



HAL
open science

Digging deeper into the impacts of different soil water systems on the date palm root architecture and associated fungal communities

Alexandre Robin-Soriano, Bryan Vincent, Kenji Maurice, Vincent Battesti, Hassan Boukcim, Marc Ducouso, Muriel Gros-Balthazard

► To cite this version:

Alexandre Robin-Soriano, Bryan Vincent, Kenji Maurice, Vincent Battesti, Hassan Boukcim, et al.. Digging deeper into the impacts of different soil water systems on the date palm root architecture and associated fungal communities. 2024. hal-04837475

HAL Id: hal-04837475

<https://hal.science/hal-04837475v1>

Preprint submitted on 16 Dec 2024

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



Distributed under a Creative Commons Attribution - NonCommercial - NoDerivatives 4.0 International License

Digging deeper into the impacts of different soil water systems on the date palm root architecture and associated fungal communities

Alexandre Robin-Soriano

alexandrerobinsoriano@gmail.com

AGAP-Institut, Univ Montpellier, CIRAD, INRAE, SupAgro, Montpellier, France <https://orcid.org/0009-0003-8040-0062>

Bryan Vincent

AGAP-Institut, Univ Montpellier, CIRAD, INRAE, SupAgro, Montpellier, France

Kenji Maurice

AGAP-Institut, Univ Montpellier, CIRAD, INRAE, SupAgro, Montpellier, France

Vincent Battesti

Lab Éco-anthropologie : CNRS, MNHN, Université Paris Cité, Paris, France

Hassan Boukcim

Department of Research and Development, VALORHIZ, Montpellier, France / ASARI, Mohammed VI Polytechnic University, Laâyoune, Morocco

Marc Ducousso

AGAP-Institut, Univ Montpellier, CIRAD, INRAE, SupAgro, Montpellier, France

Muriel Gros-Balthazard

DIADE, Univ Montpellier, CIRAD, IRD, Montpellier, France

Research Article

Keywords: Desert, Date palm, Water scarcity, Irrigation system, Metabarcoding, Arbuscular mycorrhizal fungi

Posted Date: July 29th, 2024

DOI: <https://doi.org/10.21203/rs.3.rs-4799682/v1>

License:   This work is licensed under a Creative Commons Attribution 4.0 International License.

[Read Full License](#)

Additional Declarations: The authors declare no competing interests.

Abstract

In arid regions, excessive water use threatens agricultural sustainability and overall livelihoods. It is essential to minimize water consumption to address these issues. Date palm (*Phoenix dactylifera* L.) is an emblematic crop of arid regions and a major water consumer. Tailoring current irrigation systems into new, water-efficient systems could help cope with the water consumption of this crop. Microbial communities associated with plants are essential for agricultural sustainability and could improve the water use efficiency in regions threatened by water scarcity. These communities should thus be seriously taken into account when adapting agrosystems to the current global change setting. However, no information is presently available on the effects of these modifications on date palm microbial communities. This study highlights the impact of different soil water systems (flooding and drip irrigation, natural conditions and abandoned farms) on date palm root fungal communities at different soil depths. The findings revealed that the soil water systems had a marked impact on fungal communities and that drip irrigation reduced the fungal diversity but increased the abundance of arbuscular mycorrhizal fungi. We showed that these effects were similar at all sampling depths. Finally, as the root architecture is a major determinant of water uptake, we reveal different behaviors of the root architecture under these different soil water systems to 160 cm depth. The findings of this study give new insights into the date palm root architecture and associated fungal communities, particularly in the context of the water availability crisis, which drives the adaptation of agricultural systems.

1 Introduction

Non-renewable groundwater reservoirs are the major source of irrigation water in arid regions such as Saudi Arabia (Odnoletkova and Patzek 2023). These aquifers are rapidly depleting because of their naturally slow recharge rates combined with the high water extraction rates for agriculture (Shahin and Salem 2014; Seraphin et al. 2022). This reliance on finite water resources significantly endangers agricultural sustainability and overall livelihoods in such areas, thereby highlighting the critical need for innovative water efficient management solutions.

The date palm (*Phoenix dactylifera* L.) is a major emblematic food crop of oasis agroecosystems in arid North African and Southwest Asian regions. There are currently over 100 million date palm trees worldwide (Khan et al. 2020). Date palms are of major cultural importance and a primary income source in many countries (Hadrami and Al-Khayri 2012), especially in the main producing countries: Egypt, Iran and Saudi Arabia (FAO data, 2021). This species is tolerant to abiotic stresses such as long-term drought, soil and water salinity and heat which are common in these hot arid regions (Arab et al. 2016; Hazzouri et al. 2020). Yet irrigation is crucial to maintain high date palm growth rates and yields (Carr 2012; Hazzouri et al. 2020), as reported for instance by Saad Eddin et al. (2023), who measured a 30% date yield reduction when the irrigation water input was reduced from 100–60% of the total water requirements of this crop. Date palms cultivation can consume over 13,000 m³/ha/year of water (Al-Omran et al. 2019) which can represent the highest proportions of water consumption at the scale of

arid countries like Saudi Arabia (Odnoletkova and Patzek 2023). The date palm cultivation, thus, represents a critical target for reducing the agricultural irrigation footprint (Shahin and Salem 2014).

This cultivation occurs in a gradient of conditions ranging from conventional multispecies and multicultivar farms to monoculture and monovarietal farms. Most studies carried out to investigate water consumption and water-saving solutions in date palm stands have been focused on monoculture farms. These studies identified two crucial points, i.e. the irrigation water quantity was too high and the irrigation methods used resulted in excessive water loss (Carr 2012; Al-Omran et al. 2019). Indeed, the amount of water applied often exceeds the date palm water requirements. Al-Omran et al. (2019) compared date palm water requirements to current irrigation conditions in Saudi Arabia using the Penman–Monteith method for evapotranspiration and found that the water quantities actually applied by farmers ($12,714 \text{ m}^3/\text{ha}/\text{year}$) were much higher than the calculated needs ($8342 \text{ m}^3/\text{ha}/\text{year}$). Moreover, the yearly evapotranspiration of cultivated date palms measured by Ben Aissa et al. (2019) was considered low, which was closely in line with the levels commonly noted in plant species adapted to arid conditions, thereby implying that over-irrigation should not be needed. Hence, current irrigation water quantities should be assessed and lowered to better match date palm needs and prevent excessive water use. Another way to improve the date palm cultivation water efficiency is to avoid water loss during irrigation (Carr 2012). This water loss may be partly due to overconsuming irrigation practices. Historically, the most frequently used date palm irrigation method is called the “flooding irrigation” method, which consists of bringing high amounts of water to the base of date palm trees growing in an irrigation basin. In the past, this was many carried out via channels dug in the soil between the basins, whereas this is currently often done via plastic pipes (Carr 2012). For example, flooding was used to irrigate 90% of date palms in Egypt in 2008, and as high as 96% in Saudi Arabia in 2005 (Elfeky and Elfaki 2019). Many studies on monoculture date palm farms found that flooding irrigation is outdated and inefficient compared to bubbler, sprinkler, and drip irrigation methods (Amiri et al. 2007; Al-Amoud 2008; Carr 2012; Elfeky and Elfaki 2019). These studies highlighted that drip irrigation, compared to flooding, can maintain or improve date yields, plant growth, tree health, and soil water distribution patterns, (Al-Amoud 2008; Carr 2012; Elfeky and Elfaki 2019; Mohammed et al. 2021; Zemni et al. 2022) and may also affect date palm root distribution (Daddi Bouhoun 2010). For example, in Saudi Arabia, the fields using drip irrigation consumed around $55 \text{ m}^3/\text{tree}/\text{year}$ while fields in fields irrigated by flooding received around $137 \text{ m}^3/\text{tree}/\text{year}$ (Alazba 2004). Drip irrigation systems can be installed on the soil surface or buried underground, impacting the performance and water distribution of the system (Talat Farid Ahmed 2012). In the present study, only surface drip irrigation was studied, so hereafter the term “drip irrigation” refers specifically to surface drip irrigation.

The impacts of new irrigation systems like drip irrigation on crop yields and water efficiency in date palm farms have been extensively explored (Al-Amoud 2010; Carr 2012; Elfeky and Elfaki 2019), but the effects of different water management practices on root microbial communities are still unknown. Yet microorganisms, and especially fungal communities have a significant impact on the health, growth, yield and water and nutrient uptake of plants, including date palms (Ferjani et al. 2015; Meddich et al.

2015; Abumaali et al. 2023). With the aim of boosting crop yields and agrosystem sustainability, the roles of such fungal communities along the soil-plant continuum have been studied in depth with regard to their ability to influence plant yields and tolerance to stresses (Xiong and Lu 2022). Among fungi, arbuscular mycorrhizal fungi (AMF) are a prime example of a well-studied taxon in agriculture. AMF are known to increase water and nutrient uptake in plants, improve their tolerance to abiotic stresses, such as drought stress by increasing the anti-oxidative system, while also increasing their tolerance to biotic stresses (Jaiti et al. 2007; Smith and Read 2010; Benhiba et al. 2015). In the meantime, AMF are also sensible to environmental conditions that can affect their survival, colonization capacities and community compositions. Determinants of AMF communities may be environmental parameters such as pH, water and nutrient availability, plant phenology and root architecture (Chourasiya et al. 2021), but also agricultural practices (Schreiner et al. 2007; Trinchera and Warren Raffa 2023). Assessing how external factors (e.g. soil water systems) may drive relationships between microbial communities, soil and plants could generate valuable insight to help improve the sustainability of agricultural practices and soil management.

In one of the few studies carried out to assess the effects of drip versus flooding irrigation on fungal communities, Deng et al. (2022) revealed a reduction in the abundance of arbuscular mycorrhizal and ectomycorrhizal fungi under drip irrigation, alongside an increase in the abundance of pathogenic fungi in the alfalfa rhizosphere in an arid region of China. The authors noticed an increase in soil nutrients due to reduced leaching and that nitrogen and phosphorus availability strongly influenced the fungal community compositions. These communities were thus also affected by the edaphic conditions, notably the soil depth. Several studies have highlighted a change in the fungal community profile along a soil depth gradient in nutrient-rich soils in temperate environments (Lamit et al. 2017; Schlatter et al. 2018). The authors of most of the studies noted that the fungal compositions generally differed between the topsoil (first 25 cm) and the lower soil depths (Eilers et al. 2012; Gu et al. 2017; He et al. 2023a) in both arid and temperate environments, mainly due to the high biological activity and differences in the physicochemical conditions at the surface.

In this study, we analyzed the effects of the soil water systems on fungal endophyte communities and date palm root architecture parameters.

To overcome the knowledge gap regarding these effects on fungal communities in date palm roots, we assessed the diversity and composition of fungal communities in date palm roots collected at different sites in the desertic region of AlUla (al-*U*lā: *أوليا*), Saudi Arabia. Our study focused on different soil water systems (flooding and drip irrigation, abandoned farms and natural = uncultivated conditions) and different soil depths (40, 80 and 140 cm deep). We hypothesized that the diversity and composition of microbial communities would remain constant under both drip and flooding irrigation, yet would differ significantly when compared to non-irrigated conditions (abandoned farms and natural settings). As the soils in this region have only one soil horizon over tens of centimeters or even meters deep, we assumed that physico-chemical properties would not change much vertically and thus, the fungal communities would remain stable at all of the studied soil depths.

Moreover, we evaluated the contributions of the soil physicochemical parameters on the fungal community composition. Finally, we assessed the impacts of different soil water systems on AMF communities and taxa, as AMF are symbionts that provide substantial benefits to plants, including improved water uptake in date palms (Qaddoury 2017).

The microbial communities in plant roots are closely linked to the root architecture (Saleem et al. 2018). However, the root architecture of full-grown date palms is generally unknown due to the difficulty of monitoring the root system of such large trees (Amira and Ben Salah 2014). A few studies have attempted to measure the root density of date palms in the 0 to 100 cm soil layer (Littardi et al. 2015; Tahri 2018), but this only encompasses a fraction of the date palm root system, which has been estimated to extend to at least 10 m deep, yet most of the roots are found within the top 2 m of the soil layer (Krueger 2021). We hypothesized that the soil water systems could affect the root development: (i) date palms watered with flooding and drip irrigation would not vary markedly with regard to their root parameters as they are both irrigated, and (ii) drip irrigated date palms would have an increased number of roots near the surface. Date palms growing on abandoned farms would have a higher root width as these conditions were more long-standing than the irrigated conditions. Finally, we hypothesized that uncultivated date palm trees collected in natural environments would have a low number of roots throughout the studied soil profile as they could be more concentrated in layers deeper than in those from which we collected our samples.

2 Material and Methods

2.1 Study area

Our study was conducted in the hot arid desertic region of AlUla (al-'Ulā oasis) in northwestern Saudi Arabia. The climatic conditions in this hyperarid region are characterized by high temperatures, which exceed 45°C in July and August, and rare, irregular rainfall events (30 mm to 170 mm/year) (Toumi et al. 2015). The region hosts modern extensive farms and old or abandoned traditional farms, encompassing different farming practices that were introduced during different periods (Gros-Balthazard & Battesti et al. 2023). Agriculture in the AlUla region mainly relies on non-renewable water supplies from the Saq-RAM Aquifer (Seraphin et al. 2022). In our study, date palms were sampled under different soil water systems in four distinct environments or irrigation systems: (i) date palm farms with flooding irrigation systems, (ii) date palm farms with surface drip irrigation systems, (iii) abandoned date palms in old farms, where the crops were no longer irrigated or harvested, and (iv) natural desert ecosystems hosting uncultivated, non-irrigated date palms that were located in the Sharaan Nature Reserve (northeast of the city of AlUla).

2.2 Sample collection

Overall, we collected and sampled the roots of 21 date palm trees across the target region under different soil water systems. According to farmers and a previous survey carried out by Gros-Balthazard & Battesti et al. (2023), the 14 date palm trees sampled in our study in flooding and drip irrigation

conditions and in abandoned farms were all date palms of the Barnī cv., which meant they were genetically identical. However, the genotypes of the 7 uncultivated date palms collected in natural desert conditions were unknown. Date palm roots were collected in the four defined soil water systems (flooding irrigation, drip irrigation, abandoned farms and natural environments) at various depths (40 cm, 80 cm, 140 cm). Roots were collected manually using clean tweezers, placed in a 2% cetrimonium bromide solution, and stored at 4°C until molecular analyses. For each sampling, soil was collected a few centimeters from the roots for soil physicochemical analysis and sieved through a 2 mm mesh sieve. Two methods were used to collect date palm roots: pit sampling at various depths (40 cm, 80 cm, 140 cm), and additional diversity sampling at 40 cm depth.

Pit sampling

In October 2021, the “pit samples” were collected in two pits per soil water systems: (i) flooding irrigation, (ii) drip irrigation, (iii) natural ecosystems, and (iv) abandoned farms, for a total of eight pits. The pits were all 200 cm long, 80 cm wide, and 160 cm deep and were positioned 2 m from the trunk and outside the irrigation basin, if applicable (Figs. 1a and 1b). We assessed the impact of the sampling depth on the fungal communities after collecting roots in three soil horizons at 40–60 cm (low depth), 80–100 cm (medium depth) and 140–160 cm depth (high depth) (Figs. 1a and 1c). In each horizon, we delineated three horizontal 65 cm long squares (Fig. 1d). In each square, 3 root segments (preferentially lateral, small, fresh and live roots) were sampled and pooled in an Eppendorf tube. There was a total of 9 samples per pit, i.e. three depths and three samples per depth.

Root density and root mean width were assessed based on photos taken of a quadrat placed on each horizon (the whole horizon was imaged in two photos). The quadrat was 100 cm × 50 cm, subdivided into 10 cm² squares (Fig. 1d). Six photos were taken per pit, all of which were processed with the ImageJ software to assess the root number and width.

The first four pit samples were collected from two farms located adjacently on either side of a road, while the date palm trees were of similar age. Although the two farms were close together, their irrigation systems differed, i.e. flooding irrigation for the first farm (pits N°1 and N°2), and drip irrigation for the second farm (pits N°3 and N°4). To the best of our knowledge and according to previous surveys, the drip irrigation system had been installed at least 3 years prior to the sampling. Uncultivated date palm roots were sampled in the Sharaan Nature Reserve (pits N°5 and N°6). The last pits (N°7 and N°8) were located in two old and abandoned farms, where the irrigation systems had not been used for a long time prior to sampling, i.e., respectively 7 years and decades earlier, according to local farmers.

Diversity sampling

Thirteen additional samples were collected in October 2021 and March 2022 around AIUla, always at an easier to access, depth of 40 cm, to increase the number of samples and the size of the sampling area. These samples are referred to as “Diversity samples”. Five of these samples were collected under

natural conditions in the Sharaan Nature Reserve, three were collected on farms under flooding irrigation, three under drip irrigation and two in abandoned agrosystems.

The pit and diversity sampling locations are shown in Fig. 2.

2.3 Soil chemical analysis

For each soil, the $\text{pH}_{\text{H}_2\text{O}}$, pH_{KCl} and acidification potential ($\text{AP} = \text{pH}_{\text{H}_2\text{O}} - \text{pH}_{\text{KCl}}$) were measured, complemented by the soil atomic element composition, i.e. ranging from magnesium to uranium, determined by X-ray fluorescence using an XRF S1 Titan analyzer (Bruker, Billerica, Massachusetts, USA). The soils were prepared for pH measurement by adding H_2O or a KCl solution (1 mol.L^{-1}) to a Falcon tube at 1:5 (v:v) ratio. After 1 h of mixing and decanting, the pH was measured with a pH meter (Knick 766; Knick International, Berlin, Germany). For the XRF measurements, the soil samples were placed in three plastic capsules, tamped and then sealed with Prolene film. Each capsule was measured in triplicate using the Geoexploration mode on the XRF device. For each soil, the nine measurements were averaged and calibrated according to the limit of optical detection (LOD) of each analyzed element (provided by Bruker). XRF provide the relative abundance of each measured element, they are compositional in nature. They were thus analyzed by transforming the values using the centered log ratio (clr) method so as to remove the closure effect inherent to compositional data (Reimann et al. 2012). Only major elements that varied in the different samples were retained for further analysis: magnesium (Mg), aluminum (Al), silicon (Si), phosphorus (P), potassium (K), calcium (Ca), iron (Fe), sulfur (S) and manganese (Mn).

2.4 DNA extraction, library preparation and sequencing

The metabarcoding dataset used in this study was generated in our previous study (Robin-Soriano et al. 2024), and previously deposited in the NCBI Sequence Read Archive under project number PRJNA1078326. The DNA extraction, PCR, library preparation and sequencing methods were described in Robin-Soriano et al. (2024). Briefly, roots were rinsed with sterile water, flash frozen and ground. DNA was extracted with the FastDNA Spin Kit for Soil (MP Biomedicals, Solon, USA). The 18S rRNA region was amplified with AMADf (5' GGGAGGTAGTGACAATAAATAAC 3') and AMADGr (5' CCCAACTATCCCTATTAATCAT 3') primers (Berruti et al. 2017). All PCR products were sent to Fasteris SA (Switzerland) for sequencing using an Illumina MiSeq (2 x 250 bp).

Details on the data processing pipeline are available in Perez-Lamarque et al. (2022). Briefly, operational taxonomic units (OTUs) were clustered at 97% similarity after merging forward and reverse sequences and removing chimeras. Negative controls incorporated at the DNA extraction and PCR steps were used to remove contamination using the *decontam* v.1.22.0 R package (Davis et al. 2018). Short and nonfungal sequences were filtered out of the OTU tables. Taxonomic assignments were performed using the Silva 138.1 database (Quast et al. 2013).

2.5 Statistical analysis

All analyses, graphs and calculations were performed in R v.4.3.0 (R Core Team, 2024).

To assess differences between soil water systems, the pit and diversity datasets were combined to maximize the number of samples and sampling areas. The impact of the sampling depth on the microbial community was assessed only on the basis of pit samples (because the diversity samples were obtained at a fixed depth of 40 cm with a different sampling protocol).

The alpha diversity of the metabarcoding data was quantified with Hill numbers (Alberdi and Gilbert 2019a) at orders of diversity $q = 0$ (species richness), $q = 1$ (exponential of Shannon index) and $q = 2$ (inverse of Simpson index), using the *hilldiv* package v.1.5.1 (Alberdi and Gilbert 2019b). Samples with < 1,000 reads and OTUs with < 10 reads were discarded to compare differences in alpha diversity among soil water systems and sampling depths. Differences in diversity among conditions were first assessed on the rarefied data by analysis of variance (ANOVA). Post-hoc Tukey HSD tests were then applied to conduct pairwise comparisons between groups.

We then analyzed the beta diversity of fungal compositions among depths or soil water systems. Samples with < 1,000 reads and OTUs with < 10 reads were removed. All OTU count tables were Hellinger transformed. Differences in fungal compositions were highlighted using non-metric multidimensional scaling (NMDS) performed on the Bray-Curtis dissimilarity matrix. The influences of our factors of interest (soil water systems and sampling depth) and their combined effect were assessed through permutational analysis of variance (PERMANOVA) with the *adonis2* function in the *vegan* package v.2.6-4 (Oksanen et al. 2022). Each soil water systems or sampling depth combination was then compared two-by-two through multivariate analysis of variance (MANOVA).

Differences in soil parameters between soil water systems were highlighted via principal component analysis (PCA) and assessed by ANOVA. The effects of the soil parameters and the 10 most significant taxa of class, order and family taxonomic levels on the fungal composition were assessed by distance-based redundancy analysis (dbRDA) using the *microeco* v.1.4.0 package (Liu et al. 2021) and the fungal Bray-Curtis dissimilarity matrix. The influence of each soil parameter was tested via PERMANOVA.

Differential abundance analyses (DAA) were carried out on the pit sample results from the flooding irrigation and drip irrigation systems to investigate the impact of soil water systems on taxon abundances in the irrigation systems. DAA were performed with the DESeq function of the *DESeq2* package v. 1.40.2 (Love et al. 2014).

Trophic modes of the most abundant fungal genus in each group (> 5% of total relative abundance) were retrieved using FUNGuild v.0.2.0.9000 (Nguyen et al. 2016).

2.6 Root architecture parameter measurements

Photos of the soil horizons within the quadrat were examined to measure the number of roots and mean root width in 10 cm deep layers from 10 cm to 160 cm deep in each of the eight pits. Roots were counted in each pit at each 10 cm deep bracket. For the root width, the images were analyzed using ImageJ

1.53K software. The root width (diameter) was measured with the line tool. The root widths in all layers in each pit were then averaged. Individual roots were classified in four orders according to their width and on the basis of the classification described by Tahri (2018): order 1 > 1.06 cm; order 2 > 0.72 cm; order 3 > 0.37 cm and order 4 < 0.37 cm. Hierarchical clustering based on the root order ratio was applied to check for root order organization consistency between soil water systems.

3 Results

3.1 Effects of sampling depth on the diversity and composition of fungal communities in date palm roots

The root fungal diversity and community composition in the pit dataset were compared at each sampling depth. Although the ANOVA and Tukey test revealed no significant differences in alpha diversity between root depths for species richness ($q = 0$), the diversity tended to diminish as the sampling depth increased (Fig. 3a). Although this trend was not significantly confirmed ($p > 0.05$) at higher q values when giving more importance to abundant species, differences between the low depth (40 cm) and high depth (140 cm) showed p values < 0.1 . The medium depth samples (80 cm) did not differ from those of the two other depths, i.e. the depth continuously decreased the alpha diversity. Although the diversity slightly decreased with depth, the fungal community composition was not impacted by the sampling depth, as revealed by the PERMANOVA pit sample results ($R^2 = 0.035$; $p = 0.808$) and MANOVA findings between depths (R^2 of 0.020, 0.029 and 0.030; $p = 0.898$, 0.515 and 0.706 for comparisons between low/medium, low/high and medium/high depths respectively) (Fig. 3b).

3.2 Effects of soil water systems on the diversity and composition of fungal communities in date palm roots

The fungal community diversity and composition in date palm roots in the pit and diversity datasets were compared between the soil water systems. The ANOVA and Tukey tests on Hill numbers revealed no significant differences overall in species richness ($q = 0$) between soil water systems except for the date palms in abandoned farms which had higher alpha diversity. Drip irrigated date palms had the lowest diversity at every q value. When rare species were given less weight ($q = 1$) drip showed significantly lower diversity, but no significant difference was found at $q = 2$. Our results showed a significant effect of soil water system on fungal community structure as revealed by NMDS (Fig. 3d) and assessed by PERMANOVA on the pit samples ($R^2 = 0.244$; $p = 9.999e^{-5}$) and all samples (pit + diversity) ($R^2 = 0.177$; $p = 9.999e^{-5}$). In the pit samples, no significant effects of the combination of soil water system and sampling depth were observed (PERMANOVA; $R^2 = 0.119$; $p = 0.359$). All soil water system had significantly different fungal communities. The least difference noted was between flooding and drip irrigation (hereafter referred to as 'flooding' and 'drip') (MANOVA; $R^2 = 0.071$; $p = 0.027$), while the greatest difference was between drip and abandoned (hereafter referred to as 'abandoned') (MANOVA; $R^2 = 0.168$; $p = 0.001$).

The main observed taxa (genera with > 5% total relative abundance) (Table S1) differed among the soil water groups. Flooding, drip and natural environments (hereafter referred to as 'natural') groups showed high percentages of species of AMF genera among their most represented taxa. Flooding and drip showed high percentages of *Rhizophagus* species (20.3 and 31.2% of total reads respectively), while this genus represented only 5.6% in the natural samples. Drip and natural samples also showed high percentages of *Glomus* species (22.5% and 9.24%, respectively), while the natural samples also had high percentages of species of two other AMF genera, i.e. *Sclerocystis* and *Septoglomus* (8.6 and 5.6%). Palms growing on abandoned farms only had one AMF genus, i.e. *Funneliformis* (11.1%), among its major taxa. All groups included high extents of saprotrophic fungi (according to FUNGuild) (Table S1), including: *Kraurogymnocarpa* (20.7% in flooding and 7.8% in abandoned), *Calvatia* (16.7% in flooding and 10.6% in drip), *Pseudocolus* (8.0% in drip), *Ophiosphaerella* (31.6% in natural and 18.6% in abandoned) and *Trichocladium* (14.9% in abandoned). There were differences in pathotrophic fungi present in the different soil water systems. Among the main genera, only one pathotroph was noted in the flooding conditions, i.e. *Burgoa* (5.09%). This genus was also frequently detected in drip (11.1%) and natural (5.6%) conditions. Among the other frequently observed pathotrophic fungi, *Melampsora* was found in drip (8.6%) and in natural (6.24%), *Nowakovskiella* was detected in natural (7.6%), *Exophiala* and *Scopulariopsis* (11.6 and 6.2% respectively) in abandoned conditions.

3.3 Soil chemical differences between soil water sample groups

The geochemical parameters of the soils from each soil water group sample are presented in Table 1, as assessed by principal component analysis (PCA) in Fig. S1.

With pH values > 8 on average, the soils in which the date palms were growing were all alkaline (Table 1). The $\text{pH}_{\text{H}_2\text{O}}$ values of soils exposed to drip irrigation ($\text{pH}_{\text{H}_2\text{O}} 8.04 \pm 0.54$) were significantly lower than those noted for the three other conditions ($\text{pH}_{\text{H}_2\text{O}} 8.50$ on average). The pH_{KCl} values were similar in all soil water systems. The acidification potential differed significantly between natural (-0.44 ± 0.42) and drip systems (0.18 ± 0.30). Regarding the atomic elements, the soil silicon contents were high and ranged from 69–81%, and this trend was similar among the four soil water systems. The response of the soil elements to the soil water systems depended on the atomic elements analyzed. The levels of atomic elements such as K and Fe in the soil were similar under all of the soil water systems, while Al, Ca, and Mg were the highest in soils under abandoned farms. Levels of other elements such as Mn and S were lowest in natural environments.

Table 1

Soil parameters (pH, acidification potential and atomic elements) in relation to the four studied environments/irrigation systems: flooding, drip, natural and abandoned. The results are expressed as means \pm standard deviations. Letters in bold indicate significant differences (at $p < 0.05$) between soil water systems based on ANOVA followed by Tukey's tests. The soil atomic element values were the centered log ratio transformed before statistical analysis.

Soil Parameters	Flooding n = 19	Drip n = 20	Natural n = 21	Abandoned n = 18
pH _{H₂O}	8.71 \pm 0.38 a	8.04 \pm 0.54 b	8.55 \pm 0.31 a	8.49 \pm 0.22 ab
pH _{KCl}	8.55 \pm 0.36 a	8.22 \pm 0.58 a	8.11 \pm 0.68 a	8.31 \pm 0.27 a
AP ¹	-0.15 \pm 0.40 ab	0.18 \pm 0.30 a	-0.44 \pm 0.42 b	-0.18 \pm 0.40 ab
Al (%)	8.70 \pm 4.08 c	9.63 \pm 3.00 bc	10.27 \pm 3.90 ab	13.65 \pm 1.68 a
Ca (%)	4.27 \pm 3.40 ab	4.41 \pm 4.61 ab	1.72 \pm 1.48 b	8.42 \pm 8.23 a
Fe (%)	3.05 \pm 2.43 a	2.42 \pm 1.39 a	2.41 \pm 1.47 a	2.67 \pm 1.35 a
Mg (%)	3.89 \pm 1.50 ab	3.50 \pm 1.09 b	2.60 \pm 0.66 b	4.32 \pm 1.34 a
K (%)	1.07 \pm 0.67 a	1.13 \pm 0.76 a	0.70 \pm 0.47 a	0.89 \pm 0.33 a
Mn (%)	0.054 \pm 0.057 ab	0.032 \pm 0.019 a	0.037 \pm 0.026 b	0.052 \pm 0.029 ab
P (%)	0.098 \pm 0.062 ab	0.066 \pm 0.053 b	0.093 \pm 0.033 a	0.159 \pm 0.097 a
S (%)	0.053 \pm 0.053 ab	0.102 \pm 0.135 a	0.014 \pm 0.007 b	0.056 \pm 0.054 ab
Si (%)	78.13 \pm 12.12 a	78.12 \pm 8.89 a	81.56 \pm 7.76 a	69.09 \pm 9.88 a
¹ AP = Acidification potential				

3.4 Contribution of soil parameters and major taxa to the fungal community composition

The effects of soil parameters on the fungal communities (Bray-Curtis dissimilarity matrix) were tested by PERMANOVA and graphically displayed using dbRDAs with ellipses, colored in relation to the soil water systems (Fig. 4a). Except for Si and pH, all atomic elements analyzed (Mg, Ca, S, K, Fe, Al, Mn and P) had a significant impact (at $p < 0.05$) on the fungal community composition in the different soil water systems. The contributions of major taxa to each soil water system (limited to five to not hinder the figures readability) at different taxonomic levels were also assessed (Fig. 4b, c, and d). The top three taxon classes, orders and families that contributed most to explaining the community compositions respectively belonged to: (i) Glomeromycetes, Eurothiomycetes and Dothideomycetes classes (Fig. 4b), (ii) Glomerales, Pleosporales and Onygenales orders (Fig. 4c), and (iii) Glomeraceae, Phaeosporiaceae and Gymnoascaceae families (Fig. 4d).

3.5 Flooding versus drip irrigation systems: differential abundances of fungal communities

We measured the potential impacts of agricultural practices in active date palm orchards on fungal communities by focusing on and comparing two watering systems: flooding versus drip irrigation. In these two farms, the date palm ages were similar and the trees were closely located geographically (within ≈ 200 m). Moreover, the soil parameters measured in both systems were similar (except for pH, Mg and Al; Table S2). Differential abundance analyses (DAA) were conducted to identify taxa that were differentially abundant between the two irrigation conditions (Fig. 5). For drip irrigation, the most significantly abundant taxa included several OTUs of Glomeraceae, one Melampsoraceae, one Lycoperdaceae and one Gymnoascaceae (Fig. 5a). Regarding the flooding conditions, DAA highlighted three OTUs of Eurotiomycetes (two Gymnoascaceae and one Mycolaliciaceae families), two Dothideomycetes from Cladosporiaceae and Phaeosphaeriaceae families, one Sordariomycetes (Chaetomiaceae), one Agaricomycetes, one Glomeraceae and one Tremellomycetes (Filobasidiaceae).

3.6 Impact of soil water systems on AMF communities

High proportions of Glomeromycetes (AMF fungi) were detected in the samples and found to be differentially expressed in relation to the soil water systems. We therefore focused more closely on these Glomeromycetes.

The proportion of AMF was highest among the drip sampling group, where 44.3% of the total reads concerned AMF, 34.9% natural samples, 21.4% flooding and 14.5% abandoned farms. A large majority of the AMF reads belonged to the Glomeromycetes class ($> 95\%$; 46/49 OTU), including a dominance of the Glomerales order (96.9%), followed by Archaeosporales (1.0%) and Diversisporales (0.7%), (Fig. 6a). Most of the assigned AMF reads belonged to the Glomeraceae family. Apart from Glomeraceae: (i) two AMF OTUs identified as *Ambispora granatensis* (Ambisporaceae) were detected in the abandoned (1.51% of AMF reads) and natural (0.50% of AMF reads) root samples, (ii) one OTU identified as *Redeckera fulvum* (Diversisporaceae) was detected in the root samples exposed to flooding (0.50%) and drip irrigation (0.57%), and (iii) one AMF OTU identified as *Racocetra alborosea* (Gigasporaceae) was extracted from root samples exposed to drip irrigation (1.0%) (Fig. 6b). The proportion of unassigned AMF families differed between soil water systems: 54.8% for drip; 48.2% for flooding, 41.1% for natural; 6.3% for abandoned (Fig. 6b).

3.7 Date palm root architecture under different soil water systems

After analyzing the environmental DNA, we directly monitored the date palm roots in relation to our four target soil water systems. Root numbers and root widths were quantified in 10 cm layers within all pits (Fig. 1c and 1d), and the results are presented in Fig. 7. The date palm root numbers were heterogenous

(Fig. 7a) in terms of depth and soil water systems, where: (i) date palms exposed to flood and drip irrigation showed similar root number profiles, with a clear increase around 60–70 cm deep, with the lowest number of roots noted before and after the 60–70 cm depth ; (ii) date palms growing in natural conditions showed a low number of roots (0 to 25) at all depths; (iii) date palms growing in abandoned farms (pits N° 7 and 8) had high numbers of roots close to the surface, and then the numbers decreased at a heterogenous rate with depth, i.e. the root number in pit N°7 decreased at a faster rate (from 75 to 20 roots in the first 30 cm) than those in pit N°8 (with 50 roots noted in the first 100 cm). Almost no roots were observed at the lowest depth (150–160 cm), except under date palms exposed to drip irrigation.

The patterns noted regarding the mean root width in relation to the soil water systems (Fig. 7b) differed from the root number patterns. Flooded and abandoned date palms had relatively low root diameters, which slightly increased with depth. The root diameters of date palms under drip irrigation and in natural conditions exhibited heterogenic profiles (Fig. 7b). The hierarchical clustering and distribution of date palms root orders (based on diameter) revealed a clustering related to the soil water systems (Fig. 7c and 7d). Moreover, the root orders of individual date palms exposed to the same soil water systems (e.g. two date palms growing in natural conditions) were highly similar (Fig. 7c and 7d). The date palm root samples collected from the abandoned farms had the greatest percentage of fine roots (order 4 < 0.37 mm Ø) and the lowest percentage of wider roots (order 1 > 1.06 mm Ø). Date palms exposed to drip irrigation had the greatest proportion of wider roots of order 1 (Fig. 7d).

4 Discussion

4.1 soil water systems affect the root density and root width

In our study, cultivated date palms irrigated with flooding and drip irrigation systems had a maximum root density at around 60–70 cm depth, and this density decreased notably after 100 cm. These results were in line with those of other studies (Munier 1973; Tahri 2018), where the highest densities were detected in roughly the same horizons. Moreover, no differences were observed between individuals under flooding and drip irrigation systems. This was inconsistent with our hypothesis and Bourziza et al. (2017b) who stated that date palms grown under surface drip irrigation developed more roots near the surface and these roots were thus more susceptible to desiccation. This is an important factor because flooding irrigation systems consume much higher amounts of water compared to drip irrigation (Alazba 2004; Amiri et al. 2007).

The two individual date palms investigated in abandoned farms showed a variable high number of roots at the surface. This variation may be explained by the date palm age, where individual N°8 was taller and growing on an older farm as compared to individual N°7. Daddi Bouhoun (2010) reported that the overall root density was not affected by the date palm ages, but that the hydro-edaphic properties of the soils may have an impact. Moreover, the same author estimated that respiratory roots (located at shallower

depths with respiratory functions) were more numerous in older date palm trees with higher respiratory needs. In our case, the greater number of roots noted at shallow depths in farms could actually have been respiratory roots and the number could partly be explained by the palm tree ages, which were older than those of the flooding and drip irrigation samples. As the samples were obtained on different farms, the differences in the root density profiles could be attributed to differences in the hydro-edaphic properties of the soils in the two farms.

Date palms are also frequently found growing in natural conditions. The extent of water availability (able to influence the root systems) differs between farm and natural conditions (Daddi Bouhoun 2010), i.e. date palms growing in natural conditions are not irrigated and depend exclusively on precipitation. Hence, it could be assumed that the rooting architecture of date palms in farms differs from that of trees growing in natural conditions. In our study, the root architecture of uncultivated date palms hosted in natural desert ecosystems differed greatly from that of trees growing in other environments. These individuals had a homogenous low root density at all depths, with almost no roots observed in the 150–160 cm layer. These results strongly suggest that agriculture, and probably irrigation, significantly modifies plant root systems compared to natural ecosystems.

Comprehensive descriptions of the root architecture of large plants at great depths are currently lacking. Although date palm roots have been reported to be present at depths > 10 m (Zaid and de Wet 2002), there is no evidence to support this. However, deep roots (> 20 m) have been described in *Sideroxylon lanuginosum* and *Quercus fusiformis* trees growing in a semiarid environment (Johnson et al. 2014). This rooting architecture and strategy may provide access to deep nutrients and water (McCulley et al. 2004). Soil water systems strongly affects date palms root formation. In these natural environments where water is scarce, uncultivated date palms might have developed a higher density of roots in deeper layers to get water and nutrients absent from the surface. Note also that we monitored the roots in a flat area 2 m away from the trunk. The root system is a 3D object described here with a 2D profile, so the monitored root parameters may vary with the distance from the trunk.

In deserts soils, nutrients can be heterogeneously distributed horizontally (Schlesinger et al. 1996; Maurice et al. 2023) and vertically (Eilers et al. 2012). Notably, nutrients and organic matter are mainly concentrated in the topsoil layers where most nutrient cycling occurs (Jobbágy and Jackson 2001; Eilers et al. 2012). Plant root systems often adapt to the extent of water and nutrient availability in soils (Cordeiro et al. 2020), whereas plants growing in deserts also develop adaptations to help them get established and survive in these dry and hot environments. For example, *Stipagrostis* spp. develop a rhizosheath, while accumulating fine roots that host various microorganisms. This microbiome can increase the soil moisture, modify the pH and nutrient availability, thus helping the plant to thrive in these extreme environments (Tian et al. 2019). Date palm seedlings have also been found to develop adaptations to arid conditions, with a multilayered tube organ called the cotyledonary petiole, which enables so-called remote germination in deeper soils to escape the high surface temperatures (Xiao et al. 2019).

Overall, very few studies have investigated the root parameters of adult date palms due to the difficulty of monitoring and measuring the root system of large plants. All studies that have attempted to describe root parameters in date palms were focused on agrosystems or on irrigated farming conditions (Daddi Bouhoun 2010; Littardi et al. 2015; Tahri 2018). From this standpoint, our study generated new elements and knowledge on the rooting architecture of date palms in natural conditions.

Munier (1973) reported that most date palm roots were present in the top 100 cm soil horizon. However, the author did not mention the method used in the book to investigate date palm root systems, yet his claim is often considered as a baseline (Zaid and de Wet 2002; Tahri 2018). Otherwise, Tahri (2018) measured the root density (in kg of roots/m³ of soil) and root system diameter under three date palms in 100 cm deep pits, while Daddi Bouhoun (2010) used an auger and thereby assessed the root density and root diameter in 120 cm soil profiles. To the best of our knowledge, no studies have tried to explore the date palm root architecture below 120 cm. Here we thus collected valuable data on the date palm root architecture up to 160 cm soil depth.

4.2 Fungal community diversity slightly declines with the soil depth without changes in the community composition

Here we sequenced date palm root fungal communities. These communities were composed of fungi detected within the roots (endophytes) and on their surface (rhizoplane), although the latter communities might have been reduced as the roots were rinsed before analysis. Our results revealed that fungal diversity in date palm roots slightly decreased along a depth gradient. This trend was in accordance with that observed previously in studies on soil microbial communities (Eilers et al. 2012; Hao et al. 2021; He et al. 2023b). The decreasing diversity pattern we observed could have been a direct consequence of a decrease in fungal diversity in the soils, thereby reducing the fungal pool available for horizontal soil-to-root transmission. Laurent-Webb et al. (2023) found that horizontal transmission from soil to roots was a major factor explaining fungal community composition in the roots of adults *Amaranthaceae Haloxylon salicornicum*.

Most current knowledge on soil microbial communities derives from studies on surface soils, which tend to have higher nutrient proportions and greater microbial diversity (Hao et al. 2021) than deeper soils. Fewer studies have focused on deep soil microbial communities and hence these communities are less understood (He et al. 2023b). Below the topsoil layer, the soil pH tends to increase with depth, while carbon, nitrogen and organic matter contents generally decrease along a depth gradient. In their meta-analysis, He et al. (2023b) observed that the bacterial biomass and diversity also decreased with soil depth in different environments. Geochemical properties and abiotic factors (e.g. soil pressure, reduced oxygen levels, reduced nitrogen quantity) may serve as a strong microbial community filter (Chen et al. 2016). Furthermore, plant roots select their associated microbial communities from the soil (Dang et al. 2021). Microbes may associate with plant roots in three ways: (i) horizontal transmission by direct penetration of microbes from the surrounding soil into the roots, (ii) transfer from older roots while growing, and (iii) vertical transmission of endophytes from seeds (Laurent-Webb et al. 2023).

The fungal diversity decreased with soil depth whereas the fungal community compositions were not significantly affected. However, many studies have reported the presence of significantly different microbial communities in the topsoil layer (with high nutrient contents) compared to deeper levels (Eilers et al. 2012; Gu et al. 2017; Schlatter et al. 2018; He et al. 2023a). We began our sampling at 40 cm depth (much below the topsoil layer), thereby potentially excluding the influence of the topsoil microbiome. Desert soils are also less stratified and more homogeneous than those in forests or cropfields described in other studies, which could explain the absence of differences we noted between our sampling depths. Finally, our study focused on root fungal communities while other previous studies concerned soil and rhizosphere samples.

In our study, the deepest samples were collected in the 160 cm soil layer. Although the soils were found to be mostly homogeneous along a vertical gradient, interesting features may appear in horizons below 160 cm. For example, in a study carried out in the hyperarid Atacama Desert in Chile, Horstmann et al. (2024) reported that the soil was composed of two major geological strata separated at 2 m depth. The lower gypsum stratum showed higher bacterial diversity, probably due to higher water availability in this horizon. The same structure might also prevail in AlUla soils, so the microbial communities present in deeper soil layers might differ.

We described a reduction in fungal diversity in deeper soils, but we also found that there were no community composition differences between soil depths. Wang et al. (2021) reported that microbiome multifunctionality decreased along a soil depth gradient (0-100 cm). It would be interesting to further analyze these effects to determine if the microbiome functional properties are conserved along a depth gradient.

4.3 soil water systems affect date palm root fungal communities

4.3.1 Soil water systems impact the diversity and composition of date palm root fungal communities

In our study, only drip irrigation had an effect on fungal diversity, which was lower than noted in the other soil water systems at diversity orders $q = 1$ and $q = 2$, which was out of line with our hypothesis that variations would only be detected between date palms growing in irrigated and non-irrigated conditions. As the drip irrigation systems had only been installed a few years prior to the study, this difference in drip fungal diversity could be attributed to a short-term disturbance effect due to the replacement of the irrigation system, but this effect might disappear within a few years once the system is stabilized. Otherwise, Wang et al. (2023b) reported a continuous reduction in soil fungal diversity 11 to 21 years after the application of mulched drip irrigation in cotton crop fields, indicating that changes in irrigation systems can trigger long-term changes in the fungal communities. In an arid region, Deng et al. (2022) observed lower fungal diversity in drip irrigated rhizosphere soil compared to flooding irrigated rhizosphere soil under alfalfa crops. Abumaali et al. (2023) reported lower bacterial diversity in the

rhizosphere of natural date palms under non-irrigated conditions than in the rhizosphere of cultivated date palms, in contrast to our results as we did not observe any diversity differences when comparing flooded and natural date palm fungal communities. Abumaali et al. (2023) explained this difference by the different soil physicochemical properties, yet we noted high intracondition (soil water systems) variability but no significant differences between conditions.

Compared with flooding irrigation, drip irrigation modifies the wetting and drying cycles, water distribution and chemical properties of soils (Bourziza et al. 2017b; Alnaim et al. 2022). Flooding irrigation induces regular flushing events, leaching of upper layer nutrients and salt to deeper soil layers, alongside intense short wetting events followed by drying periods. Drip irrigation reduces drainage, thus leading to more stable soil moisture conditions for the plants and microbial communities. However, surface drip irrigation induces salt accumulation on the soil surface due to the absence of leaching. The water application period with drip irrigation systems is longer and the watering is mainly concentrated in the upper soil layers, so the soil moisture levels in the deep soil layers might be less than under flooding irrigation. Although water application is more consistent with drip irrigation systems, a change in irrigation system on farms may substantially modify the water distribution and flow. This disturbance might potentially dry the deep soil layers due to the lack of leaching at the surface following irrigation, leading to lower water penetration to these depths. The abandoned farms we investigated had also been disturbed—although long before the study—by an interruption in irrigation, thereby forcing the date palms and associated communities to adapt and restructure in response to the new scant water conditions. Otherwise, from the moment of their germination, the date palms studied in the natural environment were growing in stable conditions with limited water access and scarce rainfall ($\approx 0, 1$ or 2 events/year).

The fungal community composition significantly differed among all soil water systems that we studied. This pattern has also been frequently observed in other studies where changes in irrigation systems (Deng et al. 2022; Wang et al. 2023a), water quality (Lüneberg et al. 2019), and water quantity (Wang et al. 2017) altered the microbial communities in soils and roots. However, the majority of these studies were focused on soil or rhizosphere microbiota. Here we assessed date palm root (endophyte and rhizoplane) microbiota, which differ from soil microbiota, due to the filtering effect and specific niches offered by the roots.

Fungal communities are very dependent on water conditions and nutrients (Schlatter et al. 2018) and can be affected by disturbance effects such as agricultural practices (Verbruggen and Kiers 2010; Wang et al. 2017). Roots also seem to select their fungal partners in response to abiotic and biotic stresses such as hydro-edaphic conditions through changes in root exudation and in their immune system (Rolfe et al. 2019; Deng et al. 2022).

4.3.2 Soil water systems alter the fungal taxa composition in date palm roots

Among the major fungal taxa detected in date palm roots under all soil water systems ($> 5\%$ relative abundance), most were saprotrophic according to FUNGuild v.0.2.0.9000 (Nguyen et al. 2016)

(*Kraurogymnocarpa*, *Calvatia*, *Pseudocolus*, *Ophiospaerella*, *Trichocladium*). Saprotrophs are decomposer fungi that play a key role in ecosystems by recycling organic matter (Boddy and Hiscox 2016). Their abundant presence in roots under all soil water systems and the high number of dead roots observed during our sampling (mostly under non-irrigated date palms) suggests potentially high organic matter recycling activity. Date palm saprotrophs may therefore contribute to dynamic reshaping and growth of fresh plant roots by providing ready-to-use nutrients extracted from older roots (Boddy and Hiscox 2016; Zhang et al. 2021).

The pathotrophic fungal communities associated with date palm roots differed under the different soil water systems. Among the major taxa, date palms under flooding irrigation hosted one pathotroph taxon, i.e. *Burgoa*, which is considered to be a lichen parasite (Lawrey and Diederich 2003). More abundant plant pathogenic fungi were observed in the other soil water systems, e.g. *Rhizoctonia* and *Cryphonectria*. Pathotrophs are key ecosystem elements that occupy ecological niches and compete with potential new invasive pathogens, and their presence in roots can thus represent an element of ecological stability and tolerance to new pathogenic disturbances (Seabloom et al. 2015). Hence, date palms growing in flooding irrigation conditions might be more susceptible to infection by new pathogens. For example, *Fusarium oxysporum* f. sp. *albedinis*, which causes devastating Bayoud disease in date palm stands in Morocco and Algeria, is not yet present in Saudi Arabia (Saleh et al. 2015). However, this disease is slowly disseminating eastward from North Africa and might become problematic in Saudi Arabia in the future if phytosanitary procedures are not fulfilled.

Finally, the main symbiotrophic fungi identified were almost all arbuscular mycorrhizal fungi (AMF) of various genera (seven overall). Date palms are commonly subject to mycorrhizal colonization under cultivation conditions (Ramoliya and Pandey 2003; Abohatem et al. 2011; Bouamri et al. 2014). Arbuscular mycorrhizal fungi, and particularly *Glomus* and *Rhizophagus*, were among the main genera explaining fungal community differences in date palm roots in our conditions. Among Glomeromycetes, in our samples, we almost exclusively noted OTUs belonging to Glomeraceae (Glomerales). AMF are generally ubiquitous fungi that prevail in most environments, including arid soil. Glomeraceae is often found to be dominant in soils under adverse conditions as they are opportunistic and have evolved characteristics enabling their survival in these environments (Lenoir et al. 2016). This pattern has been observed in other dryland studies (Symanczik et al. 2014; Qiang et al. 2019; Vasar et al. 2021; Harrower and Gilbert 2021; Adenan et al. 2021), in the date palm rhizosphere (Al-Yahya'ei et al. 2011), in *Coffea arabica* roots (Mahdhi et al. 2020), and in maize (Lü et al. 2020).

Compared to other soil water systems, drip irrigation induced a significant reduction in fungal diversity and an increase in the proportion and differential abundance of Glomeromycetes. These results contrast with those of Deng et al. (2022), who reported a proportional decrease in AMF in alfalfa crops under drip irrigation as compared to flooding irrigation. AMF-plant relationships can be influenced by the plant and fungal partners and by the environmental conditions, e.g. nutrient or water availability (Werner and Kiers 2015). In our conditions, we observed a reduction in fungal diversity under drip irrigation and an increase in the relative abundance of AMF. This suggests that the date palms might have filtered AMF taxa in the

roots or in the rhizosphere in response to the change of soil water systems, thereby preserving AMF from the overall decrease in diversity.

4.4 Prospects for drip irrigation as an alternative to flooding

In this study, we compared the impacts of using flooding irrigation and drip irrigation on date palm root system parameters and root fungal communities in a modern monoculture farm setting. We observed no root architecture differences between the two conditions. We found that fungal diversity was significantly lower in drip irrigated date palm roots but that proportion of AMF was higher under these conditions. Fungal communities significantly differed between these two irrigation systems.

Extensive literature, mainly on modern monoculture farms, confirms the superiority of drip irrigation over other surface irrigation methods such as bubbler, sprinkler or flooding irrigation in terms of plant growth, yield, disease reduction and water use efficiency in modern date palm cultivation (Carr 2012; Elfeky and Elfaki 2019). However, no data is currently available on the impacts of these irrigation systems on microbial communities associated with date palms. In this study of date palm root fungal communities, we found no evidence that would suggest that replacing flooding irrigation systems by drip irrigation systems would be deleterious to date palms. Therefore, our findings support the notion that shifting from flooding irrigation to drip irrigation in monoculture farms could help substantially reduce water consumption in modern date palm farms. Nonetheless, to the best of our knowledge, this is one of the few studies that have focused on investigating the impact of soil water systems on microbial communities, and it is the only one on date palm. Future studies could focus on assessing the impacts of soil water systems on microbial functions in soils and roots in relation to date palm fitness.

Surface drip irrigation nevertheless has several flaws. This irrigation method tends to increase soil moisture levels at shallow depths, leading to greater surface root development, potentially making them more susceptible to heat, wind and desiccation, while reducing soil anchorage (Bourziza et al. 2017b). Heat and evaporation at the soil surface can also lead to salt concentration on the surface (that can be mitigated with leaching steps once in a while) and in the irrigation pipes, thereby damaging and obstructing them. Subsurface drip irrigation, which is an alternative to the conventional surface drip irrigation studied here, has also been extensively studied and shown to enhance water savings and yields (Al-Amoud 2010; Talat Farid Ahmed 2012; Bourziza et al. 2017a, b). This system may be an even better alternative to flooding than surface drip irrigation and should now be studied with regard to its impact on date palm microbial communities. This system could notably be used at different depths, i.e. the soil depth would alter the water distribution, as well as root development and water conductance in the soil (Al-Amoud 2008; Bourziza et al. 2017b). In further studies, it would be interesting to assess the effects of the installation depth of this system on microbial communities. Indeed, we did not observe any microbial community differences between soil depths in our conditions when comparing surface drip irrigation and flooding irrigation, but direct water input at deeper layers could alter the community compositions in the upper and lower soil layers.

Water-saving strategies and precise irrigation systems such as drip irrigation systems are probably the best suited for extensive farms and date palm monoculture conditions, but they could be out of line with traditional or modern agroecological systems where other crops are also grown in date palm orchards (e.g. fruits, cereals, vegetables), which thus benefit from the excessive watering (carried out to meet the date palm water needs) (Battesti 2005). There is currently increased interest in agroecology in arid and oasian environments as a response to climate change to increase and diversify farm production overall (Ameur et al. 2020; Mrabet 2022). A choice thus has to be made between: (i) date palm monoculture agricultural models with adapted irrigation systems to save as much water as possible, and (ii) agroecosystems with less water use efficiency for date production but enabling crop and production diversification.

5 Conclusion

The present study generated new insight into the impacts of different irrigated and non-irrigated systems on the date palm root architecture and root fungal communities. We outlined the effects of the soil water systems on the date palm root number and root width at various depths, thus providing valuable insight into the largely unknown root architecture of mature date palms. Our analysis revealed that the irrigation system had no impact on the observed root architecture parameters, but that this architecture was affected by the interruption or absence of irrigation. Moreover, we have highlighted significant impacts of the soil water systems on the fungal community composition and on the selection of dominant taxa in the roots. We highlighted that the root sampling depth did not affect the fungal communities, yet the diversity decreased with increasing depth.

This study paves the way for gaining further essential insight into microbial communities associated with date palms under different irrigation systems in a context of increasing water scarcity. Future research will be necessary to assess further potential modifications in microbial functional traits resulting from changes in irrigation systems. Microbial communities associated with plants are key factors for agriculture sustainability and could improve the water use efficiency in regions threatened by water scarcity. They should hence be closely studied to facilitate the adaptation of agrosystems to current global changes.

Declarations

The authors declare no competing interests

Funding: This work was funded by the SoFunLand project, supported by AFALULA (*Agence Française pour le développement d'AIUla*) under the auspices of the RCU (Royal Commission for AIUla).

Acknowledgments:

We express our gratitude to everyone who helped us in the field, especially those who dug the pits in these harsh environmental conditions, including Jerome Nespoulous, Coraline Damasio, Liam Laurent-

Webb, and Stéphane Boivin. We also thank the farmers for their hospitality on their farms. We would like to thank Amelia Bourceret for her work on the elaboration of sequencing procedures and for sequences treatments.

Contributions:

A. Soriano: Conceptualization, Sampling, Formal analysis, Investigation, Data curation, Software, Writing, Review & Editing. **B. Vincent:** Formal analysis, Writing, Review & Editing. **K. Maurice:** Formal analysis, Writing, Review & Editing. **V. Battesti:** Data supply, Review & Editing. **H. Boukcim:** Project administration, Funding acquisition, Review & Editing, Supervision. **M. Ducouso:** Project administration, Funding acquisition, Review & Editing, Supervision. **M. Gros-Balthazard:** Data supply, Funding acquisition, Review & Editing, Supervision.

References

1. Abohatem M, Chakrafi F, Jaiti F et al (2011) Arbuscular Mycorrhizal Fungi Limit Incidence of *Fusarium oxysporum* f.sp. *albedinis* on Date Palm Seedlings by Increasing Nutrient Contents, Total Phenols and Peroxidase Activities. TOHORTJ 4:10–16. <https://doi.org/10.2174/1874840601104010010>
2. Abumaali DA, Al-Hadidi SH, Ahmed T et al (2023) 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. 10.1016/j.egg.2023.100195
3. 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>
4. Al-Amoud AI (2008) Performance of Bubbler Irrigation System as compared to trickle for Large Size Date Palm Tree Farm. The Canadian Society for Bioengineering Paper No. CSBE 08-172:12
5. Al-Amoud AI (2010) Subsurface drip irrigation for date palm trees to conserve water. Acta Horti 103–114. <https://doi.org/10.17660/ActaHortic.2010.882.11>
6. Alazba P (2004) Estimating Palm Water Requirements Using Penman-Monteith Mathematical Model. J King Saud Univ 16:137–152
7. Alberdi A, Gilbert MTP (2019a) A guide to the application of Hill numbers to DNA-based diversity analyses. Mol Ecol Resour 19:804–817. <https://doi.org/10.1111/1755-0998.13014>
8. Alberdi A, Gilbert MTP (2019b) hilldiv: an R package for the integral analysis of diversity based on Hill numbers. 545665. <https://doi.org/10.1101/545665>
9. Alnaim MA, Mohamed MS, Mohammed M, Munir M (2022) Effects of Automated Irrigation Systems and Water Regimes on Soil Properties, Water Productivity, Yield and Fruit Quality of Date Palm. Agriculture 12:343. <https://doi.org/10.3390/agriculture12030343>

10. Al-Omran A, Eid S, Alshammari F (2019) Crop water requirements of date palm based on actual applied water and Penman–Monteith calculations in Saudi Arabia. *Appl Water Sci* 9:69. <https://doi.org/10.1007/s13201-019-0936-6>
11. Al-Yahya'ei MN, Oehl F, Vallino M et al (2011) Unique arbuscular mycorrhizal fungal communities uncovered in date palm plantations and surrounding desert habitats of Southern Arabia. *Mycorrhiza* 21:195–209. <https://doi.org/10.1007/s00572-010-0323-5>
12. Ameer F, Amichi H, Leauthaud C (2020) Agroecology in North African irrigated plains? Mapping promising practices and characterizing farmers' underlying logics. *Reg Environ Change* 20:133. <https://doi.org/10.1007/s10113-020-01719-1>
13. Amira J, Ben Salah M (2014) Architectural Study of the Young Date Palm (*Phoenix dactylifera* L). *Root Syst* 8:425–432
14. Amiri ME, Panahi M, Aghazadeh G (2007) Comparison of bubbler, sprinkler and basin irrigation for date palms (*Phoenix dactylifera*, cv. Zahdi) growth in Kish Island, Iran. In: wflpublisher.com. <https://www.wflpublisher.com/Abstract/1146>. Accessed 3 Nov 2022
15. Arab L, Kreuzwieser J, Kruse J et al (2016) Acclimation to heat and drought—Lessons to learn from the date palm (*Phoenix dactylifera*). *Environ Exp Bot* 125:20–30. <https://doi.org/10.1016/j.envexpbot.2016.01.003>
16. Battesti V (2005) Jardins au désert: évolution des pratiques et savoirs oasiens: Jérid tunisien. IRD Éditions, Paris
17. Ben Aissa I, Bouarfa S, Roupsard O, Majdoub R (2019) Is it true that the date palm tree consumes a lot of water? Evaluation of the date palm tree transpiration using Granier's sap flow method in a Tunisian Saharan oasis. *Int J Agric Environ Food Sci*. <https://doi.org/10.31015/jaefs.2019.2.3>
18. Benhiba L, Fouad MO, Essahibi A et al (2015) Arbuscular mycorrhizal symbiosis enhanced growth and antioxidant metabolism in date palm subjected to long-term drought. *Trees* 29:1725–1733. <https://doi.org/10.1007/s00468-015-1253-9>
19. Berruti A, Desirò A, Visentin S et al (2017) ITS fungal barcoding primers versus 18S AMF-specific primers reveal similar AMF-based diversity patterns in roots and soils of three mountain vineyards. *Environ Microbiol Rep* 9:658–667. <https://doi.org/10.1111/1758-2229.12574>
20. Boddy L, Hiscox J (2016) Fungal Ecology: Principles and Mechanisms of Colonization and Competition by Saprotrophic Fungi. *Microbiol Spectr* 4. [10.1128/microbiolspec.funk-0019-2016](https://doi.org/10.1128/microbiolspec.funk-0019-2016)
21. Bouamri R, Dalpe Y, Serrhini MM (2014) Effect of Seasonal Variation on Arbuscular Mycorrhizal Fungi Associated with Date Palm. *Emirates J Food Agric* 977–986. <https://doi.org/10.9755/ejfa.v26i11.18985>
22. Bourziza R, Hammani A, Kuper M, Bouaziz A (2017) Performances du goutte à goutte enterré pour l'irrigation de jeunes palmiers dattiers. *Revue Marocaine des Sci Agronomiques et Vétérinaires* 5:5–12
23. Bourziza R, Hammani A, Mailhol J-C et al (2017b) Modélisation de l'irrigation en goutte à goutte enterré du palmier dattier sous les conditions oasiennes. *Cahiers Agricultures*.

<https://doi.org/10.1051/cagri/2017023>

24. Carr MKV (2012) The water relations and irrigation requirements of the date palm. *Expl Agric* (2013), volume 49 (1), pp 91–113 C Cambridge University Press 23
25. Chen Y, Chen G, Robinson D et al (2016) Large amounts of easily decomposable carbon stored in subtropical forest subsoil are associated with r-strategy-dominated soil microbes. *Soil Biol Biochem* 95:233–242. <https://doi.org/10.1016/j.soilbio.2016.01.004>
26. Chourasiya D, Gupta MM, Sahni S et al (2021) Unraveling the AM fungal community for understanding its ecosystem resilience to changed climate in agroecosystems. *Symbiosis* 84:295–310. <https://doi.org/10.1007/s13199-021-00761-9>
27. Cordeiro AL, Norby RJ, Andersen KM et al (2020) Fine-root dynamics vary with soil depth and precipitation in a low-nutrient tropical forest in the Central Amazonia. *Plant Environ Interact* 1:3–16. <https://doi.org/10.1002/pei3.10010>
28. Daddi Bouhoun M (2010) Contribution à l'étude de l'impact de la nappe phréatique et des accumulations gypsosolines sur l'enracinement et la nutrition du palmier dattier dans la cuvette de Ourgla (Sud Est Algérien). Badji Mokhtar Annaba University
29. Dang H, Zhang T, Wang Z et al (2021) Differences in the endophytic fungal community and effective ingredients in root of three *Glycyrrhiza* species in Xinjiang. *China PeerJ* 9:e11047. <https://doi.org/10.7717/peerj.11047>
30. Davis NM, Proctor DM, Holmes SP et al (2018) Simple statistical identification and removal of contaminant sequences in marker-gene and metagenomics data. *Microbiome* 6:226. <https://doi.org/10.1186/s40168-018-0605-2>
31. Deng Q, Wu Y, Zhao X et al (2022) Influence of different irrigation methods on the alfalfa rhizosphere soil fungal communities in an arid region. *PLoS ONE* 17:e0268175. <https://doi.org/10.1371/journal.pone.0268175>
32. Eilers KG, Debenport S, Anderson S, Fierer N (2012) Digging deeper to find unique microbial communities: The strong effect of depth on the structure of bacterial and archaeal communities in soil. *Soil Biol Biochem* 50:58–65. <https://doi.org/10.1016/j.soilbio.2012.03.011>
33. Elfeky A, Elfaki J (2019) A Review: Date Palm Irrigation Methods and Water Resources in the Kingdom of Saudi Arabia. *J Eng Res Rep* 1–11. <https://doi.org/10.9734/jerr/2019/v9i217012>
34. Ferjani R, Marasco R, Rolli E et al (2015) The Date Palm Tree Rhizosphere Is a Niche for Plant Growth Promoting Bacteria in the Oasis Ecosystem. *Biomed Res Int* 2015:153851. <https://doi.org/10.1155/2015/153851>
35. Gros-Balthazard M, Battesti V, Flowers JM et al (2023) What lies behind a fruit crop variety name? A case study of the barnī date palm from al-'Ulā oasis, Saudi Arabia. *PLANTS, PEOPLE, PLANET* 5:82–97. <https://doi.org/10.1002/ppp3.10326>
36. Gros-Balthazard M, Flowers JM (2021) A Brief History of the Origin of Domesticated Date Palms. In: Al-Khayri JM, Jain SM, Johnson DV (eds) *The Date Palm Genome*, vol 1. Springer International Publishing, Cham, pp 55–74

37. Gu Y, Wang Y, Lu S et al (2017) Long-term Fertilization Structures Bacterial and Archaeal Communities along Soil Depth Gradient in a Paddy Soil. *Front Microbiol* 8. <https://doi.org/10.3389/fmicb.2017.01516>
38. El Hadrami A, Al-Khayri J (2012) Socioeconomic and traditional importance of date palm. *Emir J Food Agric* 24:371–385
39. Hao J, Chai YN, Lopes LD et al (2021) The Effects of Soil Depth on the Structure of Microbial Communities in Agricultural Soils in Iowa (United States). *Appl Environ Microbiol* 87:e02673–e02620. <https://doi.org/10.1128/AEM.02673-20>
40. Harrower JT, Gilbert GS (2021) Parasitism to mutualism continuum for Joshua trees inoculated with different communities of arbuscular mycorrhizal fungi from a desert elevation gradient. *PLoS ONE* 16:e0256068. <https://doi.org/10.1371/journal.pone.0256068>
41. Hazzouri KM, Flowers JM, Nelson D et al (2020) Prospects for the Study and Improvement of Abiotic Stress Tolerance in Date Palms in the Post-genomics Era. *Front Plant Sci* 11:293. <https://doi.org/10.3389/fpls.2020.00293>
42. He H, Zhou J, Wang Y et al (2023a) Deciphering microbiomes dozens of meters under our feet and their edaphoclimatic and spatial drivers. <https://doi.org/10.1111/gcb.17028>. *Global Change Biology* n/a:e17028
43. He L, Sun X, Li S et al (2023b) The vertical distribution and control factor of microbial biomass and bacterial community at macroecological scales. *Sci Total Environ* 869:161754. <https://doi.org/10.1016/j.scitotenv.2023.161754>
44. Horstmann L, Lipus D, Bartholomäus A et al (2024) Persistent microbial communities in hyperarid subsurface habitats of the Atacama Desert: Insights from intracellular DNA analysis. *PNAS Nexus* 3:123. <https://doi.org/10.1093/pnasnexus/pgae123>
45. Jaiti F, Meddich A, Hadrami IE (2007) Effectiveness of arbuscular mycorrhizal fungi in the protection of date palm (*Phoenix dactylifera* L.) against bayoud disease. *Physiol Mol Plant Pathol* 71:166–173. <https://doi.org/10.1016/j.pmpp.2008.01.002>
46. Jobbágy EG, Jackson RB (2001) The distribution of soil nutrients with depth: Global patterns and the imprint of plants. *Biogeochemistry* 53:51–77. <https://doi.org/10.1023/A:1010760720215>
47. Johnson DM, Brodersen CR, Reed M et al (2014) Contrasting hydraulic architecture and function in deep and shallow roots of tree species from a semi-arid habitat. *Ann Botany* 113:617–627. <https://doi.org/10.1093/aob/mct294>
48. Khan PR, Hegazy SS, Iqbal M (2020) Date palm rachis as a raw material for wood composite industry: anatomical characteristics. *Braz J Bot* 43:601–607. <https://doi.org/10.1007/s40415-020-00612-9>
49. Krueger RR (2021) Date Palm (*Phoenix dactylifera* L.) Biology and Utilization. In: Al-Khayri JM, Jain SM, Johnson DV (eds) *The Date Palm Genome*, vol 1. Springer International Publishing, Cham, pp 3–28
50. Laity JJ (2009) *Deserts and Desert Environments*. Wiley

51. Lamit LJ, Romanowicz KJ, Potvin LR et al (2017) Patterns and drivers of fungal community depth stratification in Sphagnum peat. *FEMS Microbiol Ecol* 93:fix082.
<https://doi.org/10.1093/femsec/fix082>
52. Laurent-Webb L, Maurice K, Perez-Lamarque B et al (2023) Seed or soil: tracing back the plant mycobiota primary sources. 2023.08.04.551828
53. Lawrey JD, Diederich P (2003) Lichenicolous Fungi: Interactions, Evolution, and Biodiversity. *Bryologist* 106:80–120. [https://doi.org/10.1639/0007-2745\(2003\)106\[0080:LFIEAB\]2.0.CO;2](https://doi.org/10.1639/0007-2745(2003)106[0080:LFIEAB]2.0.CO;2)
54. Lenoir I, Fontaine J, Lounès-Hadj Sahraoui A (2016) Arbuscular mycorrhizal fungal responses to abiotic stresses: A review. *Phytochemistry* 123:4–15.
<https://doi.org/10.1016/j.phytochem.2016.01.002>
55. Littardi M, Littardi C, Bouguedoura N et al (2015) Rhizotron field observations
56. Liu C, Cui Y, Li X, Yao M (2021) microeco: an R package for data mining in microbial community ecology. *FEMS Microbiol Ecol* 97:fiaa255. <https://doi.org/10.1093/femsec/fiaa255>
57. Love MI, Huber W, Anders S (2014) Moderated estimation of fold change and dispersion for RNA-seq data with DESeq2. *Genome Biol* 15:550. <https://doi.org/10.1186/s13059-014-0550-8>
58. Lü P-P, Zheng Y, Chen L et al (2020) Irrigation and fertilization effects on arbuscular mycorrhizal fungi depend on growing season in a dryland maize agroecosystem. *Pedobiologia* 83:150687.
<https://doi.org/10.1016/j.pedobi.2020.150687>
59. Lüneberg K, Schneider D, Brinkmann N et al (2019) Land Use Change and Water Quality Use for Irrigation Alters Drylands Soil Fungal Community in the Mezquital Valley, Mexico. *Front Microbiol* 10.
<https://doi.org/10.3389/fmicb.2019.01220>
60. Mahdhi M, Tounekti T, Abada E et al (2020) Diversity of arbuscular mycorrhizal fungi associated with acacia trees in southwestern Saudi Arabia. *J Basic Microbiol* 60:322–330.
<https://doi.org/10.1002/jobm.201900471>
61. Maurice K, Laurent-Webb L, Bourceret A et al (2024) Networking the desert plant microbiome, bacterial and fungal symbionts structure and assortativity in co-occurrence networks. In Review
62. Maurice K, Laurent-Webb L, Dehail A et al (2023) Fertility islands, keys to the establishment of plant and microbial diversity in a highly alkaline hot desert. *J Arid Environ* 219:105074.
<https://doi.org/10.1016/j.jaridenv.2023.105074>
63. McCulley RL, Jobbágy EG, Pockman WT, Jackson RB (2004) Nutrient uptake as a contributing explanation for deep rooting in arid and semi-arid ecosystems. *Oecologia* 141:620–628.
<https://doi.org/10.1007/s00442-004-1687-z>
64. Meddich A, Jaiti F, Bourzik W et al (2015) Use of mycorrhizal fungi as a strategy for improving the drought tolerance in date palm (*Phoenix dactylifera*). *Sci Hort* 192:468–474.
<https://doi.org/10.1016/j.scienta.2015.06.024>
65. Mohammed M, Sallam A, Munir M, Ali-Dinar H (2021) Effects of Deficit Irrigation Scheduling on Water Use, Gas Exchange, Yield, and Fruit Quality of Date Palm. *Agronomy* 11:2256.
<https://doi.org/10.3390/agronomy11112256>

66. Mrabet R (2022) Advanced and emerging agricultural innovations for securing food, climate and ecosystems in Moroccan oasis. *J oasis Agric sustainable Dev* 4:6–15.
<https://doi.org/10.56027/JOASD.spiss022022>
67. Munier P (1973) *Le palmier-dattier*. Maisonneuve et Larose, Paris
68. Nguyen NH, Song Z, Bates ST et al (2016) FUNGuild: An open annotation tool for parsing fungal community datasets by ecological guild. *Fungal Ecol* 20:241–248.
<https://doi.org/10.1016/j.funeco.2015.06.006>
69. Odnoletkova N, Patzek TW (2023) Water resources in Saudi Arabia: trends in rainfall, water consumption, and analysis of agricultural water footprint. *npj Sustain Agric* 1:1–8.
<https://doi.org/10.1038/s44264-023-00006-w>
70. Oksanen J, Simpson G, Blanchet FG et al (2022) vegan community ecology package version 2.6-2 April 2022
71. Perez-Lamarque B, Krehenwinkel H, Gillespie RG, Morlon H (2022) Limited Evidence for Microbial Transmission in the Phyllosymbiosis between Hawaiian Spiders and Their Microbiota. *mSystems* 7:e01104–e01121. <https://doi.org/10.1128/msystems.01104-21>
72. Qaddoury A (2017) Arbuscular Mycorrhizal Fungi Provide Complementary Characteristics that Improve Plant Tolerance to Drought and Salinity: Date Palm as Model. In: Prasad R (ed) *Mycoremediation and Environmental Sustainability*. Springer International Publishing, Cham, pp 189–215
73. Qiang W, He X, Wang J, Zhao L (2019) Temporal and spatial variation of arbuscular mycorrhizal fungi under the canopy of *Hedysarum scoparium* in the northern desert, China. *Appl Soil Ecol* 136:139–147. <https://doi.org/10.1016/j.apsoil.2019.01.003>
74. Quast C, Pruesse E, Yilmaz P et al (2013) The SILVA ribosomal RNA gene database project: improved data processing and web-based tools. *Nucleic Acids Res* 41:D590–D596.
<https://doi.org/10.1093/nar/gks1219>
75. Ramoliya PJ, Pandey AN (2003) Soil salinity and water status affect growth of *Phoenix dactylifera* seedlings. *New Z J Crop Hortic Sci* 31:345–353. <https://doi.org/10.1080/01140671.2003.9514270>
76. Reimann C, Filzmoser P, Fabian K et al (2012) The concept of compositional data analysis in practice – Total major element concentrations in agricultural and grazing land soils of Europe. *Sci Total Environ* 426:196–210. <https://doi.org/10.1016/j.scitotenv.2012.02.032>
77. Robin-Soriano A, Maurice K, Boivin S et al (2024) A multimethod approach to assess arbuscular mycorrhizal fungal diversity in a hot arid and hyperalkaline region
78. Rolfe SA, Griffiths J, Ton J (2019) Crying out for help with root exudates: adaptive mechanisms by which stressed plants assemble health-promoting soil microbiomes. *Curr Opin Microbiol* 49:73–82.
<https://doi.org/10.1016/j.mib.2019.10.003>
79. Saad Eddin MR, Hassan AM, Hegazi AA et al (2023) Effects of root watering system on yield, water use efficiency and fruit quality of date palm (c.v. Siwi): a case study in the arid climate, Egypt. *Irrig Sci*. <https://doi.org/10.1007/s00271-022-00840-9>

80. Saleem M, Law AD, Sahib MR et al (2018) Impact of root system architecture on rhizosphere and root microbiome. *Rhizosphere* 6:47–51. <https://doi.org/10.1016/j.rhisph.2018.02.003>
81. Saleh AA, El_Komy MH, Eranthodi A et al (2015) Variation in a molecular marker for resistance of Saudi date palm germplasm to *Fusarium oxysporum* f. sp. *albedinis* the causal agent of Bayoud disease. *Eur J Plant Pathol* 143:507–514. <https://doi.org/10.1007/s10658-015-0703-y>
82. Schlatter DC, Kahl K, Carlson B et al (2018) Fungal community composition and diversity vary with soil depth and landscape position in a no-till wheat-based cropping system. *FEMS Microbiol Ecol* 94:fiy098. <https://doi.org/10.1093/femsec/fiy098>
83. Schlesinger WH, Raikes JA, Hartley AE, Cross AF (1996) On the Spatial Pattern of Soil Nutrients in Desert Ecosystems. *Ecology* 77:364–374. <https://doi.org/10.2307/2265615>
84. Schreiner RP, Tarara JM, Smithyman RP (2007) Deficit irrigation promotes arbuscular colonization of fine roots by mycorrhizal fungi in grapevines (*Vitis vinifera* L.) in an arid climate. *Mycorrhiza* 17:551–562. <https://doi.org/10.1007/s00572-007-0128-3>
85. Seabloom EW, Borer ET, Gross K et al (2015) The community ecology of pathogens: coinfection, coexistence and community composition. *Ecol Lett* 18:401–415. <https://doi.org/10.1111/ele.12418>
86. Seraphin P, Gonçalves J, Hamelin B et al (2022) Influence of intensive agriculture and geological heterogeneity on the recharge of an arid aquifer system (Saq–Ram, Arabian Peninsula) inferred from GRACE data. *Hydrol Earth Syst Sci* 26:5757–5771. <https://doi.org/10.5194/hess-26-5757-2022>
87. Shahin SMR, Salem MA (2014) Review future concerns on irrigation requirements of date palm tree in United Arab Emirates (UAE):call for quick actions. 8
88. Smith SE, Read DJ (2010) *Mycorrhizal Symbiosis*. Academic
89. Symanczik S, Błaszczowski J, Koegel S et al (2014) Isolation and identification of desert habituated arbuscular mycorrhizal fungi newly reported from the Arabian Peninsula. *J Arid Land* 6:488–497. <https://doi.org/10.1007/s40333-014-0021-9>
90. Tahri K (2018) Etude De L'architecture Et De La Biomasse Du Systeme Racinaire De Palmier Dattier (*Phoenix dactylifera* L.) Adulte. Mémoire de Magister, Université Mohamed Khider
91. Talat Farid Ahmed (2012) Performance assessment of surface and subsurface drip irrigation system for date palm fruit trees. *Afr J Agric Res* 7. <https://doi.org/10.5897/AJAR11.1178>
92. Tengberg M (2012) Beginnings and early history of date palm garden cultivation in the Middle East. *J Arid Environ* 86:139–147. <https://doi.org/10.1016/j.jaridenv.2011.11.022>
93. Tian Y, Ma X, Li Y et al (2019) Relationship between microbial diversity and nitrogenase activity of *Stipagrostis pennata* rhizosphere. *J Cell Biochem* 120:13501–13508. <https://doi.org/10.1002/jcb.28625>
94. Toumi N, Hussein BHM, Rafrafi S, El kassas N (2015) Groundwater quality and hydrochemical properties of Al-Ula Region, Saudi Arabia. *Environ Monit Assess* 187:84. <https://doi.org/10.1007/s10661-014-4241-4>

95. Trinchera A, Warren Raffa D (2023) Weeds: An Insidious Enemy or a Tool to Boost Mycorrhization in Cropping Systems? *Microorganisms* 11:334. <https://doi.org/10.3390/microorganisms11020334>
96. Vasar M, Davison J, Sepp S-K et al (2021) Arbuscular Mycorrhizal Fungal Communities in the Soils of Desert Habitats. *Microorganisms* 9:229. <https://doi.org/10.3390/microorganisms9020229>
97. Verbruggen E, Kiers ET (2010) Evolutionary ecology of mycorrhizal functional diversity in agricultural systems. *Evol Appl* 3:547–560. <https://doi.org/10.1111/j.1752-4571.2010.00145.x>
98. Wang H, Bu L, Tian J et al (2021) Particular microbial clades rather than total microbial diversity best predict the vertical profile variation in soil multifunctionality in desert ecosystems. *Land Degrad Dev* 32:2157–2168. <https://doi.org/10.1002/ldr.3873>
99. Wang J, He Q, Niu W, Han J (2023a) Alternate drip irrigation regulates the soil fungal community structure and metabolic function based on root–fungus interactions. *Land Degrad Dev* 34:1133–1144. <https://doi.org/10.1002/ldr.4521>
100. Wang J, Li H, Cheng Z et al (2023b) Changes in soil bacterial and fungal community characteristics in response to long-term mulched drip irrigation in oasis agroecosystems. *Agric Water Manage* 279:108178. <https://doi.org/10.1016/j.agwat.2023.108178>
101. Wang J, Niu W, Zhang M, Li Y (2017) Effect of alternate partial root-zone drip irrigation on soil bacterial communities and tomato yield. *Appl Soil Ecol* 119:250–259. <https://doi.org/10.1016/j.apsoil.2017.06.032>
102. Werner GDA, Kiers ET (2015) Partner selection in the mycorrhizal mutualism. *New Phytol* 205:1437–1442. <https://doi.org/10.1111/nph.13113>
103. Xiao TT, Raygoza AA, Pérez JC et al (2019) Emergent Protective Organogenesis in Date Palms: A Morpho-Devo-Dynamic Adaptive Strategy during Early Development. *Plant Cell* 31:1751–1766. <https://doi.org/10.1105/tpc.19.00008>
104. Xiong C, Lu Y (2022) Microbiomes in agroecosystem: Diversity, function and assembly mechanisms. *Environ Microbiol Rep* 14:833–849. <https://doi.org/10.1111/1758-2229.13126>
105. Zaid A, de Wet PF (2002) Chapter I: Botanical and systematic description of the date palm. <https://www.fao.org/3/Y4360E/y4360e05.htm>. Accessed 2 Dec 2022
106. Zemni N, Slama F, Bouksila F, Bouhlila R (2022) Simulating and monitoring water flow, salinity distribution and yield production under buried diffuser irrigation for date palm tree in Saharan Jemna oasis (North Africa). *Agric Ecosyst Environ* 325:107772. <https://doi.org/10.1016/j.agee.2021.107772>
107. Zhang K, Maltais-Landry G, Liao H-L (2021) How soil biota regulate C cycling and soil C pools in diversified crop rotations. *Soil Biol Biochem* 156:108219. <https://doi.org/10.1016/j.soilbio.2021.108219>

Figures

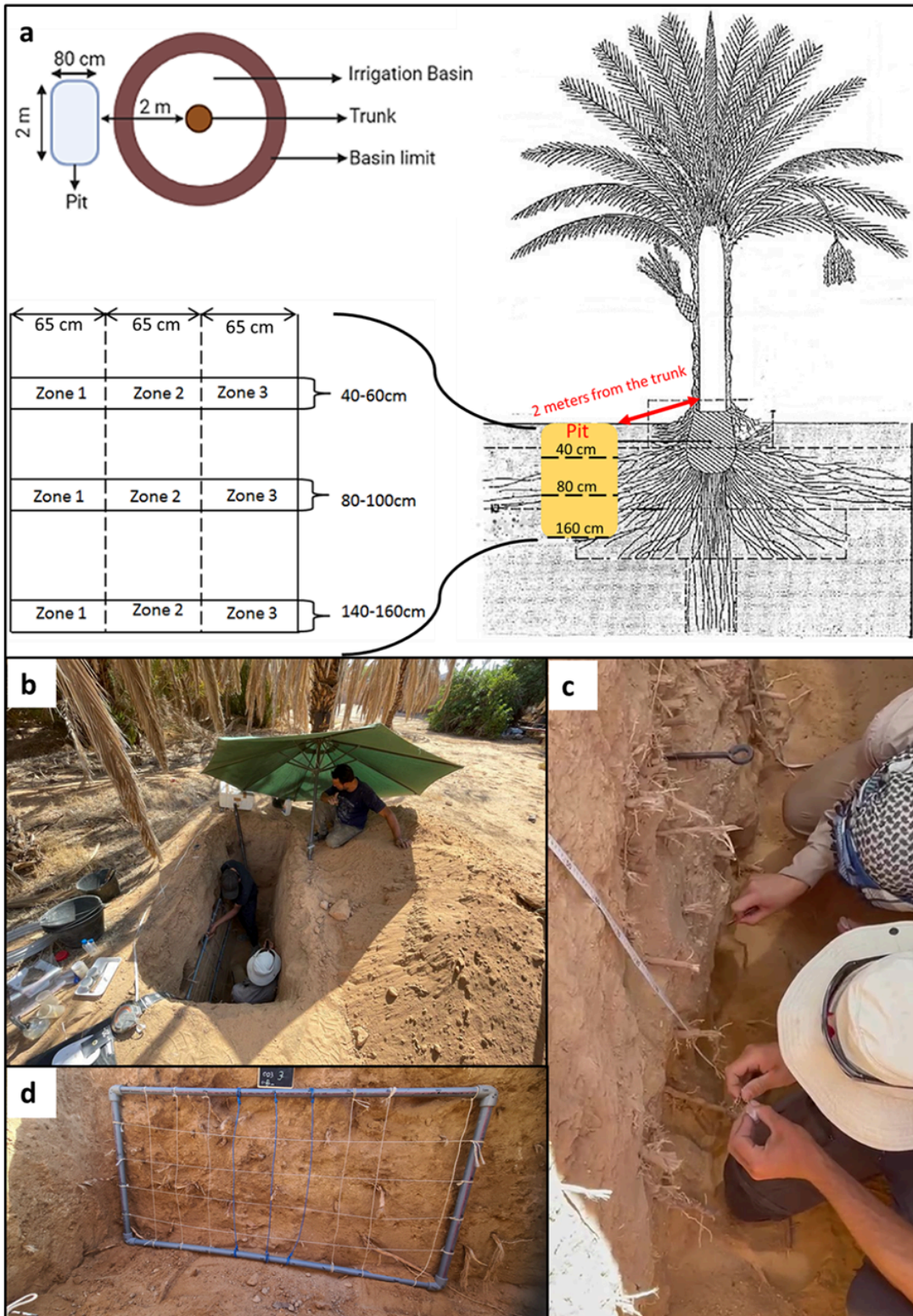


Figure 1

Illustration of the pit sampling process. **a.** Pit location relative to the sampled date palm and the pit sampling design. Adapted from (Munier 1973) **b.** Overview of a pit, the trunk of the sampled date palm is on the left in the photo. **c.** Root sampling in a pit. **d.** Use of quadrat to measure the root number and width.

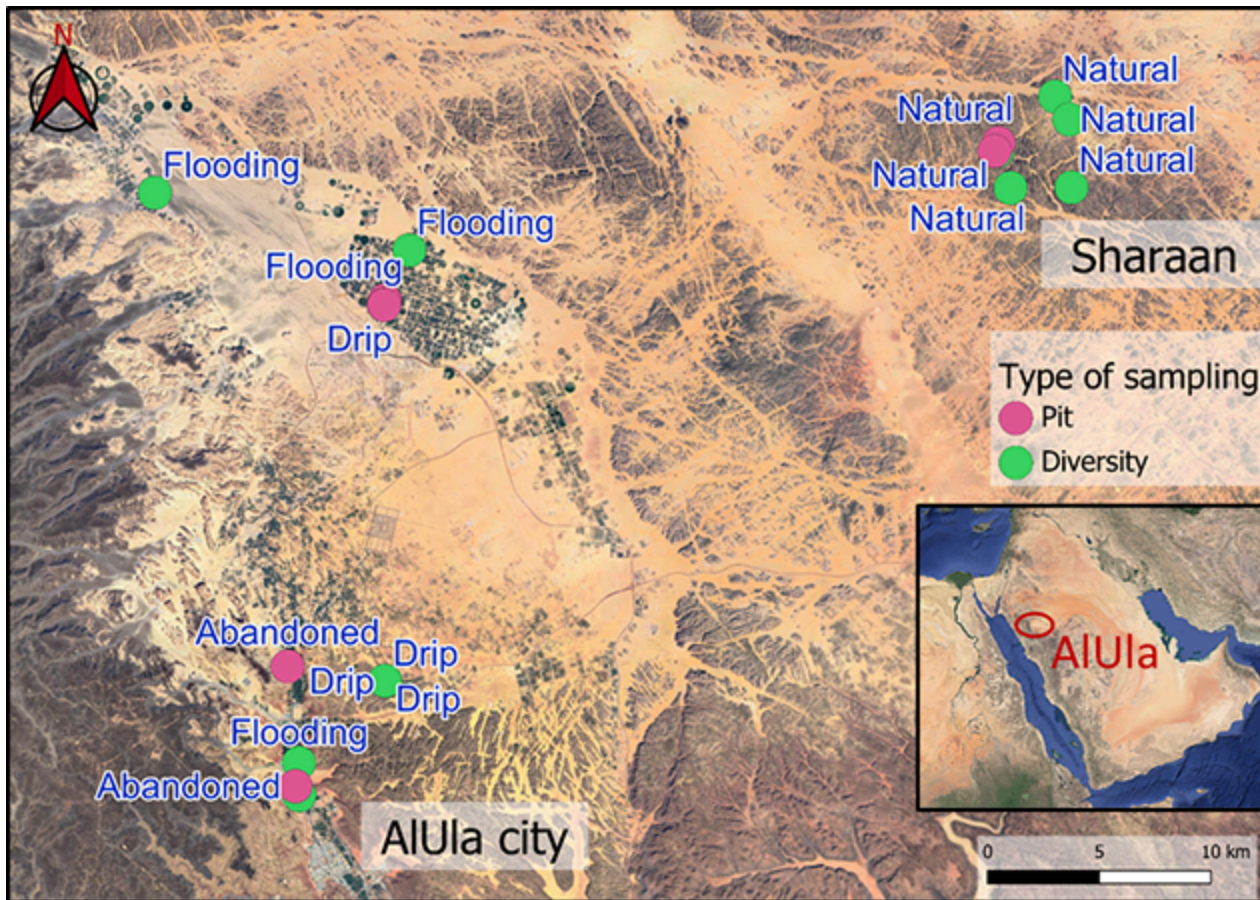


Figure 2

Locations of the date palm root sampling sites throughout AIUla region. The samples were collected by Pit sampling (180 cm deep) and Diversity sampling (40 cm deep). The date palms are classified according to the soil water systems: flooding irrigation, drip irrigation, abandoned farms and natural ecosystems.

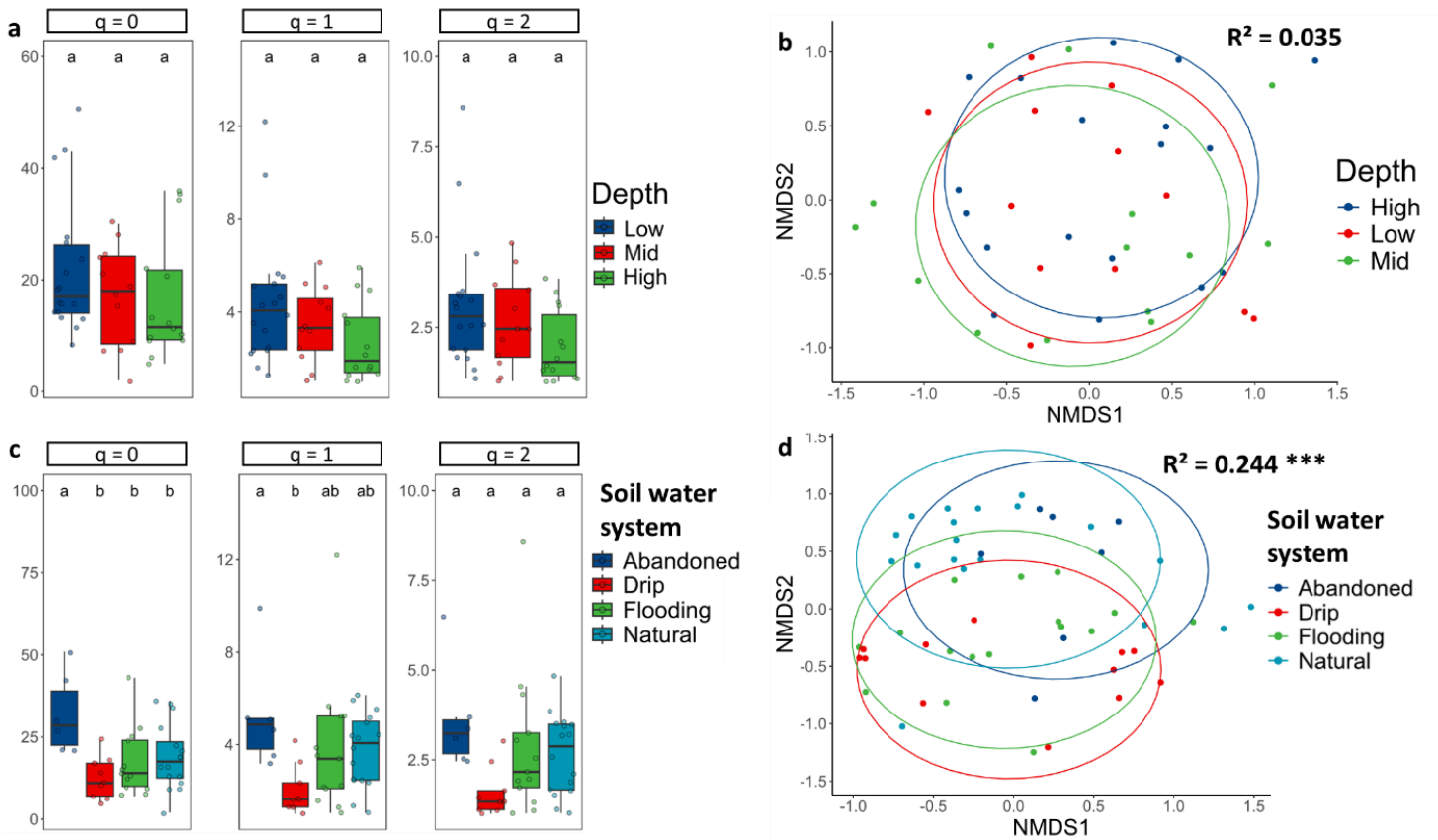


Figure 3

Alpha and beta diversity of date palm root fungal communities. The effects of sampling depth on fungal communities are presented in **panels a and b**. Only the pit sample dataset was used for this analysis: **a**. The alpha diversity measured using Hill numbers at three orders ($q = 0, 1,$ and 2) is represented with boxplots, and **b**. the distribution of fungal communities in relation to depth is visualized with an NMDS. The effects of the soil water systems on fungal communities are presented in **panels c and d**. This analysis included both diversity and pit datasets. **c**. The alpha diversity measured using Hill numbers at three orders ($q = 0, 1$ and 2), and **d**. corresponds to the distribution of fungal communities relative to soil water systems visualized with an NMDS. In each NMDS, the R^2 and associated p-value of the PERMANOVAs are shown.

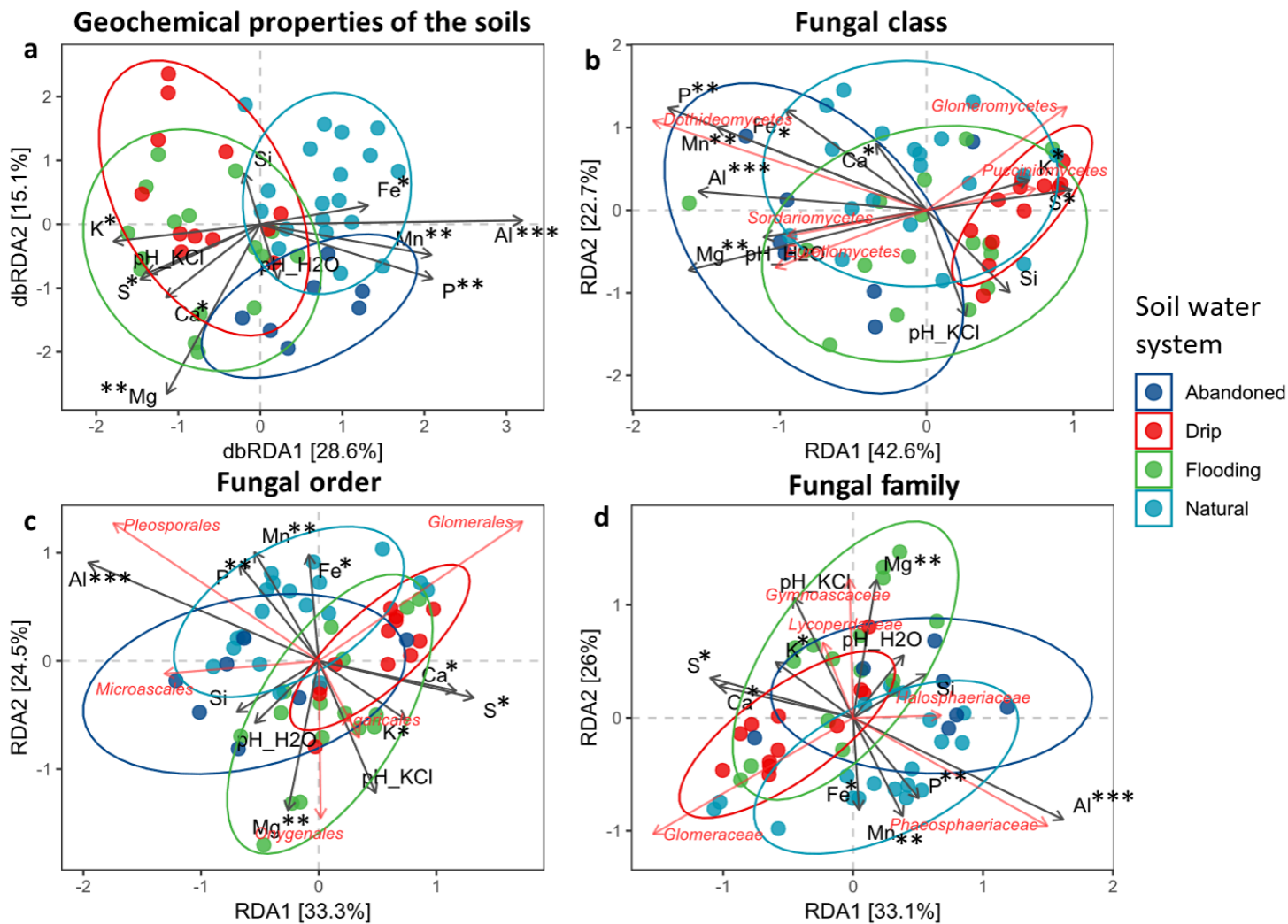


Figure 4

Distance-based redundancy analyses showing the contributions of soil parameters and major taxa to the Bray–Curtis dissimilarity matrix of 18S fungal communities hosted in date palm roots. The different soil water systems are shown with ellipses. The influence of each soil parameter was assessed by PERMANOVA while noting the respective p-values (p-value: * if < 0.05; ** if < 0.01; *** if < 0.001). **a:** soil geochemical properties in relation to the soil water systems assessed by dbRDA. **Panels b, c, and d:** contributions of soil parameters and of the five most abundant taxa at different taxonomic levels: **b.** fungal classes; **c.** fungal orders. **d.** fungal families.

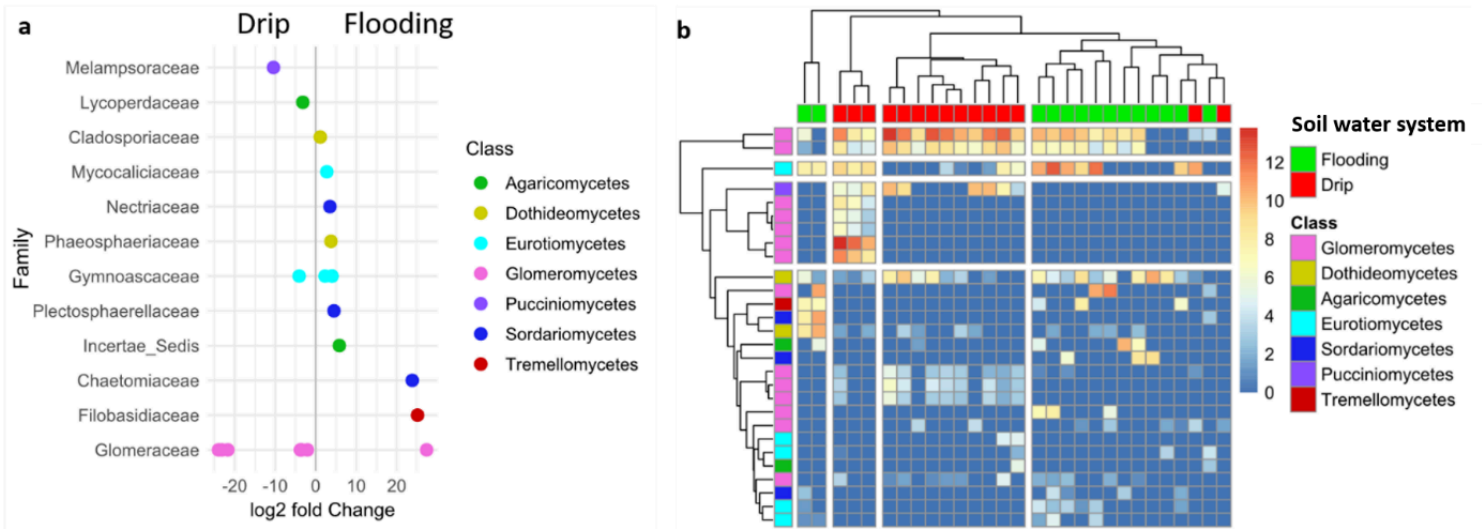


Figure 5

Differential abundance analysis of fungal communities sampled from pits of date palms growing under flooding or drip irrigation. **a**. Log2 fold changes of differentially abundant OTUs between the flooding irrigation (right) and drip irrigation (left) treatments. The families are presented in rows and colored according to the class. **b**. Clustered heatmap based on fungal communities in relation to soil water systems treatments (flooding or drip), where differentially abundant taxa are colored according to their class (color gradient based on the Log-fold changes).

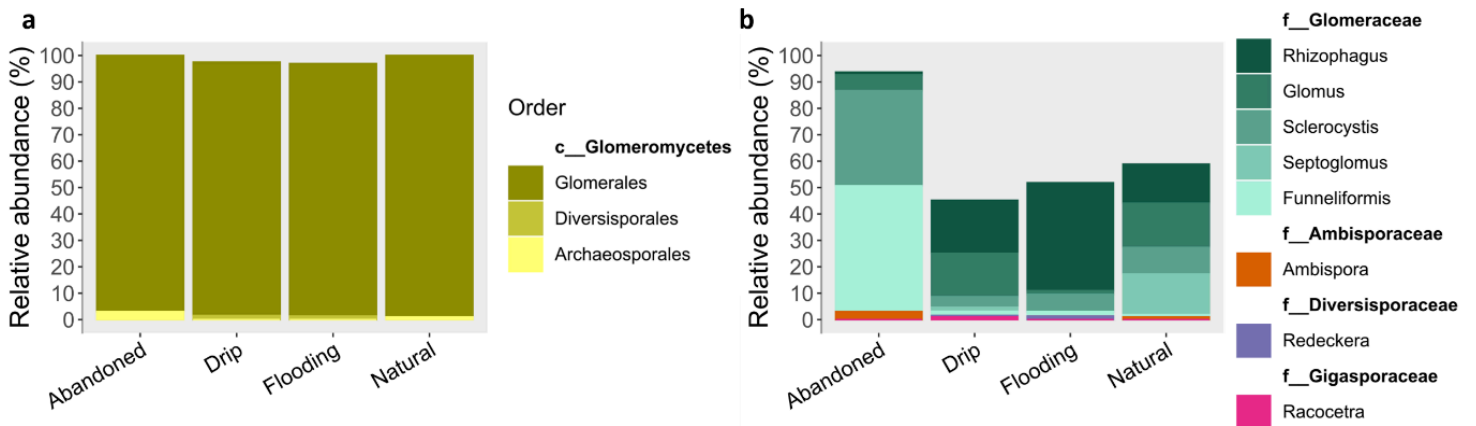


Figure 6

Relative abundance (in %) of Glomeromycetes taxa between soil water groups at different taxonomic ranks. **a**: Order taxa in the Glomeromycetes class. Glomeromycetes reads unassigned to the order taxonomic rank are not colored. **b**: Genera within the corresponding families are represented by colored gradients (in bold). The Glomeromycetes reads unassigned to the family taxonomic rank are not colored.

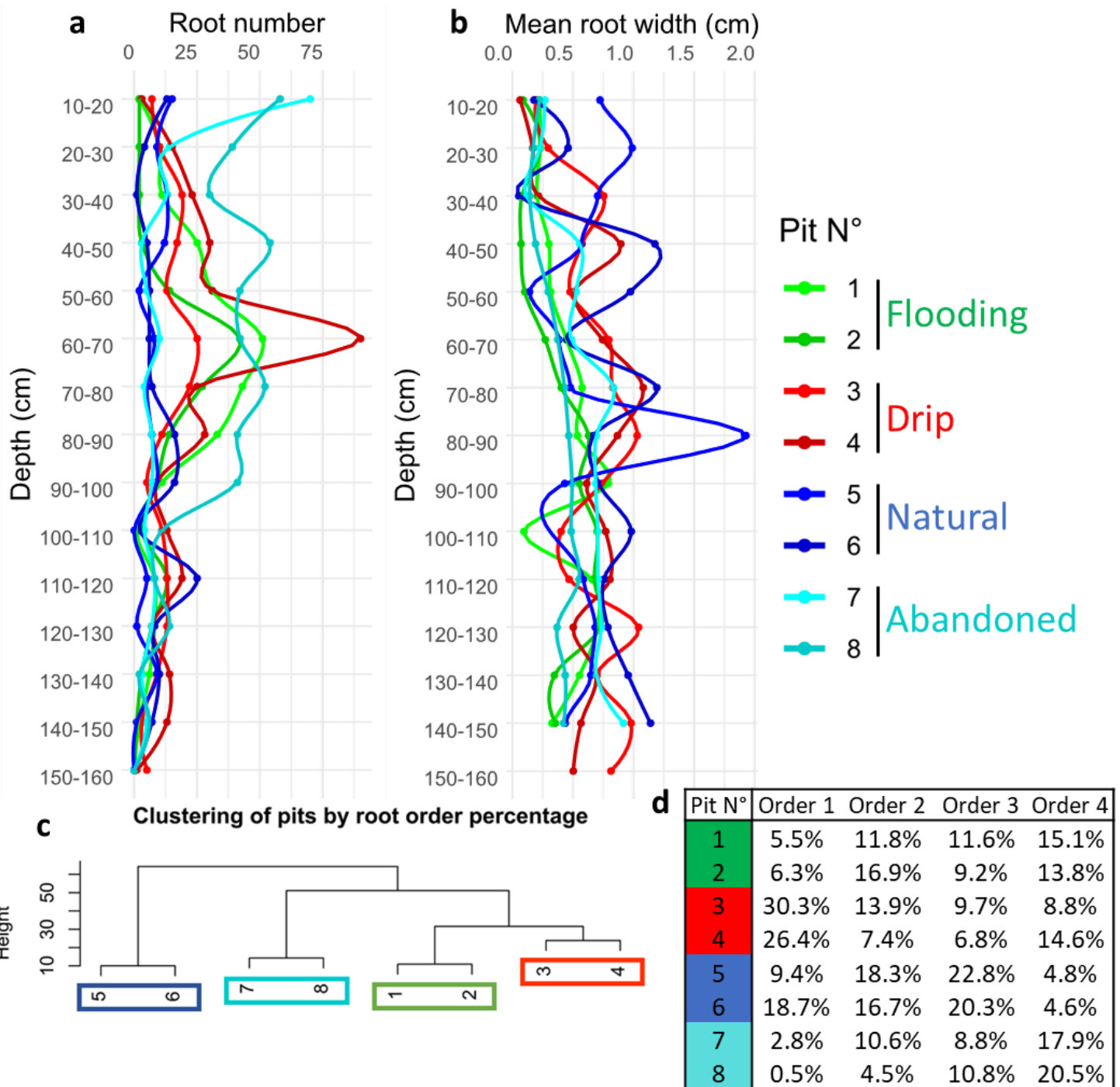


Figure 7

Root architecture analysis (root number, root width, and order) of date palms in relation to soil depth (10 cm layers, from 10 to 160 cm below ground level in 2 m horizons) and colored according to soil water systems (flood, drip, natural, and abandoned). **a**: Mean root number of date palms counted in each pit at each depth. **b**: Mean date palm root width. **c**: Clustering of pits according to the date palm root relative abundance order. **d**: details on the percentage of root orders per date palm.

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- [Supplementaryfigures.pptx](#)