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Abstract

The 930,000 km^2 Kalahari covers nearly all of Botswana, the eastern third of Namibia, and Northern Cape Province of South Africa. It is a basin-like, arid and semiarid plain 900 m or more in elevation with a long history of use of truffles by its native people. Three genera and species of desert truffles have been recorded from the Kalahari: *Kalaharituber pfeilii* is a monotypic endemic. *Eremiomyces* has also been reported from Spain and *Mattirolomyces* is a cosmopolitan genus, at least in terms of xeric habitats, but their Kalahari species, *E. echinulatus* and *M. austroafricanus*, are endemic. *Kalaharituber pfeilii* has been prized as a food by the San back into their prehistory. It is harvested for personal use but also for sale to distributors for both domestic use and European markets. Depending on rain in a region where rain is undependable, its production understandably varies strongly from year to year.

Chapter 13
Ecology and Distribution of Desert Truffles in the Kalahari of Southern Africa

James M. Trappe, Andrew W. Claridge, and Varda Kagan-Zur

13.1 Introduction

The Kalahari basin of southern Africa covers some 930,000 km^2, including most of Botswana, the eastern third of Namibia, and Northern Cape Province of South Africa. Little is known of the hypogeous fungi of southern Africa: early reports were studded with misidentifications and inadequate documentation (Marasas and Trappe 1978), despite the long history of truffles as a highly preferred food of the ! Kung San (Bushmen) indigenous people (Lee 1979; Silberbauer 1981). Verwoerd (1925) and Leistner (1967) examined several collections of hypogeous basidiomycetes in southern Africa but were hindered by the inadequate knowledge of the time; many collections were misidentified or introduced with exotic trees such as *Eucalyptus* spp. (Trappe unpublished data), and few were from the Kalahari. Moreover, the nature of these truffles was unclear in some circles as

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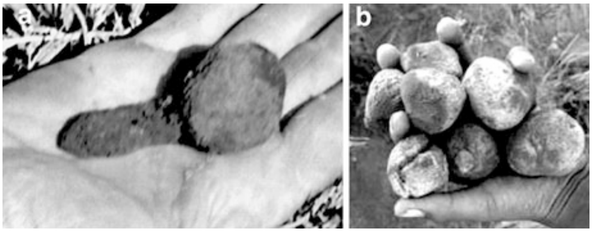

Fig. 13.1 (**a**) Kalahari truffle showing the basal "stalk" formed by a mass of entangled soil, roots, and mycelium. (**b**) Handful of mature Kalahari truffles (courtesy of Tim Turluck, Slow Foods Johannesberg, www.slowfood.co.za; all rights reserved)

late as 1971: "It is uncertain whether this species is a root parasite or a fungus" (p. 107 in Lee and DeVore 1976).

As of now, three species of Kalahari truffles are known. One, *Kalaharituber pfeilii* (Henn.) Trappe & Kagan-Zur, is well known and widely distributed in the Kalahari (Fig. 13.1); *Eremiomyces echinulatus* (Trappe & Marasas) Trappe & Kagan-Zur and *Mattirolomyces austroafricanus* (Trappe & Marasas) Trappe, Kovács and Claridge, in contrast, are known only from a few collections each (Trappe et al. 2010a, b). Given the lack of systematic survey, more species could yet be found in the Kalahari. However, it seems to have a small truffle mycota compared to several desert regions elsewhere in the world (see other chapters in Part III of this volume).

13.2 The Kalahari

13.2.1 Landscapes

The Kalahari is a more or less featureless, gently undulating sand plain dominated by three types of surface: sand sheets, longitudinal dunes, and clay pans. All of it is higher than 900 m above sea level, but mountain ranges are absent. Bedrock is exposed only in low, vertical-walled hills (Thomas and Shaw 1991; Logan 2012). AU3

The southern part of the Kalahari has no perennial surface water except for widely scattered water holes (Thomas and Shaw 1991; Logan 2012). Most rain disappears immediately into the sand or flows temporarily during and immediately after rains along short stretches of bedrock into claypans. The northern part, in contrast, has a complex drainage in which heavy rains from as far away as the Angola highlands flow southward in many streams that merge to form the perennial Okavango, Kwango, and several other rivers. These then break into numerous channels that may fill lakes, swamps, and pans. As Logan (2012) phrases it, "Thus is created the paradoxical situation of an area with extensive excess of water in a region chronically short of water."

Despite the term "featureless," a relative term, the Kalahari abounds with diverse habitats.

13.2.2 Geology and Soil

Sand characterizes the Kalahari, but that sand is derived from diverse origins (Thomas and Shaw 1991). Mineralogical studies indicate its sands represent accumulation of materials derived from local sources, including the weathering products of pre-Kalahari rocks supplemented by other material transported over relatively short distances. In general, Kalahari sands are low in organic matter, relatively calcareous, and extremely dry (Logan 2012).

The sand sheets of the eastern Kalahari apparently formed during the Pleistocene from about 12,000 to 2.6 million years before present and have occupied the same areas ever since (Logan 2012); most were wind-formed. They change little in elevation, and the sand is generally deeper than 60 m. It is often red from iron compounds, a potentially meaningful trait in distribution of *Kalahari pfeilii*, the Kalahari truffle.

In contrast to the eastern Kalahari, the western Kalahari is entirely composed of north–south-oriented dunes at least 2.5 km long, a hundred meters or more broad, and 7–70 m tall. These dunes are separated from each other by broad, parallel depressions termed a *straat*, or street.

Pans are also common in parts of the Kalahari (Leistner 1967), having resulted from surface water flow in past times of greater precipitation. Where such flows disappeared into the sand in low places, the silt they carried formed pans (Logan 2012). The pans of the southern Kalahari can be divided into three broad classes: white or calcareous, pink or slightly calcareous, and red or noncalcareous. These in turn may vary in physical and chemical characters from edge to center of the pan (Leistner 1967).

Thomas and Shaw (1991) otherwise provide a detailed description of the geology and climate of the Kalahari (also see Chap. 4 by Bonifacio and Morte).

13.2.3 Climate

The southwestern Kalahari meets the traditional definition of a desert as receiving less than 250 mm of rain per year. Moreover, it conforms to a more accurate definition in which potential evaporation is twice as great as the precipitation. As commonly the case in deserts, the southwest varies markedly between and within years in precipitation. The northeast, in contrast, cannot qualify climatically as a desert by these definitions. Nonetheless, it has no surface water; the rain drains instantly through its deep stands to produce an edaphic drought (Logan 2012).

Two principles of Kalahari rainfall are variability and uncertainty (Thomas 2002). Pike (1971) reports for the Okavango Delta that more than 75 % of rain events are low in intensity, and half the storms produce less than 10 mm of precipitation per event. Annual rainfall varies notably as well. In many years rains do not start until December or January, and sometimes no rain falls after February or March. Silberbauer (1981) reported for the Ghanzi District of the central Kalahari that from 1961 to 1965 annual precipitation ranged from about 100 to 770 mm. Most rainfalls were of low intensity, and half of them delivered less than 10 mm, but most of the annual total was from localized, violent thunderstorms. The wet season usually begins in October or November and ends in April or May, but in many years the rain commences in December or January, and some years no rain may fall after February or March. The !Kung San divide the year into five seasons (Lee 1979): spring rains, main summer rains, autumn, winter, and the spring dry season. The spring rains usually begin in October or November and mostly consist of light thundershowers that hit in one place, miss others entirely, and generally last about an hour. These rains trigger plant growth. The main summer rains in December to March bring a season of relative plenty (Fig. 13.2), depending on their highly variable timing and intensity. The dry but still warm autumn season of April or May is followed by the dry but cool to cold winter months into August. The early spring dry season begins in late August, when temperatures begin to warm, and lasts until commencement of the spring rains in October or November. The Kalahari is huge, so variations on this theme are to be found in the wetter north and drier south.

The Kalahari's relatively high elevation and predominantly clear, dry weather produce large seasonal and diurnal temperatures. Summer day shade temperatures often reach 43–46 °C and drop to 21–27 °C at night. Winter night temperatures may drop to 12 °C (Logan 2012).

13.2.4 Plants

The large diversity of Kalahari habitats on both macro- and microscales naturally results from the interaction of the diverse soils and climates over its 930,000 km^2. Most research on plant communities has been focused on the deserts of the central and southern Kalahari of Botswana, eastern Namibia, and western Northern Cape Province of South Africa (Leistner 1967; Lee 1979; Thomas and Shaw 1991). The documented collections of desert truffles of the Kalahari span these regions (Trappe et al. 2008a, 2010a).

Silberbauer (1981, Figs. 4–6) presents informative transect diagrams of the region's dune woodlands, scrub plain and pan, and thornveld. We will not repeat the details of these and other plant ecological features (Leistner 1967; Thomas and Shaw 1991, and others) for lack of specific information on habitats recorded for occurrence of desert truffles.

Fig. 13.2 Harvesting Kalahari truffles: lush growth of vegetation after intense summer rainstorms signals a good truffle fruiting season in the following winter

13.3 The Kalahari Desert Truffles

Compared to truffle-producing deserts elsewhere (see the other chapters in Part III of this volume), the Kalahari is poor in both species and genera. For example, the Kalahari has three genera, each with one species: *Eremiomyces echinulatus*, *Kalaharituber pfeilii*, and *Mattirolomyces austroafricanus*. A possible fourth also exists: specimens of an undescribed species of the genus *Tirmania* were collected by Kagan-Zur and Taylor on their Kalahari truffle collection expedition during 1990. Unfortunately, the specimens were lost, so scientific identification as well as herbarium specimen accession await further collections. In contrast, the other major desert region of the southern hemisphere, the Australian outback, has six genera and seven species (see Chap. 14 by Claridge et al.; Trappe et al. 2008b). The reason for this disparity is presently unclear, although the trend is in keeping with the general observation that the diversity of hypogeous fungi Australia-wide is unparalleled relative to other continents.

13.3.1 History of Discovery

The indigenous peoples of the Kalahari likely have used truffles for countless centuries, a presumption backed by the high regard they have for truffles as a preferred food to this day (Lee 1979; Silberbauer 1981). The first published record of Kalahari Desert truffles, however, appeared in 1897.

In the 1890s Joachim Count von Pfeil, German politician and explorer, obtained truffles in Damaraland, South-West Africa (now Namibia). He sent them pickled in vinegar in a large jar to the German mycologist Paul Christoph Hennings, who recognized them to be an undescribed species (Hennings 1897). He described and named them *Terfezia pfeilii* Henn. That name persisted for more than a century (see Trappe et al. 2008a for a brief historical review) and was accepted by Marasas and Trappe (1973), who added two additional new species to the truffles of the Kalahari: *Choiromyces echinulatus* Trappe & Marasas and *Terfezia austroafricana* Trappe & Marasas. The advent of molecular methods enabled a new, more precise way of evaluating phylogeny of fungi, and these were used to good effect by Ferdman et al. (2005). Their molecular data demonstrated that *C. echinulatus* and *T. pfeilii* each merited new and separate generic status. They described two new genera and transferred the two species accordingly: *Eremiomyces echinulatus* (Trappe & Marasas) Trappe & Kagan-Zur and *Kalaharituber pfeilii* (Trappe & Marasas) Trappe & Kagan-Zur.

Then, Trappe et al. (2010a, b) applied molecular techniques to *Terfezia austroafricana*, showing that species to belong to *Mattirolomyces*, a genus occurring in Mediterranean Europe. So, the new combination *M. austroafricanus* was formulated. With these nomenclatural corrections, the names should endure.

13.3.2 Taxonomy, Endemism, and Distribution

All taxa of Kalahari Desert truffles are described in detail, illustrated, discussed, and keyed by Trappe et al. (2008a, 2010a, b). The three genera/species of desert truffles so far discovered are all in the Ascomycota, order Pezizales, family Pezizaceae.

All three species are endemic to the Kalahari, but the genera *Eremiomyces* and *Mattirolomyces* are now known from elsewhere. Until a new species, *E. magnisporus* G. Moreno et al., was described from a semiarid habitat in central Spain (Alvarado et al. 2011), *E. echinulatus* was thought to represent both an endemic genus and species, but now only the species is endemic to the Kalahari.

Mattirolomyces austroafricanus is a species endemic to the Kalahari, but the genus *Mattirolomyces* was originally described by Fischer (1938) to accommodate *Choiromyces terfezioides* Matt. from a collection from Italy. Since then the genus *Mattirolomyces* has been found in many southern European localities (Kovács 2007), Australia (Trappe et al. 2010a), West Asia, and North America (Kovács et al. 2011). *Mattirolomyces austroafricanus*, originally described as a *Terfezia* species by Marasas and Trappe (1973), was revealed by phylogenetic analysis to belong in *Mattirolomyces* (Trappe et al. 2010a, b).

The currently known distributions of the Kalahari Desert truffles are summarized by Trappe et al. (2010a). *Eremiomyces echinulatus* is known from only three collections from 1961 to the present, one each from Botswana, Namibia, and Northern Cape Province of South Africa. Judging from these collections, it is widely distributed but infrequent. *Mattirolomyces austroafricanus* is represented by only two collections from Northern Cape Province, South Africa.

The common and much prized desert truffle from the Kalahari is *Kalaharituber pfeilii* (Fig. 13.1), represented from several collections from each of Botswana, Namibia, and Northern Cape Province of South Africa and reported without documentation from additional localities in these countries. Unfortunately, the specific localities and coordinates were not noted for any of the collections; rather, only broad regional areas are recorded (Ferdman et al. 2005), so a distribution map offers little more than is given in the first sentence of this paragraph.

13.3.3 Ecology: Key to Distribution

Little information on soils or climate has been documented for any of the collections we have examined or in the literature. In this section we summarize the review by Trappe et al. (2008a). Additional literature supplementing their review is cited in the text.

Analyses of truffle-bearing soils have been reported for only seven sites in Namibia and two in Botswana. *Kalaharituber pfeilii* tended to grow on compact, pink or sometimes white sands with a pH of 5.5–6.5, sometimes as high as 7.2. $CaCO_3$ is low, ranging from 0.3 to 3.1 %. Other observers reported the species in dips between sand dunes, but it also has been harvested in agricultural fields of various herbaceous plants (Kagan-Zur et al. 2001; Mshigeni et al. 2005).

Weather, particularly rainfall, is critical to the fruiting of Kalahari truffles as is true of all desert truffles, for example see Chap. 14 by Claridge et al. for Australian desert truffles. Thus, in his studies of the truffle-hunting !Kung San in northeastern Namibia and northwestern Botswana, Lee (1979) reported that *Kalaharituber pfeilii* did not fruit in the winter of 1964 but was common and easily obtained in the winter of 1968 (April and May) near water holes of the southern part of his study area. Silberbauer (1981) visits with the G/wi-speaking tribesmen of central Botswana, who also preferred *K. pfeilii* over other foods when available, found it mostly in April and May and at least once in January, but the season was short. Mshigeni (2001) reported finding *K. pfeilii* in northern Namibia in June at the end of the truffle season. Depending on the region, the fruiting season may extend as late as June or July, the end of the rainy season when soil and air temperatures are cooling (Fig. 13.2).

The limited literature on plants associated with truffle fruiting, as reviewed by Trappe et al. (2008a), includes shrub–grass–forb communities, cultivated fields of melons, pearl millet and sorghum, shrubs of *Vachellia hebeclada* (DC) Kyal. & Boatwr., a mixed grassveld of *Aristida* and *Eragrostis* species with scattered *Vachellia* trees. (The name *Acacia* has been applied to African species, but molecular analyses show it to differ genetically from Australian members of *Acacia*, to which that generic name was first applied; the African species reported to associate with *K. pfeilii* now are placed in the new genus *Vachellia* [Kayalangalilwa and Bruce 2013].) None of these reports are specific enough to indicate a truffle mycorrhizal host: roots of desert plants can extend farther outward than is often realized, so a fruiting truffle is not necessarily forming mycorrhizae with its nearest plant. Only careful sampling and analysis of roots and experimentation can demonstrate actual mycorrhizal associates of the Kalahari truffle. Yet, knowing which plants form mycorrhizae is requisite to understanding where it occurs for purposes of sustainable management and harvest. Anything that threatens host plants threatens the truffle.

Identity of a several *K. pfeilii* hosts was confirmed by Taylor et al. (1995), who carefully examined the "stalk" of entangled rhizomorphs, hyphae, roots, and soil from which the truffle arises (Fig. 13.1a). This work provided strong evidence of mycorrhiza formation with roots of diverse herbaceous and woody plants: probable mycelium of *K. pfeilii* formed ectomycorrhizal structures such as Hartig nets within the roots. This study was followed by application of DNA analysis by Kagan-Zur et al. (1999) to even more convincingly demonstrate colonization of wild watermelon roots by *K. pfeilii*, this time not with a Hartig net but with structures similar to those formed by *Terfezia* and *Tirmania* spp. with desert annuals on the Arabian Peninsula (see Roth Bejerano et al. in this volume). These two seminal papers provide the first scientific approach to determining the mycorrhizal hosts of *K. pfeilii* and thus form the basis for testing hypotheses about the role of plant hosts in its distribution.

Meerkats, baboons, bat-eared foxes, and hyenas have been observed to eat Kalahari truffles, presumably then dispersing the spores as do animals for hypogeous fungi around the world (Trappe and Claridge 2005). Mycophagy is also probable among any rodent species and other ground-dwelling desert animals.

13.4 The Outlook for Kalahari Desert Truffles

In 2008, a wildfire in Botswana's Central Kalahari Game Reserve, home of the Basarwa (another name for bushmen) people, raged over some 40,000 km^2 in 4 weeks (Earth Observatory 2008). Fire has always been a part of the Kalahari, both from lightning strikes and human activity. Paradoxically, wet years experience the worst fire potential, because the wet years induce fast seed germination and plant growth that rapidly dries to a high fuel load when the dry season begins. Native societies used prescribed burning, probably from ancient times (Thomas and Shaw 1991). How fire affects truffle production in the Kalahari inevitably depends on how fire affects the truffle host plants, particularly the fire sensitive ones. Probably the intense fire noted at the beginning of this paragraph is deleterious, because many plants may be killed. However, the entire topic of fire effects on truffle production, positive and negative, needs much careful research (Claridge and Trappe 2004).

Overgrazing, on the other hand, is well recognized as seriously detrimental to soils, water, and plants. Thomas (2002) elegantly describes evolution of the grazing industry in the Kalahari over time. A few highlights of his paper follow, although a full appreciation demands reading the original. Cattle have been grazing the Kalahari for a millennium or more, but until the last century limited water availability restricted use by cattle in many areas. Now boreholes dot the Kalahari landscape, enabling cattle to survive in formerly unsuitable areas; the cow is now the Kalahari's dominant mammal. With boreholes together with fencing, especially since the 1970s, the cattle populations have grown to impinge seriously on native wildlife, and concentrated grazing is opening the landscape to invasion of undesirable exotic plants and damaging truffle grounds (Khonga 2012).

Climate change will affect the Kalahari, including truffle-producing areas, potentially before the end of the twenty-first century. Precipitation may increase, but aridity may also increase because of higher temperatures and higher evaporation. As truffles have been observed to fruit in the depressions between dunes, the predicted increased mobility of dunes in this century due to increased erodibility and wind energy (Thomas et al. 2005) could bury significant areas of truffle production. Significant dune movement is predicted to occur by 2039 in the southern dune field and in the eastern and northern dune fields by 2069. All dune fields from South Africa to Angola and Zambia will likely be activated by the end of the century.

The serious problems for sustainable production, present and future, are the consequence of environmental factors and human interventions. Restoring and maintaining the health of the truffle population demands answers from research, which has been sporadic at best over the past century. Thus it is gratifying that the Botswana Agricultural College at Gaborone has established the Mahupu Project, named for the native word for truffle. It aims to address "the dwindling yields of the Kalahari desert truffle due to drought, overgrazing, and overexploitation." The project is assessing (1) various tree species and cucurbits as symbionts of the truffle fungus, (2) effect of fencing to reduce overgrazing, and (3) use of supplemental irrigation to enhance truffle yields in the field (Khonga 2012).

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