

Effects of climate on the productivity of desert truffles beneath hyper-arid conditions

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Abstract Desert truffles are edible hypogeous fungi that are very well adapted to conditions of aridity in arid and semi-arid regions. This study aims to highlight the influence of climatic factors on the productivity of desert truffles under hyper-arid climatic conditions of the Sahara Desert in Algeria, with assumptions that the more varying climatic factors, mainly rainfall, are more crucial for the development and production of desert truffles. At seven separate sites, desert truffles were collected by systematic sampling between 2006 and 2012. The effects of climate parameters of each site on the productivities (g/ha/year) of desert truffle species were tested using generalized linear models (GLMs). The annual mean of the total production recorded for all three harvested species (*Terfezia arenaria*, *Terfezia clavaryi*, and *Tirmania nivea*) was 785.43 ± 743.39 g/ha. *Tirmania nivea* was commonly present over the sampled sites with an occurrence of 70 ± 10.1 %. GLMs revealed that total and specific productivities were closely positively related to autumnal precipitations occurring during October–December, which is the critical pre-breeding period for both desert truffles and host plant species. The other climatic parameters have statistically no effect on the annual variation of desert truffle productivity.

Keywords Desert truffle · Productivity · Climate variability · Precipitation timing · Sahara Desert · Drylands

Introduction

Drylands are characterized by water scarcity and extreme seasonal weather conditions with unpredictable rainfall. Desert areas cover about 6.5 % of the Earth's surface, the equivalent of a fifth of the land surface, which is about 33 million km² (Goudie 2002; Laity 2009). In general, the prevailing ecological conditions over these regions are very restrictive to the spontaneous survival of living beings (Chenchouni 2012). Under such conditions, the Sahara Desert in North Africa is characterized by a specific vocation that involves desert truffles which are very much appreciated by the local population. Known locally as *terfez* in the northern Sahara of Algeria, the desert truffles grow and spread over habitats that provide favorable ecological conditions, principally climate (Bradai et al. 2013).

Since ecosystem productivity is very low in arid regions (Laity 2009) and therefore natural nutrient sources are, too (Harris and Mohammed 2003), desert truffles have great popularity, especially for their nutritional value and specific delicious taste. Indeed, these edible wild ascomycetes add remarkable flavor to the staple food and they are also a rich source of proteins, amino acids, fatty acids, minerals, and carbohydrates (Al-Naama et al. 1988; Bokhary and Parvez 1988; Bokhary et al. 1989). In addition, the desert truffles have been used in traditional medicine for more than two millennia without known harmful or toxic effects on their users (Al-Rahmah 2001). Due to their wide distribution in arid and semi-arid regions of the world, desert truffles are considered edible and an excellent source of nutrition since about 3,000 years (Chang 1980; Morte et al. 2008), not only because of their particular biochemical composition (Trappe

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1979; Al-Delaimy and Ali 1970; Morte et al. 2009) but also due to a range of ethnomycological uses among dryland peoples (Mandee and Al-Laith 2007).

Ecologically, they are hypogeous ascomycetes fungi living in mycorrhizal association with annual or perennial *Helianthemum* spp. plants (Cistaceae). Their range encompasses arid and semi-arid areas worldwide, including North Africa (Dib-Bellahouel and Fortas 2011; Morte et al. 2009; Bradai et al. 2014), Kalahari Desert (Ferdman et al. 2005), Southern Europe (Morte et al. 2009), and the Middle East (Alsheikh 1994; Mandee and Al-Laith 2007; Kagan-Zur and Roth-Bejerano 2008; Bawadekji et al. 2012) including Iran (Jamali and Banihashemi 2012).

In all these distributional areas of desert truffles, ecological characteristics of habitats are basically common. For example, in the Euro-Asian and Mediterranean regions, habitats of desert truffles are inland steppe zones characterized by semi-arid to arid continental climate with dry summers (i.e., no rainfall during June–September) and more or less rainy winters. Annual rainfall is ranging between 300 and 600 mm in semi-arid regions and from 50 to 250 mm in arid regions. Rainfall in these regions is often irregular, where years of drought are frequent (Kagan-Zur and Akyuz 2014).

Therefore, climatic parameters are among the most important abiotic factors that effectively control the occurrence of desert truffles (Trappe et al. 2008a, b). Among these, it is rain falling after the dry period that determines the development of truffles (Mandee and Al-Laith 2007; Bradai et al. 2014). However, most studies that investigated the bio-ecology of desert truffles give individual speculative findings about the influence of climatic factors on their occurrence and productivity (Alsheikh and Trappe 1983; Alsheikh 1994; Khabar et al. 2001; Chafi et al. 2004; Kagan-Zur and Roth-Bejerano 2008). Furthermore, very few surveys specifically have sought at what degree climate factors influence the occurrence and productivity of desert truffle species in arid or semi-arid climatic conditions.

As ecological activities of living beings are influenced by variables that are experiencing major changes in the environment (Chapin et al. 2000), we assume that the production of desert truffles is controlled by environmental factors having large variations in their habitat. Also, knowing that the arid climate in hot deserts (limiting habitat from the water viewpoint) is characterized by erratic and very low rainfall with large fluctuations of the pluviometric scheme (Laity 2009), we hypothesize that precipitation (both quantity and schedule) is the climatic factor which influences the appearance of truffles and therefore controls their growth and productivity. Thus, two questions arise here: (i) at what period of the year is rainfall critical to the development of desert truffles? (ii) Because the various climatic factors vary in space and time, what are those that affect desert truffle production under hyper-arid conditions? Moreover, the current study targets to

carry out a mid-term monitoring of productivity of desert truffle species in the northern Sahara on the one hand and determines the climatic parameters that influence this productivity on the other.

Materials and methods

Study area and sampling sites

The study area is located in the northern Sahara of Algeria, between 28° 40' N to 33° 40' N and 02° 00' E to 08° 00' E. Seven sites in this region were chosen to collect desert truffles (Fig. 1). The choice of these sites was based on the guidelines of indigenous and nomad peoples, but truffle desert hunters were also consulted. The sampled study sites are deemed to frequently produce desert truffles. According to Bradai et al. (2014), soils of the sampled sites have poor physicochemical characteristics, in which pedological analyses (Table 1) reveal that sites have non-saline soils (electrical conductivity ranged between 0.65 and 0.79 dS/m) which have a typically sandy texture and are slightly alkaline (pH ~7.60–8.05), highly deficient in soil organic matter (0.78–0.98 %), moderately calcareous (CaCO₃ content varied from 9.09 to 12.01 %), and poor in phosphorus content (23.42–25.54 ppm).

After uploading latitude–longitude data of each site into the climate interpolation software package New_LocClim version 1.10 (www.fao.org/nr/climpag/pub/en3_051002_en.asp; Grieser et al. 2006), climate information of the study sites was generated based on interpolations of long-term weather data of the nearest ten meteorological stations around the study site in question. Based on these climatic interpolations, the climate of the whole area is typically hot arid (BWh climate class according to Köppen–Geiger classification, Peel et al. 2007) with very low values of the aridity index (0.02–0.04) and De Martonne index (1.21–4.91). Furthermore, Budyko's radiation index of dryness reveals values ranging between 21.4 for the extremely northern study site (Oued Righ) to 42.6 recorded in Golea (Table 1). Indeed, mean annual temperatures are high, with absolute maxima in July–August, up to and may exceed 50 °C, and with minima in January ranging from 2 to 9 °C (Le Houérou 1990). Precipitation almost and usually occurs as very erratic rainfall with very low amount. The estimate of precipitation deficit reveals high values in all study sites (>1,370 mm/year), where the dry period lasts all year (Fig. 1).

In addition, the combination of this low rainfall with an irregular pluviometric regime that knows large interannual variability is causing long periods of drought in the Sahara Desert (Laity 2009). This supports the fact that it is precipitation, rather than temperature, which plays the role of limiting factor to the net primary production (NPP) in this ecoregion. Indeed, according to the Miami model (Lieth 1975), low

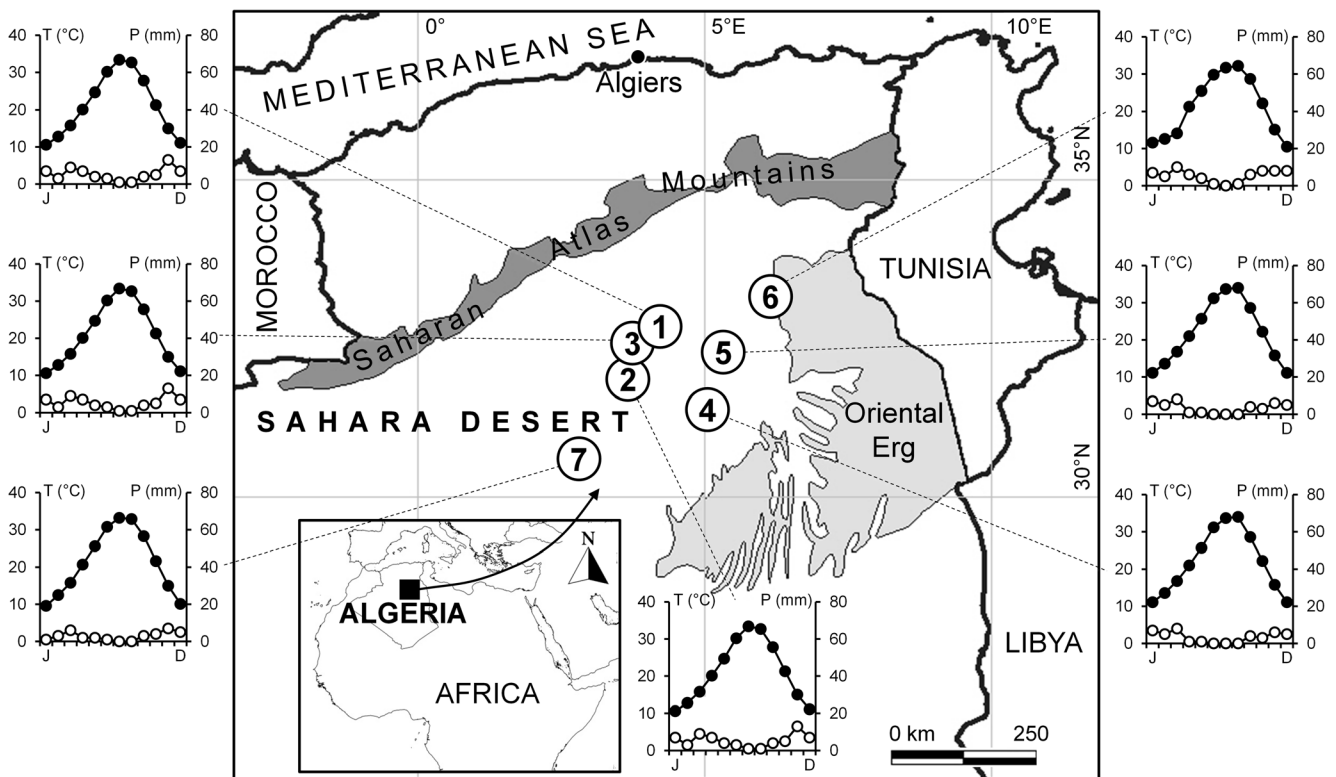


Fig. 1 Geographic location of the study area including the climatic diagrams (*solid circles* represent temperature T and *empty circles* symbolize precipitations P ; Bagnouls and Gaussien 1957) of the sampled sites

(1 Guerrara, 2 Hassi El Fehal, 3 Nomrate, 4 Oued Mya, 5 Oued N'ssa, 6 Oued Righ, 7 Golea) in the Sahara Desert of Algeria

values of NPP are related to annual precipitations; thus, the latter are seen as limiting factor since the model is based on the law of the minimum. Finally, Gorczyński's continentality index (Gorczyński 1920) of the study sites ranged between 46 and 58 (Table 1).

Desert truffle collection

Within each study site, a 1-ha plot (100×100 m) was defined for harvesting and monitoring desert truffle productivity. GPS coordinates of each plot were recorded in order to return to the same plots each time.

From 2006 to 2012, regular surveys and collections of truffles were held weekly during the period of December–March, which matches the period of desert truffle development (Chafi et al. 2004; Bradai et al. 2014). On-site, a purposive-systematic sampling was applied for harvesting all fruiting bodies of desert truffles inside the study plot, i.e., inspecting the surrounding areas of host plants belonging to the genus *Helianthemum*, where generally truffle ascocarps cause cracks and swellings in soil surfaces.

Each collected ascocarp was weighed on-site by an electronic balance (to the nearest 0.01 g), then put in a bag for species identification at the laboratory. For desert truffle species identification, the method of Ferdman et al. (2005) was used by referring to the keys of determination of Trappe

(1979). The annual productivity of desert truffles of each study site was given by the sum of weights of all collected ascocarps during the year in question expressed to 1 ha of surface.

Climatic parameters

Climatic data mainly originated from the nearest meteorological station of each study site. During each year and for each study site, we gathered the following climatic variables:

- (1) Annual mean of minimum, maximum, and average temperatures (°C)
- (2) Total annual precipitation (mm)
- (3) Cumulated precipitation (mm) recorded during October, November, and December, corresponding to the pre-growing period of both desert truffles and the host plant species
- (4) Cumulated precipitation (mm) recorded during January, February, and March, corresponding to the effective growing period of both desert truffles and the host plant species (Bradai et al. 2013; 2014)
- (5) De Martonne index I_{DM} : $I_{DM} = P / (T + 10)$, where P (mm) is total annual rainfall and T (°C) represents the annual mean of average temperatures (De Martonne 1925).

Table 1 Location, edaphic, and climatic characteristics of the study sites in the Algerian Sahara Desert

| Site characteristics | Study sites | | | | | | |
|--|--|----------------|---------|----------|------------|-----------|---------|
| | Guerrara | Hassi El Fehal | Nomrate | Oued Mya | Oued N'ssa | Oued Righ | Golea |
| Location | | | | | | | |
| Site code (Fig. 1) | 1 | 2 | 3 | 4 | 5 | 6 | 7 |
| Latitude (north) | 32° 40' | 31° 37' | 32° 20' | 31° 24' | 32° 16' | 33° 19' | 30° 40' |
| Longitude (east) | 04° 17' | 03° 43' | 03° 49' | 04° 53' | 05° 19' | 05° 54' | 03° 01' |
| Altitude above sea level (m) | 360 | 367 | 457 | 200 | 137 | 73 | 431 |
| Soil parameters^a | | | | | | | |
| Texture | Sandy texture: sand (80.6–91.7 %), silt (6.2–18.0 %), clay (1.6–3.2 %) | | | | | | |
| Electrical conductivity (dS/m) | 0.66 | 0.66 | 0.79 | 0.78 | 0.67 | 0.78 | 0.65 |
| pH | 7.88 | 7.78 | 7.96 | 8.05 | 7.6 | 7.9 | 7.84 |
| Organic matter contents (%) | 0.83 | 0.83 | 0.85 | 0.84 | 0.78 | 0.97 | 0.98 |
| Total CaCO ₃ contents (%) | 10.21 | 11.28 | 11.66 | 9.09 | 9.19 | 9.09 | 12.01 |
| Phosphorus contents (ppm) | 22.09 | 23.42 | 21.95 | 24.22 | 21.83 | 22.28 | 25.54 |
| Climate information | | | | | | | |
| Köppen classification | Hot desert arid climate (BWh) | | | | | | |
| Budyko's radiation index of dryness | 23.72 | 24.05 | 23.83 | 36.34 | 35.89 | 21.37 | 42.60 |
| Aridity index | 0.04 | 0.04 | 0.04 | 0.02 | 0.02 | 0.04 | 0.02 |
| De Martonne index | 2.62 | 1.21 | 2.73 | 2.03 | 3.67 | 4.91 | 1.29 |
| Precipitation deficit (mm/year) | 1,371 | 1,371 | 1,371 | 1,639 | 1,639 | 1,396 | 1,462 |
| Climatic NPP (g (DM)/m ² /year) | 125 | 125 | 125 | 79 | 79 | 125 | 67 |
| NPP (temperature) | 2,316 | 2,316 | 2,316 | 2,363 | 2,363 | 2,314 | 2,319 |
| NPP (precipitation) | 125 | 125 | 125 | 79 | 79 | 125 | 67 |
| Gorczynski continentality index | 51.4 | 53.5 | 52.1 | 54.3 | 52.5 | 46.8 | 58.3 |

NPP net primary production

^a According to Bradai et al. (2014)

Data analysis

Descriptive statistics were given as box plots to describe the extent of productivity values of each desert truffle species throughout the study period and study sites. To test the null hypothesis that there is no difference in annual production (g/ha) and occurrence (%) of each desert truffle species between the seven sampled sites, Pearson's chi-square test (χ^2) was applied at $\alpha=0.05$. Moreover, to model the effects of the studied climatic parameters on the annual variation of the productivity of each desert truffle species as well the total productivity (all species combined) in each site, linear models (LM) were used (Chambers 1992). In each model, the annual productivities (specific and total) at each site were associated with the annual values of climate parameters. The LM summary was given of each productivity including multiple R^2 (MR^2), adjusted R^2 (AR^2), and F statistic (F) with P value (P). R-commander {Rcmdr} was used as a statistical package for computations (Fox 2005; R Development Core Team 2014).

Results

Abundance and occurrence of desert truffle species in the experimental plots

During the period from January 2006 to March 2012, a total of 78 desert truffle ascocarps were harvested in the northern Sahara of Algeria. These ascocarps belong to two genera *Terfezia* Tul. & C. Tul. and *Tirmania* Chatin (*Pezizaceae*) that are classified into three species, namely *Tirmania nivea* Trappe, commonly called *Terfesse Labyadh* with 38 harvested ascocarps; *Terfezia arenaria* (Moris) Trappe with 24 collected ascocarps, known under the common name *Terfesse Lahmar*; and *Terfezia claveryi* Chatin, known locally as *Terfesse Lakhal*, of which 16 ascocarps have been collected during the study.

The most common and dominant species in all sampled sites was *Tirmania nivea* with an average occurrence of 70 ± 10.1 %. According to the chi-square test, there is no difference of species occurrence values between the study sites ($\chi^2=8.77$, $P=0.187$). In second position came *Terfezia arenaria*,

whom occurrence ranged between 19 and 37 % with a mean of 22.9 ± 8.1 %. The frequencies of occurrence of this species were significantly different between study sites ($\chi^2=17.02$, $P=0.009$), whereas *Terfezia claveryi* was slightly present with occurrence frequencies ranging from 0 to 17 % with an average of 9.9 ± 5 %. The occurrence *Terfezia claveryi* varied very highly significantly between the sampled sites ($\chi^2=33.69$, $P<0.001$). Indeed, not only was its presence sporadic, but it was completely absent throughout the monitoring in some sites like Oued N’ssa and Oued Righ (Fig. 2).

Variation of desert truffle productivity

Over the seven study sites and during the six study years, the average of the total annual production recorded for all species of desert truffle was 785.43 ± 743.39 g/ha, with the production being zero in some years while reaching a maximum of 2,720.00 g/ha in other years. *Tirmania nivea* was the most productive species with an average productivity of 524.79 ± 491.50 g/ha/year and a maximum output of 1,795.2 g/ha/year. Productivity values of this species experienced a wide range of variation over the years of the survey. It was followed by *Terfezia arenaria* that denoted an average productivity of 197.51 ± 209.00 g/ha/year and a maximum of 761.6 g/ha/year. The average annual production of *Terfezia claveryi* was 63.13 ± 74.71 g/ha. It had the lowest productivity values with less variability when compared with the other two species; its maximum productivity did not exceed 260.22 g/ha/year (Fig. 3).

Annual variation of desert truffle productivity

For all sites and for all harvested species, productivity of desert truffles in the northern Sahara varied from one year to

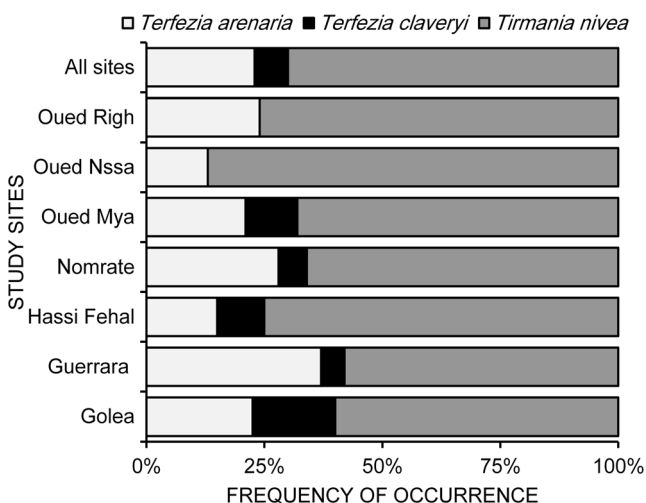


Fig. 2 Distribution of desert truffle species following the study sites in the northern Sahara Desert of Algeria

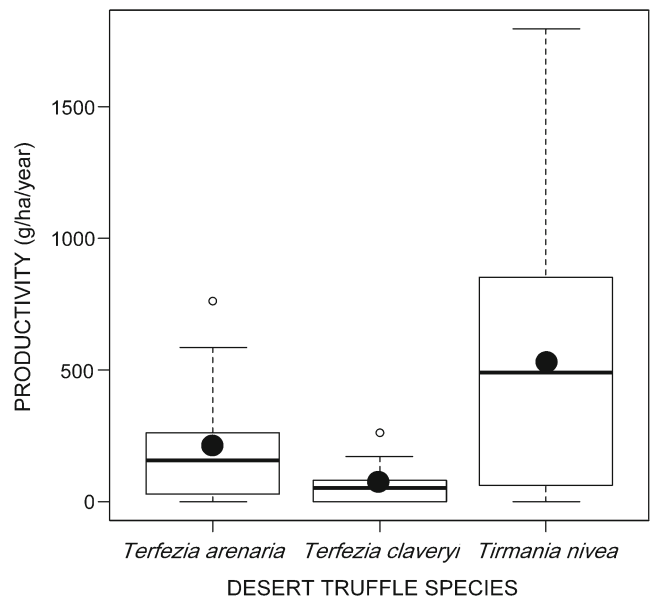


Fig. 3 Variation range of productivity of desert truffle species living in the Algerian northern Sahara region

another, especially in terms of rainfall, particularly during the period October–December. Indeed, we find that no production of desert truffles was reported during 2007, which underwent a severe drought, representing thus the driest year with an average of total annual rainfall equal to 36.20 mm. In contrast, during 2009, we collected the largest amount of truffles with an average annual production of 9.72 kg/ha and with an average annual rainfall of 124.14 mm. However, although 2011 was the wettest year of the study period with an annual total of 168.99 mm, the production of desert truffles was 1.10 kg/ha, and it remains less than that of 2009, knowing that the autumnal rainfall of 2011 was 5.69 mm, lower than that of 2009 during which the autumnal rain reached 49.20 mm.

Another obvious fact highlighting the importance of autumnal rains for desert truffle production was the total production of 2012 that attained 1.71 kg/ha. This was higher than that of 2011 (1.10 kg/ha), although annual precipitation in 2012 (42.5 mm) was significantly lower than that of 2011 (169 mm), but the autumnal rains of 2012 (23.58 mm) were larger than those of 2011 (5.69 mm). For desert truffle species, production of *Terfezia claveryi* was more disturbed by the lack of annual precipitation and autumnal rains compared to those of *Tirmania nivea* and *Terfezia arenaria*, which were the most productive, respectively (Fig. 4). The chi-square test revealed a very highly significant difference between the surveyed sites for specific productions of desert truffles ($P<0.001$).

Climatic factors affecting desert truffle production

Overall and according to the F statistics of the linear models, the tested climatic parameters had a significant effect

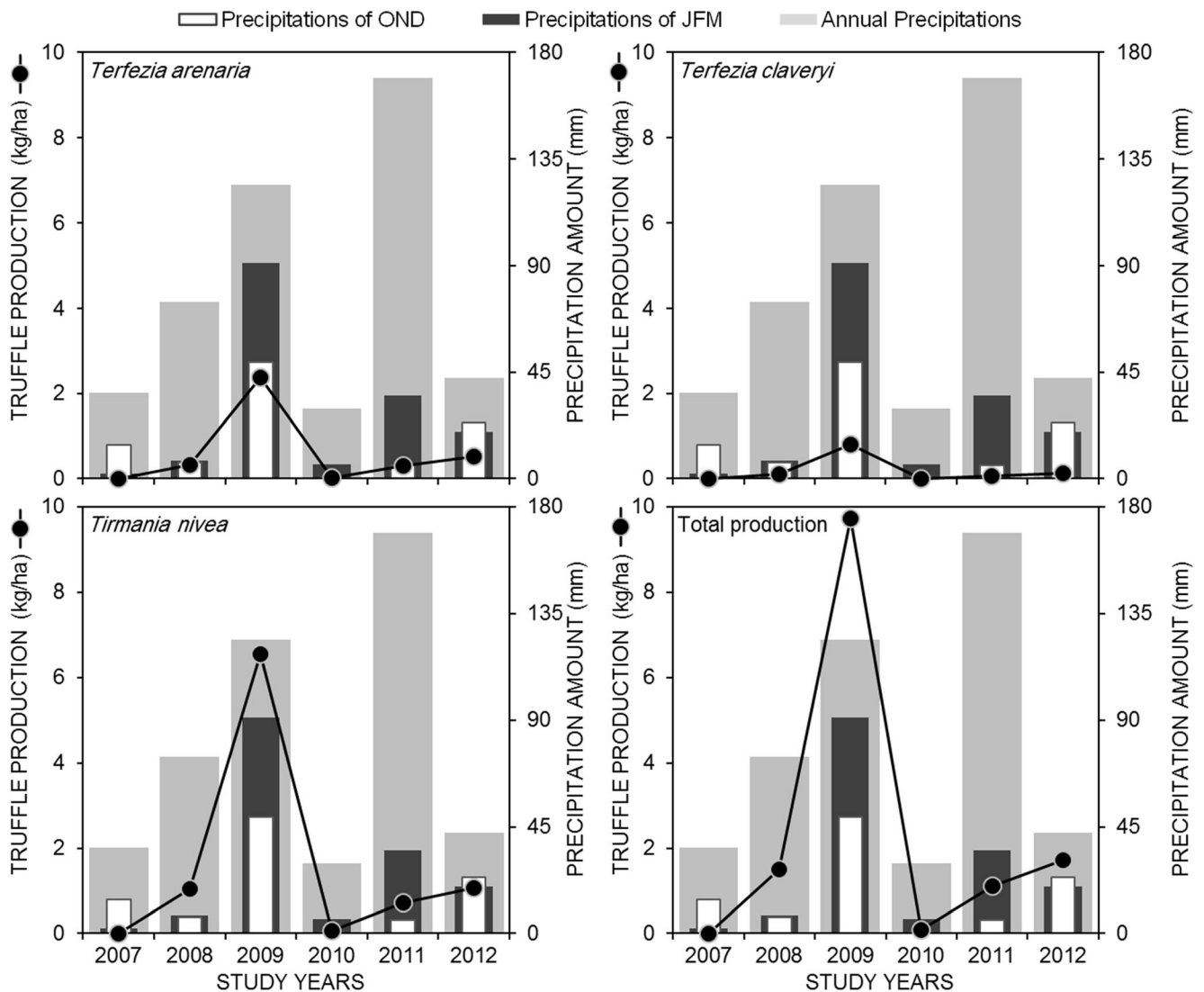


Fig. 4 Annual variation of desert truffle production in relation to precipitation amounts

($P < 0.05$) on the variation of total and truffle species productions except *Terfezia claveryi* production ($F = 2.00$, $P = 0.120$), which significantly ($P = 0.025$) decreased with the annual mean of minimum temperatures. The production of the two other species as well as the total production was found highly significantly ($P < 0.01$) related to the cumulated precipitation of October–December that represents the pre-growing period of desert truffles as well as the host plant species. However, all the other climate parameters statistically had no individual effect on desert truffle productions, although three of the four tested linear models showed that climatic parameters generally had an influence. Despite these non-significant relationships, it can be argued based on the values of LM estimates that desert truffle productions (total and specific) were constantly negatively associated with minimum temperatures and precipitation of January–March, but positively correlated with average and maximum temperatures and annual precipitations (Table 2).

Discussion

Desert truffles of the Algerian northern Sahara require a certain level of autumnal rains and mild winters so that they grow under an arid climate. It is obvious that rains falling during months of winter have no effect on the productivity of truffles. In addition, the low temperatures of winters (January–February) decrease the production of desert truffles. We recall that the first matured ascocarps often appeared at the end of January. Consequently, the impact of climatic factors is perceptible during the period preceding this first appearance.

Our findings regarding the importance of rainfall and its periodicity are quite in agreement with the literature. Indeed, well-distributed annual rainfall from October to March makes harvesting of desert truffles in Algeria successful, taking place in December–January in arid regions and March–April in semi-arid areas (Chafi et al. 2004). These specific periods of truffle harvesting are outlined by seasonal fluctuations of

Table 2 Results from the linear models of the effects of climate parameters on desert truffle species specific and total productivities in the northern Sahara Desert of Algeria (*Std. error* standard error, *AR*² adjusted *R*², *MR*² multiple *R*², *F* *F* statistic, *Temp min* mean annual of minimumtemperatures, *Temp max* mean annual of maximum temperatures, *T avg* mean annual of average temperatures, *Prec ann* annual precipitation, *Prec OND* cumulated precipitation of October–December, *Prec JFM* cumulated precipitation of January–March, *De Martonne* De Martonne index)

| Climatic variables | Estimate | Std. error | <i>t</i> value | <i>P</i> value | Estimate | Std. error | <i>t</i> value | <i>P</i> value |
|--------------------|--|------------|----------------|----------------|--|------------|----------------|----------------|
| | <i>Terfezia arenaria</i> (<i>MR</i> ² =0.83, <i>AR</i> ² =0.71, <i>F</i> =6.82, <i>P</i> =0.004) | | | | <i>Terfezia claveryi</i> (<i>MR</i> ² =0.61, <i>AR</i> ² =0.34, <i>F</i> =2.00, <i>P</i> =0.120) | | | |
| Intercept | -83.4 | 2,119.6 | -0.04 | 0.969 | 1,396.2 | 1,136.9 | 1.23 | 0.248 |
| Temp min | -43.1 | 50.7 | -0.85 | 0.416 | -71.6 | 27.2 | -2.63 | 0.025 |
| Temp max | 19.7 | 54.6 | 0.36 | 0.727 | -13.9 | 29.3 | -0.48 | 0.645 |
| Temp avg | 5.1 | 7.3 | 0.70 | 0.498 | 7.2 | 3.9 | 1.84 | 0.096 |
| Prec ann | -13.4 | 29.7 | -0.45 | 0.663 | 12.6 | 16.0 | 0.79 | 0.450 |
| Prec OND | 6.6 | 1.4 | 4.75 | 0.001 | 1.5 | 0.7 | 2.01 | 0.073 |
| Prec JFM | -1.9 | 1.6 | -1.21 | 0.255 | -0.5 | 0.8 | -0.59 | 0.571 |
| De Martonne | 517.7 | 968.6 | 0.53 | 0.605 | -394.5 | 519.5 | -0.76 | 0.465 |
| | <i>Tirmania nivea</i> (<i>MR</i> ² =0.77, <i>AR</i> ² =0.61, <i>F</i> =4.74, <i>P</i> =0.014) | | | | Total productivity (<i>MR</i> ² =0.79, <i>AR</i> ² =0.64, <i>F</i> =5.24, <i>P</i> =0.010) | | | |
| Intercept | 3,217.3 | 5,762.9 | 0.56 | 0.589 | 4,530.2 | 8,386.4 | 0.54 | 0.601 |
| Temp min | -288.0 | 137.9 | -2.09 | 0.063 | -402.7 | 200.6 | -2.01 | 0.073 |
| Temp max | 19.7 | 148.5 | 0.13 | 0.897 | 25.4 | 216.1 | 0.12 | 0.909 |
| Temp avg | 28.0 | 19.7 | 1.42 | 0.186 | 40.3 | 28.7 | 1.40 | 0.191 |
| Prec ann | 46.1 | 80.9 | 0.57 | 0.581 | 45.3 | 117.7 | 0.39 | 0.708 |
| Prec OND | 13.7 | 3.8 | 3.63 | 0.005 | 21.8 | 5.5 | 3.97 | 0.003 |
| Prec JFM | -5.5 | 4.2 | -1.29 | 0.227 | -7.8 | 6.2 | -1.27 | 0.233 |
| De Martonne | -1,265.8 | 2,633.4 | -0.48 | 0.641 | -1,142.6 | 3,832.2 | -0.30 | 0.772 |

climate factors. Only during favorable climatic conditions can truffles grow. However, in a changing world, the climate is a limiting factor for the production of truffles by influencing both host plant fitness and fungi spore germination and growth (Sitrit et al. 2014). The production of black truffles (*Tuber melanosporum* Vittad.) has declined due to climate change including precipitations of May–August (Le Tacon et al. 2014).

In several countries, there are legends that link desert truffles to storms at the beginning of the rainy season. For example, the Israeli Bedouins of Negev tell the same story as hunters of desert truffles in Morocco and Syria (Kagan-Zur and Roth-Bejerano 2008).

In general, areas where desert truffles grow are characterized by annual rainfall that varies between 50 and 380 mm. In addition, a high yield of truffles in North African countries is obtained when the annual rainfall varies from 70 to 120 mm, while in countries of Southern Europe, important productions of desert truffles coincide with annual precipitation ranging from 100 to 350 mm. In our study sites during the period 2006–2012, the annual rainfall recorded low values that ranged from 0.25 to 158 mm with a 7-year average of 75.84 ± 53.52 mm. These low precipitation amounts may be the cause of low truffle production in some years and/or sites. However, the frequency of these rainfalls is as important as

their quantity, that is to say, the importance of rainfall timing to match the early growing period of both desert truffles and host plants. Definitely, precipitations are required no later than early December in North Africa and the Middle East and no later than early October in Southern European countries (Morte et al. 2009).

The period of truffle fruiting in the northern Sahara Desert occurs quite earlier compared to that of other regions; it lasts from late winter until early spring. While in the Middle East, desert truffles appear in spring after adequate wintery rainfall. This is the same period of time required for annual host plants to complete their life cycle. In fact, many host plants support in combination the production of desert truffle ascocarps (Awameh and Alsheikh 1979; Sitrit et al. 2014).

Not only is the amount of rainfall critical for desert truffle production but also the synchronization of the rainfall period with the growth period of the host plant is among the determinant factors. Indeed, a minimum of 180 mm of well-distributed rainfall between October and March produces a dense vegetation cover with a good growth of annual plant species including *Helianthemum* spp. This growth of the host plants gives more chance for the establishment of mycorrhizae with *Terfezia* spp., which is a prerequisite for a good growth of ascocarps. However, rainfall occurring in late autumn delays germination and growth of annual host plants (Alsheikh

1994). This has negative influences on the productivity of desert truffles. Furthermore, the timing and amount of precipitation control the growth of ascocarps, as it was reported for *Picoa lefebvrei* (Pat.) Maire sub: *Phaeangium lefebvrei* (Alsheikh and Trappe 1983).

According to Alsheikh and Trappe (1983), it is mostly rainfall occurring during mid-January to late February that causes the appearance of desert truffles in Qatar. In Morocco, it is rather rains of November–January that are the most determinant (Khabar et al. 1994), whereas the germination of desert truffles in Kuwait and Egypt is controlled by precipitations of October–November (Awameh and Alsheikh 1979; Feeney 2002). However, in case of heavy rains, spores may be damaged and thus little desert truffles are produced (Feeney 2002).

The air temperature may also affect truffle productivity, not only by influencing soil temperature on the one hand, and therefore ascocarps, but also by inducing a direct impact on the physiological activities of aerial parts of the host plant and thus on the plant–fungus relationship on the other hand. Since performances of mycorrhization depend on physiological performances of the two symbionts (Morte et al. 2000; Morte et al. 2010), it is especially the minimum temperatures that can disrupt the production of truffles because they significantly affect the host plant than the fungus as temperature is considerably mitigated by soil depth. This may explain the negative effect of minimum temperatures on *Terfezia clavaryi* productivity following the GLM.

The bio-ecology of desert truffles is significantly related to changes in various environmental factors, including rainfall. Indeed, their development depends on water availability and climatic conditions, in particular seasonality and periodicity of rainfall in addition to their quantity and spatiotemporal distribution (Bokhary and Parvez 1988). Actually, rainfall of the period October–December is involved not only in germination and resumption of growth of host plant species but also in transport and infiltration of fungi spores in soil, then germination and mycelial growth of desert truffles (Bradai 2006). That is why productivities of all desert truffle species were deemed positively correlated with precipitations of this period.

Besides, the introduction of desert truffles in hot arid environments can be a useful way to use lands which hitherto were considered unproductive (Morte et al. 2000). In conclusion, desert truffles are still a mysterious footprint in dryland grounds but also a good indicator of an amazing adaptation to arid conditions in hot deserts, which is ensured by a particular biological association with desert plants that are also well adapted. Autumnal precipitations represent a significant potential for the development and production of desert truffles in regions of the Algerian northern Sahara. Desert truffles are not only natural products of nutritional, therapeutic, and economic interests; however, its good adaptation to arid climate may

change our vision for valorizing flora and fauna of drylands in a changing world.

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