eukaryotic community structures of the date palm rhizosphere. Samples were collected from one wild population, five cultivars from two farms, and a factorial fertilizer experiment (organic, chemical, and biofertilizer) in Qatar. The eukaryotic communities were sequenced using a next-generation sequencing method. A total of 2422 Operational Taxonomic Units (OTUs) were identified as belonging to 15 phyla, *Chlorophyta*, *Streptophyta*, *Imbricatea*, *Chytridiomycota*, *Ascomycota*, *Olpidiomycota*, being dominant. The wild-type date palms showed a low number of OTUs compared to cultivated date palms, potentially due to the strong influence of soil salinity and low moisture level. However, the wild-type date palm hosted the highest number of unique OTUs. PCA revealed that the eukaryotic microbiome of the wild date palms was separated from the cultivated date palms and that the eukaryotic microbial diversity varied between date palm cultivars in similar environments. Using the highest amounts of biofertilizer and chemical fertilizer decreased the species diversity within the samples. However, a high concentration of biofertilizer combined with a low concentration of chemical fertilizers enhanced the eukaryotic diversity within the samples. We conclude that cultivar type (biotic factor), type of fertilizer, and dosage (abiotic factor) play significant roles in determining the microbiome diversity of the rhizosphere. The wild date palm population could potentially host salt and drought-tolerating eukaryotes that should be further investigated for future development of biofertilizers suitable for drylands.

Keywords Fertilizer treatment · Fungi · High-throughput sequencing · Microbiome · *Phoenix dactylifera* · Protists · Rhizosphere

Introduction

The date palm (*Phoenix dactylifera*) is a popular crop tree traditionally grown in arid and semi-arid regions, and its fruits are globally valued for their nutritional and health-promoting values (Ben Chobba et al. 2013). Date palms occupy the most prominent area among the fruit trees grown in Qatar, with 7.2% of the total agricultural production (Muhammed et al. 2015). The date palm cultivars in Qatar are divided into two groups, common cultivars (e.g. Barhi, Bin Saif, Hilaini, Hilali, Hitimi, Jabri, Khalas, Khunaizi, Naboot Saif, Rotanah, Shishi) and unique cultivars (e.g., Azat, Bashbak, Berz, Disky, Niqal, Qashmak, Tarahim, Taumai Aswad, Ward, Zary) that only occur in Qatar (Muhammed et al. 2015). Most cultivation of date palm is present in the north, and central areas of Qatar, where

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the soils have low salinity levels compared to soils in other parts of the country (Muhammed et al. 2015).

Crops depend heavily on healthy soils where soil quality, fertility, and productivity reduction can occur because of agricultural practice and land use (Price et al. 2015; Cherubin et al. 2015). Indeed, various reports relate soils' health and productivity to microbial processes (Heilmann-Clausen et al. 2015; Guo et al. 2015; Stott and Taylor 2016). Modern agricultural practices, such as excessive use of pesticides and high levels of inorganic fertilizers, affect soil microbial populations, which affect the ecological process (Filimon et al. 2015; Esmaeili Taheri et al. 2015; Rangel et al. 2015; Pose-Juan et al. 2015).

Soils harbor thousands of microbial species that play dynamic roles in natural and managed agricultural soils (Abed et al. 2013; Kaisermann et al. 2015; Al-Sadi et al. 2015; Tardy et al. 2015). Eukaryotic microorganisms include most of the natural microbes and are associated with the sustainability of the soil-based ecosystem and biological processes (Crossley and Hendrix 2004; Falkowski et al. 2008; DeLong 2009; Aslani et al. 2022). The soil eukaryotic microbiome plays a role in soil structure formation, litter decomposition, and nutrient cycling (Brussaard et al. 2007; Zhao et al. 2018; TiÁskal et al. 2021). In addition, eukaryotes play a key role in soil fertility and influence prokaryotic community structure (Ali et al. 2018). There are five supergroups belonging to eukaryotes, including *Archaeplastida*, *SAR*, *Excavata*, Amoebozoa, and *Opisthokonta* (Fierer et al. 2007). They comprise about 11% of cellular biomass in the soil community (Urich et al. 2008). Fungi that belong to *Opisthokonta* are often the soil's most dominant eukaryotic species (Kazeeroni and Al-Sadi 2016). They are hugely diverse, from single microscopic cells like yeast to large macrofungi (Bridge and Spooner 2002). Like other eukaryotic microorganisms, Fungi have beneficial roles such as mycorrhizal symbiosis, soil aggregation, and plant uptake (Guo et al. 2021; Ul Haq et al. 2022). Furthermore, the macroaggregate (0.25-2 mm) limits oxygen diffusion and regulates water flow (3–7). The effect of microorganisms on soil aggregation occurs directly (through hyphal entanglement and exopolysaccharide secretion) and indirectly (through the regulation of soil organic carbon) (Daynes et al. 2012; Tisdall et al. 2012). Arbuscular mycorrhizal fungi (AMF) could augment the plant uptake of comparatively immobile nutrients, especially phosphorous and micronutrients (Guo et al. 2021). *Caragana korshinski* and *Caragana microphylla* are extensively colonized by AMF whereas host specific interaction between *Caragana microphylla* and AMF was noticed decertified grasslands in northern China desert (Ma et al. 2016). However, fungi can be harmful and be plant pathogens (Thomson et al. 2015; Guo et al. 2015; Stott and Taylor 2016). *C. radicola* is one of the pathogenic fungi that causes black score disease in date palms. Although most microorganisms are still unknown, which refers to the difficulty of their isolation from complex environmental matrices (which are not cultivable on media) (Amaral Zettler et al. 2002; Rappé and Giovannoni 2003; Bonkowski 2004).

Different abiotic variables influence the diversity of microorganisms; for example, pH frequently controls bacterial diversity (Bahram et al. 2018), climate impacts fungi (Tedersoo et al. 2014), and soil moisture influences protists (Oliverio et al. 2020). Many studies have studied the rhizosphere microbiome of plants to verify their certain roles, such as plant growth regulator (PGR), drought resistance, and salinity resistance (Abumaali et al. 2023b). Therefore, improving our knowledge about conditions for beneficial plant-associated microbiomes is essential to developing tools for improving agriculture and plant conservation (Quoreshi et al. 2019).

There is a growing number of studies on the microbiome of the date palm, and they tend to focus on fungal or bacterial communities (Ben Chobba et al. 2013; Cherif et al. 2015; Yaish et al. 2016; Mosqueira et al. 2019; Abumaali et al. 2023a). However, more comprehensive studies that focus on the effect of the genotype and the fertilizers on the eukaryotic microbiome are lacking. For that, this study aimed to identify the structure of the eukaryotic communities found in the rhizosphere between and among wild-type and cultured date palm populations and to study the effect of different fertilizers on eukaryotic microbiome diversity using high-throughput sequencing approaches. We propose the following hypothesis, (1) eukaryotic diversity from the rhizosphere of wild date palms is lower than those collected from cultivated date palms on farms, and (2) the biofertilizer enhances the eukaryotic diversity more than the chemical fertilizers.

Materials and methods

Soil samples collection

A total of 103 soil samples were collected from the rhizosphere of date palms using a small shovel, roughly 10 cm below the surface (50–80 cm from the date trees), with a high abundance of fine date palm roots, as follows: five trees were chosen randomly for sampling the rhizosphere for each cultivar (Berhi, Shishi, Nabot Saif, Khalas, and Khenezy) and the wild date palm. The samples were collected from three locations: wild date palms soil samples were collected from Umm Bab (25°13'07.8"N 50°46'04.5"E), while the cultivated date palm soil samples were collected from Qatar University Farm (25°48'2"N 50°46'02.5"E), and Rowdat Al-Faras Farm (25°49'22.3"N 51°19'58.1"E). All sampling

was conducted in March 2021. The wild date palms occur scattered along the beach at Umm Bab for a stretch of a few kilometers, the size of the plot with the different cultivars of date palms at the Qatar University farm is 2 ha, the size of the plot with different cultivars of date palms at Rowdat Al-Faras Farm is 1.7 ha, and the size of the fertilizer experiment at Rowdat Al-Faras Farm is 1.3 ha. In total, 55 soil samples (5 replicate* 5 cultivars* 2 farms + 5 samples from one wild population) were obtained to compare the eukaryotic communities in the rhizosphere of a wild date palm population (oasis ecosystem) and various cultivars grown on farms (agroecosystem). Five date palm trees were randomly chosen from the wild population and each of the different cultivars at the two farms for the sampling. The cultivated date palms in both farms had a drip irrigation system.

Impact of the chemical and organic fertilizers on eukaryotic microbial community structures in date palm rhizosphere

To assess the effect of different chemical and organic fertilizers on eukaryotic community structures in the date palm rhizosphere, 15 different fertilizer types were applied to date palm (Khalas Cultivar) at Rodat Al-Faras Research Station in a randomized complete block design (RCBD) experiment with three replications. 48 soil samples (3 replicate*15 fertilizer types + 3 control) from cultivated date palm trees rhizosphere were collected from 15 different fertilizer types in addition to control (no fertilizer). The fertilizer treatments include organic fertilizer (animal waste; 30 kg per tree per year), biofertilizer (commercial bio-fertilizer named Rewital Plus) obtained from BIO-GEN company (https://bio-gen.pl/en/); 85 g of fertilizer per 100 L of water per 15 days), and chemical fertilizer (N:P: K ration of 1.8:0.8:1 kg/date palm tree (numbers for the 100% treatment) (Table 1). The fertilizer treatments were applied for 48 months, after which the sampling occurred.

All soil samples were stored in paper bags with proper labeling until delivered to the laboratory (directly after the sampling). Following the protocol of a global project (Tedersoo et al. 2021), the soil samples were air-dried for seven days at the laboratory. After drying and removing all roots, root fragments, and rock debris from the soil, soil samples were ground by hand inside plastic bags to prevent contamination (Tedersoo et al. 2021). The composite samples were prepared by combining (pooling) five samples from the same cultivars from the same locations by the ratio (1:1:1:1:1 g), after which chemical and molecular analysis were done, and the remaining material was stored at -20 for backup.

Molecular analyses, sequencing, and bioinformatics

DNeasy PowerSoil kit (Qiagen, Germany) was used to extract DNA from composite soil samples following the manufacturer's instructions. Thirty ng of the extracted DNA samples were used as templates to amplify the V4 region of the 18S SSU rRNA gene using the TAReuk-454FWD1 (5'-CCAGCASCYGCGGTAATTCC-3') and TAReukREV3 (5'-ACTTTCGTTCTTGATYRA-3') oligonucleotides in subsequent polymerase chain reaction (PCR) amplification. Agencourt AMPure XP beads (Beckman Coulter) were used to purify the DNA, and the Agilent Technologies 2100 bioanalyzer was used to qualify the library. The qualified libraries were sequenced using the pair-end on Hiseq 2500 platform according to their insert size.

Table 1 Alpha diversity for eukaryotic communities in the rhizosphere of date palms in response to different fertilizer treatments. See Table S1 for the key to samples

Sample Name	sobs	chao	ace	shannon	simpson	coverage
L	488	530.3684	534.5833	3.098749	0.173906	0.998594
M	196	269.0286	337.4592	2.588567	0.155426	0.993624
N	611	709.7838	676.633	4.904598	0.017108	0.99826
O	520	587.1622	569.4924	3.549404	0.180337	0.998562
P	394	491.0000	471.8765	0.936699	0.770712	0.998052
Q	666	729.3818	723.2437	4.974267	0.016991	0.998293
R	398	448.5714	440.7932	3.882892	0.04259	0.998795
S	519	555.2727	556.4964	4.516013	0.037431	0.998844
T	373	406.6098	409.0341	3.279219	0.104732	0.998933
U	194	246.2857	255.8367	3.155697	0.087144	0.992159
V	490	589.1071	557.1855	4.517582	0.024453	0.99849
W	520	569.7632	563.3902	4.749396	0.025683	0.998746
X	706	782.5600	765.9148	4.841822	0.029906	0.998219
Y	874	977.9091	948.2122	4.882772	0.023747	0.99725
Z	660	697.3469	694.8379	5.098301	0.016141	0.99875
AA	798	844.7746	843.438	5.042452	0.023817	0.998305
Stand. Dev	191.7404	197.912	184.3953	1.162798	0.186143	0.001955

Raw reads were filtered to remove adaptors and low-quality and ambiguous bases. Then, the fast Length Adjustment of short reads program (Flash, v1.2.11) (Magoč and Salzberg 2011) was used to get the tags for paired-end reads. After that, the tags were clustered into Operational Taxonomic Units (OTUs) with 97% similarity using UPARSE software (v7.0.10.90) (Edgar 2013). Chimaera sequences were detected by comparing with UNITE database (v20140703) using UCHIME (v4.2.40) (Edgar et al. 2011). Then, the ribosomal Database Project (RDP) Classifier v.2.2 was used to taxonomic the OTUs representative sequences within a minimum confidence threshold of 0.6 and trained on the Silva (V138) and UNITE (Version8.2) by QIIME v1.8.0 (Caporaso et al. 2010). The USEARCH_global (Edgar 2010) was used to compare all tags to OTUs to get each sample's OTU abundance statistics table. Mothur v1.31.2 (Schloss et al. 2009) and QIIME v1.8.0 (Caporaso et al. 2010) software were used to estimate alpha and beta diversity, respectively, at the OTUs level. A 27 samples cluster was conducted by QIIME (v1.8.0) (Caporaso et al. 2010) based on UPGAMA.

OTUs Rank curve, Core-Pan OTUs of samples, and species accumulation curves were plotted with R packages v3.1.1., while principal component analysis (PCA) in OTUs was plotted with R package "ade4" by QIIME v1.8.0 (Caporaso et al. 2010). GraPhlAn created a GraPhlan map of species composition. In addition, the phylogenetic tree of species was constructed using FastTree v2.1.3 (Price et al. 2010). Furthermore, the UPGMA cluster and abundance map was done using phytools and R package v.3.5.1.

Chemical analysis

Initially, 27 composite soil samples were oven dried at 60–62 °C for 48 h to avoid the decomposition of organic materials and augment mineral extractability (Adenan et al. 2021). The dried soil samples were then crushed to a fine powder in a rotary ball mill (Retch Mill, Haan, Germany) at a speed of 250 rpm for 40 min, followed by passing through a 2 mm mesh of a standard sieve. Subsequently, three replicates of each composite soil sample were used to measure the pH, salinity, total carbon (TC), total nitrogen (TN), NO_3^-, NO_2^- as well as the concentration of chemicals elements such as Ca, K, Mg, P, Cd and Pb using standard previously published procedures (International Organization for Standardization (ISO/IEC 17025) (Adenan et al. 2021). All physiochemical analyses (pH, TSS, Salinity, and electrical conductivity) were measured using a YSI probe and employed the use of a 1:5 soil-to-distilled water ratio (Hardie and Doyle 2012). Soil nitrogen and carbon were analyzed using the elemental analyzer. 5 g of soil sample was directly analyzed by using a TOC/TN Soil Analyser. Soil nutrients for nitrates and nitrites were analyzed using a UV spectroscopy (EasyChem Analyzer Plus) (O'Dell 1993). Trace Metals were analyzed using Inductively Plasma Optical Emission Spectrometry (ICP_OES). A 0.25 g of soil was weighted into Teflon tube and digested using a combination of Nitric acid and Hydrofluoric acid followed by set at 95°c in a Hot Block Heater as per PA200.7.

Statistical analysis

Alpha diversity was measured by the observed species index, Chao index, ace index, Shannon index, Simpson index, and Good-coverage index. Samples with low sobs (OTUs number) and high Shannon index indicates low diversity and vice versa. Alpha diversity was estimated by MOTHUR (v1.31.2) (Schloss et al. 2009). Sequenced data is considered sufficient when the rarefaction curve tends to be smooth (Amato et al. 2013). Otherwise, it is suggested to increase the sample size. The Shannon and Simpson index analyses were applied to estimate eukaryotic species diversity and fungal species richness. The good-coverage index shows the coverage of the sample library. Smaller index values indicate a lower probability that sample sequences are not sequenced. This value reflects whether the sequencing results can represent the sample's real property. Beta diversity analysis was used to evaluate the differences between samples in terms of species complexity. Beta diversity analysis was carried out using QIIME(v1.80) software (Caporaso et al. 2010). The beta diversity distance was calculated using the 'OTU table biom' file. A heatmap is a data visualization technique showing a phenomenon's magnitude as color in two dimensions. Clustering of samples based on species abundance in samples (at all seven levels) was performed to reveal the similarity among samples. The heatmap of different classification levels was plotted with R package v3.4.1 and "ggplot" to complete the clustering method and 'Euclidean' distance. XLSTAT was used to investigate relationships between the composition of different soil fungal' groupings, the chemical parameters in soils, different locations sampled, and to understand the relationship between different organic fertilizers and the eukaryotic diversity. For the principal component, the PCA in OTUs was plotted with XLSTAT to visualize the linkages between the soil fungal communities and the main drivers, soil parameters and sites, and cultivars (farms with cultivated date palms, cultivars, and wild date palms).

Results

The effect of date palm genotype, biofertilzer and chemical fertilizers on the rhizosphere eukaryotic biodiversity

The Illumina 2×300 bp HiSeq 2500 platform generated 1,671,989 paired-end reads targeting the V4 region of the 18 S SSU rRNA gene. These reads were quality filtered, chimaeras removed, and combined. The final dataset comprised 1,248,673 sequences, including 2,422 OTUs from the 27 composite soil samples. A total of 2,422 eukaryotic OTUs belonging to major 15 phyla, including Chlorophyta (14.2%), Streptophyta (6.8%), Imbricatea (2.8%), Chytridiomycota (2.6%), Ascomycota (2.1%), Olpidiomycota, and other (66.8%) (Fig. 1).

The core-Pan OTUs plot analysis for eukaryotic communities isolated from the date palm rhizosphere shared 14 OTUs after removing OTUs related to other eukaryotes and OTUs that were not annotated (Fig. 2). The highest unique OTUs number was 116 OTUs obtained from wild date palms, followed by 67 and 53 OTUs obtained from the rhizosphere of Nabot saif and Shishi cultivars, respectively, from farm 1 (Rowdat Al-Faras). In contrast, the unique OTUs numbers of Nabot saif and Shishi cultivars from farm 2 (Qatar University) were 31 and 21 OTUs, respectively. At the same time, the number of unique OTUs of other cultivars (Berhi, Khalas, and Khenezy) ranged from 12 to 41 OTUs. The unique OTUs number of soil samples under fertilizer treatment conditions ranged between 3 and 45 OTUs. The lowest OTU numbers were found in 70% chemical and 100% biofertilizer (treatment 10), while the highest number was treated with 100% biofertilizer and 30% chemical fertilizer (treatment 14).

To estimate the alpha diversity within the samples, the refraction curves were first generated (Figure S1). The alpha diversity of five date palm cultivars samples (Berhi, Khenezy, Khalas, Shishi, and Nabot saif) from the two farm locations are presented along with Sobs, Chao, Shannon, and ace indexes (Table 2). The Shannon values of date palm cultivars from farm two (Qatar University farm) and wild date palm samples ranged from 3.02 to 5.2. In contrast, the lowest value was obtained from the Khenezy cultivar sample from farm one (Rowdat Al-Faras), while the highest was obtained from the Barhi cultivars sample from farm one. These results indicate that Khenezy had higher diversity than other cultivars in farms one and two. However, Barhi showed the lowest eukaryotic diversity among the samples. The sobs value for five date palm cultivars from farm two and wild-type date palm samples ranged from 402 to 778. In contrast, the lowest sobs value was obtained from the Khenezy cultivar sample from farm one, while the highest was obtained from the Khalas cultivars sample from farm two (Qatar University). The sobs value for wild-type date palm samples was 435, and the Shannon index was 3.8, indicating high diversity.

The alpha diversity of 16 samples from the Khalas cultivar that were treated with different concentrations and combinations of fertilizers is summarized in Table 1. The Shannon index for treated samples ranged from 0.94 to 5.1. In contrast, the lowest Shannon index was found in samples with 100% for both biofertilizer and chemical fertilizer, while the highest was obtained from samples treated with 30% chemical and 100% biofertilizer. The sobs values ranged from 194 to 798; the lowest value was obtained from samples treated with 70%chemical and 100% biofertilizer, while the highest value was obtained from the control samples (no fertilizer) (Table 1).

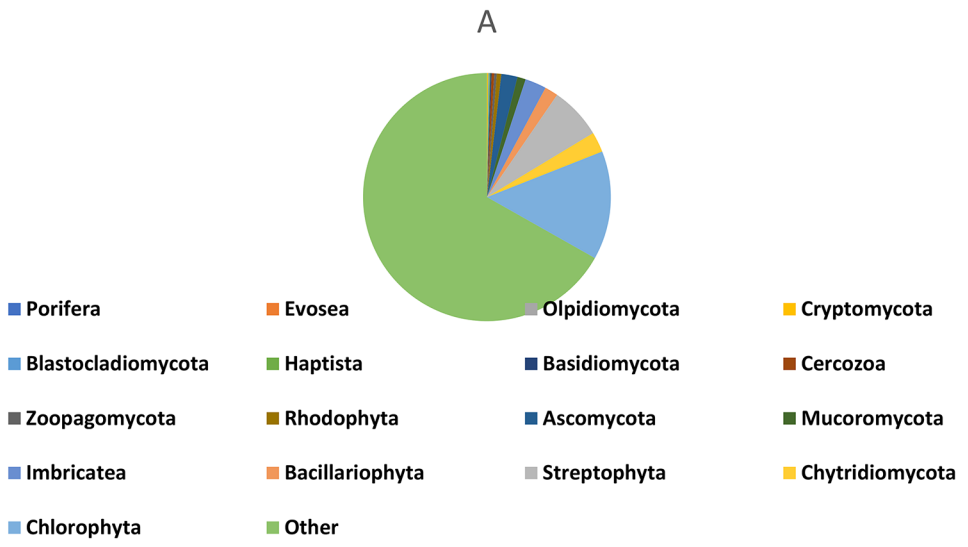

Fig. 1 The percentage for the dominant groups of eukaryotic phyla in the rhizosphere of date palms

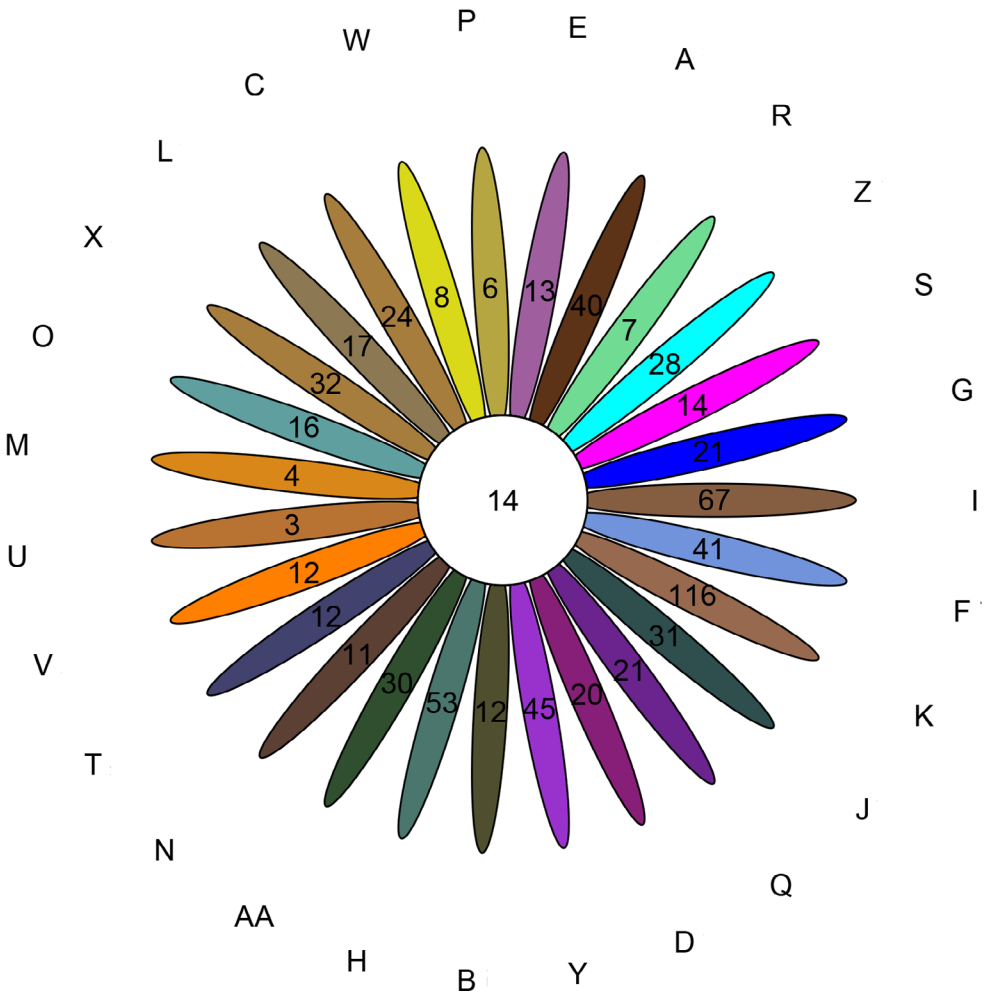

Fig. 2 Core-Pan OT Us plot for eukaryotic communities isolated from the rhizosphere of date palms from different locations, cultivars, and fertilizer treatments. The middle numbers indicate the number of OTUs in 27 composite soil samples, and the ellipse outside the center circle indicates the number of unique OTUs in each sample. For the code of samples (letters in the outer circle), please see Table S1

Table 2 Alpha diversity for eukaryotic communities in the rhizosphere of 5 date palm cultivars in two different farm locations in Qatar. See Table S1 for the key to samples

Sample Name	sobs	chao	ace	shannon	simpson	coverage
A	767	832.6316	823.877	5.208519	0.013793	0.998202
B	508	555.4583	561.8879	4.438855	0.032201	0.998616
C	493	549.4773	547.8747	3.737486	0.117452	0.998571
D	549	587.5918	589.2226	4.474969	0.028085	0.998744
E	402	461.1667	459.6211	3.026838	0.210204	0.998574
F	565	592.8409	592.1758	4.526553	0.038668	0.998983
G	563	619.6923	607.1319	4.845671	0.0185	0.998635
H	778	821.6974	824.5494	4.820036	0.02858	0.998327
I	686	750.0976	730.964	5.082244	0.016484	0.998522
J	522	576.0286	563.5798	4.889615	0.014921	0.99873
K	435	482.3571	466.044	3.817913	0.088032	0.99895
Stand. dev	124.326	126.4303	125.9112	0.663358	0.061162	0.000233

Beta diversity is a measure of the similarity of the membership and structure found between different samples. The heatmap analysis was used to investigate the relationship between the soil samples obtained from the rhizosphere of the tested date palm trees based on the relative abundance and the eukaryotic phyla relationship (Fig. 3). The results showed that the 27 samples were divided into four groups, CLU1 ($n=10$), CLU2 ($n=13$), CLU3 ($n=1$), and CLU4 ($n=3$). Group CLU1 was subdivided into sub-groups CLU1.1 and CLU1.2. The CLU1.1 included the W sample (treated with 30% chemical fertilizer), the Z sample (treated with 30% chemical, 100% organic, and 100% biofertilizer), and the O sample (treated with 100% organic and 100% biofertilizer). The CLU1.2 included seven samples, whereas

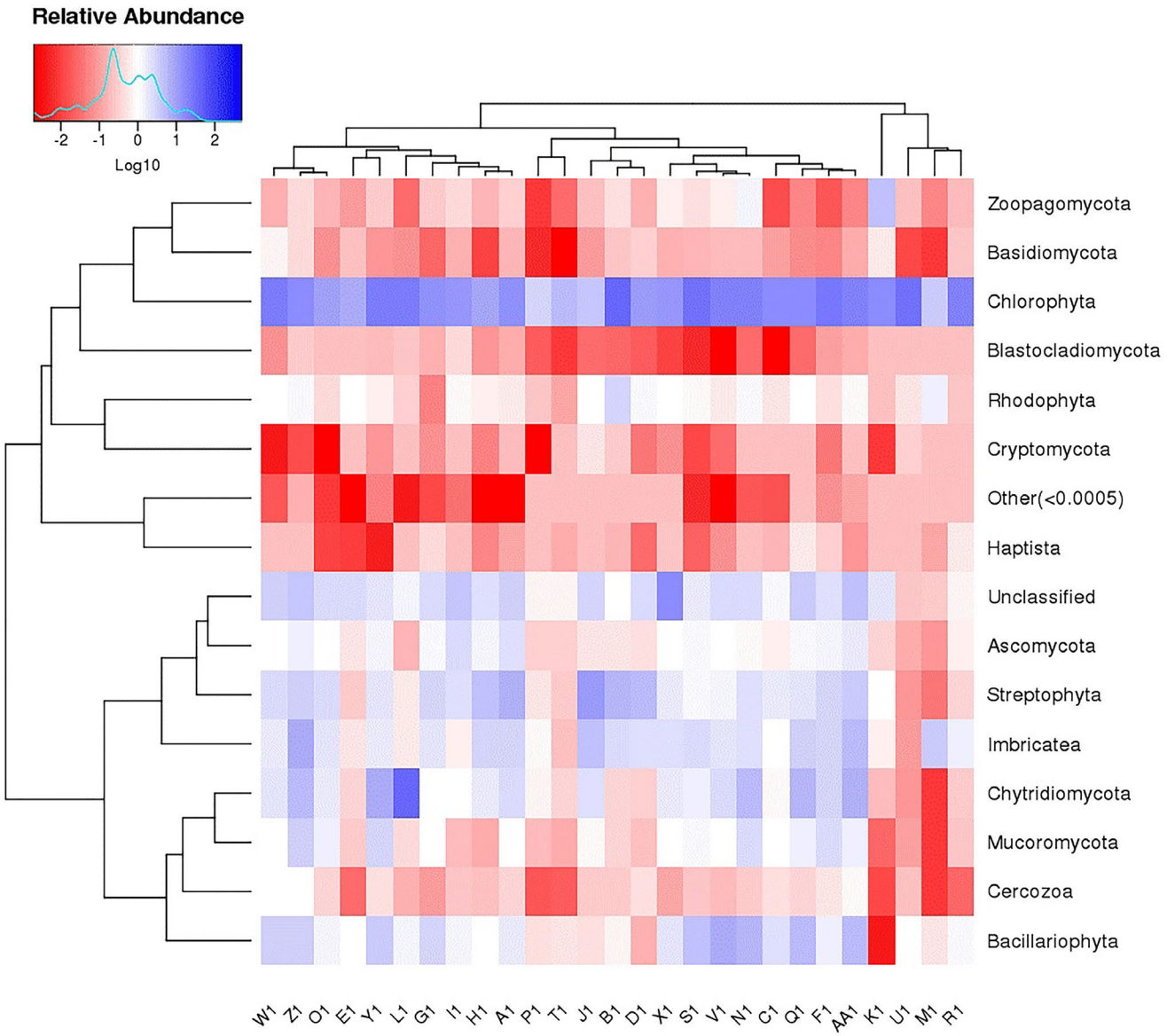

Fig. 3 The heatmap for eukaryotic phyla. The horizontal cluster indicates the similarity of specific phyla among different samples. It can be inferred that samples are likely to be similar when closer distance/shorter branch length is shown in the graph. Relative abundance values are normalized through log transformation. In addition, if any relative abundance value is "0", then the value will be replaced by half the minimum abundance value of all samples. CL OR CLU = cluster.

the E sample (Khenezy cultivar, farm one) was close to the Y sample (treated with 100% biofertilizer and 30% chemical fertilizer), and the A sample (Barhi cultivar, farm1) was close to the H sample (Khalas cultivar, farm two). The cluster CLU2 also was subdivided into the CLU2.1 sub-cluster, the P sample (treated with100% biofertilizer and 100% chemical) and the T sample (treated with 70% chemical and 100% organic), and the CLU2.2 sub-cluster with 11 samples, where the AA sample (no fertilizer, control) was closer to F sample (Khenezy cultivar, farm two), however, the "group" CLU3 included only the wild date palm sample (K) which was distinctly apart from the others. Group CLU4, with U sample (treated with 70% chemical and 100% biofertilizer), M sample (treated with 100% organic fertilizer), and R sample (treated with 100% chemical, organic and biofertilizer), where the last two samples were closer.

The horizontal groups indicate the similarity of phyla among different samples. The phyla were divided into four groups: CL1, CL2, CL3, and CL4 (Fig. 3). Group CL1 was subdivided into three sub-groups involving Bacillariophyta (sub-group CL1.1), Cercozoa (sub-group CL1.2), Mucoromycota, and Chytridiomycota (sub-group CL1.3). Cluster CL2 included Imbricatea (sub-group CL2.1), Streptophyta (sub-group CL2.2), Ascomycota, and Unclassified

(sub-group CL2.3). Cluster CL3 included Haptista and others, whereas group CL4 involved Cryptomcota, Rhodophyta (sub-group CL4.1), Blastocladiomycota (sub-group CL4.2), Chlorophyta (sub-group CL4.3), Basidiomycota and Zoopagomycota (sub-group CL4.4).

Relative abundance on class level showed that most cultivars had a similar relative abundance of eukaryotes except for the wild population (K) (Fig. 4). Chlorophyceae had the highest relative abundance among cultivars, followed by Magnoliopsida, Ulvophyceae, Bacillariophyceae, and Chytridiomycetes. In comparison, Ulvophyceae had the highest relative abundance among samples in the fertilizer experiment, followed by Chlorophyceae, Chytridiomycetes, Bacillariophyceae, and Magnoliopsida, respectively (Fig. 4). Oomycota was presented in all samples except Barhi cultivars from farm 2 (B) and samples treated with 100% organic fertilizer (M). About 40–90% of the relative abundances were unclassified eukaryotic organisms (others).

The phylogenetic tree analysis was performed based on the genus level for the 27 samples (Figure S2). The phylum Evosea had the smallest number of genera, including *Hyperamoeba* and *Didymium*. The phylum Rhodophyta included *Peyssonnelia*, *Cyanidioshyzon*, *Centroceras*, etc. The phylum Zoopagomycota involved *Mycoemilia*, *Cochlonema*, *Rhopalomyces*, etc. Chlorophyta included *Neochlorosracina*, *Prototheca*, *Symbiochloris*, etc., and Basidiomycota included *Phyllozyma*, *Kurtzmanomyces*, etc. The phylum Ascomycota had the highest number of genera, including *Cladosporium*, *Neoascochyta*, *Saccharomyces*, *Hanseniaspora*, and *Kodamaea*.

Effect of chemical properties, habitat, and fertilizer treatments on eukaryotic communities

The principal component analysis (PCA) plot (Fig. 5) showed that soil properties such as chemical concentrations, pH, salinity, fertilizers, and genotype affects the eukaryotic community structure (see Table S2 for soil chemical data of the different samples). The PCA showed that salinity, conductivity, and NO3- mg/kg soil concentration significantly correlated with other elements (NO_3-N mg/Kg soil, NO_2-N mg/ Kg soil, %C, %TN, Ca, Cd, Mg, P, Pb, and K) (r-value > 0.5). In contrast, Pb showed almost no correlation with the other elements (r value close to 0). Furthermore, the PCA suggests a relation between high C%, salinity, and high Cryptomycota and Zoopagomycota relative abundance, while Streptophyta appears to be affected by conductivity and NO_3- concentration. The samples from the fertilizer experiment showed no correlation with pH, salinity, and soil element concentrations (P, Cd, K, Mg, NO2) mg/kg soil concentration. As mentioned previously, the Khalas cultivars used in the fertilizer experiment were clustered close to Khalas samples from other Farms. In addition, the wild sample (UB) showed no correlation with other samples.

Discussions

Plant roots have a relationship with the rhizosphere microbiome communities. There are direct and indirect interactions with free-living microbes affecting plant health, growth, and productivity (Bennett et al. 2012). Through indirect interactions, the microorganism enhances nutrient availability for the plant and direct interaction with pathogens and mutualists (Morgan et al. 2005). In contrast, geographic locality,

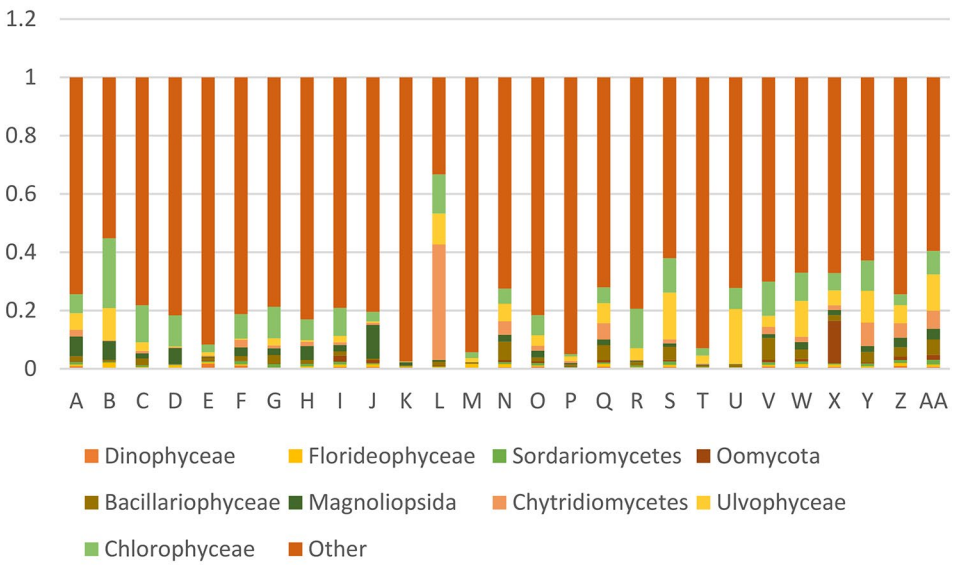

Fig. 4 Relative abundance of eukaryotic classes in soil samples. **A - J**: 5 cultivars from two farm locations and wild samples (K). **L - Z**: samples different fertilizer treatments (control = no fertilizer (AA)). For the code of samples (A-AA), please see Table S1

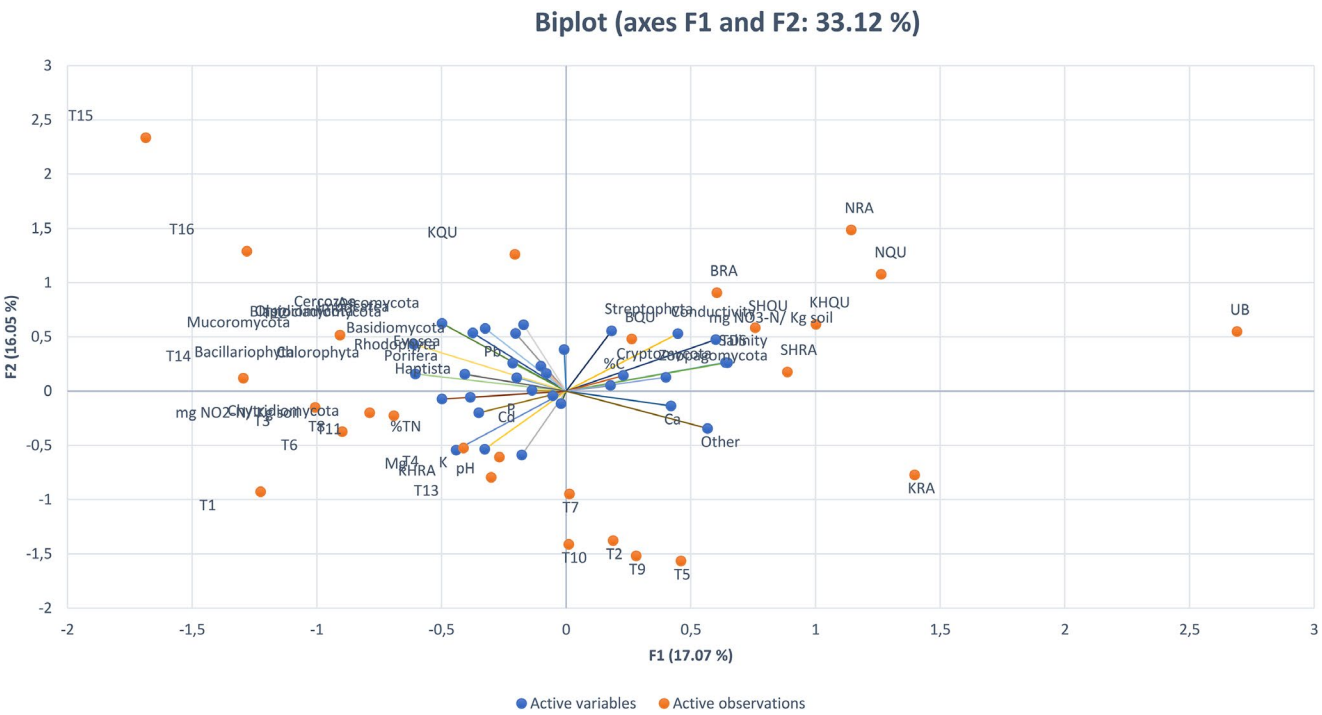

Fig. 5 Principal component analysis (PCA) plot showing the associations between chemical element concentrations, pH, salinity, eukaryotic phyla (shown in red), date palm cultivars among locations in Qatar, and fertilizer treatments (shown in blue). The significant influence of the chemical parameters & eukaryotic phyla (shown in red) is indicated by the distance of each point from the origin. For the code of samples, please see Table S1

environmental factors (abiotic stress), host identity, developmental stages, and plant properties like age and genotype (biotic stress) are considered the main driver of plant fungal endophyte diversity and composition (Hunter et al. 2014; Mefteh et al. 2017). In line with this, we found that geographic locality and cultivar type (genotype) were the main drivers of variation in eukaryotic communities in the date palm rhizosphere by using core-Pan OTUs analysis. Only 14 OTUs were shared among all samples, and the highest unique OTUs number was 116 OTUs (wild date palm microbiome population), followed by 67 OTUs (Nabot saif cultivar, farm 1) and 53 OTUs (Shishi cultivar, farm 1). Eukaryotic diversity varies among diverse crops on the same farm (Kazeeroni and Al-Sadi 2016). The observed OTUs, Shannon index, and Chao1 richness estimates of soil samples from date palm and acid limes had higher fungal diversity than soil samples from cucumbers in a semi-Oasis farm in Oman (Kazeeroni and Al-Sadi 2016). In a study on the microbiome of date palms in an oasis in Saudi Arabia, Streptophyta dominated in Sukkari cultivars and was absent in Khalas cultivars while Ascomycota dominated Khalas cultivars and was absent in Sukkari cultivars (Dhawi and Alsanie 2022). In another study at a semi-oasis farm and organic farm in Oman, Ascomycota was the most dominant phylum in most samples (date palm, acid limes, cucumber, and tomato) (Kazeeroni and Al-Sadi 2016).

Our first hypothesis that eukaryotic diversity from soil samples from wild date palms is lower than those collected from farms of different date palm cultivars was not supported. However, in contrast to Shannon diversity, the number of OTUs was low in the wild date palm compared to cultivars. The wild date palm oasis where soil samples were collected is near the beach. Thus, we expected that the long-time evolutionary history of date palms being exposed to high salinity in soil (1,5 ppt (parts per thousand) compared to between 0.4 and 0.6 ppt in the fertilizer experiment) (Adenan et al. 2021), and low freshwater availability (compared to continuous irrigation of date palms in the two farms) would have a negative impact on the eukaryotic diversity. Our result showed richness, and the effective number of species of eukaryotes from the rhizosphere of the wild date palms was in the middle range compared to the rhizosphere samples from the different date palm cultivars collected from farms. The large variation in soil salinity at the Rowdat Al-Faras, between different cultivars and the fertilizing experiment, might have been caused by excessive fertilizing of individual date palms (Darwish et al. 2005). While the exact amount of different fertilizers was controlled during the fertilizing experiment, the same was not true for the cultivars grown outside the fertilizer experiment. This could potentially explain the large variation within the farm. Further support for this comes from all soil samples

showing low salinity levels within the fertilizing experiment where the fertilizing was controlled. The soil microbial community could be altered due to soil salinization, affecting the soil nutrient cycle in terrestrial ecosystems (Zhang et al. 2019b, 2019c). Soil salinity and water availability are factors that affect the microbe's population in deserts (Rath and Rousk 2015). Usually, microbes contain 70% moisture in their cell, and soil moisture level strongly influences the gaseous exchange and liquid diffusion of microbes in the soil (Banerjee et al. 2016). Our results align with other studies that found the microbial community in the rhizosphere associated with wild and cultivated plants to differ. For example, there were significant differences in fungal community structures between the wild and reintroduced rhizosphere soil of *Magnolia sinica* in the relative abundance of taxa at the phylum level (Shen et al. 2020). Similarly, the dominant fungal phyla differed between natural and cultivated walnut trees, and naturally growing trees had a higher Shannon diversity (Bai et al. 2020). In contrast, there were no significant differences in the dominant phyla and genera in the rhizosphere of wild and cultivated soybean (Zhang et al. 2019a).

Our second hypothesis that the biofertilizer results in higher eukaryotic diversity in the rhizosphere compared to chemical and organic fertilizers was not supported by the results obtained from this study. Instead, the highest diversity in the rhizosphere was found in the treatments combining biofertilizer and chemical fertilizers. However, similar to other studies, we found the OTUs number increased with decreasing chemical fertilizer treatment concentration. Date palm trees used for fruit production at commercial levels, unlike wild-type date palms, require extra energy to maximize the yield of dates besides maintaining normal tree growth. For that, stable and high date yields depend on healthy soil structure and fertility support. Soil fertilization, involving organic or chemical fertilizer, could influence rhizosphere microbial communities by altering their food or energy sources, whereas the quality and quantity of root exudates (Kerry 2000; Van Nuland et al. 2016; Zhang et al. 2017). Our result showed that the highest richness and greatest effective number of eukaryotic species was found in the combination of 100% biofertilizer and 30% chemical fertilizers. However, bioorganic fertilizer leads to significantly higher fungal diversity in a maize-cabbage rotation system than chemical fertilizer alone (Qiao et al. 2019).

Proper agriculture management of perennial woody plants should conserve soil microbiota and allow soil microbes to enrich the rhizosphere (Maeder et al. 2002; Chaudhry et al. 2012). A study in China found that applying organic fertilizer changed not only the fungal rhizosphere but also suppressed a common soil-born pathogen that frequently causes significant losses in yields of cereal crops (*Heterodera avenae*) (Qiu et al. 2020). Organic fertilizers often enrich microbial diversity compared to chemical fertilizers in conventional agriculture (Maeder et al. 2002; Chaudhry et al. 2012). Our results showed that using highly concentrated biofertilizer enhances eukaryotic diversity when combined with low concentrations of chemical fertilizers. The fertilization practices influence the soil microbiome by altering it through the enrichment of soil chemical characteristics (Ai et al. 2015; Yao et al. 2018). In addition, inoculating plants with microbial communities has frequently been shown to support growth and yield, and combined with fertilizers, this could optimize agricultural practices (Guo et al. 2021; Khan et al. 2022; Ul Haq et al. 2022). These findings can help the management of microbiota in the date rhizosphere and improve soil management techniques for date palm management.

Conclusions

Chlorophyta, Streptophyta, Imbricatea, Chytridiomycota, Ascomycota, and Olpidiomycota were the dominant eukaryotic phyla from the date palm rhizosphere. The eukaryotic microbial communities varied between wild and cultivated date palms. The rhizosphere of the wild-type date palm had fewer eukaryotic OTUs (435) than cultivated date palms (402–778), possibly due to the strong influence of soil salinity and moisture level on microbes. However, the rhizosphere of wild-type date palms hosted the highest number of unique OTUs (116), likely reflecting selection from the stressful environment, less available nutrients, and water compared to cultivars grown on farms. PCA revealed that the eukaryotic microbiome of the wild date palms was separated from the cultivated date palms and that the eukaryotic microbial diversity varied between date palm cultivars in similar environments. The 100% biofertilizer and chemical fertilizer resulted in the lowest alpha diversity. In contrast, a high concentration of biofertilizer combined with a low concentration of chemical fertilizers enhanced the eukaryotic diversity within the community, suggesting that a combination of biofertilizers and chemical fertilizers may be needed to optimize soil health. Future research should focus on the interaction between microbial communities and fertilizers and their impact on date palm yield, quality, and stress tolerance.

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Data availability The sequence datasets generated and/or analyzed during the current study are available in the NCBI repository, https://www.ncbi.nlm.nih.gov/sra/PRJNA956269.

Declarations

Ethics approval and consent to participate This article does not contain any studies on human or animal subjects.

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References

Abed RMM, Al-Sadi AM, Al-Shehi M et al (2013) Diversity of free-living and lichenized fungal communities in biological soil crusts of the Sultanate of Oman and their role in improving soil properties. Soil Biol Biochem 57:695–705. https://doi.org/10.1016/j.soilbio.2012.07.023

Abumaali DA, Al-Hadidi SH, Ahmed T et al (2023a) Bacterial community structure and predicted function in the rhizosphere of wild and cultivated date palms: effects of fertilizers on composition and functionality. Ecol Genet Genomics 29:100195. https://doi.org/10.1016/j.egg.2023.100195

Abumaali DA, Al-Hadidi SH, Yahia MND et al (2023b) The date palm microbiome: a review. Ecol Genet Genomics 29:100212. https://doi.org/10.1016/j.egg.2023.100212

Adenan S, Oja J, Alatalo JM et al (2021) Diversity of arbuscular mycorrhizal fungi and its chemical drivers across dryland habitats. Mycorrhiza 31:685–697. https://doi.org/10.1007/s00572-021-01052-3

Ai C, Liang G, Sun J et al (2015) Reduced dependence of rhizosphere microbiome on plant-derived carbon in 32-year long-term inorganic and organic fertilized soils. Soil Biol Biochem 80:70–78. https://doi.org/10.1016/j.soilbio.2014.09.028

Al-Sadi AM, Al-Mazroui SS, Phillips AJL (2015) Evaluation of culture-based techniques and 454 pyrosequencing for the analysis of fungal diversity in potting media and organic fertilizers. J Appl Microbiol 119:500–509. https://doi.org/10.1111/jam.12854

Ali SRA, Isa MNM, Safari S et al (2018) Eukaryotic biodiversity in mixed peat ecosystems in Sarawak, Malaysia. J Oil Palm Res 30:429–450

Amaral Zettler LA, Gómez F, Zettler E et al (2002) Eukaryotic diversity in Spain's river of fire. Nature 417:137–137. https://doi.org/10.1038/417137a

Amato KR, Yeoman CJ, Kent A et al (2013) Habitat degradation impacts black howler monkey (Alouatta pigra) gastrointestinal microbiomes. ISME J 7:1344–1353. https://doi.org/10.1038/ismej.2013.16

Aslani F, Geisen S, Ning D et al (2022) Towards revealing the global diversity and community assembly of soil eukaryotes. Ecol Lett 25:65–76. https://doi.org/10.1111/ele.13904

Bahram M, Hildebrand F, Forslund SK et al (2018) Structure and function of the global topsoil microbiome. Nature 560:233–237

Bai Y-C, Chang Y-Y, Hussain M et al (2020) Soil chemical and microbiological properties are changed by long-term chemical fertilizers that limit ecosystem functioning. Microorganisms 8:694

Banerjee S, Helgason B, Wang L et al (2016) Legacy effects of soil moisture on microbial community structure and N2O emissions. Soil Biol Biochem 95:40–50

Ben Chobba I, Elleuch A, Ayadi I et al (2013) Fungal diversity in adult date palm (Phoenix dactylifera L.) revealed by culture-dependent and culture-independent approaches. J Zhejiang Univ Sci B 14:1084–1099. https://doi.org/10.1631/jzus.B1200300

Bennett AJ, Bending GD, Chandler D et al (2012) Meeting the demand for crop production: the challenge of yield decline in crops grown in short rotations. Biol Rev 87:52–71. https://doi.org/10.1111/j.1469-185X.2011.00184.x

Bonkowski M (2004) Protozoa and plant growth: the microbial loop in soil revisited. New Phytol 162:617–631. https://doi.org/10.1111/j.1469-8137.2004.01066.x

Bridge P, Spooner B (2002) Soil fungi: diversity and detection. In: Powlson DS, Bateman GL, Davies KG et al (eds) Interactions in the Root Environment: an Integrated Approach. Springer Netherlands, Dordrecht, pp 147–154

Brussaard L, de Ruiter PC, Brown GG (2007) Soil biodiversity for agricultural sustainability. Agric Ecosyst Environ 121:233–244. https://doi.org/10.1016/j.agee.2006.12.013

Caporaso JG, Kuczynski J, Stombaugh J et al (2010) QIIME allows analysis of high-throughput community sequencing data. Nat Methods 7:335–336. https://doi.org/10.1038/nmeth.f.303

Chaudhry V, Rehman A, Mishra A et al (2012) Changes in Bacterial Community structure of Agricultural Land due to Long-Term Organic and Chemical amendments. Microb Ecol 64:450–460. https://doi.org/10.1007/s00248-012-0025-y

Cherif H, Marasco R, Rolli E et al (2015) Oasis desert farming selects environment-specific date palm root endophytic communities and cultivable bacteria that promote resistance to drought. Environ Microbiol Rep 7:668–678. https://doi.org/10.1111/1758-2229.12304

Cherubin MR, Franco ALC, Cerri CEP et al (2015) Sugarcane expansion in Brazilian tropical soils—effects of land use change on soil chemical attributes. Agric Ecosyst Environ 211:173–184. https://doi.org/10.1016/j.agee.2015.06.006

Crossley PF Jr (ed) (2004) Fundamentals of Soil Ecology. Academic Press

Darwish T, Atallah T, El Moujabber M, Khatib N (2005) Salinity evolution and crop response to secondary soil salinity in two agro-climatic zones in Lebanon. Agric Water Manag 78:152–164. https://doi.org/10.1016/j.agwat.2005.04.020

Daynes CN, Zhang N, Saleeba JA, McGee PA (2012) Soil aggregates formed in vitro by saprotrophic Trichocomaceae have transient water-stability. Soil Biol Biochem 48:151–161

DeLong EF (2009) The microbial ocean from genomes to biomes. Nature 459:200–206. https://doi.org/10.1038/nature08059

Dhawi F, Alsanie SI (2022) Investigation of Microbial Community structure and diversity in the Rhizosphere of date palm (Phoenix Dactylifera L.), Sukkari Cultivar. J Hunan Univ Nat Sci 49

Edgar RC (2010) Search and clustering orders of magnitude faster than BLAST. Bioinformatics 26:2460–2461. https://doi.org/10.1093/bioinformatics/btq461

Edgar RC (2013) UPARSE: highly accurate OTU sequences from microbial amplicon reads. Nat Methods 10:996–998. https://doi.org/10.1038/nmeth.2604

Edgar RC, Haas BJ, Clemente JC et al (2011) UCHIME improves sensitivity and speed of chimera detection. Bioinformatics 27:2194–2200. https://doi.org/10.1093/bioinformatics/btr381

Esmaeili Taheri A, Hamel C, Gan Y (2015) Pyrosequencing reveals the impact of foliar fungicide application to chickpea on root fungal communities of durum wheat in subsequent year. Fungal Ecol 15:73–81. https://doi.org/10.1016/j.funeco.2015.03.005

Falkowski PG, Fenchel T, Delong EF (2008) The Microbial engines that Drive Earth's biogeochemical cycles. Science 320:1034–1039. https://doi.org/10.1126/science.1153213

Fierer N, Breitbart M, Nulton J et al (2007) Metagenomic and small-subunit rRNA analyses reveal the Genetic Diversity of Bacteria, Archaea, Fungi, and viruses in Soil. Appl Environ Microbiol 73:7059–7066. https://doi.org/10.1128/AEM.00358-07

Filimon MN, Voia SO, Popescu R et al (2015) The effect of some insecticides on soil microorganisms based on enzymatic and bacteriological analyses. Romanian Biotechnol Lett 20:10439

Guo X, Petermann JS, Schittko C, Wurst S (2015) Independent role of belowground organisms and plant cultivar diversity in legume-grass communities. Appl Soil Ecol 95:1–8. https://doi.org/10.1016/j.apsoil.2015.05.010

Guo X, Wang Z, Zhang J et al (2021) Host-specific effects of Arbuscular Mycorrhizal Fungi on Two Caragana Species in Desert Grassland. J Fungi 7:1077. https://doi.org/10.3390/jof7121077

Hardie M, Doyle R (2012) Measuring Soil Salinity. In: Shabala S, Cuin TA (eds) Plant Salt Tolerance. Humana Press, Totowa, NJ, pp 415–425

Heilmann-Clausen J, Barron ES, Boddy L et al (2015) A fungal perspective on conservation biology. Conserv Biol 29:61–68. https://doi.org/10.1111/cobi.12388

Hunter P, Teakle G, Bending G (2014) Root traits and microbial community interactions in relation to phosphorus availability and acquisition, with particular reference to Brassica. Front Plant Sci 5

Kaisermann A, Maron PA, Beaumelle L, Lata JC (2015) Fungal communities are more sensitive indicators to non-extreme soil moisture variations than bacterial communities. Appl Soil Ecol 86:158–164. https://doi.org/10.1016/j.apsoil.2014.10.009

Kazeeroni EA, Al-Sadi AM (2016) 454-Pyrosequencing reveals variable fungal diversity across Farming systems. Front Plant Sci 7

Kerry BR (2000) Rhizosphere interactions and the exploitation of microbial agents for the biological control of plant-parasitic nematodes. Annu Rev Phytopathol 38:423

Khan H, Akbar WA, Shah Z et al (2022) Coupling phosphate-solubilizing bacteria (PSB) with inorganic phosphorus fertilizer improves mungbean (Vigna radiata) phosphorus acquisition, nitrogen fixation, and yield in alkaline-calcareous soil. Heliyon 8:e09081. https://doi.org/10.1016/j.heliyon.2022.e09081

Ma F, Na X, Xu T (2016) Drought responses of three closely related Caragana species: implication for their vicarious distribution. Ecol Evol 6:2763–2773. https://doi.org/10.1002/ece3.2044

Maeder P, Fliessbach A, Dubois D et al (2002) Soil fertility and Biodiversity in Organic Farming. Science 296:1694–1697. https://doi.org/10.1126/science.1071148

Magoč T, Salzberg SL (2011) FLASH: fast length adjustment of short reads to improve genome assemblies. Bioinformatics 27:2957–2963

Mefteh FB, Daoud A, Chenari Bouket A et al (2017) Fungal Root Microbiome from Healthy and Brittle Leaf Diseased date Palm Trees (Phoenix dactylifera L.) reveals a hidden untapped Arsenal of Antibacterial and Broad Spectrum Antifungal secondary metabolites. Front Microbiol 8

Morgan JAW, Bending GD, White PJ (2005) Biological costs and benefits to plant–microbe interactions in the rhizosphere. J Exp Bot 56:1729–1739. https://doi.org/10.1093/jxb/eri205

Mosqueira MJ, Marasco R, Fusi M et al (2019) Consistent bacterial selection by date palm root system across heterogeneous desert oasis agroecosystems. Sci Rep 9:4033. https://doi.org/10.1038/s41598-019-40551-4

Muhammed NH, Ahmed OE, Ahmed TA, Al-Yafai MS (2015) Date Palm Status and Perspective in Qatar. In: Al-Khayri JM, Jain SM, Johnson DV (eds) Date Palm Genetic resources and utilization: volume 2: Asia and Europe. Springer Netherlands, Dordrecht, pp 323–351

O'Dell J (1993) Method 353.2, revision 2.0: determination of nitrate-nitrite nitrogen by automated colorimetry. Environ Monit Syst Lab US Environ Prot Agency Cincinnati Ohio

Oliverio AM, Geisen S, Delgado-Baquerizo M et al (2020) The global-scale distributions of soil protists and their contributions to belowground systems. Sci Adv 6:eaax8787

Pose-Juan E, Sánchez-Martín MJ, Herrero-Hernández E, Rodríguez-Cruz MS (2015) Application of mesotrione at different doses in an amended soil: dissipation and effect on the soil microbial biomass and activity. Sci Total Environ 536:31–38. https://doi.org/10.1016/j.scitotenv.2015.07.039

Price MN, Dehal PS, Arkin AP (2010) FastTree 2 – approximately maximum-likelihood trees for large alignments. PLoS ONE 5:e9490. https://doi.org/10.1371/journal.pone.0009490

Price GW, Astatkie T, Gillis JD, Liu K (2015) Long-term influences on nitrogen dynamics and pH in an acidic sandy soil after single and multi-year applications of alkaline treated biosolids. Agric Ecosyst Environ 208:1–11. https://doi.org/10.1016/j.agee.2015.04.010

Qiao C, Penton CR, Xiong W et al (2019) Reshaping the rhizosphere microbiome by bio-organic amendment to enhance crop yield in a maize-cabbage rotation system. Appl Soil Ecol 142:136–146. https://doi.org/10.1016/j.apsoil.2019.04.014

Qiu W, Su H, Yan L et al (2020) Organic fertilization assembles fungal communities of Wheat Rhizosphere Soil and suppresses the Population Growth of Heterodera avenae in the field. Front Plant Sci 11

Quoreshi AM, Suleiman MK, Kumar V et al (2019) Untangling the bacterial community composition and structure in selected Kuwait desert soils. Appl Soil Ecol 138:1–9

Rangel DEN, Alder-Rangel A, Dadachova E et al (2015) Fungal stress biology: a preface to the fungal stress responses special edition. Curr Genet 61:231–238. https://doi.org/10.1007/s00294-015-0500-3

Rappé MS, Giovannoni SJ (2003) The uncultured Microbial Majority. Annu Rev Microbiol 57:369–394. https://doi.org/10.1146/annurev.micro.57.030502.090759

Rath KM, Rousk J (2015) Salt effects on the soil microbial decomposer community and their role in organic carbon cycling: a review. Soil Biol Biochem 81:108–123

Schloss PD, Westcott SL, Ryabin T et al (2009) Introducing mothur: Open-Source, Platform-Independent, community-supported Software for describing and comparing Microbial communities. Appl Environ Microbiol 75:7537–7541. https://doi.org/10.1128/AEM.01541-09

Shen Q, Yang J, Su D et al (2020) Comparative Analysis of Fungal Diversity in Rhizospheric Soil from Wild and Reintroduced Magnolia Sinica estimated via high-throughput sequencing. Plants 9:600. https://doi.org/10.3390/plants9050600

Stott MB, Taylor MW (2016) Microbial ecology research in New Zealand. N Z J Ecol 40:12–28

Tardy V, Spor A, Mathieu O et al (2015) Shifts in microbial diversity through land use intensity as drivers of carbon mineralization in soil. Soil Biol Biochem 90:204–213. https://doi.org/10.1016/j.soilbio.2015.08.010

Tedersoo L, Bahram M, Põlme S et al (2014) Global diversity and geography of soil fungi. Science 346:1256688. https://doi.org/10.1126/science.1256688

Tedersoo L, Mikryukov V, Anslan S et al (2021) The Global Soil Mycobiome consortium dataset for boosting fungal diversity research. Fungal Divers 111:573–588. https://doi.org/10.1007/s13225-021-00493-7

Thomson BC, Tisserant E, Plassart P et al (2015) Soil conditions and land use intensification effects on soil microbial communities across a range of European field sites. Soil Biol Biochem 88:403–413. https://doi.org/10.1016/j.soilbio.2015.06.012

TiÁskal V, BrabcovÁ V, Větrovský T et al (2021) Complementary roles of Wood-Inhabiting Fungi and Bacteria facilitate Deadwood Decomposition. mSystems 6:e01078–e01020. https://doi.org/10.1128/mSystems.01078-20

Tisdall JM, Nelson SE, Wilkinson KG et al (2012) Stabilisation of soil against wind erosion by six saprotrophic fungi. Soil Biol Biochem 50:134–141

Ul Haq J, Sharif M, Akbar WA et al (2022) Arbuscular Mycorrhiza Fungi Integrated with single super phosphate improve wheat-nitrogen-phosphorus Acquisition, Yield, Root infection activity, and Spore Density in Alkaline-calcareous soil. https://doi.org/10.1007/s10343-022-00718-y. Gesunde Pflanz

Urich T, Lanzén A, Qi J et al (2008) Simultaneous assessment of soil microbial community structure and function through analysis of the meta-transcriptome. PLoS ONE 3:e2527

Van Nuland ME, Wooliver RC, Pfennigwerth AA et al (2016) Plant–soil feedbacks: connecting ecosystem ecology and evolution. Funct Ecol 30:1032–1042. https://doi.org/10.1111/1365-2435.12690

Yaish MW, Al-Harrasi I, Alansari AS et al (2016) The use of high throughput DNA sequence analysis to assess the endophytic microbiome of date palm roots grown under different levels of salt stress. Int Microbiol 19:143–155

Yao L, Wang D, Kang L et al (2018) Effects of fertilizations on soil bacteria and fungi communities in a degraded arid steppe revealed by high through-put sequencing. PeerJ 6:e4623. https://doi.org/10.7717/peerj.4623

Zhang Y, Dong S, Gao Q et al (2017) Soil bacterial and fungal diversity differently correlated with soil biochemistry in alpine grassland ecosystems in response to environmental changes. Sci Rep 7:43077. https://doi.org/10.1038/srep43077

Zhang J, Zhang J, Zhang P et al (2019a) Rhizosphere Fungal Diversity of Wild and Cultivated Soybeans in Field and Greenhouse Experiments. 21:7

Zhang K, Shi Y, Cui X et al (2019b) Salinity is a key determinant for Soil Microbial communities in a Desert Ecosystem. MSystems 4:e00225–e00218

Zhang W, Wang C, Xue R, Wang L (2019c) Effects of salinity on the soil microbial community and soil fertility. J Integr Agric 18:1360–1368. https://doi.org/10.1016/S2095-3119(18)62077-5

Zhao H, Li X, Zhang Z et al (2018) Drivers and assemblies of soil eukaryotic microbes among different soil habitat types in a semi-arid mountain in China. PeerJ 6:e6042