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

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**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. Adapting current irrigation systems to be more 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 the different soil water systems 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 (40, 80 and 140 cm deep). 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.

**Keywords** Desert · Date palm · Water scarcity · Irrigation system · Metabarcoding · Arbuscular mycorrhizal fungi

## 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 due to 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 and efficient water 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

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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).

In such arid conditions, 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 to 60% of the total water requirements of this crop. Date palm cultivation can consume over 13,000 $m^3$ $ha^{-1}$ $year^{-1}$ of water (Al-Omran et al. 2019) which can represent the greatest source of water consumption at the scale of arid countries like Saudi Arabia, compared to other crops as well as municipal and industrial uses (Odnoletkova and Patzek 2023). Date palm cultivation, thus, represents a critical target for reducing the agricultural irrigation footprint (Shahin and Salem 2014).

Date palm cultivation can occur in a gradient of conditions depending on the exploitation, 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 and date palm evapotranspiration was considered low thereby implying that over-irrigation should not be needed (Ben Aissa et al. 2019). 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 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 flooding the basin surrounding the base of the date palm trees with water. In the past, the water was carried out via channels dug in the soil between the basins. Nowadays, it is 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 irrigated using drip irrigation consumed around 55 $m^3$ $ha^{-1}$ $year^{-1}$ while fields irrigated by flooding received around 137 $m^3$ $ha^{-1}$ $year^{-1}$ (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. Compared to flooding which involves flushing of salt and nutrients to the deeper soil layers, drip irrigation accumulates the water in the upper soil layer, which without regular flushing events, can lead to accumulation of salts because of the heat and evaporation, but also development of roots near the surface (Bourziza et al. 2017b; Alnaim et al. 2022).

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 and root architecture are still unknown. In this study, we aim to explore the impacts of different soil water conditions on the endophytic fungal communities of date palms at different sampling depths. Indeed, 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 the sustainability of agrosystems, the roles of such fungal communities along the soil-plant continuum have been studied in depth particularly regarding their ability to influence plant tolerance to stresses (Xiong and Lu 2022). Arbuscular mycorrhizal fungi (AMF) are a prime example of a well-studied taxon in agriculture. They 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).

Fungal communities are highly 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). Assessing how external factors (e.g. soil water systems) may drive relationships between microbial communities, soil and plants provide valuable insights for improving the sustainability of agricultural practices and soil management.

In one of the few studies assessing the effects of drip versus flood irrigation on fungal communities, Deng et al. (2022) observed an overall reduction in fungal diversity under drip irrigation. Specifically, they reported a decrease in the abundance of arbuscular mycorrhizal and ectomycorrhizal fungi and an increase in pathogenic fungi in the alfalfa rhizosphere in an arid region of China. These communities were also affected by the soil depth as changes were observed 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 main difference was that the fungal compositions generally differed between the topsoil (first 25 cm) and the other 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. 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 decreased with soil depth in different environments. Most current knowledge on soil microbial communities derives from studies on surface soils, and hence deep soil microbial communities are poorly understood (He et al. 2023b).

To overcome the knowledge gap regarding the effects of sampling depths and soil water systems on fungal communities in date palm roots, we assessed their diversity and composition at different sites in the desert region of AlUla (al-ʿUlā: العلا), 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 (i) diversity would decrease and the composition of microbial communities would differ between drip and flood irrigation, as described by Deng et al. (2022). Additionally, (ii) diversity would be lower in non-irrigated conditions (abandoned farms and natural settings) due to drought, with significant differences in composition between irrigated and non-irrigated conditions. As the soils in this region have only one soil horizon over tens of centimeters or even meters deep, we hypothesize (iii) that fungal communities would remain stable at all of the studied soil depths.

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). We hypothesize that iv) AMF proportion would decrease under drip irrigation conditions compared to flooding irrigation as observed by Deng et al. (2022) on alfalfa crops.

The microbial communities in plant roots are closely linked to the root architecture (Saleem et al. 2018). In desert 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, and accumulate fine roots that host various microorganisms. This microbiome can increase 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).

However, the root architecture of full-grown date palms is 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 (Daddi Bouhoun 2010; 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). Moreover, these studies were focused on agrosystems or on irrigated farming conditions, so we lack information over root architecture of uncultivated and non-irrigated date palms and at depths over 100 cm. The present study, then provides new elements and knowledge on the rooting architecture of date palms in uncultivated conditions and at higher depths. We hypothesized that the soil water systems could affect the root development: date palms watered with flooding and drip irrigation would not vary markedly with regard to their root parameters as they are both irrigated although (v) drip irrigated date palms would have an increased number of roots near the surface which is a common trait associated with drip irrigation. Date palms growing on abandoned farms (vi) would have a higher root width in these conditions as they are older than in the irrigated conditions. Finally, we hypothesized (vii) 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 deeper layers than in those from which we collected our samples.

## 2 Materials and methods

### 2.1 Study area

Our study was conducted in the hot arid desertic region of AlUla (al-ʻUlā 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$^{-1}$) (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

In total, we collected and sampled the roots of 21 date palm trees across the target region under different soil water systems: (i) flood irrigation, (ii) drip irrigation, (iii) natural ecosystems, and (iv) abandoned farms. 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. 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.

#### 2.2.1 Pit sampling

Date palms were sampled at different depths to compare sampling depths. This samples were called the “pit samples”. In October 2021, two pits were dug per water system, totaling eight pits. Each pit measured 200 cm in length, 80 cm in width, and 160 cm in depth, located 2 m from the trunk and outside the irrigation basin where applicable (Fig. 1a and b). Roots were collected from three soil horizons—40–60 cm (shallow), 80–100 cm (medium), and 140–160 cm (deep)—to assess fungal diversity, avoiding the top-soil and aiming different root functional areas as described by Zaid and De Wet (2002). (Figure 1a and c). 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 two pits (N°7 and N°8) were located on two old, abandoned farms. According to local farmers, irrigation on these farms ceased 7 years ago for one and several decades ago for the other, prior to the sampling.

#### 2.2.2 Diversity sampling

Thirteen additional samples were collected in October 2021 and March 2022 around AlUla, 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. 1e.

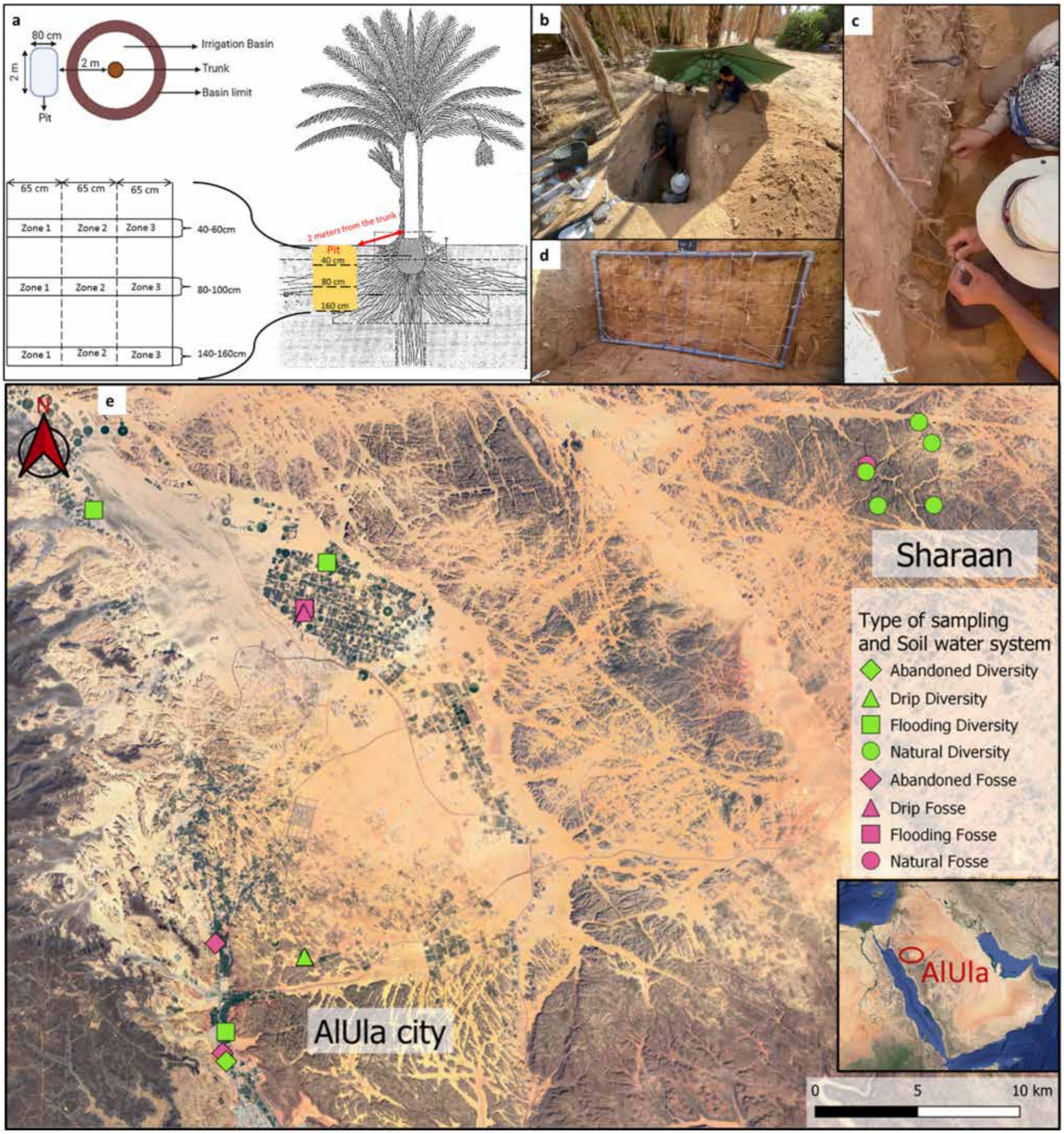


**Fig. 1** Illustration of the pit sampling process. **a.** Pit location relative to the sampled date palm and the pit sampling design. Adapted from (Munier 1973) **b.** Overview of a pit, the trunk of the sampled date palm is on the left in the photo. **c.** Root sampling in a pit. **d.** Use of quadrat to measure the root number and width. **e.** Locations of the date palm root sampling sites throughout AlUla region. The samples were collected by Pit sampling (160 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

## 2.3 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 in liquid nitrogen and ground. DNA was extracted with the FastDNA Spin Kit for Soil (MP Biomedicals, Solon, USA). The 18 S rRNA region, which provides better resolution for AMF taxa detection, was amplified with AMADf (5′ GGGAGGTAGTGACAAT AAATAAC 3′) and AMADGr (5′ CCCAACTATCCCTATT AATCAT 3′) primers (Berruti et al. 2017). All PCR products were sent to Fasteris SA (Switzerland) for sequencing using an Illumina MiSeq (2 × 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).

## 2.4 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 1.53 K 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.

## 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.

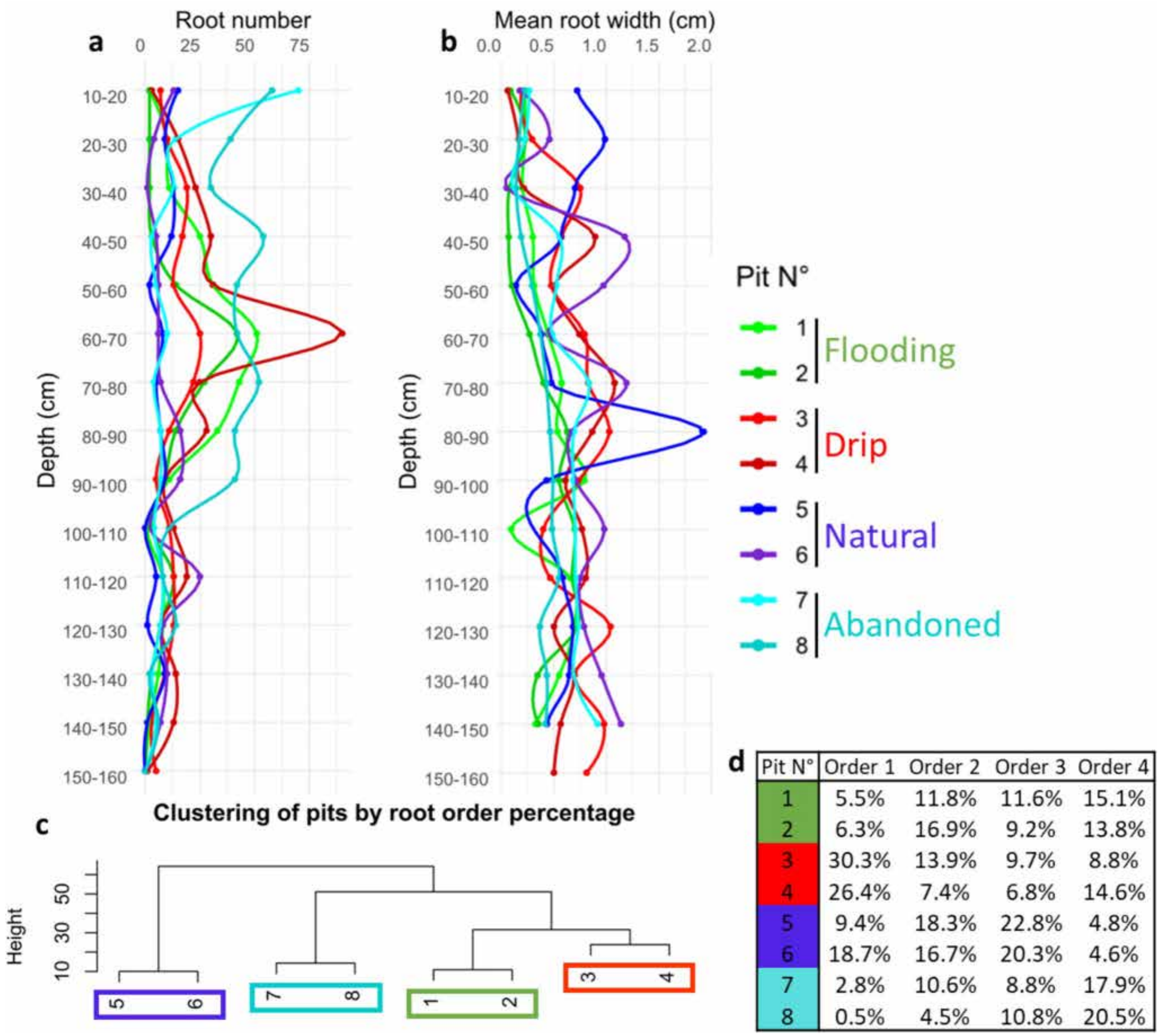
Differential abundance analyses (DAA) were carried out on the pit sample results from the flooding irrigation and drip irrigation systems to investigate the impact of soil water systems on taxon abundances in the irrigation systems. DAA were performed with the DESeq function of the *DESeq2* package v.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

## 3 Results

### 3.1 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 d), and the results are presented in Fig. 2. The date palm root numbers were heterogenous (Fig. 2a) 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



| Pit N° | Order 1 | Order 2 | Order 3 | Order 4 |
|---|---|---|---|---|
| 1 | 5.5% | 11.8% | 11.6% | 15.1% |
| 2 | 6.3% | 16.9% | 9.2% | 13.8% |
| 3 | 30.3% | 13.9% | 9.7% | 8.8% |
| 4 | 26.4% | 7.4% | 6.8% | 14.6% |
| 5 | 9.4% | 18.3% | 22.8% | 4.8% |
| 6 | 18.7% | 16.7% | 20.3% | 4.6% |
| 7 | 2.8% | 10.6% | 8.8% | 17.9% |
| 8 | 0.5% | 4.5% | 10.8% | 20.5% |

**Fig. 2** 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

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. 2b) 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. 2b). The hierarchical clustering and distribution of date palms root orders (based on diameter) revealed a clustering related to the soil water systems (Fig. 2c and d). 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. 2c and d). 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. 2d).

## 3.2 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. The ANOVA and Tukey test revealed no significant differences in alpha diversity between root depths at any q value (Fig. S1a). 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 shallow/medium, shallow/deep and medium/deep depths respectively) (Fig. S1b).

## 3.3 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.

## 3.4 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). Differential abundance analyses (DAA) were conducted to identify taxa that were

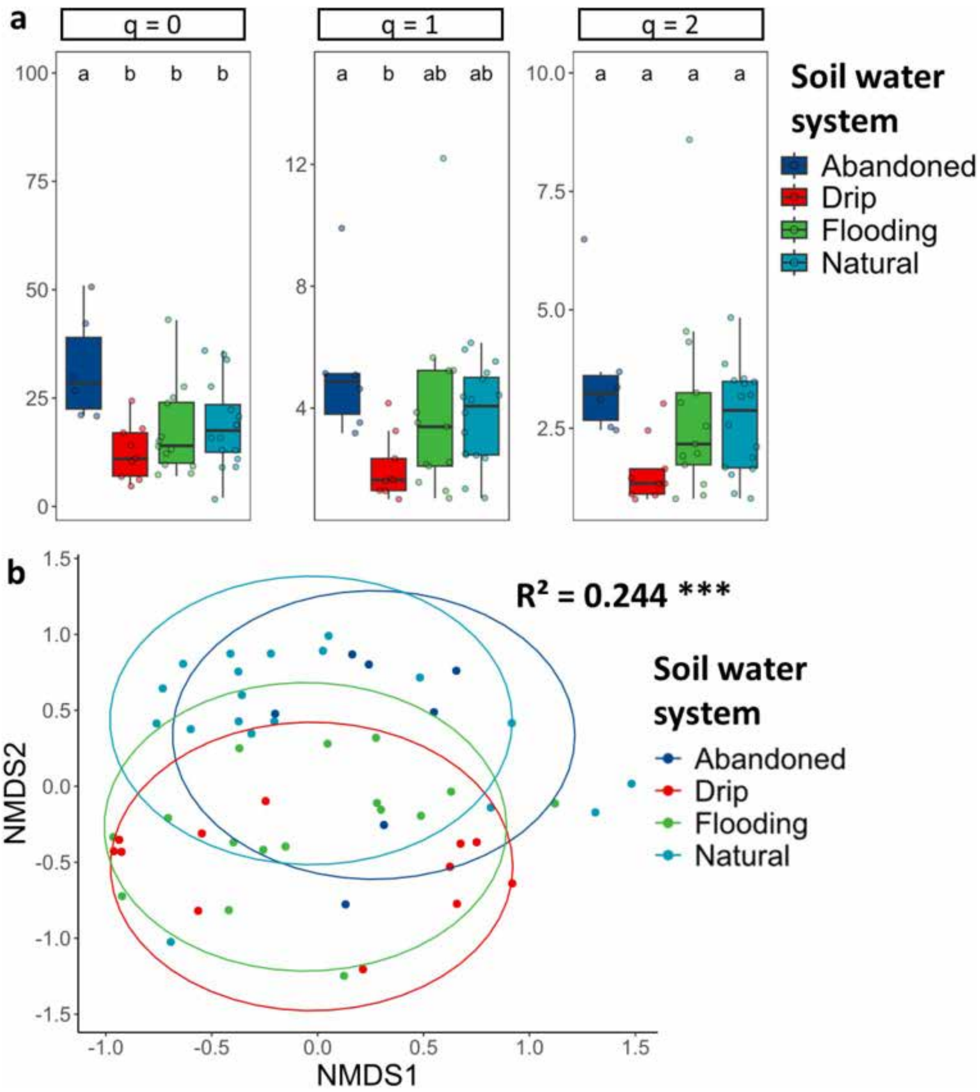


**Fig. 3** Alpha and beta diversity of date palm root fungal communities according to the different soil water systems. This analysis included both diversity and pit datasets. **(a)** The alpha diversity measured using Hill numbers at three orders (q = 0, 1 and 2). The q-value represent the importance given to the abundant species, the higher the q-value, the higher this importance. **(b)** corresponds to the distribution of fungal communities relative to soil water systems visualized with an NMDS. In the NMDS, the $R^2$ and associated p-value of the PERMANOVA are shown. *** means that the p-value is < 0,001

differentially abundant between the two irrigation conditions (Fig. 4). For drip irrigation, the most significantly abundant taxa included several OTUs of Glomeraceae, one Melampsoraceae, one Lycoperdaceae and one Gymnoascaceae (Fig. 4a). Regarding the flooding conditions, DAA highlighted three OTUs of Eurotiomycetes (two Gymnoascaceae and one Mycocaliciaceae families), two Dothideomycetes from Cladosporiaceae and Phaeosphaeriaceae families, one Sordariomycetes (Chaetomiaceae), one Agaricomycetes, one Glomeraceae and one Tremellomycetes (Filobasidiaceae).

### 3.5 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. S2). 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. 5). The proportion of unassigned AMF families differed between

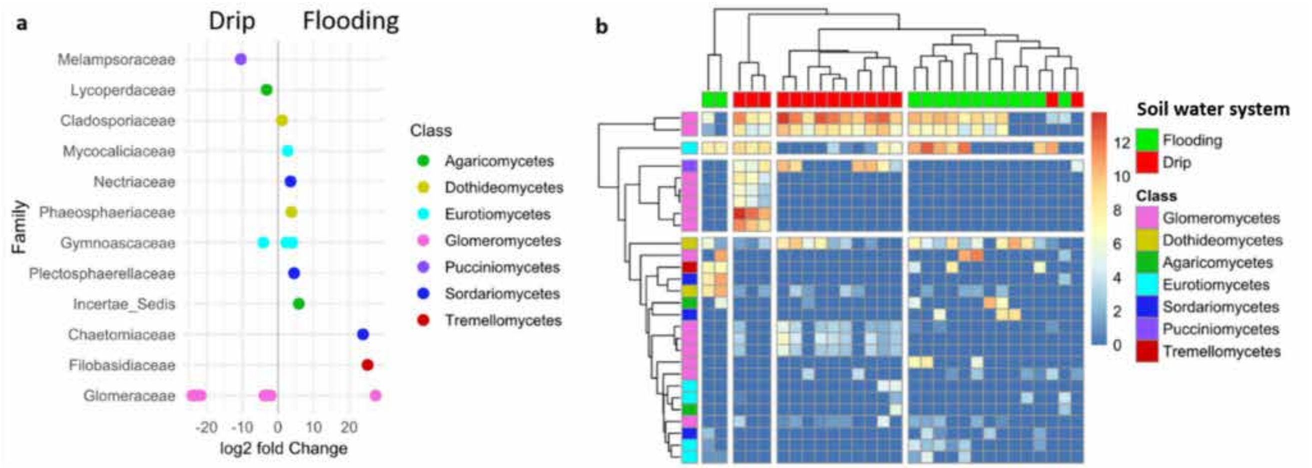


**Fig. 4** Differential abundance analysis of fungal communities sampled from pits of date palms growing under flooding or drip irrigation. **(a)** Log2 fold changes of differentially abundant OTUs between the flooding irrigation (right) and drip irrigation (left) treatments. The families are presented 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)

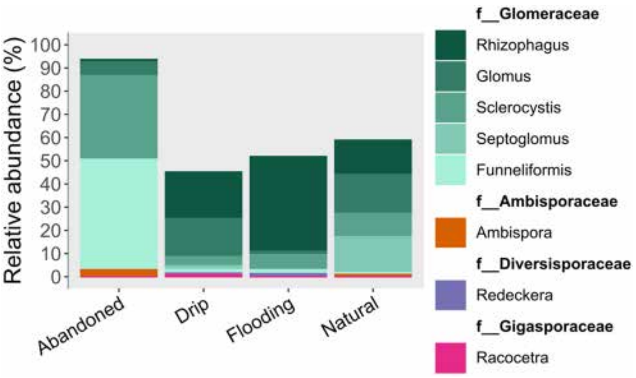


**Fig. 5** Relative abundance (in %) of Glomeromycetes taxa between soil water systems at Genera rank within the corresponding families are represented by colored gradients (in bold). The Glomeromycetes reads unassigned to the family taxonomic rank are not colored

soil water systems: 54.8% for drip; 48.2% for flooding, 41.1% for natural; 6.3% for abandoned (Fig. 5).

## 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 the flooded and drip irrigated date palms. This finding contradicted Bourziza et al. (2017b) and our hypothesis, which suggested that date palms under surface drip irrigation would develop more roots near the surface, making them 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, since individual N°8 was taller, thus older, 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 older date palm tree would have an increased number of respiratory roots (close to the surface) than younger trees, which could be an explanation for our increased number of roots near the surface on abandoned date palms, which were older than those of the flooding and drip irrigation samples. However, contrary to our hypothesis that abandoned date palms would have thicker roots, no major differences with other conditions were observed.

Date palms are also 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. Thus, the root architecture of date palms in farms likely differs from that of trees growing in natural conditions. In our study, the root architecture of uncultivated date palms 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, in accordance with our hypothesis, but with almost no roots observed in the 150–160 cm layer. These results strongly suggest that agriculture, and probably the presence of irrigation, significantly modifies plant root systems compared to natural ecosystems.

Comprehensive descriptions of the root architecture of large plants at great depths remains scarce. 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 affect date palm 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 access water and nutrients that are not available at 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. We can for example assume that observing the profile closer to the trunk would lead us to observe thicker and more numerous roots. We can also hypothesize that in irrigated conditions, the soil closer to the trunk would have an increased moisture which can lead to an increased number of roots; this point in particular might be different in non-irrigated conditions.

Date palm root architecture, then, is an important feature affecting the plant's nutrition and stress tolerance (Xiao et al. 2019; Cordeiro et al. 2020). But this nutrition is also highly affected by the microorganism and importantly by the fungal communities associated with the roots (Meddich et al. 2015; Abumaali et al. 2023).

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

Considering the importance of fungal communities on ecosystems functioning and agrosystems health and productivity, it is essential to better understand these communities especially on poorly studied environments such as arid lands (Neilson et al. 2017; Wagg et al. 2019).

The fungal communities described in date palm roots in this study were composed of fungi detected within the roots (endophytes) and on their surface (rhizoplane), although the latter communities have been reduced as the roots were rinsed before analysis. The lack of differences in fungal diversity and community composition between 40 and 160 cm supports our hypothesis, as the soil pits showed no clear stratification, and the topsoil was excluded from our analyses.

We began our sampling at 40 cm depth (much below the topsoil layer), thereby 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.

Plant roots select their associated microbial communities from the soil (Dang et al. 2021). Fungal endophyte communities may originate from (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). These communities, therefore, are not only selected by the edaphic conditions in the soil but also by the root exudates (as in the rhizosphere) and the root immune system and rhizodermis which are other filters for fungal communities and some of these could originate from the seed, and thus from the parent. We still lack information about deep soil microbiome of rhizosphere soils, further research on the rhizosphere compartment in these arid conditions could be necessary to understand the specificity of the root compartment compared to the rhizosphere compartment across depths and thus understand the role of rhizosphere's community on root communities across depths.

In our study, the deepest samples were collected from the 160 cm soil layer. Although the soils were found to be mostly homogeneous along a vertical gradient, interesting features might 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 a 2 m depth and that 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. In our sampled depths, however, no clear differences in geochemical parameters were observed between the three depths, though major geological strata may appear in deeper layers and impact more significantly the fungal communities (Supp analysis).

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

The drop in fungal diversity observed in drip irrigation conditions compared to flooding conditions was also noted by Deng et al. (2022) in the rhizosphere soils of alfalfa crops in arid regions.

Since 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. However, 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 fields, indicating that changes in irrigation systems can trigger long-term changes in the fungal communities. This implies that this disturbance effect could also be more lasting. On one hand, Deng et al. (2022) analyzed that increased diversity was linked to more stable soil ecosystem and increased plant resistance to pathogens, suggesting that the reduced diversity in drip irrigated alfalfa may be linked to lower resistance to pathogens. Following this argument, the reduced diversity could thus imply deleterious effects for the ecosystem and the date palm. On the other hand, in some systems with stresses or disturbances, bacterial and fungal diversity can increase in response to these disturbances as a response to a diversification in ecological niches due to the perturbation (Karimi et al. 2017; Labouyrie et al. 2023; Maurice et al. 2024). Systems other than drip irrigation can be seen as systems with disturbances and stress (e.g. flooding events, drought), thus increasing microbial diversity while under drip irrigation, the system can be seen as more stable over time (long period of irrigation with less amount of water).

We observed a difference in community composition between the two irrigated conditions: flooding and drip which aligned with our hypothesis. 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, most 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. Drip irrigation reduces drainage, thus leading to more stable soil moisture conditions for the plants and microbial communities. Date palm roots and associated fungal communities growing in flooding conditions, however, go through frequent wetting and drying events (Bourziza et al. 2017b; Alnaim et al. 2022). These differences in the access to water may then select fungal communities in the soil and in the roots.

Specifically, regarding the non-irrigated conditions, 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.

The fungal community composition significantly differed among all soil water systems that we studied. Major differences were observed between non-irrigated and irrigated date palms according to our hypothesis ii), but contrary to this hypothesis there was no drop in diversity compared to irrigated conditions. These differences in composition were reported by Abumaali et al. (2023) comparing “wild” date palms and cultivated ones. Unsurprisingly, the presence or absence of a regular input of water in such dry environment can affect the microbial composition in the soil, for example it might select taxa that are tolerant to drought. However, the roots can be seen as a peculiar environment that could serve as a shelter for fungal communities making them less susceptible to the hydro-edaphic conditions of the soil (Müller et al. 2017). But roots are also affected by drought, thus impacting the fungal communities inside the root. Moreover, these communities often undergo horizontal transmission from the soil, meaning that they complete at least part of their life cycle under the adverse conditions of non-irrigated soils (Laurent-Webb et al. 2023).

### 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 across 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 across 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 accross 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 under flooding irrigation conditions might be more susceptible to infection by new pathogens. Drip irrigation has been described to improve the growth and health of date palms (Carr 2012), this irrigation system may also improve the tolerance to diseases because ecological niches for pathogens are already occupied. Moreover, AMF colonization improves the tolerance of the plant to biotic stresses and Glomeraceae were found more present in drip irrigated date palms in this study. Drip irrigation may then participate in improving date palm cultivation by rendering it less susceptible to diseases. 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 spreading eastward from North Africa and may become a concern in Saudi Arabia in the future if phytosanitary measures are not enforced.

Finally, the main symbiotroph fungi identified were almost all 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 study. 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). As AMF are considered to improve nutrition, including water nutrition, of plants, an increase in AMF proportion could induce an improved water uptake for the date palm, thus, less loss of water through evaporation or percolation. Indeed, several studies have investigated the role of AMF symbiosis with crops to improve their tolerance to drought, salinity and pathogens (Al-Karaki 2013; Meddich et al. 2015; Anli et al. 2020). However, the detection of AMF sequences inside the root cannot be taken as a proof of AMF colonization of the root, nor as a proof of efficient symbiotic interaction. Thus, AMF proportion cannot be directly linked to improved benefits for the plant.

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. This suggests that the date palms might have selected AMF taxa in the roots or in the rhizosphere when the irrigation system was installed, thereby preserving AMF from the overall decrease in diversity. These results contrast with our hypothesis and the findings 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 plant and fungal partners and by the environmental conditions, e.g. nutrient or water availability (Werner and Kiers 2015).

Endophytic fungi in general can have both positive and negative impacts on the plants in arid lands. Negative impacts involve endophytes turning pathogenic, causing decreased growth, increased mortality. Positive impacts are linked to increase nutrient uptake, improved tolerance to abiotic stresses: salinity, drought, heat but also biotic stresses through the production of specialized metabolites or even increasing the plant competition with nearby vegetation for resources (Morales-Vargas et al. 2024).

### 4.4 Prospects for drip irrigation as an alternative to flooding

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 to suggest that replacing flood irrigation with drip irrigation would be harmful to date palms. On the contrary, we found that it could even improve the symbiotic fungal community by increasing the proportion of AMF even though the link between increased proportion of symbionts and increased benefits to the plant should be thoroughly checked. 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.

Drip irrigation performance may be improved when it is placed belowground as the moisture area is further from the surface, reducing even more the chances for evaporation, thus reducing water losses (Al-Amoud 2010; Talat Farid Ahmed 2012; Bourziza et al. 2017a; b). This system can 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 well suited in terms of water use efficiency for extensive farms and date palm monoculture conditions (Alazba 2004; Elfeky and Elfaki 2019), 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). If Saudian, and overall, date palm agriculture wants to transition to reduce losses of water and reduce water consumption, it is important to take into account the water use efficiency and find a balance 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 diversity and communities. These results thus demonstrate that the irrigation system has an influence on the fungal root communities which can have an influence on the plant health, growth, yields and on water nutrition.

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.

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**Author 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. Ducousso: Project administration, Funding acquisition, Review & Editing, Supervision. M. Gros-Balthazard: Data supply, Funding acquisition, Review & Editing, Supervision.

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## Declarations

**Competing interests** The authors declare no competing interests.

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