Original article

Desert soil fungi isolated from Saudi Arabia: cultivable fungal community and biochemical production

Fuad Ameen [a],[*], Saleh AlNAdhari [b], Mohamed A. Yassin [c], Ahmed Al-Sabri [a], Abobakr Almansob [a], Norah Alqahtani [d], Steven L. Stephenson [e]

[a] Department of Botany and Microbiology, College of Science, King Saud University, Riyadh 11451, Saudi Arabia
[b] Deanship of Scientific Research, King Saud University, Riyadh 11451, Saudi Arabia
[c] Agricultural Research Center, Plant Pathology Research Institute, Giza, Egypt
[d] Department of Biology, College of Science, Qassim University, Saudi Arabia
[e] Department of Biological Sciences, University of Arkansas, Fayetteville, AR 72701, USA

ABSTRACT

Desert soils harbor fungi that have survived under highly stressed conditions of high temperature and little available moisture. This study was designed to survey the communities of cultivable fungi in the desert soils of the Arabian Peninsula and to screen the fungi for the potentially valuable antioxidants (flavonoids, phenols, saponins, steroids, tannins, terpenoids, and alkaloids) and enzymes (cellulase, laccase, lipase, protease, amylase, and chitinase). Desert soil was sampled at 30 localities representing different areas of Saudi Arabia and studied for physico-chemical soil properties. Five types of soil texture (sand, loamy sand, sandy loam, silty loam, and sandy clay loam) were observed. A total of 25 saprotrophic species was identified molecularly from 68 isolates. Our survey revealed 13 culturable fungal species that have not been reported previously from Arabian desert soils and six more species not reported from Saudi Arabian desert soils. The most commonly recorded genera were *Aspergillus* (isolated from 20 localities) and *Penicillium* (6 localities). The measurements of biochemicals revealed that antioxidants were produced by 49 and enzymes by 52 isolates; only six isolates did not produce any biochemicals. The highest biochemical activity was observed for the isolates *Fusarium brachygibbosum* and *A. phoenicis*. Other active isolates were *A. proliferans* and *P. chrysogenum*. The same species, for instance, *A. niger* had isolates of both high and low biochemical activities. Principal component analysis gave a tentative indication of a relationship between the biochemical activity of fungi isolated from soil and soil texture variables namely the content of silt, clay and sand. However, any generalizable relation between soil properties and fungal biochemical activities cannot be suggested. Each fungal isolate is probable to produce several antioxidants and enzymes, as shown by the correlation within the compound groups. Desert soil warrants further research as a promising source of biochemicals.

1. Introduction

The Arabian Desert is one of the most important deserts in the world, covering a total area of 2,300,000 km^2 and making up a large part of the kingdom of Saudi Arabia (Owen et al., 2020). Desert soil is known to be rich in microorganisms that can tolerate the extreme conditions of high temperature and little available moisture. Desert fungi have protective morphological features, such as melanin in fungal cell walls, thick-walled spores, and hyphae that may cross air-filled soil pores to access nutrients and water (Barnard et al., 2013). One evolutionary adaption mechanism to survive in drought is to synthesize different metabolites (Schimel et al., 2007). Fungal metabolites such as enzymes and antimicrobial compounds have been searched widely from different environments (Keswani et al., 2019). Soil fungi are known to produce enzymes and antioxidants such as phenols and flavonoids (Arora and Chandra, 2011; Chandra et al., 2020; Hameed et al., 2017) and could be used in biotechnological applications.

Desert soil fungi have scarcely been studied as a source of novel bioactive compounds. Antimicrobial activities of desert soil fungi have been studied to some extent. Species of *Penicillium*, *Aspergillus, Mucor, Phoma, Alternaria,* and *Fusarium* recovered from desert soils have been found to display antimicrobial activities (Al-Enazi

* Corresponding author.
E-mail address: fuadameen@ksu.edu.sa (F. Ameen).

et al., 2018; El Hamd et al., 2014). Novel bioactive compounds such as cytotoxic compounds have been found from Atacama desert, China, and Egyptian desert soils (Gonçalves et al., 2016; Guo et al., 2019; Magdy et al., 2017). Arabian desert plants have been reported for novel bioactive compounds (Ameen et al., 2021a, 2021c), but Arabian desert soil has received little attention as a source of bioactive compounds.

Arabian desert soils are inhabited by a diverse fungal community, as reviewed recently by Ameen et al. (2021b). They found a total of 233 identified taxa of fungi (either at the genus, species, or higher level) in the published literature dealing with the Arabian desert soils. The review reports a total of 172 different observations that are taxonomically different identifications. In Saudi Arabia alone, 161 different identifications were reported. A minority (13) of these identifications originated from the extraction of environmental samples (metagenomic data), while the majority of the identifications (148) were cultivable fungi. A total of 119 different identifications at the species level were reported from Saudi Arabia. The genera reported most often were *Aspergillus, Alternaria, Chaetomium, Cladosporium, Fusarium, Glomus,* and *Penicillium*, all commonly found in soils. The studies reviewed by Ameen et al. (2021b), report observations from more or less randomly chosen single areas, and thus, a comprehensive survey of the Arabian desert soils is still lacking. As such, the current study was designed to isolate soil fungi from 30 localities representing different deserts in north, south, east, west, and in central Saudi Arabia. The aim was to get an overview of cultivable fungal communities in the Arabian desert soils. The second aim was to find fungal species that might be biotechnologically valuable secreting metabolites to be used in different applications. It has been established that the biochemical compounds vary with geographical location. This has prompted an effort by researchers to investigate the entire globe for finding novel compounds from different organisms and environments. The current study was directed towards the extreme environment in the deserts of Saudi Arabia, where it was anticipated that the fungi present would yield valuable and novel metabolites.

2. Materials and methods

2.1. Sample collection sites and sampling

The soil samples were collected at 30 desert localities situating in different parts of Saudi Arabia during winter 2020. The sampling areas were: Tabuk area in north-west (N) belonging to Al Nufud Al Kabir desert, around Jubail in north-east (E) belonging to Ad-Dahna Desert, Najran and Shararah in south-west (S) belonging to Ar Rub' al Khali desert, around Medina and Makkah in west (W) belonging to Ar Rub' al Khali desert, and in central (C) part around Riyadh belonging to Al Nufud Al Kabir (Fig. 1). Annual precipitation in the regions is as follows. In N (50 mm), in E (20 mm), in S (79 mm), in W (130 mm) and in C (66 mm). Annual maximal and minimal temperatures are in N (39°C and 5°C), in E (45°C and 10°C), in S (38°C and 15°C), in W (40°C and 20°C) and in C (44°C and 11°C) respectively. Sparse vegetation consisted of xerophytes in N, small herbs and shrubs in E, S, and C, and small grasses in W.

Three samples of desert soil were collected from each area. After removing the possible thin layer of debris, the samples (ca 100 g) were taken (0 – 15 cm depth) aseptically and transported to the laboratory.

2.2. Analysis of soil characteristics

Soil: water suspension at a ratio of 1:2.5 was prepared to measure the following properties: soil texture using a hydrometer (Sera Marin Hydrometer), $CaCO_3$ using a calcimeter (Eijkelkamp

Instrumentation), pH using GF Signet meter; electric conductivity (EC) using Metter Toledo meter, Na and K using a flame photometer (BWB-XP), and Ca, Mg, Cl, and HCO_3 using titration methods (Estefan, 2013).

2.3. Isolation of fungi and pure culture preparation

The soil samples were serially diluted (10^4 and 10^5), and 1 mL was spread onto the plates of potato dextrose agar (PDA) with antibiotic chloramphenicol 200 µg/L. Plates were incubated at 25°C for seven days. Individual colonies (isolates) were selected based on their morphological characteristics. The selected isolates were subcultured on PDA plates for further studies.

Fungal isolates were preserved for long-term studies as described by Gupta et al. (2020). The fungal mycelia were transferred to sterile Eppendorf tubes containing 1 mL, 30% (v/v) sterile glycerol and incubated at 28°C for five days and then maintained at -20°C.

2.4. Molecular identification of fungi

DNA extraction was carried out as described by Ameen et al. (2021c). Each fungus was inoculated to 50 mL PDB (potato dextrose broth) and placed under specific conditions for 5-7 days. After incubation, 20 gm of fungal mycelia were collected and ground up using a mortar and pestle. Then the ground fungal material was transferred into a 2 mL Eppendorf tube; extraction buffer (500 µL) was prepared by using 200 mM- 0.5% SDS, 25 mM EDTA, 1M Tris-HCl, 250 mM NaCl with pH 7.5 followed by centrifugation at 13,000rpm for 1min. The supernatant was transferred to a fresh Eppendorf tube with an equal volume of phenol: chloroform mixture (1:1 ice cold) and centrifuged at 13,000 rpm for 2 min. The supernatant was collected in a separate Eppendorf tube with chloroform (300 µL) added, and the centrifugation step was repeated for 2 min. Afterward, the supernatant was collected and added to ice-cold isopropanol (300 µL), gently mixed, and incubated at -80°C for 30 min, followed by centrifugation at 13,000 rpm for 5 min. The pellet was collected and added to ice-cold ethanol (70%) and suspended in 1 mL sterile distilled water. The quality and yield of DNA were assessed by using AGE (agarose gel electrophoresis).

ITS primers including ITS1 (5′-TCCGTAGGTGAACCTGCGG-3′) and ITS 4 (5′-TCCTCCGCTTATTGATATGC-3′) were used for molecular identification of fungi. The PCR conditions used consisted of a 5 min initial denaturation step at 95°C, 1 min of denaturation for 35 cycles done at 94°C, 30 sec of annealing done at 55°C, a 2 min extension step done at 72° C, followed by a 10 min final extension step at 72°C. A BigDye terminator sequence kit (Applied Biosystems) was used for sequencing, and the sequences obtained were identified with NCBI (BLAST software), with additional alignments using Ugene and the T-Coffee algorithm (https://www.ebi.ac.uk/, EMBL-EBI, Cambridgeshire, UK) (Ameen et al., 2021c).

2.5. Fungal activities

Each isolate was cultured in a 1 L conical flask containing potato dextrose broth PDB medium (HiMedia, India) and incubated at 28°C for 30 days. After incubation, the supernatant was cofiltered through Whatman No. 1 filter paper and extracted using an equal volume of ethyl acetate. Then, the ethyl acetate extract was evaporated by a rotary evaporator, and the dried samples were dissolved in methanol/DMSO (100 µg/µL). The crude extract was filtered (0.22 µm) for further studies. Antioxidants were analyzed using the procedure described by Ameen et al. (2021c). Briefly, the fungal extracts (1 mL) were taken to test tubes, and specific reagents for each antioxidant were added to observe the formation
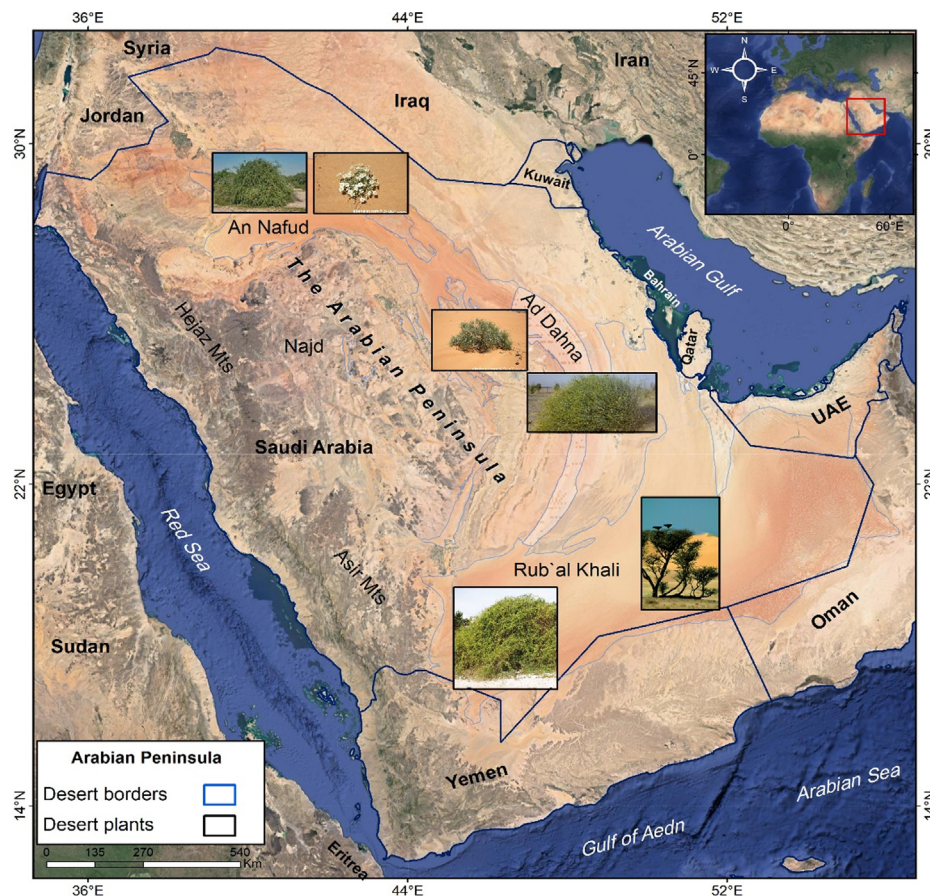
Fig. 1. Location of the sample sites in Saudi Arabian deserts.

of precipitate or emulsion or a color change. The strength of the reaction was evaluated visually and reported as +, ++, +++, ++++. The following reagents were used: Mayer's reagent (alkaloids), NaOH (flavonoids), ferric chloride (phenols), distilled water (saponins), acetic anhydride (steroids), $FeCl_3$ (tannins), chloroform (terpenoids).

Extracellular enzyme (cellulose, Laccase, Lipase, Protease, Amylase and Chitinase) were measured spectrophotometrically at 660 nm as described by Hamim et al. (2018).

2.6. Data analysis

Antioxidant results describing the level of activity (+, ++, +++, ++++) were inserted with values 1, 2, 3, 4 for data analyses. Principal component analysis (PCA) from the correlation matrix of the whole dataset (n = 68) was carried out using FactoMineR package (Lê et al., 2008) of R (Team et al., 2013) using R Studio 1.4.1717 (© 2009-2021 RStudio, PBC). Pearson correlations using the logarithmic data were also calculated.

3. Results

3.1. Soil characteristics

Soils were classified into five soil texture types; sand, loamy sand, sandy loam, silty loam, and sandy clay loam (Table 1).

3.2. Species identification

Sixty-eight different isolates consisting of 26 different species were identified (Table 2). The most common taxon was *Aspergillus*, particularly *Aspergillus niger*, which was isolated from 20 localities. *Aspergillus niger* was the only species isolated at 11 localities, but *A. terreus* was the only species present at Almajmaah (C), *A. phoenicis* at Ash Shayyit (E), *A. proliferans* at Dhahran (E), and *A. welwitschiae* at Tabuk 5 (N). The second most common genus was *Penicillium*, isolated from six localities. The species involved included *P. chrysogenum, P. glandicola,* and *P. dipodomyicola. P. goetzii* was isolated from Makkah-Mina (W) and *P. concavorugulosum* from Medina (W). In addition, the genus *Alternaria* was recorded from five different localities, with *A. consortialis* and *A. atra* isolated from Tabuk 3 (N). Two species of *Fusarium* were obtained, with *F. oxysporium* from Medina-Archers Mountain (W) and *F. brachygibbosum* from Najran 1 (S). Other taxa recorded were *Ulocladium* sp. from Tharmida-rawdhat alqaa (C), *T. longibrachiatum* from Alkharj-AlAin (C), *C. carrionci* from AlAhsa (E), *C. hawaciensi* (Makkah-Arafat)(W), *C. madrasense* (Makkah-Mina) (W), *T. variabliis* (Medina)(W), *Stemphylium* sp. (Tabuk 1 and 2) (N) (Table 2).

3.3. Fungal activities in relation to soil properties

The isolates producing most antioxidants were *Fusarium brachygibbosum* (MZ133779) from NJ1, *Aspergillus proliferans* (MZ045511) from D, *Penicillium chrysogenum* (MZ081403) from MM, *A. phoenicis* (MZ045505) from AS, and *P. chrysogenum* (MZ090907) from H (Table 3). The isolates producing most enzymes were *A. niger* (MZ133784) from NA3, *F. brachygibbosum*

Table 1
Characterization of desert soils.

Sample sites (Site code)(Texture)	Sand %	Silt	Clay	Ca2+ mEq/L	Mg2+	Na±	K±	Cl-	HCO3-	CaCO3	pH	EC S/m
Riyadh - rawdhat alkhafes (RR)(S)	89	7	4	30	15	1.6	1.3	7.5	15	31	7.4	1.2
Riyadh – aljelah (RA)(LS)	81	11	8	31	16	2.1	1.6	10	8	6.9	7.2	1.4
Tharmida - rawdhat alqaa (TRA)(LS)	78	18	4	4	13	1.6	1.9	7.5	11	63	7.4	1.2
Almuzahimiyah –almhaliah (AA)(SL)	59	29	12	14	8	21	11	7.5	8	21	7.9	2.5
Alkharj –AlAin (AAN)(S)	90	7	3	2	6	1.4	3.8	3.5	12	4.4	7.8	1.1
Almajmaah (AJT)(S)	93	5	2	8	2	37	16	2.5	10	58	7.2	1.5
Jubail (JL)(SL)	79	12	9	4	9	2.0	2.0	13	1	16	7.7	1.1
AlAhsa (ALA)(L)	39	43	23	6	10	1.9	0.6	10	8	53	7.4	3.1
Buqaya (BA)(SL)	15	68	18	4	11	1.5	1.0	7.5	6	17	7.3	2.1
Ash Shayyit (AS)(SL)	56	28	16	19	2	27	19	10	4	14	7.1	1.6
Buqaya – Aljashiah (BAH)(SL)	71	22	7	19	7	1.6	1.3	7.5	12	61	7.8	2.3
Dhahran (D)(SCL)	64	14	22	6	4	1.9	1.5	5	4	19	7.4	4.1
Makkah – Arafat (MAT)(LS)	85	4	11	7	5	2.2	1.1	7.5	3	25	7.5	1.1
Makkah – Mina (MM)(S)	92	7	1	4	7	2.4	1.2	10	4	5.0	7.7	2.1
Medina - Al Henkiyah (MA)(S)	91	6	3	4	6	1.8	0.8	8.5	1	5.6	7.8	2.1
Medina - Archers Mountain (MAM)(SL)	68	18	14	7	13	2.9	1.1	10	7	2.5	7.8	1.1
Medina (M)(SL)	72	13	15	11	7	7.9	1.7	9.8	4	8.8	7.4	4.3
Taif (TF)(SL)	74	22	4	34	36	14	28	13	8	3.1	7.4	3.3
Najran 1 (NA1)(SL)	64	21	15	6	2	2.3	0.5	6.7	3	1.9	7.5	3.1
Najran 2 (NA2)(S)	96	3	1	4	10	2.2	1.0	7.5	8	1.3	6.9	2.2
Najran 3 (NA3)(L)	48	38	14	5	8	9.3	3.6	15	8	2.5	7.2	2.2
Jazan – AlHasamah (JA)(S)	80	7	2	5	3	2.7	1.0	6.9	3	3.6	7.0	1.1
Sharurah 1 (S1)(LS)	70	8	7	30	12	2.0	1.3	7	9	7.2	7	3.5
Sharurah 2 (S2)(LS)	71	16	5	5	10	1.8	2.9	7.3	10	23	7.1	2.1
Hail (H)(SL)	65	34	14	10	8	19	14	7.9	9	11	7.4	2.7
Tabuk 1 (TB1)(S)	87	6	5	3	5	2.4	2.8	4.5	8	5.4	7.6	3.1
Tabuk 2 (TB2)(S)	90	8	3	8	3	7.2	6.3	1.5	8	8.3	7.0	1.5
Tabuk 3 (TB3)(SL)	74	10	8	5	7	3.0	3.0	2.5	2	10	7.5	2.3
Tabuk 4 (TB4)(L)	32	13	10	4	11	1.0	2.6	9.0	9	13	7.2	1.2
Tabuk 5 (TB5)(SL)	10	52	13	8	10	6.5	4.0	6.5	5	20	7.0	3.2

S = sand, SL= sandy loam, LS = loamy sand, L = loam, SiL= silty loam, SCL = sandy clay loam

(MZ133779) from NJ1, *A. phoenicis* (MZ045505) from AS, *C. madrasense* (MZ031134) from MM, *Fusarium* sp. (MZ090904) from S1 (Table 4).

The first axis of PCA using the whole dataset explained 22% of the variation (Eigenvalue 5.5). The second axis explained 14% (Eigenvalue 3.5), the third 11% (Eigenvalue 2.7), and the fourth axis explained 9% (Eigenvalue 2.3). These four axes explained 56% of the total variation. Biochemical compounds had the highest loadings of PC1 (> 0.6) (Fig. 2a). The PC1 loadings of the enzymes were around 0.5. All enzymes increase to the direction of the upper right corner

of the loadings plot, whereas all biochemical compounds increase to the direction of the lower right corner. Thus, the loadings plot indicates a correlation within the biochemical compounds, as well as within the enzymes but no strong correlation between the groups of antioxidants and enzymes. Soil physico-chemical properties had low loadings on PC1, and thus, PC1 is interpreted to describe the biochemical activities of fungi.

The second PC2 axis is interpreted to describe soil texture because Silt, Clay, and Sand had the highest loadings of PC2, varying between 0.5 and 0.75 (positive or negative). Other soil proper-

Table 2

Fungal species with their NCBI accession numbers isolated from desert soils from different areas in Saudi Arabia. Bold refers to species not reported previously from the Arabian desert soils and underlining refers to the species not reported previously from the Saudi Arabian desert soils.

Species	Accession Number	Site	Area
Alternaria chlamydosporigona	MZ133791	Riyadh - rawdhat alkhafes	Central
Alternaria sp.	MZ133790	Riyadh - rawdhat alkhafes	Central
Alternaria alternata	MZ045515	Makkah - Arafat	West
Alternaria atra	MZ090913	Tabuk 3	North
Alternaria consortialis	MZ090912	Tabuk 3	North
Alternaria sorghi	MZ133797	Almuzahimiyah -almhaliah	Central
Aspergillus niger	MZ133793	Riyadh - rawdhat alkhafes	Central
	MZ090911	Tabuk 2	North
	MZ133792	Riyadh - rawdhat alkhafes	Central
	MZ045500	Jubail	East
	MZ045502	AlAhsa	East
	MZ045504	Buqaya	East
	MZ045507	Dhahran	East
	MZ045508	Dhahran	East
	MZ045509	Dhahran	East
	MZ045510	Dhahran	East
	MZ045512	Makkah - Arafat	West
	MZ081408	Makkah - Mina	West
	MZ081409	Medina - Al Henkiyah	West
	MZ081416	Medina	West
	MZ081417	Medina	West
	MZ133783	Najran 3	South
	MZ133784	Najran 3	South
	MZ090903	Sharurah 1	South
	MZ133786	Tabuk 5	North
	MZ133788	Tabuk 5	North
	MZ045506	Buqaya - Aljashiah	East
Aspergillus oryzae	MZ081412	Medina - Archers Mountain	West
Aspergillus phoenicis	MZ045505	Ash Shayyit	East
	MZ090902	Sharurah 1	South
Aspergillus proliferans	MZ045511	Dhahran	East
Aspergillus terreus	MZ045499	Almajmaah	Central
	MZ045514	Makkah - Arafat	West
	MZ133776	Taif	West
Aspergillus welwitschiae	MZ133787	Tabuk 5	North
Aspergillus sp.	MZ133794	Riyadh - rawdhat alkhafes	Central
	MZ081410	Medina - Archers Mountain	West
	MZ133789	Jazan - AlHasamah	South
	MZ133785	Tabuk 4	North
Chaetomium madrasense	MZ031134	Makkah - Mina	West
Cladophialophora carrionci	MZ045501	AlAhsa	East
Curvularia hawaciensis	MZ045513	Makkah - Arafat	West
Curvularia nicotiae	MZ133795	Riyadh - aljelah	Central
Fusarium brachygibbosum	MZ133779	Najran 1	South
	MZ090905	Sharurah 1	South
Fusarium oxysporium	MZ081411	Medina - Archers Mountain	West
Fusarium sp.	MZ133777	Najran 1	South
	MZ133778	Najran 1	South
	MZ133780	Najran 2	South
	MZ133781	Najran 2	South
	MZ133782	Najran 3	South
	MZ090904	Sharurah 1	South
	MZ090906	Sharurah 2	South
Penicillium chrysogenum	MZ081403	Makkah - Mina	West
	MZ090908	Tabuk 1	North
	MZ090907	Hail	North
Penicillium dipodomyicola	MZ081406	Makkah - Mina	West
Penicillium glandicola	MZ081405	Makkah - Mina	West
Penicillium goetzii	MZ081407	Makkah - Mina	West
Penicillium concavorugulosum	MZ081414	Medina	West
Stemphylium solani	MZ090909	Tabuk 1	North
Stemphylium sp.	MZ090910	Tabuk 2	North
Talaromyces variabliis	MZ081415	Medina	West
Trichoderma longibrachiatum	MZ045498	Alkharj -AlAin	Central
Ulocladium sp.	MZ133796	Tharmida - rawdhat alqaa	Central
Unknown	MZ133798	Almuzahimiyah -almhaliah	Central
Unknown	MZ045503	AlAhsa	East
Unknown	MZ081413	Medina - Archers Mountain	West

ties had low loadings and, thus, of minor importance. Enzymes also had relatively high loadings on PC2. Thus, the loadings plot indicates that enzyme activities were higher when Silt and Clay were higher. The loadings plot also gives a slight indication that antioxidants were higher when Sand was higher.

Table 3

Biochemical activity of desert fungi isolates, '+' indicates low activity, '++' moderate activity, '+++' strong activity and 'empty space' no activity. Bold refers to the most active isolates and underling to the isolates raised by PCA.

Fungus (site code)	Flavonoids	Phenols	Saponins	Steroids	Tannins	Terpenoids	Alkaloids
A. chlamydosporigona (RR)	+						
Alternaria sp. (RR)		+				+	
A. alternata (MAT)							
A. atra (TB3)	+++	+	++	+	++	++	++
A consortialis (TB3)	++	+++	++	+++	+	++	++
A sorghi (AA)							
A. niger (RR)	++	+	++	+	++	++	++
A. niger (TB3)							
A. niger (RR)							
A. niger (JL)							
A. niger (ALA)	++			++			
A. niger (BA)		++		+	++	+	++
A. niger (D)	++	+	+++	++	+	++	+++
A. niger (D)	+	+	+	+	+	+	+
A. niger (D)							
A. niger (D)							
A. niger (MAT)							
A. niger (MM)	++		++	++			
A. niger (MA)		+		++			++
A. niger (M)						++	
A. niger (M)		++					
A. niger (NA3)		-	+	+			+
A. niger (NA3)	++	++	+	++	+		++
A. niger (S1)	++	+	+++	+			+
A. niger (TB5)							
A. niger (TB5)							
A. niger (BAH)							
A. oryzae (MAM)	+	++	+++		++		
A. phoenicis (AS)	**++**	**++**	**+**	**++**	**++**	**+++**	**+++**
A. phoenicis (S2)	++	+++	++	+++	++		+++
A. proliferans (D)	**+++**	**+++**	**+++**	**++++**	**+++**	**++**	**+++**
A. terreus (AJH)							
A. terreus (MAT)		++	++	++		++	++
A. terreus (TF)	++	++	++	++	+	++	+
A. welwitschiae (TB2)	+++	+	+	++	+	++	++
Aspergillus sp. (RR)		+		+			+
Aspergillus sp. (MAM)	+	++	+			+	++
Aspergillus sp. (JA)		++	++	+			++
Aspergillus sp. (TB4)							
C. madrasense (MM)	+	+	++		++		++
C. carrionci (ALA)							
C. hawaciensis (MAT)	++		++	++		++	++
C. nicotiae (RA)			++		+++	++	+++
F. brachygibbosum (NJ1)	**+++**	**+++**	**+++**	**+++**	**++**	**+++**	**++++**
F. brachygibbosum (S1)			++				++
F. oxysporium (MAM)							
Fusarium sp. (NJ1)				++			+
Fusarium sp. (NJ1)	+	+++	+++	++	+	+	++
Fusarium sp. (NJ2)	++	+	++	+	++	+	+
Fusarium sp. (NJ2)	+			++	+		++
Fusarium sp. (NJ3)				++	++		
Fusarium sp. (S1)	++			+		++	+
Fusarium sp. (S2)	++		+		++		+
P. chrysogenum (MM)	**+++**	**+++**	**++**	**+++**	**++++**	**+++**	**+++**
P. chrysogenum (TB1)	++	+	++	+	++	+	++
P. chrysogenum (H)	**+++**	**++**	**++**	**++**	**++**	**+**	**+++**
P. dipodomyicola (MM)	++	+	+++		++		++
P. glandicola (MM)	++	++	+	+	++	+	++
P. goetzii (MM)	++	+++	+	++			
P. concavorugulosum (M)	++	++	++	++	++	++	+
S. solani (TB1)	+++		+++	+		+	
Stemphylium sp. (TB2)			++	++			++
T. variabliis (M)	+++	++	++	++	++	++	++
T. longibrachiatum (AAN)	+		+		++		++
Ulocladium sp. (TRA)							
Unknown (AA)							
Unknown (ALA)							
Unknown (MAM)							

The PCA interpretations about the relation of biochemical activities and soil properties were not verified with Pearson correlation coefficients, which all were under 0.4 ($r < 0.4$; data not shown) and thus weak or not existing. PCA interpretation about the relationship of the groups of antioxidants and enzymes was verified with Pearson correlations: the members of the groups did not correlate

Table 4
Enzyme activity (U/ml, mean ± SD, n = 3) of the desert fungi isolates, 'empty space' indicates no activity. Bold refers to the most active isolates and underling to the isolates raised by PCA.

Fungus (site code)	Cellulase	Laccase	Lipase	Protease	Amylase	Chitinase
A. chlamydosporigona (RR)						
Alternaria sp. (RR)	8.3 ± 0.3	4 ± 0.1	3.5 ± 0.1	4.5 ± 0.1		
A. alternaria (MAT)						
A. atra (TB3)	8 ± 0.1	7.8 ± 0.1	9.7 ± 0.2	13 ± 0.2	10 ± 0.1	9 ± 0.1
A. consortialis (TB3)		6.8 ± 0.1		9.6 ± 0.1		
A. sorghi (AA)	18 ± 0.1			20 ± 0.2		18 ± 0.2
A. niger (RR)			10 ± 0.1			
A. niger (TB3)					8.98 ± 0.1	
A. niger (RR)		10 ± 0.3				
A. niger (JL)	9.2 ± 0.2	4 ± 0.1		3.9 ± 1		8.2 ± 0.3
A. niger (ALA)						
A. niger (BA)	10.1 ± 0.2		7.9 ± 0.3		3.4 ± 0.1	11.2 ± 0.1
A. niger (D)						
A. niger (D)						
A. niger (D)						
A. niger (D)						
A. niger (MAT)	19 ± 0.2	11.3 ± 0.1	8.4 ± 0.2	2.9 ± 0.2	9.1 ± 0.2	11 ± 0.3
A. niger (MM)						
A. niger (MA)	10 ± 0.1			7.9 ± 0.1		
A. niger (M)						
A. niger (M)						
A. niger (NA3)		9 ± 0.1			8.7 ± 0.3	
A. niger (NA3)	**18 ± 0.1**	**17 ± 0.3**	**19.3 ± 0.1**	**18 ± 0.2**	**23 ± 0.1**	**16 ± 0.2**
A. niger (S1)						
A. niger (TB5)	11 ± 0.1	8.9 ± 0.3		9.2 ± 0.3	8.3 ± 0.1	
A. niger (TB5)	10 ± 0.1		7.9 ± 0.2	6.9 ± 0.2	8.5 ± 0.1	
A. niger (BAH)						
A. oryzae (MAM)	7.2 ± 0.3	3.2 ± 0.2	4.8 ± 0.1	8.3 ± 0.2		9.2 ± 0.1
A. phoenicis (AS)	16 ± 0.1	16.7 ± 0.22	19 ± 0.2	10 ± 0.2	18 ± 0.1	21 ± 0.2
A. phoenicis (S2)	9.2 ± 0.2	10 ± 0.3	9.7 ± 0.1	4.3 ± 0.1	2.9 ± 0.2	10.2 ± 0.2
A. proliferans (D)	11.2 ± 0.1	8.6 ± 0.2	2.7 ± 0.2	17 ± 0.2		8.4 ± 0.3
A. terreus (AJH)						
A. terreus (MAT)		1.2 ± 0.1	9.3 ± 0.1	16 ± 0.2		10.6 ± 0.1
A. terreus (TF)						
A. welwitschiae (TB2)	2.7 ± 0.3	12.2 ± 0.2	9.5 ± 0.2	7.6 ± 0.2	11 ± 0.1	9 ± 0.1
Aspergillus sp.(RR)	9.2 ± 0.1		9.7 ± 0.1	8.5 ± 0.2	3.6 ± 0.3	
Aspergillus sp. (MAM)		10.2 ± 0.2	19 ± 0.2	3.2 ± 0.1	12.2 ± 0.1	
Aspergillus sp. (JA)						
Aspergillus sp.(TB4)						
C. madrasense (MM)	**18 ± 0.1**	**19 ± 0.2**	**9.2 ± 0.2**	**19 ± 0.1**	**10 ± 0.1**	**17 ± 0.1**
C. carrionci (ALA)	19.1 ± 0.1	9.2 ± 0.2	4.2 ± 0.1	19.2 ± 0.2	10 ± 0.2	5.2 ± 0.3
C. hawaciensis (MAT)	2.2 ± 0.2	1.9 ± 0.1	2.3 ± 0.3	4.3 ± 0.1	4.9 ± 0.1	3.9 ± 0.1
C. nicotiae (RA)	1.3 ± 0.1	8.7 ± 0.2	7.2 ± 0.3	9.3 ± 0.1	8.9 ± 0.1	3.2 ± 0.1
F. brachygibbosum (NJ1)	**23 ± 0.3**	**19.7 ± 0.3**	**17 ± 0.2**	**18.6 ± 0.2**	**17.3 ± 0.2**	**10.9 ± 0.2**
F. brachygibbosum (S1)	3.2 ± 0.1	12 ± 0.1			3.9 ± 0.1	
F. oxysporium (MAM)	9.2 ± 0.3	1.7 ± 0.2			10 ± 0.2	4.2 ± 0.2
Fusarium sp. (NJ1)		11 ± 0.2		10.2 ± 0.2	8.7 ± 0.3	
Fusarium sp. (NJ1)	7.9 ± 0.2		1.3 ± 0.4		11.3 ± 0.1	
Fusarium sp. (NJ2)	2.1 ± 0.1		3.2 ± 0.2		0.9 ± 0.1	
Fusarium sp.(NJ2)			8 ± 0.1			
Fusarium sp.(NJ3)					9.3 ± 0.2	10.2 ± 0.2
Fusarium sp. (S1)	**18 ± 0.1**	**11 ± 0.2**	**18 ± 0.2**	**10 ± 0.2**	**19 ± 0.2**	**10 ± 0.1**
Fusarium sp. (S2)	1.2 ± 0.1	12 ± 0.1		1.3 ± 0.1		10 ± 0.2
P. chrysogenum (MM)		20 ± 0.2		19.5 ± 0.2	2.3	
P. chrysogenum (TB1)	9.3 ± 0.2			12 ± 0.3	8.7 ± 0.3	
P. chrysogenum (H)	11 ± 0.1	9.4 ± 0.1	3.7 ± 0.1	10.3 ± 0.2	2.1 ± 0.3	12 ± 0.2
P. dipodomyicola (MM)	10 ± 0.1			11 ± 0.2		
P. glandicola (MM)	2.9 ± 0.2				12 ± 0.3	
P. goetzii (MM)	20 ± 0.1	19 ± 0.2	12 ± 0.2	9.4 ± 0.2	7.8 ± 0.2	8.6 ± 0.2
P. concavorugulosum (M)	1.9 ± 0.3			3.9 ± 0.12	2.4 ± 0.1	
S. solani (T)	10 ± 0.1	11 ± 0.2	17 ± 0.2	16.5 ± 0.2	20 ± 0.2	0.9 ± 0.1
Stemphylium sp. (TA)	10.8 ± 0.2	19 ± 0.1	2.4 ± 0.1	9.3 ± 0.1	2.1 ± 0.3	10.2 ± 0.2
T. variabliis (M)	11 ± 0.2	4.6 ± 0.3	10.3 ± 0.3	1.6 ± 0.3		
T. longibrachiatum (AL)	2.2 ± 0.1	9.2 ± 0.2	11 ± 0.1	2.8 ± 0.3	9.8 ± 0.2	3.4 ± 0.1
Ulocladium sp. (TR)	8.3 ± 0.3	20.3 ± 0.2	5.2 ± 0.1	3.9 ± 0.1	10.2 ± 0.2	5.3 ± 0.2
Unknown (ALA)	10.2 ± 0.1	3.9 ± 0.2	19 ± 0.2	20.3 ± 0.1	12 ± 0.3	3.1 ± 0.3
Unknown (MAM)	3.5 ± 0.1	10.3 ± 0.2	2.6 ± 0.1	9.7 ± 0.3	2.4 ± 0.1	10 ± 0.2
Unknown (AA)	2.5 ± 0.2	12.3 ± 0.3	2.9 ± 0.2	20 ± 0.2	2.4 ± 0.1	

with each other. Instead, the members correlated within the groups. The strongest correlation (r = 0.70) was between saponins and flavonoids. No correlation, i.e. r < 0.5 was observed only between steroids and tannins (r = 0.41). Enzymes correlated with each other as well. The strongest correlation (r = 0.65) was

PCA graph of variables

Genus

a *Alternaria*
a *Aspergillus*
a *Chaetomium*
a *Cladophialophora*
a *Curvularia*
a *Fusarium*
a *Penicillium*
a *Stemphylium*
a *Talaromyces variabliis*
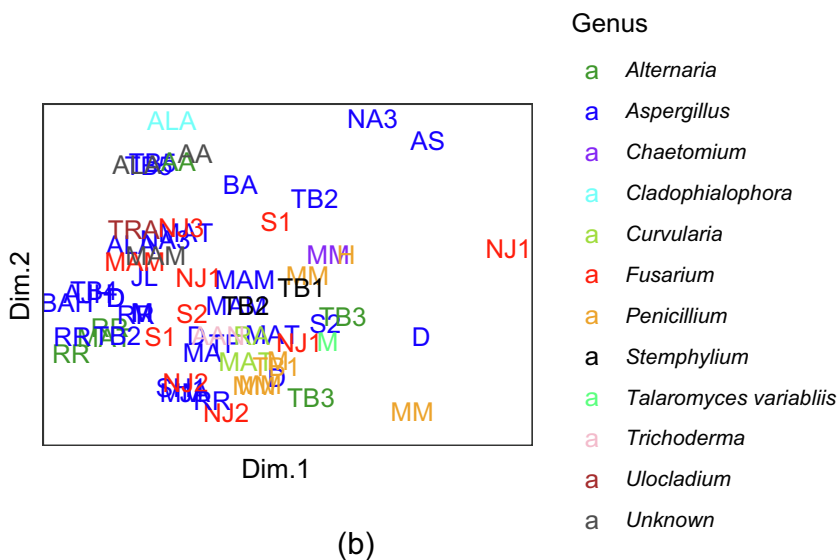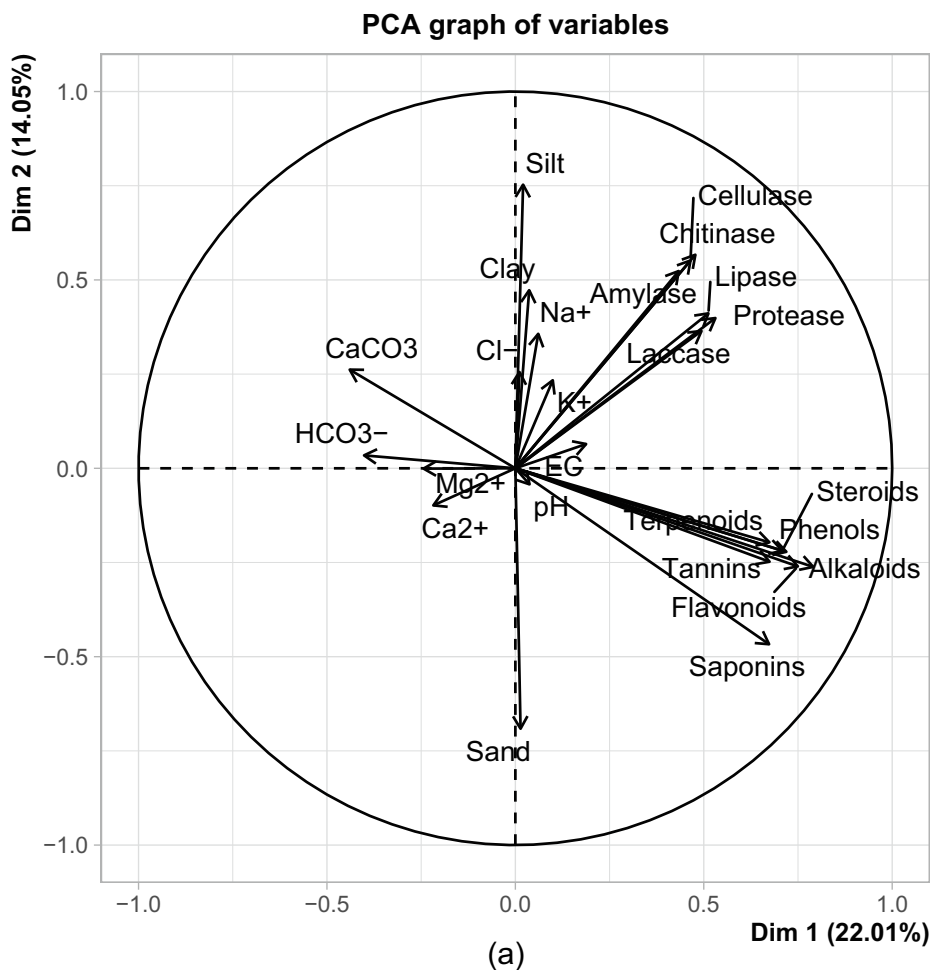a *Trichoderma*
a *Ulocladium*
a *Unknown*

Fig. 2. PCA (PC1 and PC2) of biochemicals (enzymes and antioxidants) produced by fungi isolated from Saudi Arabian desert soils and the respective soil properties; a) variable loadings plot and **b)** sample site score plot. See sample sites from Fig. 1 and Table 2.

between protease and cellulase. No correlation was observed only between amylase and chitinase ($r = 0.39$).

The sample site score plot of PC1 and PC2 shows no evident clustering of either fungal genera or sampling areas (Fig. 2b). The

most active isolate regarding both antioxidants and enzymes (increasing along PC1) was *Fusarium brachygibbosum* (MZ13377) from NJ1. The other species with high antioxidant and enzyme activities were *Aspergillus phoenicis* (MZ045505) from AS. *A. niger*

(MZ133784) from NA3 (upper right corner) had high enzyme activities. *Penicillium chrysogenum* (MZ081403) from MM (W) and *A. proliferans* (MZ045511) from D (lower right corner) had high antioxidant activities. At the left end of PC1, indicating low or no activity of these isolates, *Aspergillus* genus is dominating. Thus, *Aspergillus* had isolates of both high and low biochemical activities. These interpretations of PCA can be verified from Tables 3 and 4.

Due to the relatively low proportion of variance explained by PC1 and PC2, PC3 and PC4 were also examined. One *A. terreus* isolate (M) was removed from the sample site score plot as an outlier. Positive PC3 loadings were higher than 0.5 for HCO₃, and Sand, and on the negative side for Clay and EC (Fig. 3a). PC4 had high positive loadings for Ca^{2+}, Mg^{2+}, K^+. Thus, PC4 axis was interpreted to indicate base cations.

PC3 and PC4 describing soil properties did not give any additional interpretation to PC1 and PC2 regarding biochemical activities. Instead, the sample site scatter plot gave information on the soil properties in different areas. Fig. 3b shows the situation of sites in N, S, E, W, and C areas. In the scatter plot Fig. 3b, C and E sites situate in the opposite ends of PC3. In Fig. 3c, the sites are marked. Many of the C sites such as RR can be found from the upper right corner. Many of the E sites (D, ALA) and the S site NJ1 can be found from the left side of the scatter plot (Fig. 3c) indicating a difference in the base cations of soils. This can be partly verified from Table 1, RR, D and NJ1 sites had high base cations. However, several other sites, such as TF, AJH, AA, RA, AS and H, had also high base cations. ALA samples had average, not low base cations.

4. Discussion

4.1. Fungal community in Saudi Arabian desert soils

Desert soil properties were separated by the dominance of either sand and base cations or by silt and clay as indicated by the PCA analysis. Sand and base cation concentrations of soil differed between sites so that many central sites had higher values than many eastern sites. However, this relation shown by PCA was only partly verified by the actual concentrations. Instead, the picture is complex due to diverse soil properties, of which some are shared, and some are distinct. Thus, no strong clustering was shown by the PCA analysis. In general, the Arabian desert soil properties were much the same as previously reported elsewhere from deserts (Ma et al., 2016).

We prepared 68 isolates from the Saudi Arabian desert soils that were inhabited by 11 different cultivable fungal genera and 25 different species. The number of species was relatively low, and it is possible that the samples were overdiluted. We cannot verify the diversity of fungi in Arabian desert soils but rather studied a representative collection of fungi.

We identified 13 culturable fungal species that have not been reported previously from the Arabian desert soils according to the review of Ameen et al. (2021b) or in the articles we are aware of. These new species were *Alternaria atra, A. consortialis, A. sorghi, Aspergillus phoenicis, A. proliferans, Cladophialophora carrionci, Curvularia hawaciensis, C. nicotiae, Fusarium brachygibbosum, Penicillium concavorugulosum, Stemphylium solani, Talaromyces variabliis,* and *Trichoderma longibrachiatum.* Particularly from Saudi Arabian desert soils, six more species, namely *Aspergillus oryzae,*
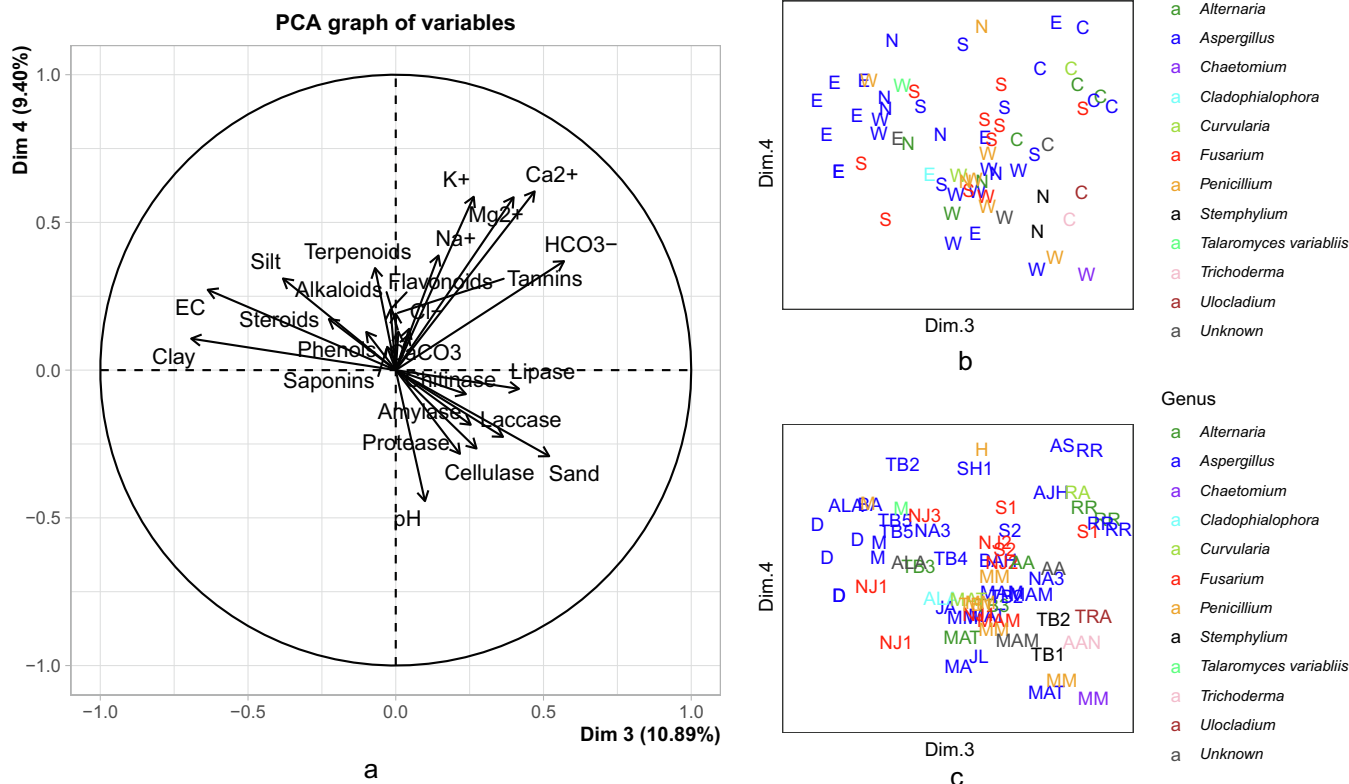

Fig. 3. PCA (PC3 and PC4) of biochemicals (enzymes and antioxidants) produced by fungi isolated from Saudi Arabian desert soils and the respective soil properties; **a)** variable loadings plot and **b)** sample site score plot marked as the location in Saudi Arabia (central (C), eastern (E), southern (S) and western (W)), **c)** sample site score plot. See sample sites from Fig. 1 and Table 2.

A. welwitschiae, Penicillium dipodomyicola, P. glandicola, P. goetzii and *Stemphylium* sp., have not been reported previously. This study did not find ten previously reported molecularly identified culturable species (*Albifimbria terrestris, Aspergillus clavatus, A. fumigatus, A. nidulans, A. nigervan, A. ochraceus, Fusarium equiseti, F. redolens, F. solani,* and *Penicillium purpurogenum*). However, comparisons between the studies are not straightforward due to the morphological identification used in older studies. Moreover, uncertainty in the molecular identifications has often been is remarkable and the species have not been identified with absolute certainty.

4.2. Fungal biochemicals

Fungi from different habitats are known to produce biotechnologically valuable chemicals. A wide variety of culturable fungal species have shown high antioxidant capacity (Cui et al., 2015; Zhou et al., 2018). Especially plant endophytic fungi have been studied a lot as reviewed recently (Toghueo and Boyom, 2019). Antioxidant potential was reported for 14% of the 87 plant endophytic fungi (Tejesvi et al., 2011). Desert plant endophytes have been reported as good antioxidant producers, more than half of fungal endophytes isolated from *Berberis aristate* and *Artemisia desterorum* had antioxidant activity (Sharma et al., 2018; Zhang et al., 2021b). Saprotrophic fungi have also been studied. A study of Zohri et al. (2017) reported that a remarkable proportion (60%) of 32 saprotrophic fungi studied produced antioxidants. Species that showed high antioxidant activity and produced high concentrations of total phenolics included *Alternaria alternata, Aspergillus flavus, A. terreus, Chaetomuim globosum, Cladosporium cladosporiodes, Penicillium roquefortii, Trichoderma pseudokoningii* and *Fusarium proliferatum. F. oxysporum* and *F. solani* produced low total phenolic concentration. *P. flavigenum* produced phenolic compounds (Tavares et al., 2018). Extreme environments, such as cold Antarctic environment, are thought to produce valuable chemicals (Duarte et al., 2018; Wentzel et al., 2019). Deserts as extreme environments have also been studied a lot (Ameen et al., 2021b; Moghaddam et al., 2021, 2020; Yadav and Meena, 2021; Zhang et al., 2021a). However, saprotrophic fungi of desert soils have been studied scarcely (Ahmed et al., 2018; Mtibaà et al., 2017). We studied 25 saprotrophic fungal species from 68 isolates.

Most of our isolates had the ability to produce enzymes and antioxidants; only six isolates did not show any biochemical activity. However, the amounts varied between the species and isolates remarkably. The same species, namely *A. niger,* had isolates of both high and low biochemical activities. The most prevalent genus of our study was *Aspergillus* that has been studied for several applications for a long time (Cairns et al., 2018; Frisvad et al., 2018; Meyer et al., 2011). *Penicillium, Chaetomium,* and *Talaromyces* species have been used to produce enzymes, for instance, to deconstruct cellulosic and lignocellulosic biomasses (Darwish and Abdel-Azeem, 2020; de França Passos et al., 2018; Frisvad et al., 2018; Méndez-Liter et al., 2020; Thapa et al., 2020). *Fusarium* sp. have several applications, from food additives and pharmaceuticals to biofuels (Alwakeel et al., 2021; Rodrigues, 2017).

In previous studies, only total phenolic concentration and flavonoids have often been measured (Huang et al., 2007; Mtibaà et al., 2017; Yadav et al., 2014; Zohri et al., 2017). Other potential antioxidants such as tannins, saponins, steroids, terpenoids, and alkaloids have scarcely been reported. We report that almost all antioxidants correlated with each other, and the fungi are probable to produce several antioxidants. The same is with enzymes; most of our enzymes correlated with each other. We conclude that each isolate is probable to produce several antioxidants and enzymes.

Several of the species producing biochemicals are pathogens. *Fusarium brachygibbosum*, which appeared to produce most biochemicals in our study, is a phytopathogen causing destructive dis-

ease, for instance, in maize, watermelon, and onion (Renteria-Martinez et al., 2015; Shan et al., 2017; Tirado-Ramirez et al., 2021). *Fusarium oxysporum* is known as a severe phytopathogen causing a common *Fusarium* wilt disease, for instance, in tomatoes and bananas (Alghuthaymi et al., 2020; Dita et al., 2018; Srinivas et al., 2019). Many species are known to produce mycotoxins (Alghuthaymi et al., 2020; Gashgari et al., 2019). *Aspergillus* species are opportunistic pathogens. The genus *Aspergillus,* including *A. niger,* causes diseases, for instance, in fruits. *Aspergillus* has also been the most studied fungal genus in biotechnological applications (Cairns et al., 2018; Cohen et al., 2021; Orfali et al., 2021). *Penicillium* sp. are also opportunistic pathogens, and many of them are continuously studied for different applications such as the antibiotics production by *P. chrysogenum* (Garcia-Estrada et al., 2020). The aspect of pathogenicity and virulence of the species must be considered when planning further studies.

PCA gave an indication of a positive relationship between the biochemical activities of fungi isolated from soil and the soil texture. However, Pearson correlations did not verify this interpretation. Therefore, we interpret that no generalizable relation exists, but many samples with high enzyme activities had relatively high silt and clay content in desert soil. Similarly, many samples with high antioxidant activities had relatively high sand content in desert soil. We did not find any previous articles reporting this relation, and therefore, the relation reported here is only tentative, needing further studies.

5. Conclusions

Biochemicals were produced by most of our isolates; out of 68 isolates, 49 produced antioxidants and 52 enzymes, while and only six isolates did not produce any biochemicals. The highest biochemical activity was observed for the isolates *Fusarium brachygibbosum, Aspergillus phoenicis, A. proliferans,* and *P. chrysogenum*. The same species (*A. niger*) had isolates of both high and low biochemical activities, which shows the need to search isolates from different environments. Each isolate is probable to produce several antioxidants and enzymes, as shown by the correlation within the compound groups. We got a tentative indication of desert soil's higher silt and clay content where the fungi with high enzyme activities were isolated. Similar tentative relation was observed with sand and antioxidant activity of fungi. However, these relationships cannot be generalized. Instead, the biochemical activities of fungi are controlled by many factors. Desert soil warrants further research as a promising source of highly bioactive fungi.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

References

Ahmed, M., El-Zayat, S., El-Sayed, M., 2018. Cellulolytic activity of cellulose-decomposing fungi isolated from Aswan hot desert soil. Egypt. J. Biol. Stud. 1, 35–48.

Al-Enazi, N.M., Awaad, A.S., Al-Othman, M.R., Al-Anazi, N.K., Alqasoumi, S.I., 2018. Isolation, identification and anti-candidal activity of filamentous fungi from Saudi Arabia soil. Saudi Pharm. J. 26, 253–257.

Alghuthaymi, M., Alshehri, W.A., Al-Maary, K.S., Bahkali, N.A., AlKahtani, M.D.F., Alarfaj, A.A., Alnadhari, S., Ameen, F., 2020. Mycotoxigenicity of Fusarium isolated from banana fruits: Combining phytopathological assays with toxin concentrations. J. King Saud Univ. 32, 1482–1485.

Alwakeel, S.S., Ameen, F., Al Gwaiz, H., Sonbol, H., Alghamdi, S., Moharram, A.M., Al-Bedak, O.A., 2021. Keratinases produced by Aspergillus stelliformis, Aspergillus sydowii, and Fusarium brachygibbosum isolated from human hair: yield and activity. J. Fungi 7, 471.

Ameen, F., Almansob, A., Al Tami, M., Al-Enazi, N., Al-Sabri, A., Orfali, R., 2021a. Epigenetic modifiers affect the bioactive compounds secreted by an endophyte of the tropical plant Piper longum. Molecules 26, 29.

Ameen, F., Stephenson, S.L., Al Nadhari, S., Yassin, M.A., 2021b. A review of fungi associated with Arabian desert soils. Nov. Hedwigia, 173–195.

Ameen, F., Stephenson, S.L., AlNadhari, S., Yassin, M.A., 2021c. Isolation, identification and bioactivity analysis of an endophytic fungus isolated from Aloe vera collected from Asir desert, Saudi Arabia. Bioprocess Biosyst. Eng. 44, 1063–1070.

Arora, D.S., Chandra, P., 2011. In vitro antioxidant potential of some soil fungi: screening of functional compounds and their purification from Penicillium citrinum. Appl. Biochem. Biotechnol. 165, 639–651.

Barnard, R.L., Osborne, C.A., Firestone, M.K., 2013. Responses of soil bacterial and fungal communities to extreme desiccation and rewetting. ISME J. 7, 2229–2241.

Cairns, T.C., Nai, C., Meyer, V., 2018. How a fungus shapes biotechnology: 100 years of Aspergillus niger research. Fungal Biol. Biotechnol. 5, 1–14.

Chandra, P., Sharma, R.K., Arora, D.S., 2020. Antioxidant compounds from microbial sources: a review. Food Res. Int. 129, 108849.

Cohen, Y., Shulhani, R., Rot, Y., Zemach, H., Belausov, E., Grinberg-Baran, M., Borenstein, M., Pivonia, S., Ezra, D., Shtienberg, D., 2021. Aspergillus niger, the causal agent of black mould disease in date fruits, infects and colonizes flowers and young fruitlets. Plant Pathol. 70, 1195–1208.

Cui, J.-L., Guo, T.-T., Ren, Z.-X., Zhang, N.-S., Wang, M.-L., 2015. Diversity and antioxidant activity of culturable endophytic fungi from alpine plants of Rhodiola crenulata, R. angusta, and R. sachalinensis. PLoS One 10, e0118204.

Darwish, A.M.G., Abdel-Azeem, A.M., 2020. Chaetomium enzymes and their applications. In: Recent Developments on Genus Chaetomium. Springer, pp. 241–249.

de França Passos, D., Pereira Jr, N., de Castro, A.M., 2018. A comparative review of recent advances in cellulases production by Aspergillus, Penicillium and Trichoderma strains and their use for lignocellulose deconstruction. Curr. Opin. Green Sustain. Chem. 14, 60–66.

Dita, M., Barquero, M., Heck, D., Mizubuti, E.S.G., Staver, C.P., 2018. Fusarium wilt of banana: current knowledge on epidemiology and research needs toward sustainable disease management. Front. Plant Sci. 9, 1468.

Duarte, A.W.F., Dos Santos, J.A., Vianna, M.V., Vieira, J.M.F., Mallagutti, V.H., Inforsato, F.J., Wentzel, L.C.P., Lario, L.D., Rodrigues, A., Pagnocca, F.C., et al., 2018. Cold-adapted enzymes produced by fungi from terrestrial and marine Antarctic environments. Crit. Rev. Biotechnol. 38, 600–619.

El Hamd, A.T.A.B.U., Abd El Raheim, M.D., El, M.A., 2014. Studies on the bioactive fungal secondary metabolites of some fungi isolated from Al-Kharj soil.

Estefan, G., 2013. Methods of soil, plant, and water analysis: a manual for the West Asia and North Africa region.

Frisvad, J.C., Møller, L.L.H., Larsen, T.O., Kumar, R., Arnau, J., 2018. Safety of the fungal workhorses of industrial biotechnology: update on the mycotoxin and secondary metabolite potential of Aspergillus niger, Aspergillus oryzae, and Trichoderma reesei. Appl. Microbiol. Biotechnol. 102, 9481–9515.

Garcia-Estrada, C., Martin, J.F., Cueto, L., Barreiro, C., 2020. Omics approaches applied to Penicillium chrysogenum and penicillin production: revealing the secrets of improved productivity. Genes (Basel). 11, 712.

Gashgari, R., Ameen, F., Al-Homaidi, E., Gherbawy, Y., Al Nadhari, S., Vijayan, V., 2019. Mycotoxigenic fungi contaminating wheat; toxicity of different Alternaria compacta strains. Saudi J. Biol. Sci. 26 (1), 210–215. https://doi.org/10.1016/j.sjbs.2018.10.007.

Gonçalves, V.N., Cantrell, C.L., Wedge, D.E., Ferreira, M.C., Soares, M.A., Jacob, M.R., Oliveira, F.S., Galante, D., Rodrigues, F., Alves, T.M.A., et al., 2016. Fungi associated with rocks of the A tacama Desert: taxonomy, distribution, diversity, ecology and bioprospection for bioactive compounds. Environ. Microbiol. 18, 232–245.

Guo, Q.-F., Yin, Z.-H., Zhang, J.-J., Kang, W.-Y., Wang, X.-W., Ding, G., Chen, L., 2019. Chaetomadrasins A and B, two new cytotoxic cytochalasans from desert soil-derived fungus Chaetomium madrasense 375. Molecules 24, 3240.

Gupta, D.R., Surovy, M.Z., Mahmud, N.U., Chakraborty, M., Paul, S.K., Hossain, M.S., Bhattacharjee, P., Mehebub, M.S., Rani, K., Yeasmin, R., et al., 2020. Suitable methods for isolation, culture, storage and identification of wheat blast fungus Magnaporthe oryzae Triticum pathotype. Phytopathol. Res. 2, 1–13.

Hameed, A., Hussain, S.A., Yang, J., Ijaz, M.U., Liu, Q., Suleria, H.A.R., Song, Y., 2017. Antioxidants potential of the filamentous fungi (Mucor circinelloides). Nutrients 9, 1101.

Hamim, A., Boukeskasse, A., Duponnois, R., Mrabet, R., Hafidi, M., 2018. Screening and quantification of enzyme activity of ericoid fungi under solid-state fermentation. J. Mater. Environ. Sci. 1431–1438. doi: 10.26872/jmes.2018.9.5.156.

Huang, W.-Y., Cai, Y.-Z., Hyde, K.D., Corke, H., Sun, M., 2007. Endophytic fungi from Nerium oleander L (Apocynaceae): main constituents and antioxidant activity. World J. Microbiol. Biotechnol. 23, 1253–1263.

Keswani, C., Singh, H.B., Hermosa, R., Garcia-Estrada, C., Caradus, J., He, Y.-W., Mezaache-Aichour, S., Glare, T.R., Borriss, R., Vinale, F., et al., 2019. Antimicrobial secondary metabolites from agriculturally important fungi as next biocontrol agents. Appl. Microbiol. Biotechnol. 103, 9287–9303.

Lê, S., Josse, J., Husson, F., 2008. FactoMineR: an R package for multivariate analysis. J. Stat. Softw. 25, 1–18.

Ma, J., Ibekwe, A. M., Yang, C. H., & Crowley, D. E. (2016). Bacterial diversity and composition in major fresh produce growing soils affected by physiochemical properties and geographic locations. Science of the Total Environment, 563, 199–209.

Magdy, W., Abdel-Motaal, F.F., El-Zayat, S.A., El-Sayed, M.A., Helaly, S.E., 2017. Nigragillin, Nigerazine B and five Naphtho-γ\$-pyrones from Aspergillus japonicus isolated from hot desert soil. Nat. Prod. J. 7, 216–223.

Méndez-Liter, J.A., de Eugenio, L.I., Nieto-Dominguez, M., Prieto, A., Martinez, M.J., 2020. Hemicellulases from Penicillium and Talaromyces for lignocellulosic biomass valorization:-a review. Bioresour, Technol, p. 124623.

Meyer, V., Wu, B., Ram, A.F.J., 2011. Aspergillus as a multi-purpose cell factory: current status and perspectives. Biotechnol. Lett. 33, 469–476.

Moghaddam, M.S.H., Safaie, N., Soltani, J., Pasdaran, A., 2020. Endophytic association of bioactive and halotolerant Humicola fuscoatra with halophytic plants, and its capability of producing anthraquinone and anthranol derivatives. Antonie Van Leeuwenhoek 113, 279–291.

Moghaddam, M.S.H., Safaie, N., Tedersoo, L., Hagh-Doust, N., 2021. Diversity, community composition, and bioactivity of cultivable fungal endophytes in saline and dry soils in deserts. Fungal Ecol. 49, 101019.

Mtibaà, R., de Eugenio, L., Ghariani, B., Louati, I., Belbahri, L., Nasri, M., Mechichi, T., 2017. A halotolerant laccase from Chaetomium strain isolated from desert soil and its ability for dye decolourization. 3 Biotech 7, 1–13.

Orfali, R., Aboseada, M.A., Abdel-Wahab, N.M., Hassan, H.M., Perveen, S., Ameen, F., Alturki, E., Abdelmohsen, U.R., 2021. Recent updates on the bioactive compounds of the marine-derived genus Aspergillus. RSC Adv. 11, 17116–17150.

Owen, Lewis, Holm, Donald August, Ochsenwald, W.L., 2020. "Arabian Desert". Encyclopedia Britannica [WWW Document]. Available from: <https://www.britannica.com/place/Arabian-Desert>. Accessed 21 August 2021.

Renteria-Martinez, M.E., Meza-Moller, A., Guerra-Camacho, M.A., Romo-Tamayo, F., Ochoa-Meza, A., Moreno-Salazar, S.F., 2015. First report of watermelon wilting caused by Fusarium brachygibbosum in Sonora. Mexico. Plant Dis. 99, 729.

Rodrigues, C. et al., 2017. Fusarium species— a promising tool box for industrial biotechnology. Appl. Microbiol. Biotechnol.

Schimel, J., Balser, T.C., Wallenstein, M., 2007. Microbial stress-response physiology and its implications for ecosystem function. Ecology 88, 1386–1394.

Shan, L.Y., Cui, W.Y., Zhang, D.D., Zhang, J., Ma, N.N., Bao, Y.M., Dai, X.F., Guo, W., 2017. First report of Fusarium brachygibbosum causing maize stalk rot in China. Plant Dis. 101, 837.

Sharma, S., Gupta, S., Dhar, M.K., Kaul, S., 2018. Diversity and bioactive potential of culturable fungal endophytes of medicinal shrub Berberis aristata DC.: a first report. Mycobiology 46, 370–381.

Srinivas, C., Nirmala Devi, D., Narasimha Murthy, K., Mohan, C.D., Lakshmeesha, T.R., Singh, B.P., Kalagatur, N.K., Niranjana, S.R., Hashem, A., Alqarawi, A.A., et al., 2019. Fusarium oxysporum f. sp. lycopersici causal agent of vascular wilt disease of tomato: biology to diversity– a review. Saudi J. Biol. Sci. 26, 1315–1324.

Tavares, D.G., Barbosa, B.V.L., Ferreira, R.L., Duarte, W.F., Cardoso, P.G., 2018. Antioxidant activity and phenolic compounds of the extract from pigment-producing fungi isolated from Brazilian caves. Biocatal. Agric. Biotechnol. 16, 148–154.

Team, R.C. et al., 2013. R: A language and environment for statistical computing.

Tejesvi, M.V., Kajula, M., Mattila, S., Pirttilä, A.M., 2011. Bioactivity and genetic diversity of endophytic fungi in Rhododendron tomentosum Harmaja. Fungal Divers. 47, 97–107.

Thapa, S., Mishra, J., Arora, N., Mishra, P., Li, H., O' Hair, J., Bhatti, S., Zhou, S., 2020. Microbial cellulolytic enzymes: diversity and biotechnology with reference to lignocellulosic biomass degradation. Rev. Environ. Sci. Bio/Technology 19, 621–648.

Tirado-Ramirez, M.A., López-Urquidez, G.A., Amarillas-Bueno, L.A., Retes-Manjarrez, J.E., Vega-Gutiérrez, T.A., López Avendaño, J.E., López-Orona, C.A., 2021. Identification and virulence of Fusarium falciforme and Fusarium brachygibbosum as causal agents of basal rot on onion in Mexico. Can. J. Plant Pathol., 1–12

Toghueo, R.M.K., Boyom, F.F., 2019. Endophytes from ethno-pharmacological plants: Sources of novel antioxidants-a systematic review. Biocatal. Agric. Biotechnol. 22, 101430.

Wentzel, L.C.P., Inforsato, F.J., Montoya, Q.V., Rossin, B.G., Nascimento, N.R., Rodrigues, A., Sette, L.D., 2019. Fungi from admiralty bay (King George Island, Antarctica) soils and marine sediments. Microb. Ecol. 77, 12–24.

Yadav, G., Meena, M., 2021. Bioprospecting of endophytes in medicinal plants of Thar Desert: an attractive resource for biopharmaceuticals. Biotechnol. Rep., e00629.

Yadav, M., Yadav, A., Yadav, J.P., 2014. In vitro antioxidant activity and total phenolic content of endophytic fungi isolated from Eugenia jambolana Lam. Asian Pac. J. Trop. Med. 7, S256–S261.

Zhang, X.-Y., Tan, X.-M., Yu, M., Yang, J., Sun, B.-D., Qin, J.-C., Guo, L.-P., Ding, G., 2021a. Bioactive metabolites from the desert plant-associated endophytic fungus Chaetomium globosum (Chaetomiaceae). Phytochemistry 185, 112701.

Zhang, X., Xu, Z., Ma, J., Zhou, D., Xu, J., 2021b. Phylogenetic diversity, antimicrobial and antioxidant potential and identification of bioactive compounds from culturable endophytic fungi associated with mangrove *Bruguiera sexangula* (Lour.) Poir. Curr. Microbiol. 78, 479–489.

Zhou, J., Diao, X., Wang, T., Chen, G., Lin, Q., Yang, X., Xu, J., 2018. Phylogenetic diversity and antioxidant activities of culturable fungal endophytes associated with the mangrove species *Rhizophora stylosa* and *R. mucronata* in the South China Sea. PLoS ONE 13, e0197359.

Zohri, A.A., Moharram, A.M., Abd El-Ghani, O.A., 2017. Antioxidant potentialities of some strains belonging to endophytic, entomopathogenic and saprophytic fungi. Eur. J. Biol. Res. 7, 76–85.