

## Desert truffle biodiversity, biology, ecology, and mycorrhizal connection in Morocco

Hicham KADDOURI<sup>1,2\*</sup>, Lahcen OUAHMANE<sup>1</sup>,  
Abdessamad TOUNSI<sup>2</sup>

<sup>1</sup>Cadi Ayyad University, Laboratory of Microbial Biotechnologies, Agrosciences and Environment (BiomAgE), Morocco;  
[hicham.kaddouri@usms.ac.ma](mailto:hicham.kaddouri@usms.ac.ma) (\*corresponding author); [louahmane@uca.ac.ma](mailto:louahmane@uca.ac.ma)

<sup>2</sup>University of Sultan Moulay Slimane Morocco, Faculty of Sciences and Techniques, Avenue Mohamed, BP 591  
Beni Mellal 23000, Morocco; [abdessamad.tounsi@usms.ac.ma](mailto:abdessamad.tounsi@usms.ac.ma)

---

### Abstract

In Morocco, there are many different types of desert truffles, including *Terfezia*, *Tirmania*, *Delastria*, *Picoa*, and *Tuber*. The Maamora Forest, Doukkala-Abda Sahel, northeast of Morocco, and the Moroccan Sahara are the four truffle regions where the geographical distribution of these ascomycetes has been noted most frequently. In addition to being a great source of protein, amino acids, carbon hydrates, and fiber, desert truffles are also regarded as a valuable source of antibiotic alternatives for pathogenic bacteria that are resistant to antibiotics. Due to the widespread appreciation of truffles, we could use these resources to develop local populations, especially in truffle-producing regions. The biodiversity of desert truffles in Morocco and other Maghreb countries is one of the characteristics of truffles that are briefly discussed in this paper review. Ecology, biology, geographical spread, and final considerations include the mycorrhizal association of truffles, biochemistry, and physiology.

**Keywords:** biodiversity; biochemistry; desert truffles; mycorrhizal association; taxonomy

---

### Introduction

Several studies have been conducted on the global importance of truffles in terms of agriculture, medicine, and economics. Although some research finding outline fungi are heterotrophic organisms, acquiring organic matter through three main modes of nutrition (symbiotic, parasitic and saprotrophic). While many species of saprophytic fungi have been successfully cultivated for a long time Oei (2003), for example, Judas ear (*Auricularia auricula*) cultivated in China since 600 before Jesus Christ or *Agaricus bisporus* dating back to 17th century, other types of fungi are more difficult to cultivate (Hall and Zambonelli, 2012). The first to understand the symbiotic nature of chimeric associations between roots and fungi, but described long ago, he named mycorrhizae from the Greek *Mukè*, fungus, and rhizome, root (Frank, 2005). Like all fungi, truffles are unable to synthesize their organic matter and use solar energy, due to the absence of chlorophyll as a pigment responsible for photosynthesis, they live in association with plants for their supply of organic substances and sugars that are important in exchange for minerals with their hosts. The reciprocal exchange between fungi and

---

Received: 10 Mar 2023. Received in revised form: 10 Feb 2024. Accepted: 23 May 2024. Published online: 28 May 2024.

From Volume 13, Issue 1, 2021, Notulae Scientia Biologicae journal uses article numbers in place of the traditional method of continuous pagination through the volume. The journal will continue to appear quarterly, as before, with four annual numbers.

their hosts defines the relationship of symbiosis. They are characterized by a mycelium that travels through the soil looking for food, penetrating the root system of the plant and causing the disruption of its structure. The association between the host plant's secondary roots (rootlets) and the mycelium leads to the formation of a structure essential for exchanges: The mycorrhiza. On the roots of the family Cistaceae, which includes the annual and perennial species of the genera *Cistus*, *Tuberaria*, and notably *Helianthemum*, the mechanism of symbiotic connection is of an ectomycorrhizal and endomycorrhizal type (Fortas and Chevalier, 1992; Slama *et al.*, 2010; Zitouni-Haouar *et al.*, 2014). In this symbiotic relationship, the plant provides the fungus with carbon, which ensures its hydromineral nutrition. Additionally, both partners protect each other from the aggressions of the soil. Therefore, in mycorrhizal species, cultivation of a single fungus is difficult, if not impossible, and is limited to the vegetative stage if the entire plant-fungus relationship is not understood. Therefore, in light of this brief introduction, it is important to focus our research on magical resources: Truffles. Truffles are ascomycetes belonging to the order of Pezizales the hypogeous fructification (Yao *et al.*, 1995). They grow and develop in the Middle East and the Mediterranean basin, mostly in semi-arid and desert regions, and are edible (Bradai *et al.*, 2015), on calcareous soil rich in calcium (Bokhary and Parvez, 1992). Terfasse, or desert truffles, are ascomycetes that only develop in arid and semi-arid regions. Desert truffles have symbiotic relationships with the roots of trees like *poplar*, *oak*, and *hazelnut* (Harrison, 1997). Generally, the most common terfess host plants are herbaceous or perennial *Helianthemums* (Khabar, 2014).

The most essential qualities of truffles are their environmental and health benefits. They are full of proteins, vitamins, minerals, carbohydrates, and fats (Bokhary *et al.*, 1987; Bokhary and Parvez, 1993). Some types of truffles, like *Tuber melanosporum* (black perigord truffle), *Tuber aestivum* (summer truffle), *Tuber magnatum* (white truffle), and others that people like for their smell (Diaz *et al.*, 2003), are also appreciated. They have a symbiotic relationship with the roots of trees such as poplar, oak, and hazelnut (Harrison, 1997). Generally, the most common terfess host plants are herbaceous or perennial *Helianthemums* (Khabar, 2014).

Desert truffles are popular for their health and nutritional benefits. A study aimed to produce fungal biomass from *Tirmania nivea*, a natural renewable resource, using an artificial growth medium. The fungal biomass was grown in potato dextrose broth and analysed for antimicrobial activity. The crude extracts showed potential as antifungal, antibacterial, antiviral, anticancer, antioxidant, anti-trypanosomal, and anti-inflammatory agents. The study highlights the potential of desert truffles as a natural renewable resource (Khaled *et al.*, 2021).

Mycorrhiza results from the association established between vascular plants and their symbiotic soil fungi. Mycorrhiza improves the ability of plants to resist environmental factors, including nutrient deficiency, water stress, and soil nuisance (Barea *et al.*, 2011). In Morocco, research works related to truffles are not yet well developed, they are of taxonomic, floristic (Chatin, 1891; Khabar, 2002), phytosociological, cytological, ultrastructural, and geographical orders (Harki *et al.*, 2010; Khabar, 2014).

It was found that mycorrhizas were closely related to desert truffles. In spite of the significance of mycorrhizal connection to desert truffles, there have been little investigations in this subject. As a result, the major goal of this study is to document the recent studies of knowledge about mycorrhiza-desert truffle interactions, identify important gaps in knowledge, and provide solutions to fill these gaps in the future studies.

## Materials and Methods

To the objective of this study, a methodology based on main steps was chosen: A documentary research on knowledge of Moroccan truffles: Google scholar, PubMed, ScienceDirect, SpringerLink, Web of Science and Scopus.

### The desert truffles and taxonomy

The *Terfezia*, *Tirmania*, *Picoa*, *Carbomyces*, *Elderia*, *Eremiomyces*, *Kalaharituber*, *Mattiolomyces*, *Mycoclelandia*, *Stouffera*, and *Ulurua* genera are the taxa that make up the family of desert truffles (Kovács and Trappe, 2013). The identification of truffles is based on taxonomic criteria: The shape of the spores, the size, the ornamentation, and the structure of the gleba and the peridium (Mello *et al.*, 2006).

Most of the morphological studies to differentiate truffle species have been done on the fruiting body, the ascocarp. Concerning the ascocarp (truffle itself), these morphological differences are observed at different levels: 1) macroscopic (size of the ascocarp, colour of the gleba, aspect of the peridium) and 2) microscopic (size of the gleba, aspect of the peridium). Gleba, aspect of the peridium and 2) microscopic (morphology of the asci and spores). The size of the fruiting body depends of course on the environment but is also species-dependent. They are also distinguished by their chemical and molecular characteristics. Indeed, the shape of the ascocarps is spherical (subglobose or piriform, glabrous) characterizing the species of *T. nivea* (Jamali and Banihashemi, 2012). Their skin is light brown or creamy white, and the pith, called gleba, is initially white or yellowish and becomes brown with age. Generally, the fruiting body is characterized by a spherical pear-shaped form of width 5-12 (20) cm, lobed or irregular. The outside is white, cream, ochre, rusty-ochre, or brown-ochre. In maturity, the gleba is compact, white, and elastic, with light pink or ochre spots and subtle white veins. It has a lovely odor. In contrast, the fruiting bodies of *T. arenaria* are 3-12 (15) cm wide, usually with a rudimentary and irregularly spherical base. The outer part is dry, beige, ochre-beige, or pink-beige and in most cases lobed, reddish-brown, grayish-blackish brown, or brown at maturity. The gleba is characterized by yellow colours and a slightly spermiac smell (Loizides *et al.*, 2012). The *T. claveryi* ascocarps collected in Morocco had the following shapes: spherical, ovoid, and cordiform, fresh weights of between 17 and 50 g. The gleba exhibited a few millimeters of spotting, and the peridium was initially pinkish-white in hue before turning brownish-black. The fertile, round, pinkish (before turning light brown), and spherical nodules in the gleba were divided by thin, pale veins. The gleba had a firm, slightly spongy texture. Hyaline, grey, spherical ascospores (18-21  $\mu$ m) with an alveolus network were found inside the asci, which were ovoid (64-68-72-84  $\mu$ m) in form. The size and shape of the ascocarps of *Tirmania* sp. transformed from sub-globular and piriform to turbine-like, with lobes or irregular morphologies (Khabar, 2016). The four main truffle growing regions in Morocco are the North-East, the Maâmora forest, the Doukkala-Abda Sahel, and the Moroccan Sahara. There are about ten species of desert truffles in these regions belongs to the genera *Tuber*, *Delastria*, *Terfezia*, *Tirmania* and *Picoa* (Hakkou *et al.*, 2022). Table 1 and 2 show desert truffle biodiversity.

**Table 1.** Desert truffle biodiversity in Morocco and other Arab nations

Genus: <i>Terfezia</i> , Systematic: Division: <i>Ascomycota</i> / Class: <i>Pezizomycetes</i> / Order: <i>Pezizales</i> / Family: <i>Terfeziaceae</i>					
Country	Taxonomy of desert truffles		Biotic and abiotic factors	Harvest period	References
Morocco	<i>Terfezia arenaria</i> (Moris)	<i>Tuber arenarium</i> Moris (1829)	Climate: Semi-arid Soil: acid, light sandy Host plant: <i>Helianthemum guttatum</i>	Mid-February to early June	(Trappe, 1971; Malençon, 1973, Abourouh, 2011; Khabar, 2016; Harir <i>et al.</i> , 2019; Abourouh, 2020; Hakkou <i>et al.</i> , 2022)
		<i>Choiromyces Leonis</i> Tul. and C. Tul. (1845)			
		<i>Rhizopogon Leonis</i> Tul. and C. Tul. (1850)			
		<i>Terfezia leonis</i> Tul. and C. Tul. (1851)			
	<i>Terfezia boudieri</i> Chatin (1891)	<i>Terfezia deflersii</i> Patouillard (1894)	Climate: Semi-arid and arid Soil: basic, gypseous and calcareous Host plant: <i>Helianthemum Lippii</i> var. <i>sessiliflorum</i> and <i>Helianthemum ledifolium</i>	March and April	(Chatin, 1891; Khabar, 2002; Roth-Bejerano <i>et al.</i> , 2004; Khabar, 2016; Abourouh, 2020)
	<i>Terfezia claveryi</i> Chatin (1891)	<i>Terfezia hafizzi</i> Chatin (1892)	Climate: Semi-arid, Arid, pre-Saharan, and Saharan Soil: basic, limestone or marl-gypsum soil Host plant: <i>Helianthemum lipii</i> and <i>Helianthemum apertum</i>	Early March to early June	(Chatin, 1891; Malençon, 1973; Alsheikh, 1994; Khabar, 2002; El Akil <i>et al.</i> , 2016; Khabar, 2016)
		<i>Terfezia hanotauxi</i> Chatin (1895)			
	<i>Terfezia leptoderma</i> Tulasne (1851)	<i>Choiromyces leptodermus</i> Tulasne and C. Tulasne (1845)	Climate: Semi-arid, Arid Soil: sandy acid or more compact, clayey and siliceous Host plant: <i>Helianthemum guttatum</i>	The third week of February and until May	(Díez <i>et al.</i> , 2002; Khabar, 2002; El Akil <i>et al.</i> , 2016; Abourouh, 2020)
<i>Terfezia olbiensis</i> Tul. and C. Tul. (1845)	<i>Choiromyces olbiensis</i> Tul. and C. Tul. (1845)	Climate: Arid Soil: sandy Host plant: <i>Pinus halepensis</i>	December and January	(Alsheikh, 1994; El Akil <i>et al.</i> , 2016)	
Genus: <i>Tuber</i> , Systematic: Division: <i>Ascomycota</i> / Class: <i>Pezizomycetes</i> / Order: <i>Pezizales</i> / Family: <i>Tuberaceae</i>					

Country	Taxonomy of desert truffles		Biotic and abiotic factors	Harvest period	References
Morocco	<i>Tuber asa</i> Tulasne (1851)	<i>Terfezia gennadii</i> Chatin (1896)	Climate: Semi-arid Soil: acidic soils sandy or more compact, clayey and siliceous soils Host plant: <i>Helianthemum guttatum</i>	End of the month of February until the end of April	(Khabar, 2002, 2016; Abourouh, 2020)
		<i>Tuber lacunosus</i> Mattiolo (1900)			
		<i>Tuber gennadii</i> (Chat) atouillard (1903)			
	<i>Tuber oligospermum</i> (Tul. and Tul.) Trape (1979)	<i>Terfezia oligosperma</i> Tul and Tul. (1851)	Climate: Semi-arid Soil: sandy Host plant: <i>Pinus pinaster</i> var. <i>atlantica</i>	December until April or May	(Khabar, 2002, 2016; Abourouh, 2020)
		<i>Delastreopsis oligosperma</i> (Tul.) Matt. (1904)			
	<i>Tuber gennadii</i> (Chatin) Patouillard (1903)	<i>Terfezia gennadii</i> Chatin (1896)	Climate: Semi-arid Soil: sandy soils or more compact, clayey, and siliceous Host plant: <i>Helianthemum guttatum</i>	March to June	(Abourouh, 2020)
<i>Tuber lacunosum</i> Mattiolo (1900)					
<i>Loculotuber gennadii</i> (Chatin) Trappe, (1992)					
Genus: <i>Tirmania</i> , Systematic: Division: <i>Ascomycota</i> / Class: <i>Pezizomycetes</i> / Order: <i>Pezizales</i> / Family: <i>Terfeziaceae</i>					
Country	Taxonomy of desert truffles		Biotic and abiotic factors	Harvest period	References
Morocco	<i>Tirmania Nivea</i> (Desf.) Trappe, 1971	<i>Tuber niveum</i> Desf. (1823)	Climate: Arid, Pre-Saharan, and Saharan Soil: sandy Host plant: <i>Helianthemum birtum</i> and <i>Helianthemum lipii</i>	From February through May	(Malençon, 1973; El Aji, 1999; El Akil <i>et al.</i> , 2016)
		<i>Terfezia ovalispora</i> Patouillard (1890)			
		<i>Tirmania ovalispora</i> Pat. (1892)			
		<i>Tirmania africana</i> Chatin (1892)			

	<i>Tirmania pinoyi</i> (Maire) Malençon (1973)	<i>Terfezia pinoy</i> Maire, (1906)	Climate: Arid, Pre-Saharan, and Saharan Soil: sandy Host plant: <i>Helianthemum birtum</i> and <i>Helianthemum lipii</i>	From February through May	(Malençon, 1973; El Aji, 1999; El Akil <i>et al.</i> , 2016)
Genus: <i>Delastria</i> , Systematic: Division: <i>Ascomycota</i> / Class: <i>Pezizomycetes</i> / Order: <i>Pezizales</i> / Family: <i>Terfeziaceae</i>					
Country	Taxonomy of desert truffles		Biotic and abiotic factors	Harvest period	References
Morocco	<i>Delastria rosea</i> Tulasne (1843)	<i>Terfezia rosea</i> (Tul.) Torrend, (1907)	Climate: semi-arid Soil: sandy Host plant: <i>Pinus pinaster</i> var. <i>atlantica</i>	From February through May	(Khabar, 2002, 2016; Abourouh, 2020)
Genus: <i>Picoa</i> Systematic: Division: <i>Ascomycota</i> / Class: <i>Pezizomycetes</i> / Order: <i>Pezizales</i> / Family: <i>Helvellaceae</i>					
Country	Taxonomy of desert truffles		Biotic and abiotic factors	Harvest period	References
Morocco	<i>Picoa juniperi</i> Vittadini (1831)	<i>Picoa juniperina</i> Tulasne (1851)	Climate: Arid, Pre-Saharan, and Saharan Soil: calcareous Host plant: <i>Helianthemum lipii</i>	February to April	(El Aji, 1999; Khabar, 2016)

**Table 2.** Real truffles “Tuber” in Morocco

Country	Taxonomy of desert truffles		Biotic and abiotic factors	Harvest period	References
Morocco	<i>Tuber Melanosporum</i> Vittadini, 1831	<i>Tuber brumale</i> Pulpa obscura, odora P. Micheli (1729)	Climate: Semi-arid and subhumid to humid Soil: well-drained and porous aerated limestone Host plant: <i>Quercus ilex</i>	November through March	(Laqbaqbi, 2020)
		<i>Tuber gulosorum</i> (Scopoli) Pico (1788)			
		<i>Tuber nigrum</i> Bulliard (1788)			
		<i>Tuber cibarium nigrum</i> Bulliard (1791)			
		<i>Tuber cibarium</i> Persoon, (1801)			
		<i>Tuber cibarium</i> Bulliard Fries (1823)			
		<i>Tuber gulonum</i> (Corda) Paoletti (1889)			
	<i>Tuber Borchii</i> Var. <i>sphaerosperma</i> Malençon (1973)	<i>Tuber sphaerospermum</i> Malençon (2006)	Climate: Semi-arid Soil: sandy Host plant: <i>Pinus halepensis</i> and <i>Pinus pinea</i>	April and May	(Malençon, 1973; Abourouh, 2020)
	<i>Tuber rufum</i> Pico, 1788	<i>Tuberum tertium</i> genus Mattioli (1544)	Climate: subhumid and humid Soil: calcareous	June to November	(Malençon, 1973)
<i>Tuber cinereum</i> Tul et C. Tul. (1844)					
<i>Tuber lucidum</i>					

	Bonnet (1884)		Host plant: <i>Quercus ilex</i>		
	<i>Tuber caroli</i>				
	Bonnet (1885) <i>Tuber rutilum</i> R Hesse, (1894)				
Country	Taxonomy of desert truffles		Biotic and abiotic factors	Harvest period	References
Morocco	<i>Tuber uncinatum</i> Chatin (1887)	<i>Tuber Aestivum</i> Vittadini (1831)	Climate: subhumid and humid Soil: Acidic soils sandy Host plant: <i>Quercus ilex</i>	September to January	(Malençon, 1973)
	<i>Tuber brumale</i> Vittadini (1831)	<i>Tuber brumale</i> Vittadini var. moschatum Ferry de la Bellone (1888)	Climate: humid Soil: calcareous Host plant: <i>Quercus ilex</i>	November to March	(Olivier <i>et al.</i> , 2018)
Algeria	<i>Tirmania</i>	<i>Tirmania pinoyi</i> (Maire)	<i>Helianthemum lippii</i> (L.) Dum.- Courset		(Bradai <i>et al.</i> , 2013)
Tunisia	<i>Terfezia</i>	<i>Terfezia boudieri</i> Chatin	<i>Helianthemum sessiliflorum</i> Desf.		(Hamza <i>et al.</i> , 2016)
Egypt	<i>Terfezia</i>	<i>Terfezia arenaria</i> (Moris) Trappe	<i>Helianthemum lippii</i> (L.) Dum. Courset		(El-Kholy, 1989)
	<i>Tirmania</i>	<i>Terfezia claveryi</i> Chatin <i>Tirmania nivea</i> (Desf.) Trappe			
Bahrain	<i>Tirmania</i>	<i>Tirmania nivea</i> (Desf.) Trappe	<i>Helianthemum kabiricum</i> Del.		(Mandael and Al-Laith, 2007)
	<i>Phaeangium</i>	<i>Phaeangium lefebvrei</i> Pat.			
Kuwait	<i>Tirmania</i>	<i>Tirmania nivea</i> (Desf.) Trappe	<i>Helianthemum kabiricum</i> Dei.		(Alsheikh and Trappe, 1983)
Jordan	<i>Terfezia</i>	<i>Terfezia claveryi</i> Chatin	<i>Helianthemum</i> Spp.		(Janakat <i>et al.</i> , 2004)
Iraq	<i>Terfezia</i>	<i>Terfezia claveryi</i> Chatin	<i>Helianthemum</i> Spp.		(Dahham <i>et al.</i> , 2016)
Saudi Arabia	<i>Terfezia</i>	<i>Terfezia claveryi</i> Chatin	<i>Helianthemum vesicarium</i> Boiss. <i>Helianthemum</i> <i>kabiricum</i> Del. <i>Helianthemum</i> <i>lippii</i> (L.) Dum.		(Sawaya <i>et al.</i> , 1985; Bokhary <i>et al.</i> , 1987; Hashem and Al-Obaid, 1996; Janakat <i>et al.</i> , 2005; Schillaci <i>et al.</i> , 2017)
		<i>Terfezia boudieri</i> Chatin			
		<i>Tirmania</i>			
	<i>Tirmania pinoyi</i> (Maire)				
	<i>Picoa</i>	<i>Picoa juniperi</i> Vittad.			
		<i>Picoa lefebvrei</i> (Pat.) Maire			
<i>Phaeangium lefebvrei</i> (Pat.) Maire					

### Geographical distribution of truffles

Geographically, truffles are spread in arid and semi-arid areas around the Mediterranean Basin and the Middle East (Bradai *et al.*, 2015). The study conducted in Morocco by Khabar (2002), announces three sites that have been designated as truffle areas, are the forest of Maamora which is located in the northwest, east of Rabat the soil is acidic in nature, and a semi-arid climate. The second area located in the east and southeast of Morocco, it consists of the eastern high plateau of Morocco which is characterized by a soil of limestone nature and an arid climate and sub-Saharan. The last area is the plain of Abda located east of the city of Safi, this area

is characterized by limestone soil and a semi-arid climate. Thus, according to Abourouh (2011) and Khabar (2016), four major areas have been identified truffle growing in Morocco, they are the Oriental, the Maâmora forest, the Sahel of Abda-Doukkala, and the Moroccan Sahara.

Ten species may be found in Morocco's semi-arid and arid areas, where yearly rainfall is low and average temperatures are high (Zniber *et al.*, 2022). They are associated to *Cistus*, *Pinus*, and many other species, but the *Helianthemum* is where they are more frequently found (Zniber *et al.*, 2022). Some of Morocco's desert truffles are found in the country's south. The first is terfes red du Tafilalet, also known as *T. claveryi* (*T. hafizi* Chat.). It is situated close to Ksar Es-Souk, Boudenib, and Figuig (Abou Lakhel and Bni Guil areas), in the regions of Tendrala, Ain Beni Mather, Erfoud, Bouarfa, and Bou Bernous (Khabar, 2016; Bermaki *et al.*, 2017). Using *H. lipii* as a host plant, it can be collected following the rains that occur from March to May. Additionally, *T. boudieri* can be found a few kilometres east of Safi in the Had Hrara and Abda plain in the Oualidia area. Additionally, it can be found in the areas around Ain Beni Mather and Erfoud. More significantly, it can be found in the March and April harvested *Helianthemum* species *H. lipii* and *H. ledifolium* in the desert plains. *Ti. nivea* and *Ti. pinoyi* have been discovered as two additional species that fall under the umbrella of the genus *Tirmania*. Ain Beni Mather, Tendrala, Bouarfa, Erfoud, Figuig, and Rissani are among the south-easterly areas where they are dispersed. The crop season lasts from early December to early March when *H. hirtum* serves as the host plant.

In other countries Tunisia, Algeria, Egypt, Libya, Iraq, Saudi Arabia, Kuwait, Syria, Palestine and Iran are among the countries where desert truffles are found. Additionally, they are found in the southern regions of France, Spain, Italy, Greece, and Portugal, in the Mediterranean Basin (Khabar, 2016). *T. claveryi* is found in the African nations of Libya (Hashem *et al.*, 2018), Tunisia, Algeria, Egypt (Khabar, 2016), and even in France and Spain (particularly in the southern semi-desert regions) (Khabar, 2016). Additionally, *T. boudieri* can be found in Libya and Egypt, sometimes in Tunisia and Algeria under the *Helianthemum lipii*, and occasionally under the *Rhathierium suaveolens* Desf.

In Tunisia, the desert truffles are mainly found in the country's center and south.

In Algeria, truffles are grown in the regions of Bechar (Taghit, Kenadssa, Tabelbala, Béni Abbes, Abadla), Ouargla (Oued Mya), Tindouf, Timimoun, Touggourt, Tamanrasset (Montagnes du Hoggar), El Golea, Ghardaïa, Biskra, Djelfa, Batna, Boussaâda, Saida, Naama, Mécherai, Laghouat (Chevalier, 1984).

In France, Spain, Portugal, Hungary, and northern Serbia one finds *Terfezia boudieri*, *Terfezia claveryi*, *Terfezia olbiensis*, *Terfezia leptoderma*, and *Terfezia arenaria* (Maire, 1906; Malençon, 1973; Diaz *et al.*, 2003; Culleré *et al.*, 2010).

In addition, the following species are found in Turkey, Syria, Lebanon and the Middle East, *Picoa lefebvrei*, *Picoa juniperi*, *Tirmania nivea*, *Tirmania pinoyi*, *Terfezia boudieri*, *Terfezia arenaria*, *Terfezia leptoderma*, and *Terfezia claveryi* were identified by Alsheikh and Trappe in 1983.

Four truffle species were identified in the non-Mediterranean Asian countries like Saudi Arabia, Bahrain, Qatar, and Kuwait during the census. The desert white truffle species *Tirmania nivea* is locally known as Zubaidi. Consumers prefer the latter species over the other. *Terfezia boudieri*, *Terfezia claveryi*, and *Picoa lefebvrei* are two types of brown truffles known locally as kholaiissi (Al-Laith, 2010).

## Truffle biology

A recent study carried out by Desert truffles are hypogeous fungus that create a symbiotic relationship with *Cistaceae* family plants and the reproductive methods and biochemical mechanisms behind the ectendomycorrhizal relationship of these fungi are unknown (Marqués-Gálvez *et al.*, 2021). *Terfezia claveryi* Chatin and *Tirmania nivea* Trappe, two highly prized edible desert truffles, have had their genomes sequenced



and compared to those of other *Pezizomycetes*. In the same context, Marqués *et al.* (2021) identified fungal genes involved in sexual reproduction in desert truffles as well as genomic and secretomic features distinct from other *Pezizomycetes* in desert truffles, such as the proliferation of a significant number of gene families with unknown Pfam domains and a number of small, species or desert truffle-specific secreted proteins that were differentially managed in the symbiosis. The factors that induce sexual reproduction of the truffle are not known, and many burned sites, where the vegetative presence of the truffle has been verified, remain non-productive. Laboratory studies on unicellular and filamentous Ascomycetes have highlighted the importance of factors such as substrate modification (including nutrient restriction), light, pH and atmospheric conditions, inducing either vegetative or sexual reproduction (Debuchy *et al.*, 2010). Very few studies have identified the factors leading to fructification in macromycetes mushrooms, but it appears that abrupt changes in temperature, nutrient availability, and water availability may all have an impact on the growth of the mycelium and lead to the formation of fructifications (Kües and Liu, 2000; Oei, 2003). According to Pacioni *et al.* (2014) hydric stress encourages the commencement of young ascocarp in truffle, and the mycelium's strong activity (measured by CO<sub>2</sub> emission) precedes their creation. In general, it appears that a moderated water stress is advantageous to the vegetative growth of the truffle (rate of mycorrhization). Olivera *et al.* (2014) indicating that careful irrigation is necessary to encourage the maintenance of truffles.

### **Development of the ascocarp and method of reproduction of the truffle**

As is typical for ascomycetes, the mycelium haplotype forms the ectomycorrhizas of truffle (Rubini *et al.*, 2014). The genes present locally at the level of the ectomycorrhizas will act as the individual mother during reproduction, forming the gleba, the sterile chair of the ascocarp, in which they participate through nourishment. An isotopic CO<sub>2</sub> measurement experiment allowed researchers to track the carbon produced by the host tree's photosynthetic process, demonstrating that the ascocarp's carbon-based nutrition comes from the tree through the ectomycorrhizas, which is connected to the ascocarp through previously unrecognized connections (Le Tacon *et al.*, 2013). The source of other compounds (phosphate, azote, etc) has not been able to be identified by this method, although they may be directly absorbed into the soil by the truffle mycelia (Barry *et al.*, 1994) and/or involve bacteria, such as azote fixators of the *Bradyrhizobiaceae* family (Antony-Babu *et al.*, 2014) for *T. magnatum* (Barbieri *et al.*, 2010).

The ascocarp, which is enclosed by the gleba, contains thousands of intensely pigmented spores that make them resistant to passing through a digestive tube (Piattoni *et al.*, 2014). It has been established that these spores are the result of heterothallic sexual reproduction (Rubini *et al.*, 2011), despite Truffle's long-held homothallic reputation. This hypothesis had been advanced due to the absence of heterozygosis observed in one of the first studies using codominant genetic markers (two markers for microsatellites that allow for the detection of different alleles, or heterozygosis (Bertault *et al.*, 2001). The possibility of a crossover between two individuals within this haploid species would thus have been made more likely by the presence of heterozygotes. However, it is likely that only the gleba's ADN was extracted and/or that the two microsatellite markers used were not sufficiently polymorphic (carried little genetic variability). A few years later, the sequencing of the truffle genome souche haploid Mel28 (Martin *et al.*, 2010). The existence of a sexual allele was shown (MAT1-2-1, abbreviated as MT2 that is indicative of heterothallism. The sexually antagonistic sequence MAT1-1 (abbreviated as MAT1) has subsequently been identified (Rubini *et al.*, 2011). When the ADN of the spores is extracted using a specific procedure, which 1) concentrates the ascospores and 2) rips apart the asques and the paroi of the spores, it confirms that the truffle is a heterothallic mushroom (Paolocci *et al.*, 2006). As a result, the genotype of the mother is determined by working with the gleba's ADN, and the genotype of the father can be determined by comparing the genotype of the mother to the zygote, which was obtained by working with

the spores ADN. Because other species cannot directly achieve the parental genotypes, Truffe's particularity makes it an original biological function model.

### Ecological studies on desert truffles

In the Great Sahara of Morocco, the location of desert truffles is proven in soils of homogeneous texture, such as calcareous, aerated, and sandy soils, sometimes, they are located in soils of calcareous sandy loam nature (Khabar, 2016). The existence of desert truffles is rarely noted in acid soils. It is interesting to point out that species of the genus *Helianthemum* are often symbiotic with desert truffles as *Helianthemum lipii* Pers., *H. birtum* Mill, *H. asperum* Lag, Ex Dunal, *H. ledifolium* (L.) Mill. etc. The organic matter concentration, fertility, and exchange capability of soil must be low. Desert truffles need phosphate, nitrogen, potassium, calcium, and iron, yet it has been found that low levels of phosphate and iron enhance mycorrhizal potential. It should be noted that the mycorrhization potential is increased when phosphate and iron contents are low. The quantity and frequency of rainfall is a significant limiting factor for desert truffles in terms of climatic conditions. In general, rain is needed in the winter and spring months, but for some species, rain is needed both in the winter and spring. Desert truffles can be found in a variety of bioclimatic phases, including dry, semi-arid, sub-Saharan, and Saharan, based on just-released research. Despite being in a desert setting, the regions of Beni Guil and Abu Lakhel have the highest concentrations of desert truffles. 17.9 °C on average for the low and 18.6 °C on average for the high. As a result, these two places experience precipitation that is on average 170 millimetres per year. The development of truffles is greatly aided by the significant amounts of rainfall that fall in these regions throughout the night and early in the morning, as well as by dewfall, thunder, and lightning. The great desert and the bulk of these characteristics are found in southern Morocco (Bermaki *et al.*, 2017). In other parts of the globe, Saudi Arabia is conducting ecological research on desert truffles. Precipitation was listed by Hashem *et al.* (2018) as another essential element for the growth of the arid truffle. Reduced precipitation may change the host plant's physiological makeup and cause a decline in the production of spores and ascocarps. Additional factors include the weather, ambient temperature, and the physicochemical properties of the earth. The two main host plants on alkaline soils are *H. ledifolium* and *H. salicifolium* (L.) Mill. The reaping season starts in early December, and rain falls in October and December.

### Truffle life cycle

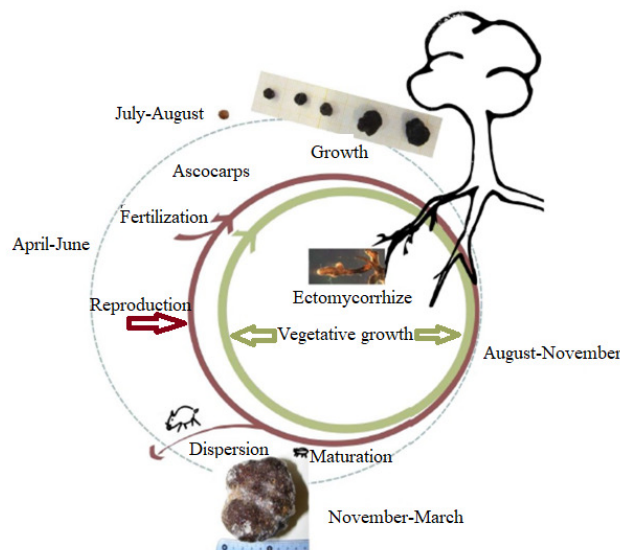
In the context of defining the symbiotic view cycle of truffles, it is necessary to talk about the emergence and functioning of the mycorrhizal association. The fungi colonize the surfaces and the cortex. Externally, tiny fungal hyphae efficiently explore the soil. 90% of all plants depend on this symbiotic relationship, which differs in the anatomical structures, fungal taxa, and plant families involved (Brundrett, 2002; van der Heijden *et al.*, 2015). The fossil record and phylogenetic analyses date the emergence of mycorrhizal communities to the Ordovician, where they played an important role in the colonizing of emerging terrestrial plants (Le Tacon and Selse, 1994; Remy *et al.*, 1994). Indeed, the fossil structure found is very similar to that of the arbuscular endomycorrhiza (AM) formed. Today, there are only 244 known species of Glomeromycetes with about 80% of all plants (Smith and Read, 2008). More recently, 100-200 Ma ago, ectomycorrhizal associations emerged (van der Heijden *et al.*, 2015). This association concerns woody plants belonging to the families of Cistaceae, Pinaceae, Fagaceae, Tiliaceae, etc (Brundrett, 2002), which dominate the Mediterranean temperate and boreal forests (Smith and Read, 2008). The loss of genes is responsible for cellulose and lignin degradation (Plett and Martin, 2011). However, ectomycorrhizal fungi (ECMs) are endowed with a catalytic capacity to utilize soil

organic and mineral matter (Rineau *et al.*, 2012). It is crucial to note that, for instance, the truffle, can develop in pure culture using cellulose as a source of carbon (Mamoun and Olivier, 1991).

The truffles are ascomycetes with hypogeous fruiting that grow underground from 5 to 10 cm deep. Throughout the world, more than hundreds of different species of truffles are known, and regularly the discovery of new species is observed. Taxonomically, these mushrooms belong to the order *Pezizales* and the family *Tuberaceae* and *Pezizaceae* (El Enshasy *et al.*, 2013). For centuries truffles belonging to the family *Tuberaceae* are widely edible, so the latter knew various lineages mainly truffle mushrooms (Læssøe and Hansen, 2007). Worldwide, the *Tuber* genus of the *Tuberaceae* family includes about 180 species (Bonito *et al.*, 2010). The *Tuber* genus truffles that found in Europe's temperate forests, New Zealand, Australia, America and Asia are qualified as culinary quality (Kinoshita *et al.*, 2011; Berch and Bonito, 2016). Generally, the desert truffles that grow in semi-arid and arid regions like Morocco, Egypt, Tunisia, Saudi Arabia, Syria, Kuwait, Iraq, and South Africa belong to the genus of *Tirmania* and *Terfezia* (El Enshasy *et al.*, 2013, Bradai *et al.*, 2015). *Tuber melanosporum*, *Tuber brumale*, *Tuber aestivum*, *Tuber indicum*, *Tuber uncinatum*, *Tuber himalayense*, and *Terfezia claveryi* are species of black truffles. Whereas, *Tuber magnatum*, *T. aculatum*, *T. borchii*, *T. latisporum*, *T. japonicum*, *T. oregonense*, and *Tirmania nivea* are the white truffles (Wang and Marcone, 2011). The Italian species (Eastern Europe) *T. magnatum* has been declared the most expensive truffle (Mello *et al.*, 2006). Therefore, it is important to point out that, in the Italian markets, the price of one kilogram of this species is 8000 dollars (Jeandroz *et al.*, 2008). Truffles are characterized by a genome with a large molecular weight; *T. melanosporum*, for example, has a 125 Mb genome (Chen *et al.*, 2014).

Truffles are ectomycorrhizal fungus with symbiotic roots, characterized by a complicated life cycle, the mycelium establishing symbiotic connection with host species primarily with the roots of several trees, including *hazelnut*, *pine*, *poplar*, *oak*, and *eucalyptus* (Mello *et al.*, 2006; Patel, 2012).

Since truffles grow their sexual fruiting bodies underground, insects and mammals are necessary for spore distribution (Læssøe and Hansen, 2007). The haploid spore develops into haploid free-living mycelium after ascospores have been released, creating an ectomycorrhizal connection with the roots of host plants. The ascoma-bearing asci, which is the sexual fruiting body, is then generated by the aggregation of hyphae (Figure 1) (Paolocci *et al.*, 2006; Chen *et al.*, 2019).



**Figure 1.** The annual life cycle of the truffle (Taschen, 2015)

For example, the cycle of life for truffles, *Tuber melanosporum* is a truffle fungus, the fruiting of this species is localized in open woodlands. During the vegetative phase, the formation of mycelium in the soil is seen, developing ectomycorrhizal relationships with many plant groupings (Figure 1). Its most well-known host species mainly for inoculation are oaks (*Quercus* spp., Fagaceae) and hazels (*Corylus* spp., Betulaceae) (Olivier *et al.*, 2012). According to Comandini *et al.* (2006), *Cistus* are fewer known hosts for the presence of truffle species or the genus *Tuber*, or *arbutus*; (a species of small tree shrubs of the family Ericaceae) (Lancellotti *et al.*, 2014). It is, therefore, necessary to point out that, the burnt is an important indicator of the presence of mycelium of truffles in the ground (Streiblová *et al.*, 2012). It is most observable in spring. In some places, few or no burns are visible, but the name always refers to the area where the truffle grows. When these burnt areas are productive, the fruiting of the truffle ascomycetes begins in spring, we speak of a period known as birth that can last until the end of July (Kulifaj, 1984). After a few months, the development and enlargement of the ascocarp are in the soil releasing a particular aroma (sulfur compounds such as dimethyl sulfide and alcohols such as 2-methyl-1-propanol and 1-octen-3-ol (Splivallo *et al.*, 2011). From November until the first frosts in the soil, it reaches its spore and aromatic maturity.

### Considerations of biochemistry and physiology

The desert truffles have a distinctive economic and medicinal significance and are extensively used throughout the globe. Polysaccharides have been found to be present in medicinal mushrooms, and these polysaccharides have been shown to have antibacterial and anticancer properties (Schillaci *et al.*, 2017). Rare reports on the chemistry and makeup of truffles, which frequently represent their economic importance, are extremely rare. Truffles are a fantastic and plentiful supply of carbs, fiber, high-quality protein, and amino acids (Murcia *et al.*, 2003; Mandel and Al-Laith, 2007). According to estimates, proteins make up 20% of the dry bulk of desert truffles, which is more than the majority of plants and fungi. Desert truffles are also frequently suggested for their therapeutic benefits against a variety of diseases (Murcia *et al.*, 2003; El Enshasy *et al.*, 2013). Additionally, truffles are a particularly abundant source of a number of chemical compounds with clinically significant anti-inflammatory, antimutagenic, antibacterial, and anticarcinogenic properties (Murcia *et al.*, 2002; Al-Laith, 2010; Dib-Bellahouel and Fortas, 2011). Truffles are also said to have anti-inflammatory and antioxidant qualities (Murcia *et al.*, 2002; Kagan-Zur *et al.*, 2013).

Truffles contain bioactive organic components like ergosterol, phenolic acids, carotenoids, flavonoids, and phenolic derivatives, which account for their antioxidant activity (Al-Laith, 2010; Villares *et al.*, 2012). In a separate study, Bouzadi *et al.* (2017) determined the protein (16.3% and 18.5%), fat (6.2 and 5.9%), and carbohydrate (67.2 and 65%) content of Libyan wild truffle (*Terfezia* and *tirmania*). Other studies indicate that *Terfezia* and *Tirmania* ascocarps (fruiting bodies), which are found in desert truffles, are well-known delicacy that are heavily promoted primarily for their flavour and nutritive value (Kagan-Zur *et al.*, 2014). Thus, *Terfezia boudieri* contains saturated and unsaturated fatty acids, such as behenic, stearic, margoric, pentadecanoic, arachidic, palmitoleic, palmitic, stearic, oleic, linoleic, and linolenic, according to Bokhary *et al.* (1989) and Bouzadi *et al.* (2017) also reported an abundance of potassium, iron, proteins and phenolics in (black truffle) *Terfezia claveryi* and *Tirmania nivea* (white truffle). Numerous researchers, like Chellal and Lukasova (1995), Janakat *et al.* (2004) and Janakat *et al.* (2005), have established the therapeutic qualities of desert truffles, including their antibacterial and antimicrobial properties. Splivallo (2008) about two hundred different secondary metabolites have been found in truffles, including terpenoids, flavonoids, fatty acids, essential oils, phenolics and aromatic chemicals, the dry biomass of Iraqi truffles (*Tirmania pinoyi*, *Terfezia claveryi* and *Tirmania nivea*) contains 9.7 and 25.5% phosphorus, 8.1% to 13.8% protein and 16.6% to 24.8% carbohydrates, as described by (Hussain and Al-Ruqaie, 1999). Also included in truffles are the important minerals K, Na, Ca, Al, Zn, Mn, and Mg (Wang and Marcone, 2011). Furthermore, up to 80% of truffle

biomass is comprised of insoluble polysaccharides, hemicelluloses, chitin and pectin (Cheung, 1997). Desert truffles also contained bioactive substances such as phenols, anthocyanin and carotenoids (Gouzi *et al.*, 2013). In addition to noticing that the desert truffle fruiting bodies contain a significant quantity of sugar (15.4%), Slama *et al.* (2009) noted that only 2.02% of the various individual sugars determined are soluble and the remaining 10.5% are insoluble. Truffles from the desert are rich in calcium, potassium, phosphorus, magnesium and iron. For instance, *Terfezia boudieri* provides adequate levels of potassium, calcium, phosphorus, and magnesium. Truffles found in the desert typically have higher calcium content than black and white truffles (*Tuber melanosporum* and *Tuber magnatum*). To have a clear understanding of the desert truffles present in Morocco, a detailed study will be necessary. All of these facts, however, make desert truffles an intriguing topic for future researchers of these valuable fungus. It's important to note that a study the general and spore-related aspects of *Terfezia claveryi*, including germination and spore quantity (Al-Sheikh and Trappe, 1990). On modified Melin-Norkrans agar medium and potato dextrose media, desert truffle mycelia grew best at neutral pH, suggesting its potential use for the productive and effective creation (generation) and cultivation of desert truffles for commercial purposes (Morte *et al.*, 1994; Morte and Honrubia, 1995; Morte and Honrubia, 1997). There are several stringent laboratory and physio-biochemical conditions for good desert growth and productivity. Pérez-Gilabert *et al.* (2001) described the characterization and biochemical properties of the inactive *Terfezia claveryi*. Due to the fact that desert truffles can grow under circumstances of water stress, several studies have examined the effects of polyethylene glycol induced osmotic stress on two desert truffles (Mexal and Reid, 1973; Coleman *et al.*, 1989; Navarro-Ródenas *et al.*, 2011). According to Navarro-Ródenas *et al.* (2011) who discovered that it increased under dry conditions, alkaline phosphatase (ALP) activity is a major indicator of the metabolic activity of these fungi. They found that *Terfezia claveryi* strain TcS2 and *Picoa lefebvrei* strain OL2 are two species of desert truffles that have been demonstrated to be able to withstand water stress at pressures lower than 1.07MPa. Even the formation of mycelial inoculum in these arid truffles was found to be enhanced by water stress. According to Akyüz *et al.* (2012) *Terfezia boudieri* arid truffles have medicinal uses and contain phenolic compounds, antioxidants and other minerals.

### **Mycorrhizal association of truffles**

Desert truffles are culinary mushrooms that require plant roots as a living environment in order to thrive. In addition to the significant nutrients they contain, they also contain a high concentration of therapeutically beneficial secondary metabolites (Zniber *et al.*, 2022). There are approximately 10 species that may be found in the semiarid and arid climate zones of Morocco, which are characterised by low yearly rainfall and high average temperatures (Zniber *et al.*, 2022). They may be related to the *Cistus* and *Pinus* species as well as a few other species, but they are most frequently found with the *Helianthemum* species (Zniber *et al.*, 2022). In the same sense, a group of edible hypogeous fungus known as desert truffles that create mycorrhizal symbiosis with perennial and annual plants shrubs from plant family *Cistaceae*, which is adapted to arid and semi-arid regions (Kovács and Trappe, 2013; Roth-Bejerano *et al.*, 2014). These areas are recognised by an aridity index AI 0.5, which is the proportion between yearly precipitation and interest evapotranspiration, as well as by poorly fertile soils with a sandy texture and low inputs of organic substances, according to the United Nations Educational, Scientific, Cultural Organization (1979) and Bonifacio and Morte (2014). Additionally, desert truffles interact with a mutualistic partner with mycorrhizal fungi and exist in symbiosis with plants. According to several studies by Díez *et al.* (2002), Mandeel and Al-Laith (2007) desert truffles in Algeria's Sahara region have symbiotic relationships with *Helianthemum lippii*. The hypogeous ascomycetes develop mycorrhizal associations that share mutualistic relationships with several species of *Helianthemum* roots, according to (Mandeel and Al-Laith, 2007; Kagan-Zur *et al.*, 2014). Another study cites that Mutualistic symbionts help

their host plants develop and survive in certain environment conditions (Morte *et al.*, 2010). For instance, *Terfezia claveryi* mycorrhizas stimulate the assimilation of phosphorus, nitrogen and potassium in *Helianthemum almeriense*, which increases the plant's survival during droughts (Morte *et al.*, 2000). Because of this interaction, the expression of plant and fungal aquaporins as well as the amount of hydrogen peroxide in roots are finely regulated (Navarro-Ródenas *et al.*, 2013; Marqués-Gálvez *et al.*, 2020). Several *Terfezia* species, including *T. boudieri* and *T. claveryi*, as well as *Tirmania* species, including *T. Nivea* and *T. pinoyi*, have been found to have mycorrhizal associations with *Helianthemum lippii*. They also form advantageous mycorrhizal connections with *Helianthemum* species like *H. ledifolium* and *H. salicifolium* (Awameh and Alsheikh, 1980; Kovács and Trappe, 2013). *Helianthemum* species form both ectomycorrhizal and ecto-endomycorrhizal connections (Claridge *et al.*, 2013). Although these species have been observed to lack a Hartig net and their mantle in the roots of the endomycorrhizal desert truffles, they still display undifferentiated hyphae, as seen, for example, in associations between *Helianthemum spp.* and a number of species of *Terfezia* and *Tirmania* (Dexheimer *et al.*, 1985). Thus, it is very important to mention that ectendomycorrhiza is the name for the kind of mycorrhiza created by these fungi (EEM). EEMs have a thin, disorganised fungal mantle covering the colonised roots, intercellular Hartig nets, intracellular hyphae that enter cortical cells and create coil-like structures, and all of these features (Morte *et al.*, 1994; Yu *et al.*, 2001). Intercellular or intracellular mycorrhizal structures can rely on a variety of factors, according to another relatively recent study. In field conditions, low auxin, low phosphate, and/or low water availability favour the intracellular mycorrhizal form, while in vitro, high auxin, phosphate, and/or water concentrations favour the intercellular mycorrhizal form (Navarro-Ródenas *et al.*, 2012; Gutiérrez *et al.*, 2003; Zaretsky *et al.*, 2006). Due to this, it is possible to consider desert truffles as a type of intermediary connection between real ecto and endomycorrhizal interactions. But the division between these two typical mycorrhizal connections is crystalline and fluid at the same time. It should be noted that the traits and characteristics of mycorrhizal relationships are usually and frequently determined by both internal and external factors. The ability of mycorrhizal associations to endure some degree of harsh environmental conditions is superior to plants in dry and semiarid areas of the world (Morte *et al.*, 2009). A few varieties of truffle, including *Terfezia claveryi* and *Picoa lefebvrei* (*Phalangium lefebvrei*), are hypogeous ascomycetes that thrive in semiarid climates on marl and gypsum rich soils. Additionally, these species establish mycorrhizal connections with the bulk of perennial and annual *Helianthemum* species (Honrubia *et al.*, 1992). An ectomycorrhizal link exists between *Helianthemum ovatum* and *Helianthemirhiza hirsuta* (Kovács *et al.*, 2011). This specific association has a simple mycorrhizal system with borders that are often cottony, straight or slightly curved, bending, or tortuous, and vary in colour from ochre to brown. A thorough investigation into desert truffles and their interactions with different plants was carried out by (Kovács *et al.*, 2002). The interaction with plants and ensuing behaviour of both partners under aseptic conditions were investigated using modified Melin-Norkrans (MMN) substrates enriched with various phosphate concentrations. In order to assess the changes caused by *Terfezia terfezioides* interaction with *Robinia pseudoacacia* and *Helianthemum ovatum*, this task was carried out. Black locust colonisation has frequently stayed delicate and weaker than the *Helianthemum's* root system. Only in *Helianthemum* do the intercellular hyphae usually create a Hartig net with such finger like structures; without prior clear evidence, these kinds of contacts could not be classified as mycorrhizae. This is one of the few essential characteristics. They also observed that the RFLP profiles of the nuclear DNA ITS of 19 fungal fruiting bodies that had been concurrently collected from the same habitat showed no appreciable variation. They also showed that the three randomly selected specimens' ITS sequences shared similarities. The inconsistency between these types emphasizes the necessity for the creation and design of species-specific PCR primers, which could play a significant role in clearly identifying the host plants. A mycorrhizal relationship was created by *Helianthemum almeriense* Pau, *Terfezia claveryi* and *Picoa lefebvrei*. In their important, thorough review of the mycorrhizal associations of desert truffles with the genus *Helianthemum*, Gutierrez *et al.* (2004) examined the

morphological traits of this association. Additionally, they discussed the structure and ultrastructure of the established mycorrhizae of this plant species with *Terfezia claveryi* and *Picoa lefebvrei* as well as the morphology of the mycorrhizal associations in which *Helianthemum almeriense* is one of the partners. To further investigate the fungal inocula and mycorrhizal connections with plants and subsequent plantations, a knowledge of the use of biotechnological tools and management methods has been developed and introduced for a select few *Terfezia* species. According to Morte and Honrubia (1997) agar or modified Melin-Norkrans (MMN) inocula can be used straight from the plates as inocula for the creation and synthesis of *in vitro* mycorrhization". Since they are mycorrhizal, true *Terfezia* species have been used in mycorrhizal bioassay tests with plants, mainly from the genus *Helianthemum* (Kovács *et al.*, 2002). They thoroughly examined the truffle's anatomy and ultrastructure, and they investigated *Terfezia terfezioides'* relationships with *Robinia pseudoacacia* and *Helianthemum ovatum in vitro*. Morte *et al.* (2008) carried out a comparable study based on the techniques employed in the efficient synthesis of mycorrhiza between desert truffles and *Helianthemum* species. Agar or modified Melin-Norkrans (MMN) media can be used to make inocula, according to Morte *et al.* (1994) and Morte and Honrubia (1997). According to the source of the fungal inocula (whether it be from spores or mycelia), the source of the plant (whether it be seedlings or micro propagated plantlets), and the culture conditions, Morte *et al.* (2008) conducted a similar investigation into the processes involved in the efficient synthesis of mycorrhiza between *Helianthemum* species and desert truffles. Khanaqa (2006) different research, suggested cultivating desert truffles in plantations with *Olea europaea*, which would have a double beneficial effect. The tree will increase water retention, lessen soil erosion, and enhance soil fertility. According to Lopez Nicolás *et al.* (2013), the compound -cyclodextrin was effective at encouraging the mycelial growth of *T. claveryi*. It was discovered that the dominant sunflower species in Libya, *Helianthemum kahiricum* and *Helianthemum lippii*, developed mycorrhiza with arid truffles (Bouzadi *et al.*, 2017). Mycorrhizal connections can be formed by the majority of desert truffles, but *Terfezia claveryi* and *Picoa lefebvrei* are the two most frequently cited candidates for this particular quality. to improve farming, ecological, and biotechnological practises in dry and desert landscapes implementing mycorrhizal technology could prove to be a crucial component in Saudi Arabia's improvement of many arid plants. This area needs to be carefully and thoroughly explored.

## Conclusions

Desert truffles are both highly valuable commercially and highly beneficial medically. However, further study is still needed to better our understanding of the taxonomy of desert truffles and to conduct in-depth analyses of their biochemical and medicinal properties. Both molecular and morphological methods should be used for this study. A potent technique, *in vitro* mycorrhization also has positive effects on Morocco's conservation of truffle biodiversity. It might boost these indicators as well as the development, production, and overall calibre of desert truffles. The precise taxonomic delimitation of truffles using conventional and molecular technologies, as well as their bioprospecting via biotechnological interventions, have attained special importance because of the high market value and financial benefits that truffles offer.

Given the importance of truffles we have fixed the main objective of this scientific review is to optimize the cultivation conditions of some southeastern truffles in Morocco based on mycorrhization. To achieve this objective, we first presented a brief bibliographic analysis of the geographical distribution of desert truffles throughout the world, particularly in Morocco, including their biology, ecology, host plants, chemical compositions, and mycorrhizal association.

### Authors' Contributions

KH, OL and TA Conceptualization KH, OL and TA writing original draft; KH, OL and TA writing, review and editing.

All authors read and approved the final manuscript.

### Ethical approval (for researches involving animals or humans)

Not applicable.

### Acknowledgements

This research received no specific grant from any funding agency in the public, commercial, or not-for-profit sectors.

### Conflict of Interests

The authors declare that there are no conflicts of interest related to this article.

### References

- Abourouh M (2011). Truffes du désert du Maroc: Diversité et modes d'exploitation. 6ème Rencontre de Mycosilva, Mértola (ADPM) Portugal. <https://tinyurl.com/3afza3zz>
- Abourouh M (2020). Restauration de la forêt de chêne liège pour le développement et la valorisation des truffes dans la forêt de la Maâmora, FAO, Terfess et truffes de la Maâmora, importances biologique, écologiques et socio-économique. <https://tinyurl.com/ymuz79t7>
- Akyüz M, Kirbağ S, Kurşat M (2012). Ecological aspects of the arid and semi-arid truffle in Turkey: Evaluation of soil characteristics, morphology, distribution, and mycorrhizal relationships. Turkish Journal of Botany 36:386-91. <https://doi.org/10.3906/bot-1103-4>
- Al-Laith AAA (2010). Antioxidant components and antioxidant, antiradical activities of desert truffle (*Tirmania nivea*) from various Middle Eastern origins. Journal of Food Composition Analysis 23:15-22. <https://doi.org/10.1016/j.jfca.2009.07.005>
- Alsheikh A, Trappe J (1983). Desert truffles, the genus *Tirmania*. Transactions of the British Mycological Society 81:83-90. [https://doi.org/10.1016/S0007-1536\(83\)80207-1](https://doi.org/10.1016/S0007-1536(83)80207-1)
- Al-Sheikh A, Trappe J (1990). Features and analysis of spore germination in the brown kame *Terfezia claveryi*. Journal of Mycology 72:495-99. <https://doi.org/10.1080/00275514.1980.12021210>
- Alsheikh AM (1994). Taxonomy and mycorrhizal ecology of the desert truffles in the Genus *Terfezia*. Ph.D. dissertation. Oregon State University, Corvallis, pp 239. <https://tinyurl.com/3stmvbb5>
- Antony-Babu S, Deveau A, Van Nostrand JD, Zhou J, Le Tacon F, Robin C, ... Uroz S (2014). Black truffle associated bacterial communities during the development and maturation of *Tuber melanosporum* ascocarps and putative functional roles. Journal Environmental Microbiology 16:2831-2847. <https://doi.org/10.1111/1462-2920.12294>
- Awameh MS, Alsheikh A (1980). Ascospore germination of black kame, *Terfezia boudieri*. Journal of Mycology 72:50-54. <https://doi.org/10.1080/00275514.1980.12021154>



- Barbieri E, Ceccaroli P, Saltarelli R, Guidi C, Potenza L, Basaglia M, ... Ryahi O (2010). New evidence for nitrogen fixation within the Italian white truffle *Tuber magnatum*. Journal of Fungal Biology 114:936-42. <https://doi.org/10.1016/j.fumbio.2010.09.001>
- Barea J, Palenzuela J, Cornejo P, Sánchez-Castro I, Navarro-Fernández C, López-García A, ... Azcón-Aguilar C (2011). Ecological and functional roles of mycorrhizas in semi-arid ecosystems of Southeast Spain. Journal of Arid Environments 75:1292-301. <https://doi.org/10.1016/j.jaridenv.2011.06.001>
- Barry D, Staunton S, Callot G (1994). Mode of the absorption of water and nutrients by ascocarps of *Tuber melanosporum* and *Tuber aestivum* a radioactive tracer technique. Journal Canadian Journal of Botany 72:317-22. <https://doi.org/10.1139/b94-04>
- Berch SM, Bonito G (2016). Truffle diversity (Tuber, Tuberaceae) in British Columbia. Mycorrhiza 26:587-94. <https://doi.org/10.1007/s00572-016-0695-2>
- Bermaki FZ, Khabar L, Ezzanega A (2017). Bioecology of desert truffles in the province of Figuig in Eastern Morocco. Journal Revista Mexicana de Micología 46:29-36. <https://doi.org/10.33885/sf.2017.46.1174>
- Bertault G, Rousset F, Fernandez D, Berthomieu A, Hochberg ME, Callot G, Raymond M (2001). Population genetics and dynamics of the black truffle in a man-made truffle field. Journal Heredity 86:451-58. <https://doi.org/10.1046/j.1365-2540.2001.00855.x>
- Bokhary H, Parvez S (1993). Chemical composition of desert truffles *Terfezia clavaryi*. Journal of Food Composition Analysis 6:285-293. <https://doi.org/10.1006/jfca.1993.1031>
- Bokhary H, Suleiman A, Basalah M (1989). The fatty acid components of the desert truffle Al Kamah of Saudi Arabia. Journal of Food Protection 52:668-69. <https://doi.org/10.4315/0362-028x-52.9.668>
- Bokhary H, Suleiman A, Basalah M, Parvez S (1987). Chemical composition of desert truffles from Saudi Arabia. Canadian Institute of Food Science Technology Journal 20:336-341. [https://doi.org/10.1016/S0315-5463\(87\)71328-5](https://doi.org/10.1016/S0315-5463(87)71328-5)
- Bokhary H, Parvez S (1992). Soil mycoflora from truffle native areas of Saudi Arabia. Mycopathologia 118:103-107. <https://doi.org/10.1007/BF00442538>
- Bonifacio E, Morte A (2014). Soil properties. Desert truffles: phylogeny, physiology, distribution, domestication 57-67. [https://doi.org/10.1007/978-3-642-40096-4\\_4](https://doi.org/10.1007/978-3-642-40096-4_4)
- Bonito GM, Gryganskyi AP, Trappe JM, Vilgalys R (2010). A global meta-analysis of *Tuber* ITS rDNA sequences species diversity, host associations and long-distance dispersal. Journal Molecular Ecology 19:4994-5008. <https://doi.org/10.1111/j.1365-294X.2010.04855.x>
- Bouzadi M, Grebenc T, Turunen O, Kraigher H, Taib H, Alafai A, ...Shamekh S (2017). Characterization of natural habitats and diversity of Libyan desert truffles. Journal of Biotech 7:1-10. <https://doi.org/10.1007/s13205-017-0949-5>
- Bradai L, Bissati S, Chenchouni H (2013). Etude mycologique et bioécologiques de la truffe blanche du désert (*Tirmania nivea* Desf. Trappe 1971) dans la région de Oued M'ya (Ouargla, Sahara algérien). Journal Revue des Bioresources 3:6-14. <https://doi.org/10.12816/0008856>
- Bradai L, Bissati S, Chenchouni H, Amrani K (2015). Effects of climate on the productivity of desert truffles beneath hyper-arid conditions. International Journal of Biometeorology 59:907-915. <https://doi.org/10.1007/s00484-014-0891-8>
- Brundrett MC (2002). Coevolution of roots and mycorrhizas of land plants. New phytologist 154:275-304. <https://doi.org/10.1046/j.1469-8137.2002.00397.x>
- Chatin M (1891). Contribution à l'histoire botanique de la truffe: kamé de Damas (*Terfezia clavaryi*). Journal Bulletin de la Société Botanique de France 38:332-35. <https://doi.org/10.1080/00378941.1891.10828584>
- Chellal A, Lukasova E (1995). Evidence for antibiotics in two Algerien truffles *Terfezia* and *Tirmania*. Pharmazie 50:228-229. <https://tinyurl.com/2wdj6e5n>
- Chen J, Li JM, Tang YJ, Xing YM, Qiao P, Li Y, ...Guo SX (2019). Chinese black truffle associated bacterial communities of *Tuber indicum* from different geographical regions with nitrogen fixing bioactivity. Frontiers in Microbiology 10:2515. <https://doi.org/10.3389/fmicb.2019.02515>

- Chen P-Y, Montanini B, Liao W-W, Morselli M, Jaroszewicz A, Lopez D, ...Pellegrini M (2014). A comprehensive resource of genomic, epigenomic and transcriptomic sequencing data for the black truffle *Tuber melanosporum*. *Gigascience* 3:2047-217X-3-25. <https://doi.org/10.1186/2047-217X-3-25>
- Cheung PCK (1997). Dietary fibre content and composition of some edible fungi determined by two methods of analysis. *Journal of the Science of Food Agriculture* 73:255-260. <https://tinyurl.com/yckmfrrv>
- Chevalier G (1984). Une nouvelle méthode de production de plants mycorhizés par la truffe, l'inoculation en motte roulée Melfert. *Journal Agronomie* 4: 211. <https://tinyurl.com/2bsxtjyr>
- Claridge AW, Trappe JM, Paull DJ (2013). Ecology and distribution of desert truffles in the Australian outback. In: *Desert Truffles*, Springer, pp 203-214. [https://doi.org/10.1007/978-3-642-40096-4\\_14](https://doi.org/10.1007/978-3-642-40096-4_14)
- Coleman MD, Bledsoe CS, Lopushinsky W (1989). Pure culture response of ectomycorrhizal fungi to imposed water stress. *Canadian Journal of Botany* 67:29-39. <https://doi.org/10.1139/b89-005>
- Comandini O, Contu M, Rinaldi A (2006). An overview of *Cistus* ectomycorrhizal fungi. *Mycorrhiza* 16:381-395. <https://doi.org/10.1007/s00572-006-0047-8>
- Culleré L, Ferreira V, Chevret B, Venturini ME, Sánchez-Gimeno AC, Blanco D (2010). Characterization of aroma active compounds in black truffles, *Tuber melanosporum* and summer truffles, *Tuber aestivum* by gas chromatography olfactometry. *Food Chemistry* 122:300-306. <https://doi.org/10.1016/j.foodchem.2010.02.024>
- Dahham SS, Al-Rawi SS, Ibrahim AH, Majid ASA, Majid AMSA (2016). Antioxidant, anticancer, apoptosis properties and chemical composition of black truffle *Terfezia claveryi*. *Saudi Journal of Biological Sciences* 25:1524-1534. <https://doi.org/10.1016/j.sjbs.2016.01.031>
- Debuchy R, Berteaux-Lecellier V, Silar P (2010). Mating systems and sexual morphogenesis in ascomycetes. *Cellular Molecular Biology of Filamentous Fungi* 499-535. <https://doi.org/10.1128/9781555816636.ch33>
- Dexheimer J, Gerard J, Leduc J-P, Chevalier G (1985). Étude ultrastructurale comparée des associations symbiotiques mycorhiziennes *Helianthemum salicifolium*, *Terfezia claveryi* et *Helianthemum salicifolium*, *Terfezia leptoderma*. *Canadian Journal of Botany* 63:582-591. <https://doi.org/10.1139/b85-073>
- Diaz P, Ibáñez E, Senorans F, Reglero G (2003). Truffle aroma characterization by headspace solid phase microextraction. *Journal of Chromatography A* 1017:207-214. <https://doi.org/10.1016/j.chroma.2003.08.016>
- Dib-Bellahouel S, Fortas Z (2011). Antibacterial activity of various fractions of ethyl acetate extract from the desert truffle, *Tirmania pinoyi*, preliminarily analyzed by gas chromatography mass spectrometry (GC-MS). *African Journal of Biotechnology* 10(47):9694-9699.
- Diez J, Manjón JL, Martin F (2002). Molecular phylogeny of the mycorrhizal desert truffles (*Terfezia* and *Tirmania*), host specificity and edaphic tolerance. *Mycologia* 94:247-259. <https://doi.org/10.1080/15572536.2003.11833230>
- El Aji A (1999). Contribution à l'étude des Terfez des parcours de l'oriental marocain: Germination des ascospores in vitro et mycorhization de l'*Helianthemum ledifolium*. Mémoire de Troisième Cycle en Agronomie, École Nationale d'Agriculture, Meknès. <https://tinyurl.com/43stvm3>
- El Akil M, Outcoumit A, Ouazzani Touhami A, Benkirane R, Douira A (2016). Study of eastern Morocco desert truffles. *International Journal of Current Research* 8:33922-33929.
- El Enshasy H, Elsayed EA, Aziz R, Wadaan MA (2013). Mushrooms and truffles: Historical bio-factories for complementary medicine in Africa and in the Middle East. *Evidence Based Complementary and Alternative Medicine* 2013:620451. <http://dx.doi.org/10.1155/2013/620451>
- El-Kholy H (1989). Genetical and physiological studies on truffles. PhD. Thesis, Fac, of Agric, Cairo University, Egypt.
- Fortas Z, Chevalier G (1992). Effet des conditions de culture sur la mycorhization de l'*Helianthemum guttatum* par trois espèces de terfez des genres *Terfezia* et *Tirmania* d'Algérie. *Journal Canadian Journal of Botany* 70:2453-60. <https://doi.org/10.1139/b92-303>
- Frank B (2005). On the nutritional dependence of certain trees on root symbiosis with belowground fungi. *Journal Mycorrhiza* 15:267-275. <https://doi.org/10.1007/s00572-004-0329-y>
- Gouzi H, Leboukh M, Bouchouka E (2013). Antioxidant and antiradical properties of methanolic extracts from Algerian wild edible desert truffles (*Terfezia* and *Tirmania*, Ascomycetes). *International Journal of Medicinal Mushrooms* 15. <https://doi.org/10.1615/IntJMedMusbr.v15.i5.50>

- Gutiérrez A, Morte A, Honrubia M (2003). Morphological characterization of the mycorrhiza formed by *Helianthemum almeriense* Pau with *Terfezia claveryi* Chatin and *Picoa lefebvrei* (Pat.) Maire. Mycorrhiza 13:299-307. <https://doi.org/10.1007/s00572-003-0236-7>
- Hakkou S, Sabir M, Machouri N (2022). Le Maroc truffier, la répartition géographique des truffes et truffes du désert et leur productivité. Revue Marocaine des Sciences Agronomiques et Vétérinaires 10:395-407.
- Hall IR, Zambonelli A (2012). Laying the foundations in edible ectomycorrhizal mushrooms, Berlin, Heidelberg: Springer, pp 3-16. [https://doi.org/10.1007/978-3-642-33823-6\\_1](https://doi.org/10.1007/978-3-642-33823-6_1)
- Hamza A, Zouari N, Zouari S, Jdir H, Zaidi S, Gtari M, Neffati M (2016). Nutraceutical potential, antioxidant and antibacterial activities of *Terfezia boudieri* Chatin, a wild edible desert truffle from Tunisia arid zone. Journal Arabian Journal of Chemistry 9:383-89. <https://doi.org/10.1016/j.arabjc.2013.06.015>
- Harir M, Bendif H, Yahiaoui M, Bellahcene M, Zohra F, Rodríguez-Couto S (2019). Evaluation of antimicrobial activity of *Terfezia arenaria* extracts collected from Saharan desert against bacteria and filamentous fungi. 3 Biotech 9:281. <https://doi.org/10.1007/s13205-019-1816-3>
- Harki E, Farah A, Bouseta A (2010). Volatile compounds from four species of Moroccan truffles. Vice Editor in Chief 12:10.
- Harrison MJ (1997). The arbuscular mycorrhizal symbiosis in plant microbe interactions, Springer, pp 1-34: [https://doi.org/10.1007/978-1-4615-6019-7\\_1](https://doi.org/10.1007/978-1-4615-6019-7_1)
- Hashem A, Alqarawi AA, Shah MA, Wirth S, Egamberdieva D, Tabassum B, Abd\_Allah EF (2018). Desert truffles in Saudi Arabia: Diversity, ecology, and conservation. Microbial Resource Conservation 353-369. [https://doi.org/10.1007/978-3-319-96971-8\\_13](https://doi.org/10.1007/978-3-319-96971-8_13)
- Hashem AR, Al-Obaid AM (1996). Mineral composition of soil and wild desert truffles in Saudi Arabia. Journal of King Saud University 8:5-10.
- Honrubia M, Cano A, Molina-Ninrola C (1992). Hypogeous fungi from southern Spanish semi-arid lands. Journal Persoonia Molecular Phylogeny Evolution of Fungi 14:647-653.
- Hussain G, Al-Ruqaie IM (1999). Occurrence, chemical composition, and nutritional value of truffles: an overview. Pakistan Journal of Biological Sciences 2:510-514. <https://doi.org/10.3923/pjbs.1999.510.514>
- Jamali S, Banihashemi Z (2012). Fungi associated with ascocarps of desert truffles from different parts of Iran. Journal of Crop Protection 1: 0-0.
- Janakat S, Al-Fakhiri S, Sallal AK (2004). A promising peptide antibiotic from *Terfezia claveryi* aqueous extract against *Staphylococcus aureus* *in vitro*. Phytotherapy Research: An International Journal Devoted to Pharmacological Toxicological Evaluation of Natural Product Derivatives 18:810-813. <https://doi.org/10.1002/ptr.1563>
- Janakat SM, Al-Fakhiri SM, Sallal A (2005). Evaluation of antibacterial activity of aqueous and methanolic extracts of the truffle *Terfezia claveryi* against *Pseudomonas aeruginosa*. Saudi Medical Journal 26:952-955.
- Jeandroz S, Murat C, Wang Y, Bonfante P, Tacon FL (2008). Molecular phylogeny and historical biogeography of the genus *Tuber*, the true truffles. Journal of Biogeography 35:815-829. <https://doi.org/10.1111/j.1365-2699.2007.01851.x>
- Kagan-Zur V, Roth-Bejerano N, Sitrit Y, Morte A (2013). Desert truffles: Phylogeny, physiology, distribution and domestication. Springer Science and Business Media.
- Kagan-Zur V, Roth-Bejerano N, Sitrit Y, Morte A (2014). Desert truffles: Phylogeny, physiology, distribution and domestication. Springer Science and Business Media.
- Khabar L (2002). Etudes pluridisciplinaires des truffes du Maroc et perspectives pour l'amélioration de production des Terfess de la forêt de la Maamora.
- Khabar L (2014). Mediterranean Basin: North Africa. In: Desert Truffles, pp 143-158. [https://doi.org/10.1007/978-3-642-40096-4\\_10](https://doi.org/10.1007/978-3-642-40096-4_10)
- Khabar L (2016). Les terfess et les truffes du Maroc: Biodiversité et valorisation. Éditions Universitaires Européennes.
- Khaled JM, Alharbi NS, Mothana RA, Kadaikunnan S, Alobaidi AS (2021). Biochemical profile by GC-MS of fungal biomass produced from the Ascospores of *Tirmania nivea* as a natural renewable resource. Journal of Fungi 7:1083. <https://doi.org/10.3390/jof7121083>
- Khanaqa A (2006). Truffle production in the Kingdom of Saudi Arabia-potential and limitation. Journal of Applied Botany and Food Quality 80(1):14.

- Kinoshita A, Sasaki H, Nara K (2011). Phylogeny and diversity of Japanese truffles (*Tuber* spp.) inferred from sequences of four nuclear loci. *Mycologia* 103:779-794. <https://doi.org/10.3852/10-138>
- Kovács G, Bagi I, Vágvölgyi C, Kottke I, Oberwinkler F (2002). Studies on the root associations of the truffle *Terfezia terfezioides*. *Acta Microbiologica et Immunologica Hungarica* 49:207-213. <https://doi.org/10.1556/amicr.49.2002.2-3.6>
- Kovács GM, Balazs TK, Calonge FD, Martin MP (2011). The diversity of *Terfezia* desert truffles: new species and a highly variable species complex with intrasporocarpic nrDNA ITS heterogeneity. *Mycologia* 103:841-853. <https://doi.org/10.3852/10-312>
- Kovács GM, Trappe JM (2013). Nomenclatural history and genealogies of desert truffles in Desert truffles: phylogeny, physiology, distribution and domestication, pp 21-37: Springer. [https://doi.org/10.1007/978-3-642-40096-4\\_2](https://doi.org/10.1007/978-3-642-40096-4_2)
- Kovács GM, Trappe JM (2014). Nomenclatural history and genealogies of desert truffles. Desert Truffles: Phylogeny, physiology, distribution, domestication 21-37. [https://doi.org/10.1007/978-3-642-40096-4\\_2](https://doi.org/10.1007/978-3-642-40096-4_2)
- Kovács GM, Trappe JM (2014). Nomenclatural history and genealogies of desert truffles. Desert Truffles. Springer. Pp 21-37. [https://doi.org/10.1007/978-3-642-40096-4\\_2](https://doi.org/10.1007/978-3-642-40096-4_2)
- Kües U, Liu Y (2000). Fruiting body production in basidiomycetes. *Applied Microbiology Biotechnology* 54:141-152. <https://doi.org/10.1007/s002530000396>
- Kulifaj M (1984). *Tuber melanosporum* Vitt.: Contribution à l'étude de la morphogenèse et de la physiologie de l'ascocarpe. <https://tinyurl.com/2p86aut9>
- Læssøe T, Hansen K (2007). Truffle trouble: what happened to the Tuberales? *Mycological Research Journal* 111:1075-1099. <https://doi.org/10.1016/j.mycres.2007.08.004>
- Lancellotti E, Iotti M, Zambonelli A, Franceschini A (2014). Characterization of *Tuber borchii* and *Arbutus unedo* mycorrhizas. *Mycorrhiza* 24:481-86. <https://doi.org/10.1007/s00572-014-0564-9>
- Laqbaqbi A (2020). La truffe entre France et Maroc ou d'un coté à l'autre de la Méditerranée. *Journal Imprimerie GRAPHO* 12. <https://tinyurl.com/3r63trk6>
- Le Tacon F, Selosse M-A (1994). La place des symbioses mycorrhiziennes dans l'évolution et la colonisation des continents par la vie. *Acta Botanica Gallica* 141:405-419. <https://doi.org/10.1080/12538078.1994.10515177>
- Le Tacon F, Zeller B, Plain C, Hossann C, Bréchet C (2013). Carbon transfer from the host to *Tuber melanosporum* mycorrhizas and ascocarps. *Plos One*. <https://doi.org/10.1371/journal.pone.0064626>
- Loizides M, Hobart C, Konstantinides G, Yiangou Y (2012). Desert truffles: The mysterious jewels of antiquity. *Field Mycology* 13:17-21. <https://doi.org/10.1016/j.fldmyc.2011.12.004>
- López-Nicolás JM, Pérez-Gilbert M, García-Carmona F, Lozano-Carrillo MC, Morte A (2013). Mycelium growth stimulation of the desert truffle *Terfezia claveryi* chatin by  $\beta$ -cyclodextrin. *Journal Biotechnology Progress* 29:1558-1564. <https://doi.org/10.1002/btpr.1791>
- Maire M (1906). Contributions à l'étude de la flore mycologique de l'Afrique du Nord. *Journal Bulletin de la Société Botanique de France* 53:clxxx-ccxv. <https://doi.org/10.1080/00378941.1906.10831941>
- Malençon G (1973). Champignons hypogés du nord de l'Afrique I. Ascomycetes. *Persoonia-Molecular Phylogeny Evolution of Fungi* 7:261-279.
- Mamoun M, Olivier J (1991). The effect of carbon source and form of mineral nitrogen on the development of *Tuber melanosporum* (Vitt) in pure culture. Application to production of mycelium biomass. *Agronomy* 11:521-527. <https://doi.org/10.1051/agro:19910609>
- Mandeel QA, Al-Laith AAA (2007). Ethnomycological aspects of the desert truffle among native Bahraini and non-Bahraini peoples of the Kingdom of Bahrain. *Journal of Ethnopharmacology* 110:118-29. <https://doi.org/10.1016/j.jep.2006.09.014>
- Marqués-Gálvez JE, Miyauchi S, Paolucci F, Navarro-Ródenas A, Arenas F, Pérez-Gilbert M, ... Morte A (2021). Desert truffle genomes reveal their reproductive modes and new insights into plant, fungal interaction and ectendomycorrhizal lifestyle. *New Phytologist Foundation* 229:2917-32. <https://doi.org/10.1111/nph.17044>
- Marqués-Gálvez JE, Morte A, Navarro-Ródenas A (2020). Spring stomatal response to vapor pressure deficit as a marker for desert truffle fruiting. *Mycorrhiza* 30: 503-12. <https://doi.org/10.1007/s00572-020-00966-8>

- Martin F, Kohler A, Murat C, Balestrini R, Coutinho PM, Jaillon O, ... Percudani R (2010). Périgord black truffle genome uncovers evolutionary origins and mechanisms of symbiosis. *Journal Nature* 464:1033-38. <https://doi.org/10.1038/nature08867>
- Mello A, Murat C, Bonfante P (2006). Truffles: much more than a prized and local fungal delicacy. *Federation of European Microbiological Societies Microbiology Letters* 260:1-8. <https://doi.org/10.1111/j.1574-6968.2006.00252.x>
- Mexal J, Reid C (1973). The growth of selected mycorrhizal fungi in response to induced water stress. *Canadian Journal of Botany* 51:1579-1588. <https://doi.org/10.1139/b73-20>
- Morte A, Honrubia M (1995). Improvement of mycorrhizal synthesis between micro propagated *Helianthemum almeriense* plantlets with *Terfezia clavaryi* (desert truffle). *Science Cultivation of Edible Fungi* 2:863-868.
- Morte A, Honrubia M, Gutiérrez A (2008). Biotechnology and cultivation of desert truffles. *Mycorrhiza* 467-483. <https://doi.org/10.1007/978-3-540-78826-3>
- Morte A, Lovisolo C, Schubert A (2000). Effect of drought stress on growth and water relations of the mycorrhizal association *Helianthemum almeriense* *Terfezia clavaryi*. *Mycorrhiza* 10:115-119.
- Morte A, Navarro-Ródenas A, Nicolás E (2010). Physiological parameters of desert truffle mycorrhizal *Helianthemum almeriense* plants cultivated in orchards under water deficit conditions. *Journal Symbiosis* 52:133-139. <https://doi.org/10.1007/s13199-010-0080-4>
- Morte A, Zamora M, Gutiérrez A, Honrubia M (2009). Desert truffle cultivation in semiarid Mediterranean areas. *Mycorrhizas Functional Processes Ecological Impact* 221-233. [https://doi.org/10.1007/978-3-540-87978-7\\_15](https://doi.org/10.1007/978-3-540-87978-7_15)
- Morte, M, Honrubia, M (1997). Micropropagation of *Helianthemum almeriense*. In: Bajaj, YPS (Ed). *High-Tech and Micropropagation VI. Biotechnology in Agriculture and Forestry*, vol 40. Springer, Berlin, Heidelberg. [https://doi.org/10.1007/978-3-662-03354-8\\_12](https://doi.org/10.1007/978-3-662-03354-8_12)
- Morte MA, Cano A, Honrubia M, Torres P (1994). *In vitro* mycorrhization of micro propagated *Helianthemum almeriense* plantlets with *Terfezia clavaryi* (desert truffle). *Agricultural Food Science* 3:309-314. <https://doi.org/10.23986/afsci.72700>
- Murcia MA, Martínez-Tomé M, Jiménez AM, Vera AM, Honrubia M, Parras P (2002). Antioxidant activity of edible fungi (truffles and mushrooms): losses during industrial processing. *Journal of Food Protection* 65:614-622.
- Murcia MA, Martínez-Tomé M, Vera A, Morte A, Gutierrez A, Honrubia M, Jiménez AM (2003). Effect of industrial processing on desert truffles *Terfezia clavaryi* Chatin and *Picoa juniperi* Vittadini: proximate composition and fatty acids. *Journal of the Science of Food Agriculture* 83:535-541. <https://doi.org/10.1002/jsfa.1397>
- Navarro-Ródenas A, Bárzana G, Nicolás E, Carra A, Schubert A, Morte A (2013). Expression analysis of aquaporins from desert truffle mycorrhizal symbiosis reveals a fine-tuned regulation under drought. *Molecular Plant Microbe Interactions* 26:1068-1078. <http://dx.doi.org/10.1094/MPMI-07-12-0178-R>
- Navarro-Ródenas A, Lozano-Carrillo MC, Pérez-Gilabert M, Morte A (2011). Effect of water stress on in vitro mycelium cultures of two mycorrhizal desert truffles. *Mycorrhiza* 21:247-253. <https://doi.org/10.1007/s00572-010-0329-z>
- Navarro-Ródenas A, Pérez-Gilabert M, Torrente P, Morte A (2012). The role of phosphorus in the ectendomycorrhiza continuum of desert truffle mycorrhizal plants. *Mycorrhiza* 22:565-575. <https://doi.org/10.1007/s00572-012-0434-2>
- Oei (2003). *Mushroom cultivation: appropriate technology for mushroom growers*. Backhuys Publishers, 3<sup>rd</sup> Ed., Leiden the Netherlands.
- Olivera A, Bonet JA, Oliach D, Colinas C (2014). Time and dose of irrigation impact Tuber melanosporum ectomycorrhiza proliferation and growth of *Quercus ilex* seedling hosts in young black truffle orchards. *Mycorrhiza* 24:73-78. <https://doi.org/10.1007/s00572-013-0545-4>
- Olivier J, Savignac J, Sourzat P (2012). *Truffe et trufficulture* FANLAC Editions. JP, France.
- Olivier J, Savignac J, Sourzat P (2018). *Truffle and truffle cultivation*. Fanlac. France.
- Pacioni G, Leonardi M, Di Carlo P, Ranalli D, Zinni A, De Laurentiis G (2014). Instrumental monitoring of the birth and development of truffles in a *Tuber melanosporum* orchard. *Journal Mycorrhiza* 24:65-72. <https://doi.org/10.1007/s00572-014-0561-z>
- Paolocci F, Rubini A, Riccioni C, Arcioni S (2006). Reevaluation of the life cycle of *Tuber magnatum*. *Applied and Environmental Microbiology* 72:2390-2393. <https://doi.org/10.1128/AEM.72.4.2390-2393.2006>



- Patel S (2012). Food, health and agricultural importance of truffles. *Current Trends in Biotechnology and Pharmacy* 6(1):15-27.
- Pérez-Gilbert M, Morte A, Honrubia M, García-Carmona F (2001). Partial purification, characterization, and histochemical localization of fully latent desert truffle, *Terfezia claveryi* Chatin, polyphenol oxidase. *Journal of Agricultural Food Chemistry* 49:1922-1927. <https://doi.org/10.1021/jf001009n>
- Piattoni F, Amicucci A, Iotti M, Ori F, Stocchi V, Zambonelli A (2014). Viability and morphology of *Tuber aestivum* spores after passage through the gut of *Sus scrofa*. *Journal Fungal Ecology* 9:52-60. <https://doi.org/10.1016/j.funeco.2014.03.002>
- Plett JM, Martin FJ (2011). Blurred boundaries: life style lessons from ectomycorrhizal fungal genomes. *Trends in Genetics* 27:14-22. <https://doi.org/10.1016/j.tig.2010.10.005>
- Remy W, Taylor TN, Hass H, Kerp H (1994). Four hundred million year old vesicular arbuscular mycorrhizae. *Proceedings of the National Academy of Sciences* 91:11841-11843. <https://doi.org/10.1073/pnas.91.25.1184>
- Rineau F, Roth D, Shah F, Smits M, Johansson T, Canbäck B, ...Lindquist E (2012). The ectomycorrhizal fungus *Paxillus involutus* converts organic matter in plant litter using a trimmed brown rot mechanism involving Fenton chemistry. *Journal Environmental Microbiology* 14:1477-1487. <https://doi.org/10.1111/j.1462-2920.2012.02736.x>
- Roth-Bejerano N, Li Y-F, Kagan-Zur V (2004). Homokaryotic and heterokaryotic hyphae in *Terfezia*. *Antonie Van Leeuwenhoek* 85:165-68. <https://doi.org/10.1023/b:anto.0000020283.99376.55>
- Roth-Bejerano N, Navarro-Ródenas A, Gutiérrez A (2014). Types of mycorrhizal association. *Journal Desert Truffles: Phylogeny, physiology, distribution, domestication* 69-80. [https://doi.org/10.1007/978-3-642-40096-4\\_5](https://doi.org/10.1007/978-3-642-40096-4_5)
- Rubini A, Belfiori B, Riccioni C, Tisserant E, Arcioni S, Martin F, Paolocci F (2011). Isolation and characterization of MAT genes in the symbiotic ascomycete *Tuber melanosporum*. *New Phytologist* 189:710-722. <https://doi.org/10.1111/j.1469-8137.2010.03492.x>
- Rubini A, Riccioni C, Belfiori B, Paolocci F (2014). Impact of the competition between mating types on the cultivation of *Tuber melanosporum*: Romeo and Juliet and the matter of space and time. *Journal Mycorrhiza* 24:19-27. <https://doi.org/10.1007/s00572-013-0551-6>
- Sawaya W, Al-Shalhat A, Al-Sogair A, Al-Mohammad M (1985). Chemical composition and nutritive value of truffles of Saudi Arabia. *Journal of Food Science* 50:450-53. <https://doi.org/10.1111/j.1365-2621.1985.tb13425.x>
- Schillaci D, Cusimano MG, Cascioferro SM, Di Stefano V, Arizza V, Chiaramonte M, ... Gargano ML (2017). Antibacterial activity of desert truffles from Saudi Arabia against *Staphylococcus aureus* and *Pseudomonas aeruginosa*. *International Journal of Medicinal Mushrooms* 19. <https://doi.org/10.1615/intjmedmushrooms.v19.i2.30>
- Slama A, Fortas Z, Boudabous A, Neffati M (2010). Cultivation of an edible desert truffle *Terfezia boudieri* Chatin. *Journal African Journal of Microbiology Research* 4:2350-2356.
- Slama A, Neffati M, Boudabous A (2009). *International Symposium on Medicinal and Aromatic Plants-SIPAM2009* 8532009:285-290.
- Smith S, Read D (2008). *Mycorrhizal symbiosis* third Edition introduction. *Mycorrhizal Symbiosis* 1-9.
- Splivallo (2008). Biological Significance of truffle secondary metabolites. In: Karlovsky P (Ed). *Secondary metabolites in soil ecology soil biology*, Springer, Berlin, Heidelberg 14:141-165. [https://doi.org/10.1007/978-3-540-74543-3\\_8](https://doi.org/10.1007/978-3-540-74543-3_8)
- Splivallo R, Ottonello S, Mello A, Karlovsky P (2011). Truffle volatiles: from chemical ecology to aroma biosynthesis. *New Phytologist* 189:688-699. <https://doi.org/10.1111/j.1469-8137.2010.03523.x>
- Streiblová E, Gryndlerova H, Gryndler M (2012). Truffle brûlé: an efficient fungal life strategy. *FEMS Microbiology Ecology* 80:1-8. <https://doi.org/10.1111/j.1574-6941.2011.01283.x>
- Taschen E (2015). Interactions biotiques et biologie reproductive de la truffe noire, *Tuber melanosporum* (Vittad.): des truffières spontanées aux plantations. Université Montpellier 2, Sciences et Techniques.
- Trappe JM (1971). A synopsis of the Carbohycomycetaceae and Terfeziaceae (Tuberales). *Transactions of the British Mycological Society* 57:85-92. [https://doi.org/10.1016/S0007-1536\(71\)80083-9](https://doi.org/10.1016/S0007-1536(71)80083-9)
- van der Heijden MGA, Martin FM, Selosse MA, Sanders IR (2015). Mycorrhizal ecology and evolution: the past, the present, and the future. *New Phytologist* 205:1406-1423. <https://doi.org/10.1111/nph.13288>

- Villares A, García-Lafuente A, Guillamon E, Ramos A (2012). Identification and quantification of ergosterol and phenolic compounds occurring in Tuber spp. truffles. *Journal of Food Composition Analysis* 26:177-182. <https://doi.org/10.1016/j.jfca.2011.12.003>
- Wang S, Marcone MF (2011). The biochemistry and biological properties of the world's most expensive underground edible mushroom: Truffles. *Journal Food Research International* 44:2567-2581. <https://doi.org/10.1016/j.foodres.2011.06.008>
- Yao Y, Spooner B, Hawksworth D (1995). Author citation of the generic name *Peziza* (Pezizales, Pezizaceae). *Systema Ascomycetum* 14:17-24.
- Yu TE, Egger KN, Peterson LR (2001). Ectendomycorrhizal associations characteristics and functions. *Mycorrhiza* 11:167-177. <https://doi.org/10.1007/s005720100110>
- Zaretsky M, Kagan-Zur V, Mills D, Roth-Bejerano N (2006). Analysis of mycorrhizal associations formed by *Cistus incanus* transformed root clones with *Terfezia boudieri* isolates. *Plant Cell Reports* 25:62-70. <https://doi.org/10.1007/s00299-005-0035-z>
- Zitouni-Haouar FE-H, Fortas Z, Chevalier G (2014). Morphological characterization of mycorrhizae formed between three *Terfezia* species; desert truffles and several Cistaceae and Aleppo pine. *Mycorrhiza* 24:397-403. <https://doi.org/10.1007/s00572-013-0550-7>
- Zniber I, Boukcim H, Khabar L, Ducouso M, Henkrar F, El Mouttaqi A, Hirich A (2022). Characterization of desert truffles in the Great Moroccan Sahara: A Review. *Environmental Sciences Proceedings* 16:55.



The journal offers free, immediate, and unrestricted access to peer-reviewed research and scholarly work. Users are allowed to read, download, copy, distribute, print, search, or link to the full texts of the articles, or use them for any other lawful purpose, without asking prior permission from the publisher or the author.



**License** - Articles published in *Notulae Scientia Biologicae* are Open-Access, distributed under the terms and conditions of the Creative Commons Attribution (CC BY 4.0) License.

© Articles by the authors; Licensee SMTCT, Cluj-Napoca, Romania. The journal allows the author(s) to hold the copyright/to retain publishing rights without restriction.

**Notes:**

- **Material disclaimer:** The authors are fully responsible for their work and they hold sole responsibility for the articles published in the journal.
- **Maps and affiliations:** The publisher stay neutral with regard to jurisdictional claims in published maps and institutional affiliations.
- **Responsibilities:** The editors, editorial board and publisher do not assume any responsibility for the article's contents and for the authors' views expressed in their contributions. The statements and opinions published represent the views of the authors or persons to whom they are credited. Publication of research information does not constitute a recommendation or endorsement of products involved.