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Alert: Saharan Oases wheat genetic resources in danger

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Introduction

An important work of the description of wheat landraces collected in the Saharan oases has been carried out by Ducellier (1920), Miège (1924a,b), Ciferri and Garavini (1941) and Erroux (1952, 1954 and 1958). A summary of these investigations was published by Erroux (1962). Collecting missions in the Saharan oases were also carried out over the last decades by Perrino *et al.* (1976) and Guarino *et al.* (1991) in Algeria, Benlaghlid *et al.* (1990) in Algeria and Morocco and Al Alazzeh *et al.* (1982), Perrino *et al.* (1984) and Hammer and Perrino (1985) in Libya. All these studies highlighted the peculiarity of Saharan oases wheat concerning morphology and environmental adaptation.

Wheat landraces traditionally cultivated in the Saharan oases are generally early maturing (Ducellier, 1909), have short and thick stems (Zhukovsky, 1964) and high spike fertility (Erroux, 1962). They include awned and awnless forms, referred by Ducellier (1920) as *aristatum* and *muticum*, respectively, and intermediate forms generally grouped under the term short-awned or *breviaristatum*. Many forms are of the *inflatum* type, their glumes being inflated, angulate at their basis and with a more or less prominent keel (Ducellier, 1920). Awns are often in the shape of hooks and present a dilatation of their basis (plate 1). In some cases, a variation in awn morphology can be observed along the same spike. Finally, Ducellier (1920) reported a high occurrence of morphological anomalies, particularly the insertion of leaf blades just at the basis of the spike or even between two stages of spikelets.

The differences observed between wheat landraces from Sahara and those cultivated in surrounding areas are likely to be a result of a restricted exchange

Plate 1 ■ Spikes (frontal and lateral view) of two Saharan bread wheat landraces, Bent Embarka (left side) and El Hamra (right side), both from Adrar, Touat (Algeria). *(Source : M. Zaharieva)*

of germplasm as Saharan oases are isolated from the rest of the country. In addition, because of their limited production, cereals produced within the oases were traditionally auto-consumed and the exchange of seeds with other regions was limited until the last century (Benlaghlid *et al.,* 1990). Diverse varietal types accumulated successively over time in the oases where spontaneous crossing and natural selction were promoted, leading to intermediate forms or to new forms, all difficult to associate with the referential types already known (Ducellier, 1929). Finally, germplasm from other regions is not expected to adapt quickly to the very specific Saharan climatic conditions. The wheat landraces, probably introduced long time ago, have been subjected over centuries to strong selection pressures related to the physical constraints of the oases environment, particularly heat, drought and salinity (Chevalier *et al.,* 1932). Saharan oases wheat landraces are consequently expected to have developed tolerance to abiotic stresses.

The present chapter, after characterizing the Saharan environment and the different factors that could have facilitated the introduction of germplasm from surrounding regions (eg, movements of population, military conquests, development of trade routes), summarizes our knowledge about Saharan wheat, the different species and forms and their presumed origins, dates and ways of introduction, and underlines their diversity and agronomic value. It represents an attempt to stimulate international efforts to rescue, analyze and more efficiently use Saharan wheat genetic resources in wheat breeding programs.

The Saharan environment

General characteristics

A desert is defined as a barren or desolate area. Deserts can be dry regions of little rainfall, extreme temperatures, and sparse vegetation, or regions of permanent cold that are largely or entirely devoid of life. With 9,100,000 km^2, Sahara is the third largest desert after Antarctica (13,829,430 km^2) and the Arctic (13,726,937 km^2) and the first hot desert, before the Arabian Desert (2,330,000 km^2) and the Gobi desert (1,300,000 km^2) (figure 1).

Sahara's boundaries are the Atlantic Ocean on the West, the Atlas Mountains, the Algerian High Plateaus and the Mediterranean on the North, the Red Sea on the East, and the Sudan region and the Niger Valley on the South. The Sahara covers large parts of Algeria, Chad, Egypt, Libya, Mali, Mauritania, Morocco, Niger, western Sahara, Sudan and Tunisia (figure 2) and represents nearly 10% of the African continent area.

The landscape of Sahara has been shaped over time by wind and includes sand dunes (around 25% of the area), sand sheets, sand seas (*ergs*), gravel-covered plains (*regs*), barren stone plateaus (*hamadas*), sand stone plateaus (*tassilis*), mountains, oasis depressions, ephemeral riverbeds (*wadis*) and salt flats. Several deeply dissected mountains, many volcanic, rise from the desert, like the Aïr, Hoggar, Saharan Atlas, Tibesti, Adrar des Iforas, and the Red Sea hills. The highest peak in the Sahara is the Emi Koussi (3,445 m), a volcano in the Tibesti Mountains of northern Chad.

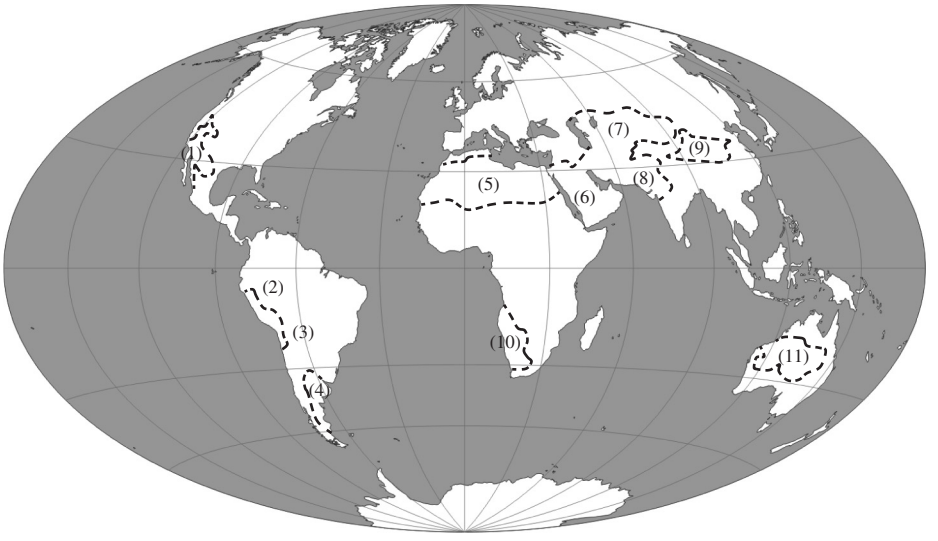

Figure 1 ■ The main hot deserts of the world: (1) Great Basin desert, (2) Peruvian desert, (3) Atacama desert, (4) Patagonian desert, (5) Sahara desert, (6) Arabian desert, (7) Turkmenistan desert, (8) Great Indian desert, (9) Gobi desert, (10) Kalahari and Namibian deserts, (11) Australian desert.

Figure 2 ■ Boundaries of the Sahara desert and countries which have part of their territory covered by this desert.

Climate

Sahara is one of the hottest and driest places in the world (Perret, 1935). The average annual temperature is 30°C but during the hottest months temperature can exceed 50°C. The boundaries of the Sahara desert correspond traditionally to the isohyets of 100 mm on the North and 150 mm on the South (Walton, 2007). According to Wickens (1998) the northern limit of the Sahara coincides with the northern limit of date palm (*Phoenix dactylifera* L.) cultivation and the southern limit of esparto (*Stipa tenacissima* L.). The southern limit of the Sahara is also the southern limit of *Cornulaca monacantha* Del. and the northern limit of *Cenchrus biflorus* Roxb., an annual grass typical of the Sahel.

The precipitation in the desert is very irregular with some parts of the Sahara that do not receive rainfall for decades. Most of the surface water found in the Sahara today is in the form of seasonal or intermittent streams. The only permanent river is the Nile that flows from Central Africa to the Mediterranean Sea. There are, however, numerous rivers that originate outside of the Sahara and enter the Sahara through underground waterways. On the South, the majority of the surface water comes from the Nile River and other rivers that feed into Lake Chad. On the North, the greater part of the water flows from the Atlas Mountains and highlands of Libya, Tunisia and Algeria.

The climate in Sahara has undergone various changes over the last thousands of years (table 1). During the last glacial period, the Sahara was much larger than it is today. During the end of the glacial period (10th millennium

Table 1 ■ Evolution of climatic conditions in Sahara since 21st millennium BCE (adapted from Adams, 1998 and Guo *et al.*, 2000).

Period	Climate
21,000-11,800 BCE	Dry and cold (full glacial period)
11,800-10,800 BCE	Rapid increase in temperature and moisture
10,800-7,500 BCE	Cold and dry (Younger Dryas)
7,500-7,100 BCE	Conditions become moister
7,100-6,900 BCE	Slight drying
6,900-5,900 BCE	Moist
5,900-4,500 BCE	Moderately dry
4,500-2,500 BCE	Moist
2,500-2,100 BCE	Very dry (as dry as at present)
2,100-1,700 BCE	Slightly moister than present
Aft-1,500 BCE	Remaining about as dry as at present

BCE) precipitation in the desert increased. During the Neolithic subpluvial or Holocene wet phase (from *c.* 7,500 to 3,000 BCE) which itself included slightly wetter and drier periods, the natural vegetation was a savanna. From 3,000 BCE, severe drought episodes occurred which had devastating effects on water resources and distribution of animal and plant populations (Kröpelin *et al.*, 2008). Extreme aridity started around 2,500 BCE and was complete by 1,500 BCE (Hassan, 2000). Evaporation exceeded precipitation, the level of water in lakes like Lake Chad falls, and most rivers became ephemeral (Austen, 2010).

The Sahara desert can be divided according to its present climatic characteristics into three geographic zones. The northern Sahara reaches the Mediterranean Sea in Egypt and portions of Libya and borders Mediterranean areas, characterized by a winter rainy season, in Cyrenaica and the Maghreb. Its northern limit corresponds to the northern limit of date palm cultivation (Wickens, 1998). The central Sahara is hyper-arid, with sparse grassland, desert shrub, and trees in the *wadi* where moisture collects. The southern Sahara is bounded by the Sahel, a belt of dry tropical savanna with a summer rainy season that extends across Africa from East to West (Walton, 2007).

Factors of diffusion of crops and management techniques across the Sahara

Population migrations, military conquests and development of trade roads were the main factors which stimulated the creation of oases and diffusion of crops and their management techniques across the Sahara (see Chronology of key events of Sahara history in appendix 1).

Population migrations and military conquests

Present population

Today, Sahara has a population of only 4 million inhabitants, one of the lowest population densities on earth (roughly 1 person for 0.44 km^2). Most of the people living in the Sahara are nomads who move from region to region throughout the desert, or people who live in cities or villages of the oases. The main ethnic groups present in the Sahara are the Arabs, Chleuhs and Berbers (endonym *Amazight*) on the North-West of Sahara, the Berbers of the Algerian and Tunisian oases of northern Sahara and the Tuaregs and Tubu in central and southern Sahara.

The Tuaregs (endonym *Imuhagh*) are a Berber people living in the Saharan parts of Niger, Mali, and Algeria, with a traditionally nomadic pastoralist lifestyle. The Tuareg language is a branch of the Berber language. The Tubu (= rock people) live mainly in northern Chad (around the Tibesti mountains), southern Libya, north-eastern Niger and north-western Sudan. They speak Tebu, a Saharan subfamily of the Nilo-Saharan languages family. Most Tubu are herders and nomads, though many are now semi-nomadic. They are divided in two closely associated people, the Teda and the Daza. Several waves of population from different origins have successively moved to the Sahara over time.

First human occupations

The earliest known hominoid fossil, *Oligopitchecus savage*, found in Fayyum (Egypt), is 33 million years old (Rasmussen and Simons, 1988). About 7 million years ago, proto-humans diverged into a separate evolutionary tree, and soon afterwards (approximately 5 million years ago), Africa began to crack along its eastern ridge, leading to the formation of the Red Sea and the emergence of the great Rift Valleys (Stamps *et al.*, 2014). About 3.7 million years ago, the *Australopithecus* marked the beginning of human culture, symbolised by tool making, the use of fire, and organised settlements (Sahnouni and de Heinzelin, 1998). Around 2 million years ago, the *Homo erectus* stood up and left Africa to colonise Asia and Europe, and 200,000 years ago, the Neanderthals evolved.

Neanderthal sites in North Africa include Haua Fteah', near Marsa Sousa in Libya and Jebel Irhoud, Temara and Tangier in Morocco. An admixture with other human populations occurred between 86,000 and 37,000 years ago (Sánchez-Quinto *et al.*, 2012). After this last date, much of North Africa was occupied by tall, large-brained, and powerfully built humans, known as the Cro-Magnon who could be the direct ancestors of the Berbers. Stone implements dated to the late Acheulean and the Aterian cultures were found in numerous sites from the Fezzan area. Around 20,000 years ago humans began migrating out of the area and spread their culture all around the Mediterranean Sea. Archaeological research confirmed that the Maurusian culture, a Berber

culture, flourished around 22,000 BCE (Bouzouggar *et al*., 2008). The skeletal remains of a population named Mouillans were said to date between 15,000 and 10,000 BCE. These settlements were typically small, of about 100 individuals.

Radiocarbon data from 150 archaeological excavations in the eastern desert of Egypt, Sudan, Libya, and Chad revealed close links between climatic variations and prehistoric occupation during the past 12,000 years and reflected the transition from initial settlement after the onset of humid conditions to the exodus resulting from gradual desertification (Kuper and Kröpelin, 2006). Eastwards and southwards shifting of the desert margin contributed to the emergence of the pharaonic civilization along the Nile and influenced the spread of pastoralism throughout sub-Saharan Africa, respectively.

Neolithic period

During the wetter period of the Neolithic subpluvial (from 7,500 BCE) many groups of dark skinned hunters and collectors coming from the East, possibly from the present Ethiopia, moved to the Sahara territory. They could be the ancestors of the Fulbe who inhabit now Niger, Mali, Burkina Faso, Mauritania and other countries out of the Sahara. The recollection of wild grasses practiced among human groups occupying the Sahara at this time progressively evolved towards farming (Wendorf *et al.,* 1998). Between 5,000 and 4,000 BCE the dark skinned population was replaced by white skinned Berber populations from the North (constituted by the Tuareg and Tubu peoples) moving southwards.

Predynastic and dynastic periods of Egypt

By 5,500 BCE, small tribes living in the Nile Valley region developed into a series of cultures demonstrating control of agriculture and animal husbandry. The Merimde culture which developed in Lower Egypt from 5,000 to 4,200 BCE (Bogucki, 1999) had natural links with the Fertile Crescent and western Asia and cultivated wheat, sorghum and barley (Eiwanger, 1999). The Badarian culture (4,400-4,000 BCE) closely related to the Nubians and North-East Africans (Shaw, 2002) was followed by the Amratian (Naqada I, 4,000-3,500 BCE) and Gerzeh (Naqada II, 3,500-3,200 BCE) cultures. Over a period of about 1,000 years, the Naqada culture developed into a powerful civilization controlling people and resources of the Nile Valley (Redford, 1992). They also traded with Nubia to the South, the oases of the western desert to the West, and the cultures of the eastern Mediterranean and Near-East to the East (Brace *et al*., 2006; Richter *et al*., 2011).

Around 2,500 years BCE the wet phase of the Sahara came to its end. A climatic change gradually turned the Sahara into a desert. The Sahara became an almost impenetrable barrier separating the Mediterranean coast and North Africa from the rest of the continent. As Sahara progressively dried, human groups abandoned their settlements, some moving to less arid mountainous

regions and others retreating to the South towards the Sahel and East towards the Nile Valley. These last populations, in addition to Neolithic farmers from the Middle East played a major role in the formation of the Egyptian pre-dynastic states as they brought their food crops (mainly from tropical origin), sheep, goats and cattle to the Nile Valley.

The horse, which played an important role in the human colonization of the desert and in military conquests, was introduced into Egypt in 1,660 BCE by the Hyksos, a people from West Asia who invaded the eastern Nile Delta, ending the 13th Dynasty of Egypt (Redford, 1992). Rupestry gravures found in different parts of the Sahara indicate that horses and two-wheeled chariots were used to traverse the desert during the period 1,500-1,000 BCE (Reygasse, 1932; Vaufrey, 1939).

Military conquests of the antiquity

Herodotus (5th century BCE) wrote that the Berber people Garamantes hunted from four-horse chariots, herded cattle and farmed dates (Mattingly *et al*., 2007). They created a kingdom in Zinchecra (Fezzan, Libya) on the hills of Messak Settafet, which constituted the first proto-historical state formation in the heart of the African desert (Mori, 2008). Archaeological evidence indicates that the main cultural phase in Zinchecra lasted during the period 1,000-400 BCE. Roman texts only tell us about military conflicts with Garamantes. Pliny the Elder (23-79) considered them as brigands who blocked peaceful travel and the historian Tacitus (*c.* 56-117) described them as "a wild race incessantly occupied in robbing their neighbours". According to Strabo (*c.* 64 BCE-24) and Pliny the Elder, the Garamantes also quarried amazonite in the Tibesti Mountains. The Garamantes built underground water galleries called *foggaras* to collect fossil water. A minimum of 617 of these *foggaras* are known in the Fezzan (Mattingly *et al*., 2007). Their crops consisted of grapes, figs, barley and wheat. They exchanged wheat, salt and slaves for imported wine and olive oil. They developed a network of sites controlling the Saharan caravan routes, as attested by archaeological and epigraphic sources (Mercuri *et al*., 2009). Germa (or Garama), the later capital of the Garamantes in the first century, had a big market used as a transit point for caravans. Germa was conquered by Septimius Severus in 202 (Birley, 1999) but the decline of the Garamantian culture may have started before, due to worsening climatic conditions or overuse of non-renewable water resources. The Fezzan remained outside Islamic control until the 11th or 12th century, but new trans-Saharan trade routes developed through Morocco and Algeria, and the influence of the Garamantes on the development of the desert diminished.

Between 1,200 and 800 BCE, the maritime trade along the Mediterranean coast developed, pioneered by the Phoenicians who settled along the Mediterranean coasts. By 800 BCE, they colonized Carthage (Qart Hadasht meaning the

new city in Phoenician) and established confederates along the coast (eg, Acholla, Hadrumete, Thabraca, Saldae, Tipasa, Siga, Abyle, and Lixos) and kingdoms in northern Sahara, overwhelming the first Berber inhabitants. During the 5th century BCE, Hanno II of Carthage (also called Hanno the Navigator) created new Phoenician colonies in the western part of Sahara (Fage *et al.,* 1979). By the beginning of the 5th century BCE, Carthage became the commercial center of the West Mediterranean region. The city subjugated the Libyan tribes and took control of the entire North African coast from modern Morocco to the borders of Egypt (Dillon and Garland, 2005) as well as Sardinia, Malta, the Balearic Islands, and the western half of Sicily (Aubet, 2001). They never penetrated deeply into the Sahara but traded with West Africa (Daniels, 1970). Carthage became a terminus for West African gold, ivory and slaves. West Africa received salt, cloth, beads and metal goods (Shillington, 1995).

In 525 BCE, the last pharaoh of the 26th Dynasty, Psamtik III, was defeated by Cambyses II, King of Persia in the battle of Pelusium in the eastern Nile delta. Egypt joined Cyprus and Phoenicia in the 6th satrapy of the Achaemenid Empire. Thus began the first period of Persian rule over Egypt (also known as the 27th Dynasty) which ended around 402 BCE. After an interval of independence, during which three (28th, 29th and 30th) indigenous dynasties reigned, the Persian King Artaxerxes III (358-338 BCE) reconquered the Nile Valley for a brief second period (343-332 BCE) called the 31st Dynasty of Egypt.

In 332 BCE, Alexander III of Macedon (356-323 BCE), commonly known as Alexander the Great, conquered Egypt (Ring *et al.,* 1994) and was pronounced the son of the deity of Amun at the Oracle of Siwa Oasis in the Libyan desert (Grimal, 1992). During his stay in Egypt, he founded Alexandria, which became the prosperous capital of the Ptolemaic Kingdom after his death (Arrian de Selincourt, 1976).

In 146 BCE, the Romans occupied and destroyed Carthage. This was the beginning of a long domination by Rome over North Africa. The Jugurthine War that took place in 112-106 BCE constituted another important phase in the Roman subjugation of Northern Africa. During this war the Romans defeated Jugurtha (Berber *Yugerten*), nephew and adopted son of Micipsa, King of Numidia. Numidia became a Roman province in 46 BCE.

Roman troops faced a constant threat from the Saharan regions and built a network of forts and walls on the southern frontier. In 25 BCE Aelius Gallus led an expedition across the Red Sea against the Sabaeans of *Arabia Felix* (Yemen). In 19 BCE, Septimus Flaccus crossed the Tibesti Mountains and reached the Niger River. In 41 Gaius Suetonius Paulinus crossed the Atlas Mountains, western Sahara and Mauritania and arrived at the northern area of the Senegal River and probably the western Niger affluents. During the same period, Julius Maternus explored the Lake Chad area and described the abundance of animals in northern Nigeria. An expedition organized by Nero to discover the sources of the Nile River reached Meroe in Nubia in 62. According to Plinius the Elder,

another expedition got at Sudan in 68. Roman objects were found in the Sahara, particularly along the western caravan routes. There is evidence of Roman commercial activities in Akjoujt and Tamkartkart near Tichit in actual Mauritania (Salama, 1990).

Between 618 and 621, the Sassanid Persian army defeated the Roman (Byzantine) forces in Egypt, the East Roman Empire's granary (Frye, 1983) and occupied the province. After the fall of Alexandria, the Persians gradually extended their rule southwards along the Nile (Dodgeon *et al.,* 2002).

Jewish and Christian migrants

Following the 1st century Great Revolt (66-70 BCE), 30,000 Jewish slaves were settled throughout Carthage by the Roman emperor Titus. After the Bar Kokhba revolt against Trajan (115-117), Jewish communities were again largely expelled from Judea and sent to various Roman provinces in North Africa. During the Roman times, Moroccan Jews began to trade within Sahara and mixed with Berbers living in the M'zab, Touat, Tafilalt, Draa and Sous. Some Berbers began to practice Judaism (Albertini, 1929). Another exodus could have occurred after the defeat of Dhu Nuwas, the Jewish Himyarite king of Yemen in 520 or 525 (Stillman, 2012). Finally, during the 10th century, when the social and political environment in Baghdad became increasingly hostile, many Jewish communities left for the Maghreb, constituting a distinctive social group of traders throughout the Mediterranean further called *Maghrebi*. When the 5th Caliph Abd al-Malik ibn Marwan (646-705) conquered Morocco, he exiled the Jewish community of Tamentit to the desert of Ajaj. The presence of Jewish communities has been attested in many Berber *ksurs* (fortified villages) all along southern Morocco and in the adjacent Sahara, at Outat (near Tafilalt), Figuig, Alhamada (Touat) and Tamentit (Horowitz, 1887).

At the beginning of the 3rd century Christianity expanded rapidly in Egypt but in the middle of the same century severely suffered persecution under the reign of the Emperor Decius (249-251). The early 4th century in Egypt began with renewed persecutions under the reign of Diocletian (284-305). Many Christians left the towns for the desert. When the persecution stopped, some remained in the desert and created Christian monasticism (Jakobielski, 1992). Roman Catholic faith persisted in North Africa for several centuries after the completion of the Arab conquest. There is evidence of religious contacts with Christians of Arab Spain. A Christian community was reported in 1114 in Al Qal'a of Beni Hammad, in central Algeria. Christians continued to live in Tunis and Nefzaoua in the South of Tunisia up until the early 15th century.

Expansion of Islam

After the Hejira (journey of the Islamic prophet Muhammad and his followers from Mecca to Medina in 622), the expansion of Islam started with

small groups of Muslims coming from the Arabian Peninsula. They were well received as they wanted to abolish slavery. The further decision of the governors of the Omeyyade Calife of Damas to restablish slavery led in 742 to the Kharedjite insurrection. The Berber revolts against the Umayyads led to the foundation of new oases in the desert. According to Al-Bakri (*c.* 1014-1094), Sufrite Kharijites settled the town of Sijilmasa (in southestern Morocco, along the River Ziz in the Tafilalt oasis) in 757-758. The M'zabites, a branch of a large Berber tribe, the Iznaten, which lived in large areas of middle southern Algeria and became Muslims of the Mu'tazili school, moved to the M'zab Valley at the beginning of the 10th century and converted its inhabitants (Amat, 1888).

In general, Islam was carried out in Africa by merchants rather than armies. It spread first using the well-established trade routes of the East coast. From the 8th century Islam expanded gradually in the oases of Sahara. Adherence to Islam and its code of law favoured the development of scholarly and commercial networks connecting Muslims across the desert and beyond. The pursuit of gold and other goods encouraged waves of migrations of North Africans into desert oases (Lydon, 2005). By the 10th century many of the merchants at the southern end of the trade routes were Muslims. By the 11th century the rulers began to be converted. The first to be converted was the King of Gao, around 1000. The king of Ghana accepted Islam around 1070. By the 11th century, the Almoravids attempted a religious reform in the Sahara. By the 14th century, the ostentatious pilgrimage to Mecca of the Emperor of Mali, Mansa Musa, alerted the wider Muslim world to the existence of gold mines in western Africa, and attracted many more Muslim visitors in this region (Lydon, 2005). In the late 16th century, the Moroccan Sultan Ahmad al-Mansur (1549-1603) attempted to take over trans-Saharan trade by securing the principal salt mine of Taghaza and invading the centres of Gao and Timbuktu of the Songhai Empire. By the 18th century, Saharan towns tended to be governed by Muslim scholars who functioned as regional judges ruling on civil, commercial, political, and religious matters. These semi-sedentary communities maintained alliances with nomadic groups who provided protection services to town dwellers, farming communities and trans-Saharan travelers. However, the Sahara was never ruled by a single nation despite attempts by Morocco to extend its power to the southern desert-edge.

The development of trans-Saharan routes

The early routes

The trans-Saharan trade dates back to prehistoric times, although it is almost impossible, based on historical documents and archaeological record, to be precise about its nature and extent. During the Naqadan era (about 4,000-3,200 BCE), predynastic Egyptians traded with Nubia to the South, the oases of

the desert to the West, and the cultures of the eastern Mediterranean to the East (Shaw, 2002).

The early routes included the Wadi Hammamat, Abu Ballas, Darb el-Arba'in and Garamantean routes (figure 3). The Wadi Hammamat became a major route from the Nile to the Red Sea during the 1st Dynasty (3,100-2,890 BCE) although evidence of Pre-Dynastic occupation (4,000-4,500 BCE) was also found along the route (Byrnes, 2007). It ran from Qift (or Coptos), located 43 km North of Luxor (ancient Thebes) on the East bank of the river Nile to Al-Qusayr (ancient Leucus Limen) on the coast of the Red Sea. The Abu Ballas Trail, established during the Old Kingdom (2,686-2,181 BCE) led from Ain Asil (Balat) in the Dakhla oasis (situated about 300 km West of the Nile Valley) *via* Kufra to Ounianga in north-eastern Chad (Kröpelin and Kuper, 2006; Förster, 2013). The Darb el-Arba'in (or Forty Days' Road), connecting Asyut (located on the western bank of the Nile, Upper Egypt) with El Fasher in North Darfur (Sudan) through Kharga oasis, Salima and the Wadi Howar was also used during the Old Kingdom for the transport and trade of gold, ivory, spices, wheat, animals and plants (Burr and Collins, 2006). Later, Romans protected the route by building forts and small outposts, some including large settlements and cultivation. The Garamantean road was created by the Garamantes as early as 1,000 BCE to connect their territory to the Mediterranean. From 800 BCE, it was used by Carthage for trade with West Africa. Trade continued during Roman times. By the 1st century CE, the Legio III Augusta secured this road

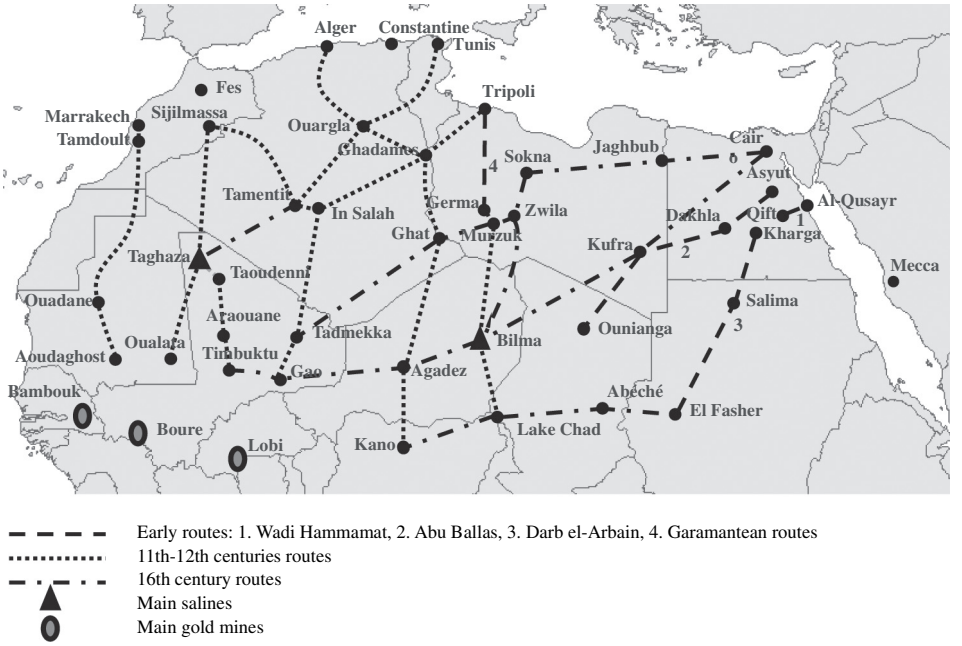

Figure 3 ■ The main trans-Saharan routes.

on behalf of Rome, safeguarding the southern border of the empire for two and half centuries (Burr and Collins, 2006).

The role of donkey and camel

Important factors in the development of trade and transportation across the Saharan desert during this period were the introduction of donkeys and camels and their use for transportation. The ancestors of the modern donkey (*Equus africanus asinus*) are the Nubian and Somalian subspecies of African wild ass (Beja-Pereira *et al.,* 2004). Remains of domestic donkeys dating to the 4th millennium BCE were found in Ma'adi in Lower Egypt. Donkeys could have been domesticated during the 7th or 8th millennium BCE either in Nubia or in Egypt (Bökönyi, 1991). Donkeys are represented in the archaelogical sites of Oued Djerat (Tassili) and Mathendous (Libya) dating back 5,000 BCE and skeletons of three domestic donkeys were found in an Egyptian tomb dated to 4,500-4,000 BCE (Clutton-Brock, 1992). The domestication of the donkey probably played an important role in the mobility of pastoral cultures and development of long-distance trade across Egypt. During the 4th Dynasty of Egypt (2,613-2,494 BCE) donkeys were used as dairy, meat and pack animals (Olsen, 1996). Donkeys may have been rare and exotic in Central Sahara, since unambiguous representations of domesticated donkeys are absent from Saharan rock art.

The introduction of the camel in the 3rd century strongly participated in the economic, political, and cultural development of North and West Africa (Bulliet, 1975). Camels were probably domesticated in the Arabian Peninsula to be used as pack animals towards the end of the 2nd millennium BCE. The introduction of camels in the southern Levant around 930 BCE could be linked to the exploitation transportation and trade of copper in this the region during the reign of Pharaoh Shoshenq I (*c.* 945-924 BCE) (Sapir-Hen and Ben-Yosef, 2013). Camels, which can travel over much longer distances than donkeys and mules, gave the Berber tribes who lived on the northern fringes of the great desert more mobility. It allowed them to extend their influence over a vast territory, and establish regular routes between the oases of the Mediterranean hinterland and the trading centers of western Sudan (Lydon, 2005).

The apogea of Saharan trade

The trans-Saharan caravan trade began to take place on a regular basis during the 4th century CE. The peak of trade extended from the 8th century until the late 16th century. In western Sahara, several roads linking northern Morocco to the Sahel (the area between the Sahara Desert and the Sudanian Savanna, from the Atlantic Ocean to the Red Sea). In the middle of the 11th century, Al-Bakri described a trans-Saharan route that ran from Marrakech to Aoudaghost on the southern edge of the Sahara, via Tamdoult. This route was used for the transport of gold during the time of the Ghana Empire

(Mauny, 1949). New routes were developed particularly during the 11th and 12th centuries mainly on the West and Central part of Sahara. Western trade routes involved the Oualata Road (from Sijilmasa to Oualata through Taghaza), the Taghaza trail (from Taghaza to Timbuktu) and the route from Ouargla to Gao (through Tamentit, In Salah and Tadmekka). Traders used these routes to obtain gold from the Bambuk, Boure or Lobi goldfields. The Central routes included the Ghadames Road (from Tripoli, *via* Ghadames, Ghat and Agadez to Gao and the Niger River) and the Bilma Trail (from Tripoli through Murzuk to Bilma in North-East Niger, before reaching Kano and the Lake Chad). Later (16th century) East-West routes were also developed, from Cairo to Tadmekka through Sokna, Zwila and Ghat, from Cairo to Gao *via* Kufra, Bilma and Agadez, and from El Fasher to Kano, *via* Abéché and the Lake Chad.

According to Ibn Battuta (*c.* 1304-1368), the average size per caravan was 1,000 camels, fattened for a number of months in the Maghreb or the Sahel before being assembled into a caravan. The caravans were guided by Berbers who knew the desert and could ensure safe passage. The survival of a caravan required careful coordination. The ancestral rivalry between Tubu and Tuareg peoples became a matter of competition for the control of trade in the Sahara, their influence areas being divided in a North-South line that crossed the Tenere and the Fezzan. In the oases of Tenere, the Tuaregs controlled the caravans while the Tubus gathered salt and dates.

Caravan routes progressively influenced the economic, political, and cultural life of a large part of the African continent until the end of the 19th century. By overcoming the natural barrier of the desert, these routes promoted commercial exchanges between Africa, Europe, and Asia, which in turn led to political and cultural relations among the various peoples involved. The diffusion of Arabic as a *lingua franca* gave a considerable impulse to diplomatic, commercial, and cultural exchanges.

During this period, powerful kingdoms were established in West Africa based on trade rather than conquest. The first kingdom to establish full control over the southern end of the Saharan trade was Ghana (situated between the Senegal River to the West and the Niger to the East). Ghana remained the dominant kingdom of West Africa from the 8th to the 13th century. The prosperity resulting from its activities is evident in the town of Jenne, already a thriving town on the Niger by 800 CE. By the 11th century, at least three camel routes crossed central and western Sahara in a North-South direction, with a number of trails connecting them at different latitudes and a number of stops determined by the presence of water or salt.

The most precious of the commodities moving to the North was gold. Genoa, Florence and Venice started using gold for coins by the 13th century and the European kingdoms followed their example. Ghana controlled the traffic from Bambuk, in the valley of the Senegal River. Around 1050, Ghana conquered Aoudaghost, but the development of new goldmines around Bure

reduced the trade through this city and benefited the Kaniaga Kingdom also known as the Sosso. Under King Soumaoro Kanté, the Sosso conquered the Mandinka Kingdom. At the battle of Kirina (*c.* 1235) the Mandinka prince Sundiata Keita defeated the Sosso and started to develop the Mali Empire that would extend later from the Atlantic coast to the Niger River.

The most important commodity transported to the South with the caravans was salt, essential in the diet of African agricultural communities. Salt mines of the Sahara were controlled by Berber tribes from the North and sometimes by Africans. Bilma Trail was the primary route for the exchange of slaves and ivory from the South against salt from the North. Traders from the North (Maghreb, Spain, Italy and Egypt) also brought copper (either in its pure form or as brass, the alloy of copper and zinc), a wide range of metal goods as weapons and armour, cloth, paper and books. Kola nuts from the South and cowry shells from the North were used as currency.

Finally, slaves coming mainly from the region around Lake Chad were sent to Arab purchasers in the North. The West African states imported highly trained slave soldiers. It has been estimated that from the 10th to the 19th century some 6,000 to 7,000 slaves were transported North each year (Fage, 2001). The main points of arrival and sale in the Sahara were Nul Lamta and Sijilmasa (Morocco), Ouargla (Algeria), Djerid (Tunisia) and Kanem (Chad).

By the 16th century, a number of trading centers grew at the intersections of the main routes. Their position and the increasing demand for African goods generated by European and American markets made them part of a vast commercial network. Products coming from Persia, India or China through the Silk Road were bought and sold in Timbuktu, Chinguetti, or Sijilmasa while Ghanaian gold was sent to the workshops and courts of Europe.

The decline of Sahara trade

An important cause for the decline of Sahara trade was the development of maritime trade between Europe and West Africa, after the conquest of new African regions by European countries. The conquest began in 1402 with the expedition organised by the Kingdom of Castile to the Canary Islands. Dom Henrique of Portugal (1394-1460), better known as Henry the Navigator, was however the first European to methodically explore and conquer Africa. In 1420 he sent an expedition to secure the strategic Archipelago of Madeira. In 1431, the Portuguese annexed the Azores. They reached Cape Bojador in 1434 and Cape Blanco in 1441 and built a fortress on the island of Arguin, in modern day Mauritania in 1443. In 1455 and 1456 Portugese expeditions followed the Gambia River and explored the Bijagos islands and the Cape Verde archipelago. In 1471, Fernão Gomes reached modern Ghana and founded A Mina (the mine), later renamed Elmina. In 1479, Portugal and Castile signed the Treaty of Alcáçovas. The treaty settled disputes between the two kingdoms over the

control of the Atlantic. The Castilian control of the Canary Islands and the Portuguese possession of the Azores, Madeira and the Cape Verde islands were recognised. The Portuguese obtained the rights to lands and islands to be further discovered.

The Portuguese established trading factories (*feitorias*) and bulking centers at strategic locations (eg, Arguin, Cape Verde Islands, Elmina). They bartered wheat bought in Safi, horses and clothes for gold, ivory, and slaves (Ricard, 1955; Worth, 2009). The first settlers who colonized the Canary and Madeira islands started to produce wheat for their own subsistence. Later, the quantity cultivated was sufficient to export wheat to Portugal, Morocco, the Saharan coast and West Africa (Magalhães Godinho, 1965). Bread was available at the beginning of the 18th century at the local market of Elmina (Youngs, 1973).

The cities and towns along the trans-Sahara trade routes began to decline in influence. The victory of Morocco against the Songhai Empire at Tondibi in 1591 also strongly affected the trans-Saharan trade, which started to decline from the 17th century. The kingdoms and empires of the Gulf of Guinea started to develop with the slave trade, practiced until the 19th century by the Portuguese, Dutch, English and French.

By the middle of the 19th century all the main Saharan commercial arteries were drying up, a main cause being the increase of commercial navigation along the West coast of Africa managed and controlled by Europeans (particularly the Portuguese) which provided a safer and faster alternative to the long journeys across the desert, whose success or failure depended on the local tribes. Another reason was the growth of French colonial power in the region and the consequent dismantlement of the political and economic system that had shaped traditional life for centuries. Most trading centers entered a long–term decline marked by progressive isolation and decay.

With the independence of nations in the region in the 1960s, the North–South routes were cut by national boundaries. National governments were hostile to Tuareg nationalism and made few efforts to support trans-Saharan trade. The Tuareg Rebellion of the 1990s further disrupted routes. All efforts today to revitalize the ancient caravan towns are frustrated by the increasing desertification of the Sahara and the consequent displacement and urbanization of nomadic tribes.

The Saharan oases

The term *oasis* derives from the Ancient Greek *o*ασις, which comes directly from the Demotic Egyptian wḥỉ. The same Egyptian source produced *wahe* in Coptic and *wahah* in Arabic. An oasis is an isolated area of vegetation in a desert, typically surrounding a spring or similar water source. Oases also provide habitats for animals and even humans if the area is big enough. At the

global level, oases planted with palm date represent around 1 million ha, and feed almost 10 million people. Oases are numerous in Sahara, but their total area is only 8,000 to 9,000 km^2.

In the Sahara, although there are classical references to direct travel from the Mediterranean to West Africa (Daniels, 1970), most of the trade was conducted through middlemen, inhabiting the area and aware of passages through the desert. The location of oases was of critical importance for trade and transportation routes in desert areas. Caravans had to stop in the oases to ensure supplies of water and food. In many cases, political or military control of an oasis meant control of trade on a particular route. For example, the oases of Awjila, Ghadames and Kufra, situated in modern-day Libya, have been vital to both North-South and East-West trade in the Sahara. The main oases are presented on figure 4 and information about their location, history and agricultural characteristics is provided in Appendix 2.

Establishment of oases in Sahara

The establishment of oases in the Sahara, mainly led by water availability, occurred at different historical periods (appendix 2). In some cases, the region has been inhabited since Neolithic times and the oases have been settled later. The first Saharan oases seem to have been established with the cultivation of date palm, domesticated in the Arabian Peninsula around 5,000 BCE. Archaeological data from Hili, close to the oasis of Al-Aïn (within the Emirate of Abu Dhabi, in the present United Arab Emirates), indicate that oases were established in the Arabian desert 3,000 BCE (Cleuziou and Costantini, 1982). Most Egyptian oases were settled in the period 3,100-2,181 BCE, during the Early Dinastic Period or the Old Kingdom (Redford, 1992). These oases include Siwa, Bahariya, Farafra and Dakhla within the western (or Libyan) Desert of Egypt. Radiocarbon dating of material remains (fauna, pottery, and chipped stone) however allowed assigning the oasis of Kharga to the Tasian culture (the oldest-known Predynastic culture in Upper Egypt, around 4,500 BCE), when nomadic populations of the Sahara took refuge in ecologically more favorable areas such as the oases and the Nile Valley (Kuper and Kröpelin, 2006).

Studies based on both genetic and archaeological information attributed these first neolithic settlements to migrants from the Fertile Crescent bringing agriculture to this region (Zvelebil, 1986; Diamond, 1999; Bellwood, 2005). In Tunisian, Algerian and Moroccan Sahara, many oases were created by Berbers escaping the Roman occupation. Some oases of Algeria and Tunisia have been Roman military outposts.

Most oases played an important role in the establishment of trade routes used by the caravans (freight, passengers and pilgrims) and the development of the trade of gold, salt and slaves between North and sub-Saharan Africa.

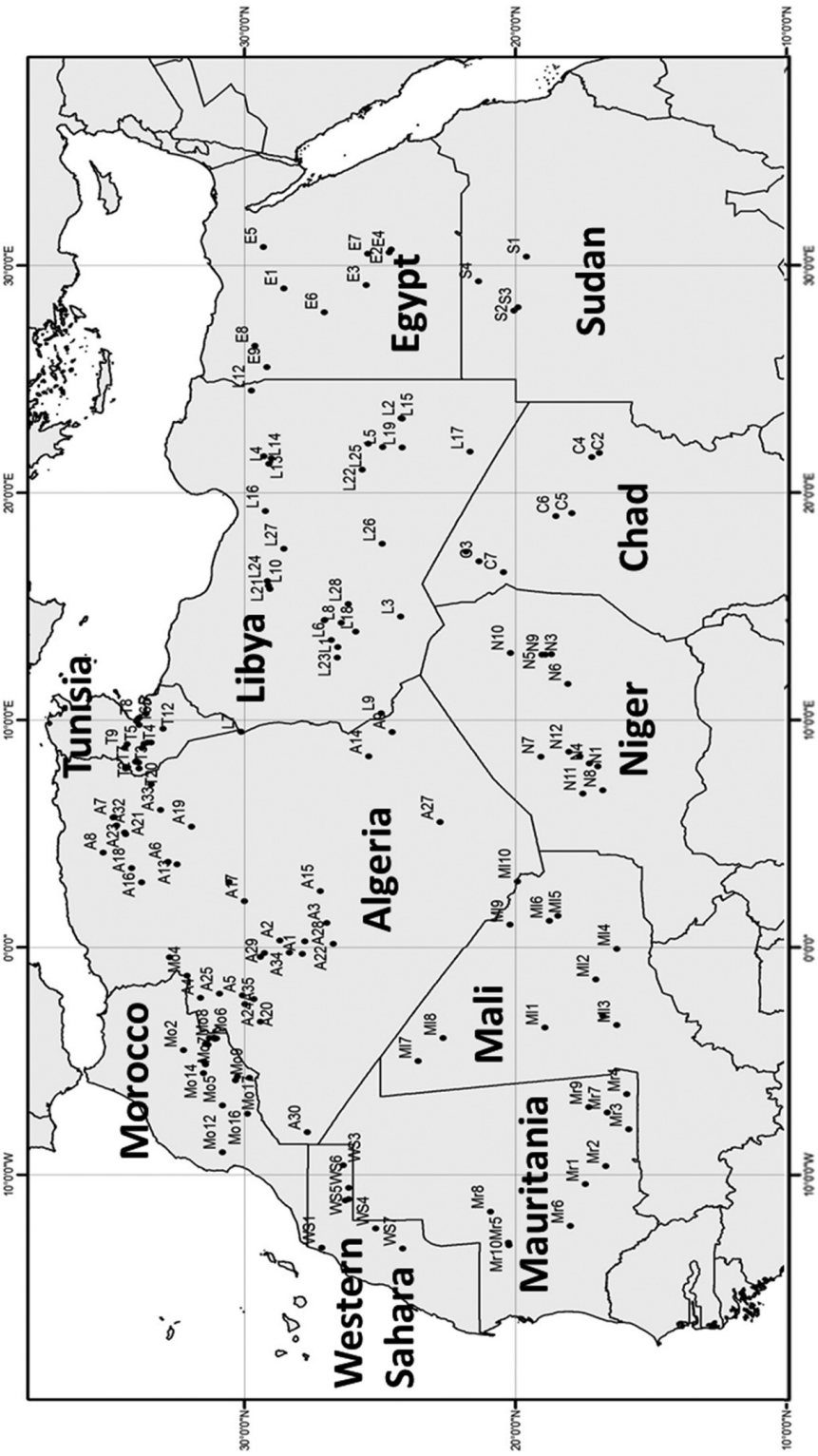

Figure 4 ■ Oases distribution in Sahara.
The letters and numbers refer to the name of the oases listed in appendix 2.

Reciprocally, some oases could have been created or developed because they could serve as relays on these desert roads. Manpower often came from slaves, particularly between the 8th and 14th century CE (Lacoste, 1990). Finally, some oases have been developed later, after the first drillings at the end of the 19th century CE and the creation of palm groves devoted to the export of dates (eg, Ziban, El Oued, M'zab, El Golea) (Bouzaher, 1990).

Agriculture in the oases

Saharan oases have very specific climatic conditions. During the day, the temperature can reach 45°C. The difference of temperatures between night and day is more than 20°C and can reach over 30°C. Relative humidity can be very low when the wind is coming from the South (*chamsin* in Egypt, *sirocco* or *simoun* in Algeria). Oases soils are always alkaline, frequently saline (sulfates, chlorides and carbonates) and generally poor in potassium, phosphorus and nitrates (Chevalier *et al.,* 1932).

The transition from desert to oasis signifies an abrupt change from extremely low to very high population densities and from extensive to intensive modes of resource extraction. Animal husbandry, commerce, industrial activities and agriculture are juxtaposed to create a remarkably intricate system seeking to utilize the resources of an inhospitable environment through risk avoidance (Clancy-Smith, 1994).

Agriculture was probably introduced into the oases from the Nile Valley (Chevalier, 1949). The origin of agriculture in the Nile Valley is itself commonly attributed to cultural diffusion from the Middle East through the *wadis* that link the Red Sea to the East bank of the Nile. The First and Second Dynasties (3,100-2,686 BCE) marked the onset of a developed system of writing, and the development of the oasian culture of cereals, fruit trees, vegetables and medicinal and ornamental plants (Bard, 2003).

Classification of Saharan oases

Oases have developed through the Sahara through a lot of effort. In most depressions (eg, Souf) the basins managed for the culture had to be constantly protected against sand. In other regions, dugs, irrigation canals (*seguias*), impoundments and drains were built. Sometimes (eg, Gourara) the gardens were installed on the slopes of *wadis*. Elsewhere they were created in the spreading basins, where temporary torrents came down from mountains and ravines in order to collect some sediment from these mountains. Finally oases were also installed around water sources. Some oases are isolated (eg, Ouargla), other are grouped (eg, Oued Righ with 47 oases along 150 km) (Bouzaher, 1990; Zella and Smadhi, 2006).

A first classification of Saharan oases can be based on access to water. Clouet (1995) distinguishes intra-desertic oases using groundwater (eg, Borku in northern Chad), piedmont oases collecting water from Mountain rivers (eg, Tamerza and Mides in Tunisia) and plain oases irrigated by dams (eg, along the Nile Valley where water from the river, whose level fluctuates depending on seasonal flooding, covers the land regularly fertilized by silt deposition). Finally, oases can also be found in *ghouts* (funnels, depressions between the dunes where water infiltrated, eg, El Oued, Algeria).

De Haas (2001) also considers three types of oases, the river oases, the groundwater oases, and the spring oases. The first ones are located along rivers, where water is used for irrigation in fields placed on the banks or in alluvial plains. They are generally prosperous, thanks to guaranteed flows of water bringing down fine sediments to the fields and maintaining soil fertility (Kassah, 1998). River oases include the huge oasis systems of the Nile and the Drâa, Tafilalt-Ziz, Dadès and the Todgha basins in Morocco. Groundwater oases are located in areas where groundwater is close enough to the surface to be tapped. Groundwater is extracted using *norias* for lifting water into small aqueducts or by digging underground tunnels or *foggaras*. These systems require high labour costs and a high degree of organisation at a community level. Agriculture is less intensive and more sensitive to changes in water tables than in river oases. In some oases of Algeria, groundwater is very close to the surface and the cultivation of date palms is possible without irrigation. Spring oases are located close to small, local springs. No elaborate techniques are required to tap water and these spring oases are less labour intensive than groundwater oases. This type of oasis can be found in Jérid, Nafzaoua, Gafsa and Gabes in Tunisia (Kassah, 1998) and in the Bani region in Morocco (de Haas, 1998).

Zella and Smadhi (2006) distinguish oases located in *erg* troughs where irrigation water is extracted by wells and drilling (eg, Ouargla), oases situated in *ghouts* (eg, El Oued), river oases (eg, M'zab, Bechar) and oases of troughs alimented in water by *foggaras* (Adrar, Timimoun). The principle of the *ghout* is based on the realization of a concentric bowl of around ten meters deep. The digging is stopped when approaching the top of the groundwater water. The palms are planted at the bottom of the depression. The advantage of this technique is to protect the crops against the winds. It however requires permanent maintenance to avoid the sanding of the *ghout*. The traditional irrigation system in the Saharan oases is based on the *foggara* (Remini *et al*., 2014). The *foggaras* (called *khettara* in Morocco) consist of large subterranean tunnels to capture the little water rain retained in the foothills and lead it to cultivated plots. They are very similar to the *qanats* that were created about 3,000 years ago on the North-West of the Iranian plateau (Goblot, 1979; Briant, 2001). The discovery of complete *foggaras* networks dating from the 5th century BCE in the oasis of Kharga (Wuttmann *et al*., 2000) supports the hypothesis of an introduction

during the Achaemenid occupation. The *foggaras* could have been introduced later (around 200 BCE) by the Garamantes in the Fezzan oases (Mattingly, 2007). *Foggaras* have been reported in more than 35 countries worldwide (Hofman, 2007). Almost 22,000 *qanats* are still functional in Iran (Boustani, 2008).

Oases can also be classified according to the cropping system practised (Ferry and Toutain, 1990). In the first type (A), complementary irrigation to the grove is no longer possible or is being abandoned, due to the lack of water or of labor. Agricultural work is limited to the collection of dates and sometimes to the pollination of date trees (Mauritanian Adrar, Ifoghas in Mali). In the second type (B), directly available water resources are sufficient and supplementary irrigation is not necessary. Maintenance work of the data palms is limited to the minimum (pollination and harvest) and there are no sub-cultures. The dominant activity within the oasis is not the date palm, but rather the raising of sheep and goats and the pasture for camels is sourced outside the oasis (oases of Sudan, Chad). The third type of oases (type C) is irrigated and planted with palm trees and a few associations of crops (Tagant in Mauritania). The last type of association (type D) is that of palm cultivation, with underlying cultures (plate 2).

Plate 2 ■ Oasis with association of crops (date palms, fruit trees, cereals and forages) in the region of Tamanrasset, Algeria.

(Source: S. Oumata)

This association was already present in Arabia during the Nabataean period in the 4th century BCE (Bouchaud, 2013). Agriculture is conducted with the overlay of two or three strata creating the "oasis effect". The first (highest) layer is formed of date palms reaching a height of 15-30 m and whose leaves filter the sunlight and maintain freshness. The proportion of the cultivated area devoted to the palm tree is high in some oases (eg, almost 100% in Adrar, 80% in Ourgla) but is generally comprised between 50 and 60% (Toutain et *al*., 1988; Guillermou, 1993). An intermediate, shrubby layer includes fruit trees (apple, orange, apricot and peach, banana and pomegranate) and henna and punica whose vines grow on the palm and fruit trees. The lowest herbaceous layer, in the shade, includes cereals (wheat, barley, sorghum) and forages associated to sedentary stock-raising (case of Jérid, Zagora and Djanet), market gardening (including many oasis varieties) and medicinal plants. Some oases, generally located in the valleys, are characterised by the cultivation of cash crops (eg, Tafilalt). The fodder plants provide feed for livestock herds, whose excrement maintains soil fertility. An extensive list of crop repertoried in Saharan oases is provided by Battesti (2005). Some crops could have been introduced early (date palm, jujube, almond, pomegranate, figs, olives) or by the Arabs (eggplant). Most of them are however originated from America or Asia and have been cultivated for a few centuries in the oases.

The high crop diversification observed today in most oases is consequently quite recent. Historically, cereal cultivation took place in different regions according to the climatic conditions faced by the Sahara. During the wet periods, crops were cultivated along the Chad, Niger and Saoura rivers. During the drying phases, agriculture concentrated in the oases, around the locations where superficial water was more abundant.

Wheat in the oases

Wheat and barley are probably, after date palm, the most important crops in the oases. As in East Asia, wheat could have been imported first in small quantities as a luxury food destinated to the dominant class of the oasian society (Van der Veen, 2003). Wheat grown in the Saharan oases was poorly known until the beginning of the 20th century. The presence of wheat in the oases cropping systems had been previously reported by several travelers like Follie (1792) and Adams (1810), but the description of the landraces that were cultivated was imprecise or even erroneous (Erroux, 1962).

Wheat is generally sown soon after the autumn rains (September, October) to avoid loss of water by drainage and evaporation (Chevalier, 1932). When rain is sufficient during this period and if additional rain occurs in spring (March to May), grain production can be abundant. Sowing occurs sometimes in November or December, when water availability is sufficient (Ducellier, 1920). In Timinoun, Mercadier *et al.* (1946) reported a late sowing of early wheat

landraces in February, after the green spikes of barley are harvested to prepare *frik* (roasted spikes). Traditionally, wheat was sown by hand, with 3 to 8 grains by seeding hole, 60 cm spacing (Chevalier, 1932) and cultivated under date palms. Chevalier (1932) however reported in the Aïr and Dire regions wheat fields without tree cover and windbreaks, just protected against animals by thorny fences (*zeribas*).

After sowing, the crop is irrigated when required. The soil is continuously weeded to eliminate competition of wild plants and reduce evapotranspiration. The frequency of irrigations decreases as the crop is maturing (Chevalier, 1932). In the Hoggar (plate 3), wheat is sown in small plots which have been previously flooded and wheat plants do not receive attention until the harvest (Nicolaisen and Nicolaisen, 1997). During the growth cycle, farmers frequently bring small amounts of fresh soil between the plants (Nicolaisen and Nicolalsen, 1997) and sometimes gypsum (*tin*) to mitigate salinity effects.

No treatment against rusts is needed as these diseases are absent in the oases (Chevalier, 1932). Grasshoppers and birds are the main enemies of wheat crops in the oases. Wheat is harvested in spring, with sickles and plants are gathered into sheaves (plate 4). Grain yield generally reaches 1.0 to 1.5 $t.ha^{-1}$. Chevalier (1932) reported maturity dates of beginning of February in the Aïr and beginning of March in the Gao-Timbuktu region.

Plate 3 ■ Farmer in his wheat field in the region of Tamanrasset, Algeria.
(Source: S. Oumata)

Plate 4 ■ Harvested wheat in the region of Adrar, Algeria. Wheat plants are gathered into sheaves to facilitate further transport and threshing.
(Source: S. Oumata)

Wheat species cultivated in the oases

The presence of wheat (*Triticum* spp.) has been reported in many oases, particularly in Algeria, Libya and Morocco (appendix 2). Both hexaploid (2n = 6x = 42, BBAADD genome) and tetraploid (2n = 4x = 28) wheats can be found while diploid (2n = 2x = 14) wheats have never been reported. Wheat diversity is described hereafter according the ploidy level and the nomenclature used follows Dorofeev *et al*. (1979) traditional classification of the genus *Triticum*. At species level, we also indicate in brackets the corresponding name according to van Slageren (1994) genetic classification, when mentioned for the first time. Botanical varieties nomenclature used by Erroux (1962) in his description of Saharan wheat, recently revised by Zaharieva *et al*. (2014) according to Dorofeev *et al*. (1979), is applied here.

Hexaploid wheat

Four hexaploid species were found in the Saharan oases. Among them, bread wheat, *Triticum aestivum* L. (= *T. aestivum* L. subsp. *aestivum*) and club wheat, *T. compactum* Host (= *T. aestivum* L. subsp. *compactum* (Host) MacKey) are the most common. Spelt wheat, *T. spelta* L. (= *T. aestivum* L. subsp. *spelta* (L.) Thell.) and Indian dwarf or shot wheat, *T. sphaerococcum* Perc. (= *Triticum aestivum* L. subsp. *sphaerococcum* (Perc.) MacKey) are more sporadically reported.

Ducellier (1920) distinguished, among the Saharan hexaploid wheats, speltoid or *saharae* forms referred as *T. spelta* L. *var. saharae* L. Ducellier, and compact or *oasiculum* forms referred as *Triticum vulgare* Host (= *T. aestivum*) var. *oasiculum* L.D. (the name *aestivum* not being accepted by all botanists at this time). The *saharae* forms present characteristics that are intermediary between true spelt wheat and *inflatum* bread wheat (Erroux, 1962). Similar intermediate forms have been reported by Kuckuck (1964) in the Shahrekord region of Iran. Speltoid bread wheats have narrow spikes, resistance to shattering, and straight, arched, semi-adherent and keeled glumes. Their grain is sometimes compressed like that of the European spelt wheat, sometimes more or less rounded like that of bread wheat, but differs from the latter by its texture and composition. The *oasiculum* forms are characterized by short, compact and fertile spikes, high number of flowers (until 12) by spikelet, pubescent glumes and thick (straight or hooked) awns. This classification of Saharan wheat was used by Maire (1940) in his Flora of Sahara. Similarly, Chevalier (1932) reported the presence of two main forms among Saharan oases wheats, the African spelt wheat referred as *T. spelta* var. *saharae* Ducellier, and the oasian bread wheat referred as *T. vulgare* Host. var. *oasicum* Ducellier, described by Schiemann (1932) as *T. aestivo-compactum* Schiem.

Erroux (1962) distinguished within the hexaploid wheats i) typically Saharan, ii) speltoid and iii) compactoid forms and iv) landraces with attenuated Saharan characteristics. He classified them into botanical varieties based on the presence and size of awns (*aristatum, muticum* and short-awned or *breviaristatum* forms), compactness of spikes, pubescence, shape and color of glumes, color of awns and color of grains. He distinguished on this basis a total of 32 botanical varieties. Twenty five of them belong to the Asian bread wheat, *T. aestivum* L. subsp. *hadropyrum* (Flaksb.) Tzvel. The European bread wheat, *T. aestivum* L. subsp. *aestivum*, is represented by only three botanical varieties. Finally, four varieties characterized by Erroux (1962) as compactoid, belong to club wheat, *T. compactum*.

The forms described by Erroux (1962) as typically Saharan correspond in the classification of Dorofeev *et al*. (1979) to the Asian wheat *T. aestivum* subsp. *hadropyrum* convar. *inflatum* (Vav.) A. Filat. et Dorof. The forms described as speltoid (with bread and spelt wheat traits) make part of *T. aestivum* convar. *inflatum* and convar. *rigidum* (Vav.) A. Filat. et Dorof. Landraces with attenuated Saharan characteristics are included in the Asian wheat convar. *semi-rigidum* A. Filat. et Dorof. and in the European wheat *T. aestivum* subsp. *aestivum*. Wheats considered as compactoid are classified as *T. compactum* convar. *inflatum* Vav. et Kob.

True spelt wheat (*T. spelta*) forms were identified by Flaksberger (1930) in Ducellier's collection of Saharan wheat maintained by the Vilmorin-Andrieux seed company, and by Miege (1924b) in Niger. Miège (1924a) reported the presence of Indian dwarf wheat, *T. sphaerococcum* in Morocco and Mali.

Tetraploid wheat

Tetraploid wheats were found in some oases. Three species were reported: durum wheat, *T. durum* Desf. (= *T. turgidum* L. subsp. *durum* (Desf.) Husn.), emmer wheat, *T. dicoccon* Schrank (= *T. turgidum* L. subsp. *dicoccon* (Schrank) Thell.) and Polish wheat, *T. polonicum* L. (= *T. turgidum* L. subsp. *polonicum* (L.) Thell.) (Erroux, 1962; Benlaghlid *et al*., 1990; Guarino *et al*., 1991).

Lethielleux (1943) considered the cultivation of durum wheat as quite frequent in the oases but erroneously included the landraces Bouch and Fartass into this species. Conversely, Chevalier (1932) and Erroux (1962) emphasized the limited occurrence of durum wheat in Sahara. The presence of durum wheat has however been reported in the oases of Algeria (Ducellier in Chevalier, 1932) and Morocco (Miege, 1924a) as well as in Mali (Chevalier, 1920) and Mauritania (Miege in Chevalier, 1932). Erroux (1962) signaled the presence of cultivated emmer in Wadi al Shatii (Fezzan region) in Central-West Libya. Polish wheat has been reported for a long time in the mountainous regions of North Africa (eg, the landrace Safra, in the Aures, Algeria) where it was cultivated in well drained soils in a sunny position. In Morocco, it was known under the name of wheat of Mogador at the end of the 18th century (Miege, 1950). It is frequently found in the durum wheat fields (Miege, 1950). Ducellier (1930) and Benlaghlid *et al.* (1990) noted its presence in the oases of Tafilalt (Morocco).

Landraces present in the Saharan oases

Most names of the Saharan wheat landraces are related to the religion, or refer to plant, spike and grain characteristics (Zaharieva *et al.,* 2014). But, as already emphasized by Erroux (1962), Benlaghlid *et al.* (1990) and Zaharieva *et al.* (2014), the nomenclature of landraces is frequently imprecise. The same landrace can have several names according to the oasis or the village it originated, making difficult the comparison of germplasm grown in different locations, particularly in the absence of precise morphological description. For example, the landrace Fartass is also called Fertass (Ghat, Tassili n'Ajjer and Illizi, Algeria), Fritissa (Fezzan, Libya) and Bekma, Sdouni, Sfaïa, Tayab or Tayba (Libya) (Erroux, 1962). Conversely, the same name can refer to different forms, with different morphological characters and belonging to different botanical varieties. For example, the landrace El Hamra, also called El Kharma o Hamra (the red in Arabic) contains forms with red spikes belonging to var. *transcaspicum* (Vav.) Mansf. or *turcomanicum* (Vav. et Kob.) Mansf. In some cases, the same name can be used in different regions for landraces belonging to different species. The term Cheguira (blonde in Arabic) has been used to characterize landraces belonging to the bread wheat botanical varieties *hostianum* (Clem.) Mansf. and *meridionale* (Körn.) Mansf. in the Hoggar, Algeria (Ducellier, 1929) and to durum wheat in the Tafilalt, Morocco

(Benlaghlid *et al.*, 1990). The name Hadrache refers to the bread wheat botanical varieties *submeridionalinflatum* Palm. and *subhostinflatum* Palm. in the Fezzan, Libya (Erroux, 1962) and to Polish wheat in the Tafilalt, Morocco (Benlaghlid *et al.*, 1990). The term Chedjara (syn. Hachadi) can apply to Saharan durum wheat, to bread wheat landraces cultivated in the Tell and to awned Saharan bread wheat (Erroux, 1991).

Hexaploid wheat

Among the typically Saharan bread wheat landraces the most frequent are Bahatane, Bel Mabrouk, Bent Embarka, El Mansouri, Fartass and Soukni. The landrace Bahatane (syn. Bahtane) was reported in the Hoggar (Erroux, 1962), Touat and Gourara (Benlaghlid *et al.,* 1990). Bel Mabrouk (also known as Ben El Mabrouk) was considered to have good yields in Beni-Abbes (Béchar), Timimoun (Gourara), Adrar (Touat) and Aoulef (Tidikelt) (Erroux, 1962). Bent Embarka (syn. Bent Embarek, Bent Mbarek), meaning "daughter of the felicity", which includes a broad range of different botanical varieties, was reported in the Algerian oases of El Golea and Timimoun (Ducellier, 1920) and in the Tidikelt (Erroux, 1962), Touat and Gourara (Benlaghlid *et al.,* 1990). El Mansouri was widely cultivated in the Algerian oases (Ducellier, 1930; Erroux, 1962) and in the Tafilalt, Morocco (Benlaghlid *et al.,* 1990). The presence of Fartass, also known as Fertass or Fritissa, was reported in Beni-Abbes and Béchar (Algeria) and in the Fezzan, Libya (Erroux, 1962). The presence of Soukni has been noted in the Fezzan (Erroux, 1962), Touat and Gourara (Benlaghlid *et al.,* 1990).

The group of speltoid bread wheats includes the landraces Ali Ben Maklouf, Djeghloul, El Hamra, Khalouf, Farina and Manga. Ali Ben Maklouf (comprising different botanical varieties, all characterized by a white spike) was reported in the Gourara and Touat, as well as in Timimoun in Algeria (Erroux, 1962). In this last oasis, it was highly appreciated for the fabrication of couscous and bread and farmers used it for their auto-consumption because of its productivity, resistance to birds and taste (Foley, in Erroux, 1962). Djeghloul, cultivated in Timimoun (Erroux, 1962) and the Tafilalt (Benlaghlid *et al.,* 1990), was productive and resistant to birds, but its taste was not appreciated (Foley, in Erroux, 1962). El Hamra, which cultivation has been reported in the Hoggar (Ducellier, 1920), Tidikelt (Erroux, 1962) and Touat (Benlaghlid *et al.,* 1990) in Algeria has a big grain, easy to mill and was appreciated for its taste. Khalouf was mainly present in Ouargla (Passager, 1957). Erroux (1962) observed that this landrace was disappearing because of the specialization of this oasis in the production and commercialization of dates. Farina was known by the Fezzan's farmers as difficult to thresh and not very productive, but resistant to lodging and shattering and providing a flour of excellent quality (Erroux, 1991). The term Farina always apply to speltoid wheats with red spikes (which explains the term El-Khamra used in some oases). It could come from the term *far*

used by the Romans to characterize spelt wheat (Portères, 1958). Cultivated in the Hoggar as well as in the oases of Tamanrasset, In Salah and El Golea, the landrace Manga was reported as resistant to lodging despite its high stature (Erroux, 1962). Erroux (1962) also noted the existence of forms with attenuated speltoid characters and consequently easier to thresh, called Hoggari in some villages of Libya.

Saharan bread wheat landraces with attenuated characteristics include Aourig, Bouch, Chedjara, Cheguira, Ghati, Khreci, Saharoui and Père de Foucauld. Aourig (Baharoui in Wadi al Shatii) was not well appreciated by the Fezzan's farmers, as a date had the same name (Erroux, 1991). Aourig presents a continuous serie of forms belonging to the botanical varieties *aestivum*, *suberythrospermum* (Vav.) Mansf. and *suberythorsperminflatum* Palm., all with white and glabrous glumes and red grain. The landrace Bouch is a mixture of types sharing awned, white, pubescent and compact spikes, mainly cultivated in the Fezzan, Tassili n'Ajjer, Hoggar and in Djanet. The landraces Chedjara, cultivated in the Saoura Valley (Ducellier, 1920) and Cheguira, described by Passager and Barbançon (1956) in the Taghit oasis, are close to Bouch. Ghati, as other landraces belonging to the botanical variety *aestivum* (previously described by Erroux as *T. vulgare* var. *erythrospermum* Körn.) could have been introduced with durum wheat (Ducellier, 1920). Khreci has a high tillering capacity and is productive but susceptible to shattering. Its straw was valued as feed for animals and its grain produced high quality flour (Erroux, 1962). Saharoui was cultivated in the North of Sahara (Ducellier, 1930). It is similar to Ghati but with longer awns. Pere de Foucauld differs from Bouch by a lower spike compactness and shorter glumes (Ducellier, 1920).

Saharan compact wheats (*T. compactum*) involve the forms Fartass, El Klouf, Farina and Tabelbala. The term Fartass applies to a large range of forms all characterized by the absence of awns or short awns and mainly cultivated in Beni-Abbes and Ghardaia (Erroux, 1962) and in the Tafilalt (Benlaghlid *et al.,* 1990). El Klouf has very compact, white, pubescent and short-awned spikes and white grains and belongs to the botanical variety *subsericinflatum* Vav. et Kob. (Erroux, 1991). The term Farina (also used in some regions to describe speltoid wheats as indicated above) is used in the Fezzan to characterize a form with very compact, red and awnless spike, inflated glumes and white grain that can be classified in the botanical variety *crassicepsinflatum* Vav. et Kob. Some Farina forms with both *breviaristatum* and *inflatum* traits have been reported in Beni-Abbes and Ghardaia by Erroux (1962) and classified by this author in the botanical variety *subsericinflatum* Vav. et Kob. The landrace Tabelbala identified by Erroux (1962) in Tabelbala (Beni-Abbes), close to Farina but with red grain, has been included in the botanical varieties *subalbicepsinflatum* Vav. et Kob. and *wittmackinflatum* Vav. et Kob. The four botanical varieties represented in the Saharan compact wheats are also present in Afghanistan (Erroux, 1962; Zaharieva *et al.,* 2014).

Interestingly, all the typical compact wheats are concentrated in the North of the Sahara, in a crescent including (from the East to the West) the oases of Ouargla, Ghardaia, Beni-Abbes, Tabalbala and Tafilalt.

Spelt wheat (*T. spelta*) landraces are poorly represented in the oases. One spelt wheat landrace, Abdassalem, with awnless spike and glabrous and white glumes, was identified by Flaksberger (1930) during his examination of a collection of Saharan wheats collected by Ducellier. It was considered, by this author, as an atypical form of the botanical variety *album* (Al.) Körn. Miege (1924b) also identified spelt wheat forms in the Kaouar, near Bilma (Niger), very susceptible to shrivelling and to rusts. He classified this form in the botanical variety *rubrivelutinum* Körn.

Indian dwarf wheat (*T. sphaerococcum*) landraces have been essentially reported in Mali and Morocco. Miège (1924b) reported in Mali the presence of the landrace Catona. This landrace, quite early and resistant to shrivelling, has been classified by this author in the botanical variety *echinatum* Perc. Miege (1924a) identified in the Draa region (Morocco) a landrace with short stem and white and short spike. Chevalier (1932) characterized the form Nanya from Goundam (Mali) as belonging to *T. sphaerococcum*, but with some compactoid traits.

Tetraploid wheat

The sample of emmer wheat found in the Fezzan and described by Erroux (1962) had red and glabrous glumes, black awns and vitreous, long and pale-amber grains and was included in the botanical variety *pseudorufum* Flaksb.

As mentioned by Chevalier (1932) and Erroux (1962), durum wheat is not frequent in the Saharan oases. A small number of varieties close to the landrace Acheb, characterized by white spikes and awns and belonging to the botanical variety *leucurum* Körn., were found in Algeria. Chevalier (1920) mentioned in Tumbuktu (Mali) the presence of a population belonging to the botanical variety *leucurum*. Ducellier (1929) described a durum wheat landrace collected by Maire in the Hoggar, characterized by short and rounded glumes. Its white or reddish, opaque and starchy grain was similar to that of Poulard wheat, *T. turgidum* L. (= *T. turgidum* L. subsp. *turgidum*). Miège identified a durum wheat (botanical variety *affine* Körn.) mixed with bread wheat in samples collected by Monod in Mauritania (Chevalier, 1932). In the Tafilalt, Benlaghlid *et al.* (1990) described the population Cheguira as having long spikes, strong and sharp glumes with prominent heel, and long, white or black awns. This population has also been reported by Chentoufi *et al*. (2014) in the Ziz Valley. Erroux (1991) mentioned the cultivation of the population Tarouzi in the Algerian oases. Erroux (1962) and Guarino *et al.* (1991) reported the presence of the population Amekkaoui, with compact spikes and short awns, in the Hoggar.

Polish wheat landraces were sporadically reported. Miege (1924a) found two main types in Morocco. The first one had short spikes (4-7 cm) with 16 to 22 spikelets and white glumes and was subdivided in a form with white spikes, long grains (11 mm) and another with black awns and short grains (9 mm). The second type had bigger spikes (8-10 cm), 24 to 33 spikelets, and white glumes and awns and was subdivided in a form with broad spikes (30 mm) and another with narrow spikes (20 mm). All these forms were tall and late-maturing (201 to 208 days) and had high tillering. The Polish wheat landrace found by Benlaghlid *et al.* (1990) was cultivated on a very small scale, near the village of Rissani, in a degraded oasis where date palms were strongly affected by the *bayoud*, *Fusarium oxysporum* f.sp. *albedinis*, leading to a direct exposition of the wheat to sunlight and heat stress. This landrace, called Hadrache by the farmers, was late maturing and has short awns and spikes, white, glabrous, narrow and long glumes, and long, red and vitreous grains. All these samples belong to the subsp. *polonicum* convar. *compactum* Ser., as described by Dorofeev *et al.* (1979).

Origin of Saharan wheats

The first introductions of wheat in Sahara probably occurred together with the development of agriculture. Agriculture was already well established in Egypt around 6,000 BCE (Hugot, 1968). In Libya, agriculture was presumably introduced from Egypt and the Nile Valley (Pelling, 2008). Höbler and Hester (1969) reported important food production in this country around 5,950 BCE. In the case of Tunisia, Algeria and Morocco most studies agree with an East to West Neolithic spread combined with later maritime introductions (Linstädter, 2008; Oliveira *et al.*, 2012).

Hexaploid wheat

Bread wheat is the main *Triticum* species grown in the oases of the Sahara, along its southern margins, from Mauritania to Sudan, and in parts of Ethiopia (Chevalier, 1932). Bread wheat grains are present in tombs in Egypt throughout the dynastic period (Darby *et al.*, 1977). Although the wheats are one of the most common cereals in the oases of Sahara (Gast, 2000), they are only sparsely cultivated further South.

Typically Saharan bread wheat is characterized by the *inflatum* and *breviaristatum* characteristics of the spike (Erroux, 1962). Vavilov (1987) mentioned the presence of these traits in bread wheat in both Asia (Turkestan, Iran, Afghanistan) and the Saharan oases. Ducellier (1929) noted on his side the similarity of the Bahatane short-awned form collected by Maire in the Hoggar with the *breviaristatum* forms described by Vavilov in Asia. Flaksberger (1930) was however the first one to establish a relationship between Saharan and

Asiatic bread wheat, based on the observation of North African samples of the Vilmorin-Andrieux collection. The potential relationship between Saharan and Asiatic wheat was further emphasized by Erroux (1962).

Saharan speltoid wheats have many traits in common with spelt wheat. This last species first appeared in the South-West of Iran during the 8th millennium BCE, from hybridization between cultivated emmer and *Ae. tauschii* Coss. subsp. strangulate (Eig) Tzvel. (Dvorak *et al.,* 1998; Talbert *et al.,* 1998). Free-threshing types appeared by mutation are at the origin of bread wheat (Kerber and Rowland, 1974). The presence of intermediate forms, with semi-adherent glumes and spikes difficult to thresh were reported in Turkestan, Iran and Afghanistan by Vavilov (1987) who classified these forms in a specific group. The speltoid wheat landraces present in the Saharan oases could have resulted from the introduction of intermediate forms from Asia or from hybridizations between spelt and bread wheat having occurred within the oases.

Additional arguments have been recently provided by glutenin polymorphism to support the hypothesis of an Asiatic origin for typically Saharan bread wheats and speltoid wheats. The number of alleles detected at *Glu-B3* (9 alleles) in Saharan wheat by Bellil *et al.* (2012) was the same as that found by Darbandi *et al.* (2010) in Iranian cultivars and seven of them were present in both collections. The allele *b* was the most frequent at the *Glu-D3* locus in Saharan cultivars as it was in Iranian cultivars. It was present not only in the typical Saharan landraces Bel Mabrouk, El Mansouri and Fartass but also in the speltoid landraces El Hamra and Manga.

Saharan wheat with attenuated forms suggests recent introductions from the high plateaus, the mountains or the coast on the North or from Niger and Chad on the South. This hypothesis is reinforced by the finding of Zeven (1980), who reported the absence of hybrid necrosis genes in Mediterranean wheats, a majority of wheats with the Ne_1^m gene in the Sahel and an intermediate proportion of wheat carrying this gene in the Sahara oases. Introductions from the North mainly concern landraces belonging to the botanical variety *aestivum* (previously described by Erroux as *T. vulgare* var. *erythrospermum* Körn.) that could have been introduced together with durum wheat (Ducellier, 1920). Introductions from the South present a high proportion of forms belonging to the botanical varieties *hostianum* and *aestivum* (Erroux, 1962).

Compact wheat or club wheat, *T. compactum*, is the second hexaploid species in importance in the Saharan oases. It differs from other species principally by the action of the compactum (*C*) locus which in its dominant form results in a compact spike (Nilsson-Ehle, 1909). The view that a mutation at the *C* locus in bread wheat, *T. aestivum*, gave rise to compact wheat is generally accepted (Johnson *et al.*, 2008). The subconvar. *roshanum* (Korzh.) A. Filat. et Dorof. that includes all the forms described in the Saharan oases, is distributed mainly in the mountainous regions of Afghanistan and Tajikistan (Porteres, 1958) suggesting an introduction from this region, probably through

Egypt (Chevalier, 1938). Interestingly, compact wheat was found in the oases of Oman by Al Khanjari (2005), who also suggested an introduction from Egypt. Compact wheat is ecologically a typical mountain species susceptible to drought and high temperatures during grain filling (Vavilov, 1987). Some forms may be however well adapted to dryland areas (Gul and Allan, 1972).

The presence of spelt wheat, *T. spelta*, has been sporadically reported in the Saharan oases. Current data suggest that European forms and some of the Asian forms of spelt wheat are derived from hybridization of emmer with free threshing hexaploid wheat. At least for some of the spelt wheat forms, the free-threshing hexaploid parent could have been compact wheat (Schiemann, 1932; Mac Key, 1966). Zeven and Zhukovsky (1975) postulated the existence of a center of diversity in the Saharan oases. However, Abdassalem, the spelt wheat landrace reported by Flaksberger (1930) belongs, according to the author, to the botanical variety *album* which makes part of the group of European spelt wheats, mainly cultivated in southern Germany, Switzerland, France and Spain (Dorofeev *et al.,* 1979). Spelt wheat is well adapted to poor soils (Jacquot *et al*., 1960; Pavićević, 1985) and to drought during grain filling (Morgan, 1980).

Indian dwarf wheat or shot wheat, *T. sphaerococcum*, has been traditionally grown in North-West India and East Baluchistan (Pakistan) (Ellerton, 1939). It is characterized by its semidwarf stature (60-70 cm), erect and rigid appearance, earliness, resistance to yellow rust, small ears, and semi spherical grains (Percival, 1921). It appeared as a result of mutation at the *S* gene which imposed a significant alteration in grain shape (Salina *et al*., 2000). This mutation could have occurred around 2,500 BCE in Afghanistan or in the North-West of the Indian subcontinent from where it moved eastward (Zeven, 1980). Based on the diversity of *T. sphaerococcum*, Singh (1946) concluded that it might have originated in the Indus plain. Twelve botanical varieties of this species have been recorded by Singh (1959) in this region. Indian wheat was present in the Sind Valley during the Harappan culture (2,300-1,700 BCE) (Vishnu-Mittre, 1974). The occurence of this species has been reported at archaeological sites from the Kashmir Valley to the Deccan Plateau, East to the Ganga Valley (Kajare, 1991; Lone *et al*., 1993) and West to Mehrgarh on the margin of the Indus Plain (Costantini, 1984; Meadow, 1996), suggesting that Indian wheat was one of the main winter crops in the ancient South Asian cultures (Mori *et al*., 2013). In Africa, landraces have been essentially found on the southern (Mali) and south-western (Mauritania) borders of Sahara (Portères, 1958). According to Zeven (1980), wheats that carry the hybrid necrosis gene Ne_1^w like *T. sphaerococcum* could have spread to the Sahel through the Arabian Peninsula and Sudan which could explain the present main area of cultivation of this species. Its tolerance to high air temperatures during grain filling (Dorofeev *et al*., 1979), xerophytic characteristics (few erected and rigid leaves) but susceptibility to high soil temperatures (Vavilov, 1987) have probably favoured its adaptation to the irrigated conditions of the Sahel.

Tetraploid wheat

Diffusion of emmer wheat, reconstituted thanks to the study of grain remains from archaeological excavations indicates a presence during the early Neolithic in Egypt, the Ethiopian highlands, the Arabian Peninsula and in Morocco (Zaharieva *et al.,* 2010). Remains of emmer wheat dating from 5,500-4,650 BCE were found in the oasis of Faiyum in Egypt (Caton-Thompson and Gardner, 1934; Wendrich and Cappers, 2005). Samples found in Egyptian tombs dating from the 5th Dynasty (2,494-2,345 BCE) and the 12th Dynasty (1,991-1,802 BCE) have been classified by Erroux (1962), according to their description by Schulz (1916) and Aberg (1950), in the botanical variety *rufum* Flaksb. The emmer landrace found in the middle of the 20th century in the Fezzan and described by Erroux (1962) has been classified by this author in the botanical variety *pseudorufum*, included by Szabó and Hammer (1996) in the subsp. *dicoccon* which contains the *European* forms of emmer. The two varieties only differ in glume color (Szabó and Hammer, 1996) and differ from the landraces collected in Oman by Filatenko and Hammer (2014) which are intermediate between Asiatic (subsp. *asiaticum* Vav.) and Abyssinian (subsp. *abyssinicum* Vav.) forms. Miege (in Portères, 1958) noted that North African emmers had coleoptiles with two veins, as European emmers, and not a coleptile with 4-6 veins as Indo-Abyssinian emmers. These results, taken together, suggest a close relationship between the emmer wheats from Europe and North Africa. North African emmer wheat (including the forms collected in the Sahara) could have been introduced from the Iberian Peninsula where this species is still grown (Zaharieva *et al*., 2010). As postulated by Hopf (1975), additional introductions could have occurred from Turkey (through Libya) and Greece (through Sicilia). According to Porteres (1958), these forms could also have hybridized with other forms coming from Egypt. Emmer wheat was still reported in the Ouergha region in Morocco by Miège (1924a) and by Ducellier in mixture in oat fields in Algeria (Erroux, 1991).

Durum wheat evolved from previously domesticated emmer stands in the eastern Mediterranean and was first cultivated in Syria dating back to 7,500 BCE, shortly after emmer wheat (Salamini *et al.,* 2002; Luo *et al.,* 2007). Due to the difficulty of distinguishing between archaeological remains of free-threshing wheats (tetraploid durum and hexaploid bread wheat) the further diffusion history of this crop is however unclear. According to Chevalier (1932), the durum wheat landraces grown in the Sahara oases originated from neighboring regions and would have been introduced later than bread wheat. This was confirmed by the presence in durum wheat cultivated in the Tafilalt of the gliadin subunit γ 45 (Benlaghlid *et al*., 1990) the presence of which is associated to high gluten quality and characterizes durum wheat from Mediterranean origin (Damidaux *et al*., 1978). The diagram of isozymes of these two accessions was also characteristic of North African populations (Kobrehel and Feillet, 1975) supporting a recent introduction from the Mediterranean Basin.

Durum wheat with compact spikes cultivated in Oman (Al Khanjari, 2005) could have been introduced from Egypt (Perrino, 1991). There is, however, no evidence that the few durum populations with compact spikes found in the Hoggar share the same origin.

Polish wheat, also named Grecian wheat, wheat of Cairo, and sometimes Egyptian wheat, can be found in small areas of the Mediterranean region, Russia and in other regions of Asia. It probably originated in Turkey from durum wheat by mutation for a factor *P* (long glumes and grains) (Dorofeev *et al*., 1979) and seems to have accompanied durum wheat in its diffusion (Vavilov, 1987). Polish wheats found in Saharan oases were probably introduced from neighbor regions. The landrace Hadrache, described by Benlaghlid *et al*. (1990) in the Tafilalt does not differ morphologically from the forms cultivated sporadically in other regions of Morocco. It could have been introduced with durum wheat. Polish what is rarely grown alone in Morocco and the cultivation of durum and Polish wheats in mixture is common in this country (Grillot, 1948). Morever, in some villages, Polish wheat is supposed to bring bad luck when cultivated alone (Miege, 1924a).

The potential ways of introduction of different types of wheat are summarized in figure 5. The use of molecular markers would considerably help to validate those hypotheses.

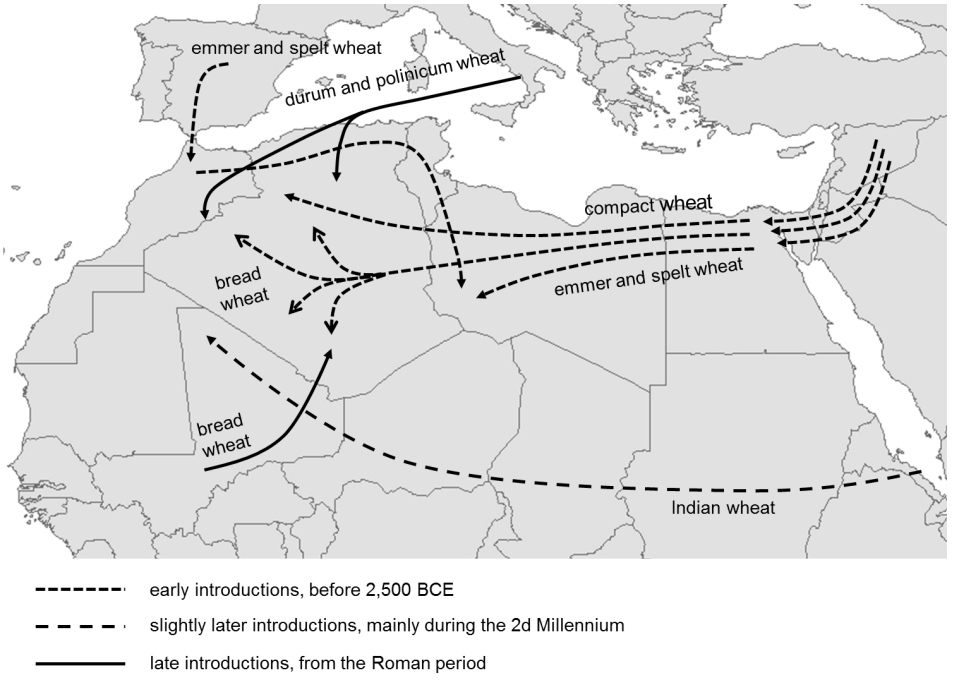

Figure 5 ■ Hypothetic routes for the origin of Saharan oases wheats.

Possible dates of introduction of wheat into Sahara

The ways and dates of introduction of wheat into North Africa are still under discussion. It has been considered for a long time that naked wheats were brought by the Arab civilization during the 7th century CE (Zhukovsky, 1964; Vavilov, 1987). Different opportunities exist, however, for an earlier, pre-Islamic diffusion of wheat to the oases of the Sahara. Moreover, the different species and groups distinguished within Saharan bread wheat could have different origins and dates and ways of introduction (Zaharieva *et al.,* 2014).

Neolithic and pharaonic times

The presence of agricultural human settlements in North Africa since the late Neolithic (Linstädter, 2008) could have favored an early introduction of different forms of wheat into Sahara. Berthelot (1927) and Chevalier (1932) emphasized the fact that the agriculture of the predynastic period on the Nile and that of the Sahara during the Stone Age had the same origin and shared similar crops and techniques. Based on this information, Chevalier (1949) postulated an early introduction of wheat from the East (Nile Valley) into Sahara, during the most recent wet period, the wet Neolithic period (from 5,000 to 2,500 BCE) that allowed easy communications between the Nile Valley and Sahara. The first wheats could have been introduced in the Sahara during the 5th (Clark, 1962) or 6th millennium BCE (Hester, 1968). The presence in the Saharan oases of speltoid and compactoid types progressively leading to *inflatum* bread wheat also supports the hypothesis of an early introduction. These types could have maintained, due to their isolation, the former stages of their evolution (Erroux, 1979). In drier periods, a chain of highlands in the Sahara called Saharan Fertile Crescent that linked the savanna areas at the East with those at the West, could have served as a route by which plants, animals and men migrated (Höbler and Hester, 1969). Then, they may have spread quickly throughout the Sahara (Seddon, 1968). After the beginning of the dry period (around 2,500 BCE) the area of cultivation was limited to the oases and the Sudan zone.

The earliest introductions could have concerned emmer wheat. The diffusion of domesticated emmer wheat, one of the basic plants in neolithic agriculture, has been described by Zaharieva *et al.* (2010). This crop has been reported in Egypt from 4,800-4,400 BCE (Wetterstrom, 1993) and remained the predominant wheat species until the end of the 1st millennium BCE in Nubia (Ryan *et al.*, 2012) and Egypt (Newton *et al.*, 2013). Ballouche and Marinval (2003) reported also its presence in Kaf Taht el-Ghar (North Morocco) from 5,477 BCE. However, the oldest remains of emmer wheat in the Sahara, found

at Zinchecra, a settlement of the Garamantes in the Fezzan, were dated only 900-400 BCE (van der Veen, 1992). The wheat remains found in the archaeological site of Garama in the Fezzan suggests a progressive replacement of emmer by bread wheat in this region from the period 100-500 CE (Mattingly *et al.*, 2001; Pelling, 2005).

Typically Saharan bread wheats with *inflatum* and *breviaristatum* characteristics of the spike and speltoid forms, with semi-adherent glumes and spikes difficult to thresh both seem to have their origin in Turkestan, Iran or Afghanistan. Their presence in the Saharan oases could testify to an ancient introduction in North Africa, likely during the last wet period (before 2,500 BCE). It is not clear if the first forms introduced in the Sahara were true Spelt wheats originated from South-West Iran or intermediate forms (with semi-adherent glumes and spikes difficult to thresh) as those reported in Turkestan, Iran and Afghanistan by Vavilov (1987). After the progressive introgression with new bread wheat forms, Saharan farmers probably selected intermediate forms that kept some speltoid traits conferring better adaptation to hot winds but relatively easier to thresh compared to *T. spelta*.

The oldest remains of compact wheat were found in the site of Tell Ramad in Syria (7,000 BCE) (Renfrew, 1969). Its presence was reported in Egypt from the 5th millennium BCE (site of Merimdah Beni Salami) (Renfrew, 1969) and it was cultivated in this country probably until 2,500 BCE (site of Afyeh) (Chowdhury and Buth, 1971). Its introduction in Sahara could have taken place before this period and probably during the wet period 4,500-2,500 BCE that allowed easy communications between the Nile Valley and Sahara. Interestingly, some grains of compact wheat were frequently found in emmer remains in Egypt (Helbaek, 1956) suggesting that the two species could have diffused almost simultaneously.

Considering that *T. sphaerocccum* appeared no earlier than 2,300 BCE in India (Vishnu-Mittre, 1974), this species should not have reached Africa much before the 2nd millennium BCE. Moreover, a late introduction, during the French colonization of Morocco, Mali and Niger, should not be excluded. It could also have been introduced as an impurity in bread wheat cultivars seeds from India.

Achaemenid Empire

Further introductions from Iran and Central Asia could have occurred during the Achaemenid occupation of Egypt when contacts between Iran and Egypt were particularly intense. These introductions could have concerned in particular emmer wheat and typically Saharan bread wheats. Their spread into Sahara could have been slower due to the dry conditions already affecting the region.

Phoenicians, Garamantes and Romans

Gsell (1908) considered that wheat had been introduced into the Saharan oases before the Carthaginian domination or even before the Phoenician colonization, after the beginning of agriculture formally described in Libya by Herodotus (484-425 BCE) and the cultivation and consumption of wheat reported by Hecataeus of Miletus (*c.* 550-476 BCE). The early development of maritime activity in the Mediterranean and contacts of the Phoenician civilization with Africa (Broodbank, 2006), the development of Carthage and its exploitation of the gold and copper mines in the Sahara, Sahel and Ghana (Barbaza, 2005; Mattingly *et al.,* 2006), implementation of settlements and military posts surrounded and supported by intensive agricultural zones during the 1st millennium BCE (Mattingly and Sterry, 2013) and the intensive commercial activities developed during the Nabataean period (1st century BCE to 1st century CE), between Persia, Middle East, Arabia and Egypt (Bouchaud, 2013) represent different opportunities for the introduction of wheat into the Saharan oases. The presumed European origin of the emmer wheats found in North Morocco (Ballouche and Marinval, 2003) and Sahara (Erroux, 1962) could be explained by intensive exchanges between Mediterranean regions during the 1st millennium BCE and particularly by the contacts between Phoenician and Garamantes (Daniels, 1970). Similarly, Abdassalem, the vestigial spelt wheat landrace reported by Flaksberger (1930), which belongs to the group of European spelt wheats, could have been introduced at this period.

Durum wheat was probably massively introduced into North Africa during the Roman Imperial period (27 BCE-284 CE). Maghreb was then considered, alongside Egypt, as the "bread-basket" of Rome and Pline (23-79) emphasized the excellent quality of semolina prepared with North African durum (Jasny, 1944). Oliveira *et al.* (2012) reported that durum landraces from North-West Africa clustered more closely with those from the Central Mediterranean than with those from South-West Europe (Iberian Peninsula), suggesting repeated introductions from the former region to North Africa. Durum wheat could have spread later in the periphery of Sahara (Mali and Mauritania). Miège (1924a) suggested some similarities between Moroccan and Mauritanian durum wheats, related to the similarity of climates between the two countries. According to Ducellier (1920), some hexaploid wheats with attenuated characters like Aourig (Fezzan), Ghati (Fezzan, Hoggar) and Saharaoui (Biskra) could have been introduced in the oases from the North, together with durum wheat. Erroux (1962) suggested that Aourig, also called Baharaoui, came from Chad, being more frequenly found in Mourzouk, on the road to Chad *via* Gatroum. The name Baharoui derives from *Bahr*, meaning a body of water (such as lake, river, or sea) in Chadian language. The population Baharoui presents some similarities with the population Kanem, a Chadian wheat landrace which name is related to the Kanem Empire (*c.* 700-1376) situated

at the southern end of the trans-Saharan trade route between Tripoli and the Lake Chad.

Durum wheat forms with compact spikes could have eventually been introduced before the non-compact forms from Egypt where wheat was cultivated already from the Hellenistic Period (323-31 BCE).

From the Hegira until the apogea of Saharan trade

Watson (1974) argued that the economy established by Muslim traders enabled the diffusion and adaptation of many crops and farming techniques among different parts of the Islamic world. According to this author, many crops from Africa, China and India were introduced throughout Islamic lands. It has been considered for a long time that naked wheat was brought by the Arabic civilization during the 7th century (Zhukovsky, 1964; Vavilov, 1987). Decker (2009) challenged this hypothesis showing that crops such as durum wheat, Asiatic rice and sorghum were already cultivated widely and consumed under the Roman and Sassanid empires, centuries before the Islamic period. However, the expansion of Islam and the development of trade routes could have intensified the exchanges across Sahara, between Sahara and Sahel and between Sahara and the Arabian Peninsula.

The presence of wheat in northern Sahel is attested for around ten centuries. According to Al Bakri (translated by de Slane, 1913) and Abu al-Fida (1273-1331) (translated by Reinaud, 1848), wheat was cultivated in the oasis of Aoudaghost on the way from Sijilmasa to the Kingdom of Ghana. Yaqut al-Hamawi (1179-1229) wrote in his geographical dictionary (the Mujam al-Buldan) that wheat played an important role in the economy of Borkou and Kanem. Two centuries later, Al-Omari confirmed the importance of wheat as a food in this region (Gaudefroy-Demombynes, 1927). Al-Dimashqi (1256-1327) reported that wheat was cultivated in Gao (capital of the Songhai empire) on the banks of the Niger (Mehren, 1923). Wheat was introduced in the region of Lake Chad from Ouargla (Tourte, 2005). Chevalier (1932) described its presence in the actual Mali (cultivated around the Gourma lake, at 15°N, by the Bellas, ex-slaves of the Tuaregs), Niger (near Birmi N'Koni in the Adar Doutchi along the Komadougou river, at 14°N), Nigeria (Sokoto and Bornou regions, at 12°N), Chad (Kanem, Ouadaï and Dar-Sila regions, between 11 and 12°N) and Central African Republic (in Ndellé at 8°N, introduced from Ouadaï). According to Tourte (2005), wheat consumed by Berbers and Arabs established in sub-Saharan cities was first supplied by trans-Saharan caravans. Then these residents started the cultivation of wheat in their new locations.

According to Mauny (1949), wheat cultivation could have been introduced in the Sahel from Egypt through the Sahara since Neolithic times. Conversely, Barth (1858) postulated that wheat present in Northern Nigeria was introduced only recently (about 1750) and remained rare and expensive. This introduction

more probably occurred after the conquest of North Africa by the Arabs, as attested by references in various Arabic sources, and the development of maritime trade.

The occurrence of wheat in the Sahel is frequently associated with the presence of Arab and Berber populations, who came from the North, and presumably brought with them the tradition of consuming and cultivating this crop. Al-Bakri reported that at Aoudaghost, the local production only partly satisfied the demand, leading to importation from the "Moslem lands" (Bilad al-Islam), ie, North Africa. It is possible that wheat was imported to Aoudaghost from Sijilmasa, where, according to Al-Bakri, an excellent variety was cultivated. Ibn Battuta mentioned that wheat sold at the town of Takadda (to the East of Gao on the way to Aïr), was consumed there by merchants and strangers only.

Another way of introduction of wheat in the Sahel could have been through the development of maritime trade and the increased movement of germplasm. A good example is the exportation of wheat from the Archipelago of Madeira to the Saharan coast and West Africa (Magalhães Godinho, 1965). Wheat cultivation started in these islands in the 15th century with the introduction of wheat from Portugal. Further introductions from North Africa and Europe associated with new settlers arriving to the islands in the 17th and 18th centuries (Vieira, 1983) led to a high diversity of forms, mostly with awned spikes and glabrous glumes belonging to the botanical varities *ferrugineum* (Alef.) Mansf., *milturum* (Alef.) Mansf. and *creticum* (Mazz.) Mansf. (dos Santos, 2009).

Further crosses between Saharan and Sahelian forms, the latest originated from North Africa, Portugal and other regions is likely to have produced the attenuated forms that can be observed today. Bread wheat cultivated in the Sahel includes a high proportion of attenuated forms belonging to the botanical varieties *hostianum* and *aestivum* (Erroux, 1962). Attenuated forms were also found within Sahara along traditional caravan routes. This is for example the case of Baharoui (= Aourig) belonging to the botanical variety *aestivum* found in Murzuk, a stop in the Fezzan on the North-South trade route across the Sahara (Erroux, 1991). Erroux *et al.* (1962) mentioned the existence of continuous series from types with attenuated Saharan characters to types with pronounced Saharan characters constituted by botanical varieties like *hostianum, subhostianum* (Vav.) Mansf. and *subhostinflatum*, or *meridionale submeridionale* (Vav.) Mansf. and *submeridionalinflatum*.

Recent introductions

Introductions also occurred during the period of French colonization. The fact that in case of bad cereal harvests farmers increasingly sold dates to buy wheat could have favoured the introduction of exogenous varieties (Hardy, 1878). Erroux (1962) reported the presence in some oases of improved bread wheat varieties like Florence-Aurore, an early-maturing cultivar released in

1936 and widely cultivated in North Africa (Ammar *et al.,* 2011). The exchange of seeds, limited until this date, has been favoured by the construction of new roads across Sahara before and after the independence (Fontaine, 2005). Several recently introduced durum wheat landraces and commercial varieties have been mentioned by Bellil (2012) in the Algerian oases. The development in Sahara of wheat cultivation under center pivot irrigation (Campano, 1996) that allows high yields but require high input levels and the use of high-yielding varieties is expected to accelerate the substitution of traditional Saharan landraces by modern varieties.

General trends in the evolution of Saharan wheats

Saharan wheats represent a "melting pot" (Ducellier, 1929) constituted by successive historical contributions of different species. Based on our present knowledge, we can hypothesize that these species arrived in the following order: emmer and spelt wheat (from Europe and Egypt), bread and compact wheats (from Egypt), *T. sphaerococcum* (from Sudan), durum wheat (from the Mediterranean Basin for non compact forms, and from Egypt for compact forms) and Polish wheat (mixed with durum wheat, mainly from the Mediterranean Basin).

Hulled wheats were consequently the first to be introduced in Saharan oases, with a further trend of attenuation of spelt and emmer characters through hybridization with naked wheats that arrived later (Portères, 1958), the true hulled forms becoming relict crops. This progressive loss of interest in hulled wheats, associated with the difficulties of threshing and milling, have also been observed in other regions (Zaharieva *et al*., 2010).

In parallel, a competitive advantage has probably favored the introduction of hexaploid wheats because of their better ecological flexibility (particularly evident in the case of bread wheat), compared to tetraploid wheats. As a consequence, emmer wheat has almost disappeared, durum wheat is mainly found at the periphery of the Sahara, and Polish wheat is sporadically present.

The ecological conditions of the Saharan oases tended to give the hexaploid wheats a "Saharan facies" (Ducellier, 1920), mainly characterized by compact ears, high number of flowers per spikelet, earliness, non-immunity to fungal diseases and eventually a tendency to branching spikelets. On the other side, the introgression of spelt wheat by bread wheat led to new (speltoid) forms with higher number of flowers per spikelet than in the hulled species (Ducellier, 1920).

In opposition to Chevalier (1932) who referred to Saharan wheats as "true botanical relics", Portères (1958) considered the Saharan oases as a secondary center of wheats diversification with interspecific hybridization between

genetic elements from distinct origins at different historical eras. This is probably true and explains the peculiarity of the Saharan wheats and their uncomparable value as genetic resources. Unfortunately, their diversity is actually threatened and many forms have already disappeared.

Genetic diversity of Saharan wheats

Ducellier (1920), Miege (1924a) and Erroux (1962) highlighted the broad diversity in Saharan wheat for spike and grain morphology. A wide variation was found by these authors for awn length, awn morphology, glume size, spike compactness, number of flowers per spikelet, and spike and grain color. Diversity studies of Saharan wheat based on biochemical markers were initiated by Benlaghlid *et al*. (1990). These authors analyzed the polymorphism of gliadins, glutenins and isoenzymes, using the methods of Bushuk and Zillman (1978), Payne *et al*. (1981) and Kobrehel and Feillet (1975), respectively, on 18 tetraploid and hexaploid landraces from the Tafilalt, Touat and Gourara. Gliadins revealed different patterns between two accessions of El Mansouri from the Tafilalt, one classified as *subhostianum* (pubescent) and the other as *suberythrospermum* (glabrous). The landrace Fartass from Tafilalt showed specific high-molecular-weight HMW subunits. The isoenzymes *e* and *f* were found to be present in the accessions of El Mansouri and absent in Bahatine, Bel Mabrouk, Bent Embarka and Ghati. The first landrace belongs to the speltoid type while the other landraces correspond to attenuated Saharan forms. The remaining hexaploid landraces (El Hamra and Manga) were characterized by the presence of the isoensyme *e* only. In the case of tetraploid wheat, similar patterns were found for two Cheguira durum wheat accessions (one with white awns and the other with black awns).

The allelic variation at the glutenin loci was studied by Bellil *et al*. (2012) in a set of bread landraces collected in Algerian oases, using SDS-PAGE. A total of 32 alleles were detected at six glutenin loci, which in combination resulted in 36 different patterns including 17 for HMW and 23 for LMW glutenin subunits. One new allele was found in Saharan wheat, at the *Glu-B1* locus. All loci, except *Glu-D1*, displayed a genetic variability higher than 0.50, *Glu-B3* being the most polymorphic (0.81). The number of alleles detected at the *Glu-1* and *Glu-3* loci was higher than in French and Czech cultivars.

In summary we can observe that genetic diversity studies on Saharan wheats, based on gliadins, glutenins and isoenzymes polymorphism, never involved large numbers of accessions. In addition, none of them was repeated over time to allow analyzing the evolution of diversity and the eventual reduction of allele diversity. It is consequently urgent to consider using high thoroughput genotyping tools to have a more general and dynamic vision of the diversity in this germplasm.

Saharan wheat landraces, potential resources for wheat breeding

Cereals grown in the Saharan oases often face water stress, due to very low rainfall, insufficient and irregular irrigation, and very high evapotranspiration. Temperatures are very high during grain filling (35 to 40°C) and present large diurnal differences. Salinity problems are frequent (Toutain, 1977). Having evolved in such constraining environment, Saharan wheat is expected to present useful tolerance traits and could represent "interesting objects of hybridization" (Ducellier, 1920).

Identification of useful traits

Ducellier (1920), Ciferri and Garavini (1940) and Erroux (1962) noted the high spike fertility of Saharan wheats, a trait that could be useful to improve this yield component in modern varieties. Meunier (1978) evaluated landraces from South Moroccan and South Algerian (Tademait) oases in the conditions of Achouria, Errachidia and Zagora (Morocco) and noted a high number of fertile spikelets per spike in almost all accessions.

Wheat landraces traditionally cultivated in the Saharan oases are generally early maturing (Ducellier, 1909) which allows them to avoid terminal drought stress. Reguieg *et al.* (2014) evaluated eighteen landraces of bread wheat from the Adrar region (Gourara) for earliness. The landrace Sabbaga (quick in Arabic) appeared to be the earliest despite a long grain filling period.

Ducellier (1920) mentioned a high level of drought tolerance in Saharan wheat, and Toutain (1977) reported drought tolerance in the landrace Fartass under the conditions of the Moroccan oases. Meunier (1978) noted a better drought tolerance in the landraces from South Morocco, compared to those from South Algeria. Considering that the use of any drought tolerance related trait and its further application in breeding should be however first considered in relation to the type of stress (intensity, timing) faced by the crop in a given environment (Tardieu *et al.*, 2012), these first observations need consequently to be confirmed and refined through evaluation in other drought prone environments.

According to Ducellier (1920) the pubescence present in a majority of Saharan wheat represents a trait of adaptation to high temperatures. Rodriguez (1932) recommended the cultivation of the Saharan wheat El Klouf (or El Krelof), close to El Mansouri, in the Castilla y León Province (Spain) for its capacity to produce high yield under drought and heat stress. In the South of Spain, De Arana (1934) observed a better heat tolerance of El Klouf, compared to local landraces. Erroux (1952) noted in the Fezzan oases the high level of tolerance to high temperatures of all locally cultivated wheats. The same author observed in Timimoun that most Saharan landraces had at least an acceptable

level of tolerance to salinity. Toutain (1977) highlighted the high level of salinity tolerance in the landrace Fartass.

Ali Ben Maklouf, El Mansouri, Farina and Khreci were reported to have a good bread-making quality (Erroux, 1962), but our knowledge of the bread-making quality of Saharan wheat is still based on punctual observations. As for other traits, there is an urgent need for a broader evaluation.

Utilization in breeding programs

The utilization of Saharan landraces in wheat breeding has been limited by the difficulty of cultivating these landraces out of their environment of origin, because of their extreme susceptibility to yellow rust (Ducellier, 1920; Vavilov, 1964). This characteristic makes it difficult to maintain collections outside the oasis.

A mass selection experiment carried out in Adrar by Erroux (1962) allowed the isolation, from different landraces, of pure lines with improved characteristics. Mass selection was also carried out within Fartass forms in the station of Zagora (Morocco) in 1970 (Meunier, 1978).

Some crosses were made in experimental stations in Algeria with the cultivar Pusa/Mentana without, however, performing the creation of new cultivars. In France, Schribaux bred new wheats derived by crossing the compact wheat landrace El Klouf with the variety iI having as progenitors the bread wheat varieties Rieti, Epi carré and Inversable (Desprez, 1927).

In Rome, Strampelli used the wheat El Krelof (or Klouf) in some wheat crosses, probably in the attempt to introduce earliness and short stature in wheat (achieved in the 1920s thanks to the Japanese variety Akakomugi). In 1910, by crossing the Italian variety Rieti by El Krelof, he obtained the mutation today known as *hooded*. In the *hooded* mutant type (*hd*), awns are shorter and bent at the base and glumes are reduced to a hook or bent round on themselves to form a close spiral, characters than can be observed in Saharan wheats.

In the experimental station of Zamora of the Instituto de Cerealicultura, in Spain, the same landrace El Klouf was used as a progenitor for its earliness, short stature, high productivity and quality and tolerance to drought and heat. It was used, together with the varieties Bon-Fermier, Blé Seigle and Square Head, in a complex cross leading to the variety Hybrid L. 4. This variety was extensively cultivated under rainfed conditions in Castilla and Aragón (De Arana, 1934). El Klouf was also crossed with the bread wheat varieties Thaw and Warren from Australia, Hope from Canada, Yeoman from England, the durum wheat line R. 10.244 from Russia, as well as with einkorn, *Triticum monococcum* L. accessions (De Arana, 1934).

In Morocco, an outstanding durum wheat line 1658 was obtained by crossing the durum landrace Reach by the Saharan form Amekkaoui. This line was subsequently released under the name Zeramek (Jlibene and Nsarellah, 2011).

Threats on Saharan cropping systems and wheat genetic resources

Oasian agriculture basically worked for centuries as a complex, subsistence based and intensive farming system. Traditionally, oases have played an important role as commercial and administrative centres for nomadic populations and have created a specific culture. During the last 30-40 years, modes of the life of the Sahara oases have changed drastically (Ishiyama, 2011). Oases are actually under serious threat and their development is facing a variety of constraints that include discrepancy between demographic pressure and urbanization and the capacity of ecosystems, maladjustment of oasis-based operators in regard to economic activities (tourism services, commercial circuits), modifications in lifestyles and consumption patterns to the detriment of local craft industries, absence of adequate attention being given in public policies to the specific nature of oasis conditions (particularly in the fields of research, agriculture and education) and socio-economic changes such as development of non-agricultural activities, urbanization and migration to cities (especially of the younger population) (Barathon *et al*., 2005; El Mahjoub, 2011) and their degradation or destruction would represent a tremendous loss of cultural heritage (Gangler, 2008).

In some cases, degradation of oases cropping systems is due to a lack of maintenance of equipment and poor management of resources. The maintenance of *foggaras* is particularly crucial. A total of 907 *foggaras* has been reported in the oases of Touat, Gourara and Tidikelt. This hydraulic and cultural heritage deteriorates from one year to another due to technical and social problems (Remini and Achour, 2008). Other factors such as salinization of the soil and water (Brooks *et al*., 2003) or encroachment of sand dunes (Hidore and Albokhair, 1982) can also result in declining productivity of oases and destroying traditional cropping systems (Ferry and Toutain, 1990). Lack of maintenance also increases the damage caused by the locust bean moth (*Ectomyelois ceratoniae*), the old world mite (*Oligonychus afrasiaticus* McGreg) or boufaroua and the bayoud that drastically affected some palmgroves (Dubost, 1986).

Another factor of degradation is the excessive exploitation of natural resources, through the development of large-scale agricultural projects like the Kufra Project in Libya (Wilkinson, 1978) and the big farms created following the Agricultural Development Law (1983) in Gassi-Touil, Souf, El-Meniaa, Zelfana, Touat-Gourara-Tidikelt in Algeria (Otmane and Kouzmine, 2013). The objectives of those projects were to sustain the economic development of the Saharan regions and reduce domestic food dependency, especially in cereals. Several decades after, the results are still limited and these realizations are endangering the water resources. Agricultural oasis systems are totally dependent on groundwater resources that have not been recharged since the wetter period of Late Pleistocene and Early Holocene times (Brooks *et al*.,

2003). Excessive exploitation of these resources can lead to a rapid decline in groundwater resources and significant land degradation.

All these changes represent a threat to regional socio-economic functioning of oases, but also about the potential loss of valuable germplasm (White, 2007). Intensification leads to the introduction of highly productive cultivars (reinforced by political factors and agricultural extension offices) that progressively replace the traditional landraces. Surveys conducted in the Siwa oasis of Egypt from 1919 to 2006 indicate that diversity of perennial crop remained relatively stable through time but that few traditionally cultivated annual species or landraces have been lost (Nabhan, 2007).

The risk of losing the genetic diversity present in the Saharan oases was first expressed by Erroux (1962). Using these indications, Guarino *et al*. (1991) planned an expedition in the Hoggar and by comparing the landraces present in six oases (Abalessa, Ideles, In Amguel, Mertoutek, Tahifet and Tazrouk) in 1977 and 1988 concluded that no significant genetic erosion had occurred during this decade. In the Ziz Valley (Morocco), Chentoufi *et al.* (2014) noted that genetic erosion is slowed by farmers' preferences for landraces, some farmers keeping at least small plots for traditional varieties even when they increasingly grow modern varieties. Most of the information available is however still punctual and based of the presence-absence of landraces and des not permit to have a global evaluation of the loss of allelic diversity in the Saharan oases. We consequently urgently need a more global analysis using pertinent indicators of biodiversity assessment (e.g. richness, evenness, divergence) (Jarvis *et al*., 2007).

Conclusion

Saharan wheat represents a valuable source to improve diversity and tolerance to abiotic stresses, of great interest in the current period of global warming. Some of the studies reported in this paper were, however, conducted a long time ago and most focused on some specific oases.

Saharan wheat deserves a new, global inventory and a detailed analysis of their diversity taking advantage of new advanced technologies, particularly the use of molecular markers. Such tools might also contribute to answer some questions concerning its origin and ways of diffusion. On the other hand, a large-scale phenotyping of existing collections is needed to confirm its potential value and identify potential progenitors to be used in wheat breeding programs. It is urgent to study these genetic resources, threatened by genetic erosion induced by the degradation of ecological conditions and distribution of seeds of modern cultivars.

As emphasized by Harlan (1970), "*for the sake of future generations, we must collect and study wild and weedy relatives of our cultivated plants as well*

as the domesticated races. These sources of germplasm have been dangerously neglected in the past, but the future may not be so tolerant. In the plant breeding programs of tomorrow we cannot afford to ignore any source of useable genes."

The fear of losing forever Saharan wheat genetic resources, already expressed by Erroux (1962), could become soon a reality. There is consequently an urgent need to collect, conserve (*ex situ* and in *situ*), analyze and evaluate Saharan wheat genetic resources to increase their utilization in breeding programs as well as to stop their genetic erosion.

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Appendix 1 ■ Chronology of key events of Sahara history.

Period	Event
c. 35,000 BCE	Appearance of the man of Cro-Magnon and development of the Acheulean and the Aterian cultures
c. 20,000 BCE	Migration of the man of Cro-Magnon around the Mediterranean Sea
22,000 BCE	Development of the Maurusian culture
15,000 BCE	Development of the Mouillan culture
c. 7,500 BCE	Beginning of a wet phase, known as Neolithic subpluvial, migration of dark skinned hunters and collectors from the East (present Ethiopia) to Sahara
c. 5,500 BCE	Development of agriculture and animal husbandry in the Nile Valley
5,000-4,000 BCE	Dark skinned populations replaced by white skinned Berber populations from the North (Tuareg and Tubu peoples)
5,000-4,200 BCE	Merimde culture in Lower Egypt, cultivation of cereals (emmer wheat, sorghum and barley), exchanges with the Fertile Crescent and western Asia
4,400-4,000 BCE	Flourishing of the Badarian culture (related to the Nubians) in Upper Egypt
4,000-3,200 BCE	Naqada culture in the Nile Valley, exchanges with Nubia, the oases of the western Egyptian desert, eastern Mediterranean and the Near East
3,100-2,890 BCE	Establishment of the Wadi Hammamat route (from the Nile to Red Sea)
2,649-2,150 BCE	Establishment of the Abu Ballas Trail (from Dakhla oasis to north-eastern Chad)
c. 2,500 BCE	End of the wet phase in the Sahara
1,660 BCE	Introduction of the horse in Egypt
1,200-800 BCE	Development of maritime trade along the Mediterranean coast by the Phoenicians
c. 1,000 BCE	Establishment of the Garamantean routes (from the Fezzan to the Mediterranean sea)
900 BCE	The Garamantes create the kingdom of Zinchecra
c. 814-813 BCE	Carthage founded by the Phoenicians
5th century BCE	Creation of Phoenician colonies in the western part of Sahara
525-404 BCE	Achaemenid (Persian) occupation of Egypt, development of Egyptian western desert oases
c. 460 BCE	Expedition of Hannon to the Draa River (Morocco)
343–332 BCE	The Persian King Artaxerxes III reconquers the Nile Valley
332 BCE	Egypt conquered by Alexander III of Macedon
305-30 BCE	Establishment of the Ptolemic Dynasty, the last dynasty of ancient Egypt. Ptolemy (*c.* 367-283 BCE) recognizes the importance of oases, not only as a source of taxation but also as bases from which to launch raids
200 BCE	Occupation of the North of Sahara by the Numidian Kingdom, allied with the Romans
146 BCE	Carthage conquered and destroyed by the Romans
112–106 BCE	Jugurthine war, beginning of the domination of Rome over North Africa

Appendix 1 ■ Chronology of key events of Sahara history (*continued*).

Period	Event
1st century BCE	The Nabateans develop trade with Persia, Middle East, Arabia and Egypt
70-66 BCE	Jewish slaves settled throughout Carthage by the Roman emperor Titus
46 BCE	Numidia annexed to the Roman Empire
27 BCE	Beginning of the Roman Imperial period, development of durum wheat cultivation in the Mediterranean basin
25 BCE	Expedition of Aelius Gallus to Yemen across the Red Sea
19 BCE	Expedition of Septimus Flaccus to the Niger River, through the Tibesti Mountains
41	Expedition of Gaius Suetonius Paulinus to the northern area of the Senegal River, through the Atlas Mountains, western Sahara and Mauritania
62	Expedition organized by Nero in Nubia
115–117	Jewish revolt against Trajan, Jewish communities sent to various Roman provinces in North Africa
202	Germa (capital of the Garamantes) conquered by Septimius Severus
3rd century	Introduction of the camel in Sahara and development of the Saharan oases
429	North Africa conquered by the Vandals, a Germanic tribe that had migrated to Iberia, before being expelled by the Visigoths
c. 525	Jewish exodus after the defeat of the Jewish Himyarite king of Yemen
533–534	Vandalic War, in which Justinian I reconquers the Africa province for the Eastern Roman (Byzantine) Empire
618-621	Romans defeated by the Sassanid Persian army in Egypt, the Persians gradually extend their rule southwards along the Nile
622	Hejira (journey of the Islamic prophet Muhammad and his followers from Mecca to Medina)
644	Beginning of the Islamic conquest of the Maghreb by Uqba ibn Nafi
681	The Muslim arab army led by Uqba ibn Nafi reaches Morocco
739	Beginning of the Great Berber Revolt
757-758	Sijilmasa founded by the Kharijites
852	Foundation of the Kanem Kingdom in Chad
c. 1000	The King of Gao converted to Islam
1050	Aoudaghost conquered by the Kingdom of Ghana
1070	The king of Ghana converted to Islam
11th century	Almoravids religious reform in the Sahara
1235	The Mandinka prince Sundiata Keita defeats the Sosso at the battle of Kirina, development of the Mali Empire
1324	Development of Timbuktu
1440	Beginning of European slavery
1464	Development of the Kingdom of Gao
1493	Development of the Songhai Empire

Appendix 1 ■ Chronology of key events of Sahara history (*continued*).

Period	Event
1591	Victory of Morocco against the Songhai Empire at Tondibi
1644	War of Charr Babba between Zawaya and Hassan tribes in western Sahara
1830	Beginning of the French colonization of Algeria
1844-1862	Battles of the oases (Biskra, Zaatcha, Laghuat) in resistance to the French colonization
1864-1880	Revolt of the Ouled Sidi Cheikh in Algeria
1885	Victory of the Mahdist against the English army in Kharthoum
1916	Great Tuareg revolt
1921	Libya occupied by the Italian army
1951	Independence of Libya
1962	Iindependence of Algeria
1969	Treaty of Ifrane between Algeria and Morocco about the exploitation of Sahara
1970	Big cultivation project launched in the oasis of Kufra, Libya
1976	The Sahrawi Arab Democratic Republic (SADR) is proclaimed by the Polisario Front which claims sovereignty over the entire territory of western Sahara
1983	Agricultural development law in Algeria, creation of big irrigated farms in the oases
1990	Tuareg revolts in Niger and Mali

Appendix 2 ■ List of the main Saharan oases with their location, history, agricultural characteristics and presence of wheat.

No	ID	Locality	Province	Region	History	Agricultural characteristics	Wheat
					Algeria		
1	A1	Adrar	Adrar	Touat	Ancient settlement; strategic point on the trade route between North and West Africa	Date palm, fruits, peanuts, vegetables, forages, cereals (wheat, barley, oat)	yes
2	A2	Aougrout	Adrar	Gourara	Old Zenete Berbers settlement	Date palm, vegetables, forages, wheat, barley	yes
3	A3	Aoulef	Adrar	Tidikelt	Trade relay between Northern Sahara and Mali	Date palm, alfalfa, millet, vegetables, cereals	yes
4	A4	Béchar	Bechar	Saoura	Trade center at the junction of trans-Saharan roads	Date palm, vegetables, figs, almonds, cereals	yes
5	A5	Beni-Abbes	Bechar	Saoura	Inhabited during the Neolithic	Date palm	yes
6	A6	Berriane	Ghardaia	M'zab	Inhabited during the Neolithic, occupation of the region c. 9,500 BCE	Date palm, forages	yes
7	A7	Biskra	Biskra	Ziban	Known during Roman times as Vescera	Date palm (Deglet Nour), figs, olives, citrus, apricots, grapes, forages, cereals	yes
8	A8	Bou Saâda	M'Sila	Saharan Atlas	A pilgrimage town since the Hegira; important caravan center	Date palm, grapes	N/A
9	A9	Djanet	Illizi	Tassili n'Ajjer	Inhabited since Neolithic (c. 9,000-10,000 BCE); founded in the Middle Ages by the Tuaregs; stop on the trade route from Ghat to Niger	Date palm, vegetables (potato, sugar beet, tomato), fruits (olives, citrus), cereals	yes
10	A10	El Golea (El Menia)	Ghardaia	M'zab	Founded in the 10th century; inhabited by Zenete Berbers	Date palm (180,000 trees), forages, cereals	yes
11	A11	El Oued	El Oued	Oued Souf	Inhabitants would have come from Yemen (Arabic and Hebrew Semitic tribes) about five centuries ago	Date palm, olives, figs, grapes, apricots, citrus, madder, tobacco, vegetables, forages, cereals	yes
12	A12	Filiach	Biskra	Ziban	Burials indicating human occupation several millennia ago	Date palm (140,000 trees), olives, vegetables	N/A

Appendix 2 ■ List of the main Saharan oases with their location, history, agricultural characteristics and presence of wheat (*continued*).

No	ID	Locality	Province	Region	History	Agricultural characteristics	Wheat
13	A13	Ghardaia	Ghardaia	M'zab	Built thousand years ago by the M'zabites	Date palm, vegetables, forages, cereals	yes
14	A14	Iherir	Illizi	Tassili n'Ajjer	Since neolithic times; prehistoric art dated to 9,000 BCE found in the area	Date palm, figs, grapes, root crops, cereals	yes
15	A15	In Salah	Tamanrasset	Tidikelt	Historically a trading town (slaves, ivory, gold from South, European goods from the North)	Date palm (200,000 trees), fruits, vegetables	yes
16	A16	Laghouat	Laghouat	Saharan Atlas	Inhabited since neolithic times (c.9000-6000 BCE); city founded in the 11th century	Date palm, wheat, barley, oat, grapes, olives, citrus, fruits; sheep, cattle	yes
17	A17	Marhouma	Bechar	Saoura	Rock engravings since neolithic times	Date palm, forages, vegetables	N/A
18	A18	Messaâd	Djelfa	Saharan Atlas	Known during Roman times as Castellum Dimmidi, Roman garrison (198-240 CE)	Date palm, fruits, pastures	N/A
19	A19	Ouargla	Ouargla	Tidikelt	Founded, according to Ibn Khaldun, during the 10th century	Date palm, forages, cereals	yes
20	A20	Ougarta	Bechar	Saoura	Prehistoric presence; stop for caravans on the trade road towards the South	Date palm	N/A
21	A21	Ouled Djellal	Biskra	Ziban	Founded in 13th century	Date palm (Deglet Nour), figs, pomegranates, grapes, cereals (bread and durum wheat)	yes
22	A22	Reggane	Adrar	Touat	Founded in 10th century; the last town on the Tanezrouf track to Mali	Date palms, vegetables	N/A
23	A23	Sidi Khaled	Biskra	Ziban	Roman remains and rock engravings around the neighboring town Ouled Djellal	Date palm (100,000 trees, Deglet Nour) figs, grapes, pomegranates, apricots, vegetables	N/A
24	A24	Tabelbala	Béchar	Saoura	Founded in 11th century; a stop on the caravan routes linking southern Morocco to the Sahel	Date palm (140,000 trees); wheat (*T. compactum*), sheeps, goats, camels	yes

Appendix 2 ■ List of the main Saharan oases with their location, history, agricultural characteristics and presence of wheat (*continued*).

No	ID	Locality	Province	Region	History	Agricultural characteristics	Wheat
25	A25	Taghit	Bechar	Saoura	Many neolithic rock engravings in the area	Date palm (137,450 trees); sheeps, goats, camels, cattle, chickens	yes
26	A26	Taghouzi	Adrar	Gourara	Founded in 12th century	Date palm, cereals (wheat, barley)	yes
27	A27	Tamanrasset	Tamanrasset	Hoggar	Originally established as a military outpost to guard the trans-Saharan trade routes	Date palm, citrus fruits, apricots, almonds, cereals, corn, figs	yes
28	A28	Tamentit	Adrar	Touat	From early history to 100 CE Gaetuli Berbers; from 100 to 600: Hebrew occupation; crossroads in the caravan trade (13th-14th century)	Date palm (25 varieties), legumes (pea, lentil), wheat, barley, cotton	yes
29	A29	Timimoun	Adrar	Gourara	Stone tools testify an human occupation in prehistoric times	Date palm, wheat, barley	yes
30	A30	Tindouf	Tindouf	Saoura	Built in 1852 by members of the Tajakant tribe on the site of a former ksar of 16th century	Date palm, wheat, barley, oat, grapes, olives, citrus, fruits; sheep, cattle	yes
31	A31	Tiout	Naama	Atlas	Rock carvings from 9,000 BCE; ancient ksar of 15th century	Date palm (excellent quality local varieties Feggous Aghrass)	N/A
32	A32	Tolga	Biskra	Ziban	Roman remains	Date palm (more than 500,000 trees; Deglet Nour), figs, pomegranates, cereals	yes
33	A33	Toggourt	Ouargla	Oued Righ	Founded in 15th century	Date palm, wheat, barley, oat, grapes, olives, citrus fruits, figs, apricots, alfalfa	yes
34	A34	Tsabit	Adrar	Gourara	Starting point for caravans travelling to Mali	Date palm, legumes, cereals (bread and durum wheat, barley, oat); camels, sheeps	yes
35	A35	Zeghamra	Bechar	Saoura	Founded by the Ayt Khebbach, a tribe of southeastern Morocco	Date palm, vegetables, fruits	yes

Appendix 2 ■ List of the main Saharan oases with their location, history, agricultural characteristics and presence of wheat (*continued*).

No	ID	Locality	Province	Region	History	Agricultural characteristics	Wheat
					Chad		
36	C1	Aouzou	Tibesti	Tibesti	N/A	Date palm, cereals (wheat, millet); camels, goats	yes
37	C2	Archei	Fada	Ennedi	Rock paintings from 9,000 BCE; permanent settlement from 4,000 BCE	Permanent water (guelta); camels	N/A
38	C3	Bardaï	Tibesti	Tibesti	First report from the German explorer Gustav Nachtigal (1869)	Date palm, cereals, vegetables	yes
39	C4	Fada	Fada	Ennedi	Military post from 1914	Date palm, figs, wheat	yes
40	C5	Faya-Largeau	Faya	Borkou	Served as a center for trans-Saharan trade	Date palm, cereals	yes
41	C6	Yarda	Borkou-Yala	Borkou	Rock drawings, caravan route from the Kufra oasis to Lake Chad through Bourku	Maize, wheat, millet	yes
42	C7	Zouar	Zouar	Tibesti	Rock carvings and paintings (25,000-8,000 BCE)	Date palm, millet, maize, wheat, barley	yes
					Egypt		
43	E1	Bahariya	Giza	Middle Egypt	Inhabited from c. 5,000 BCE; an important transit point for the caravan tracks	Date palm, olives, mangos, apricots, oranges, grapes, wheat, rice, corn	yes
44	E2	Baris	New Valley	Upper Egypt	On the Darb el-Arba'in trade road connecting Egypt to Sudan	N/A	N/A
45	E3	Dakhla	New Valley	Upper Egypt	Settled by nomadic hunter-gatherers c.10,000 BCE; tombs from 2,200 BCE; hydraulic system from the Persian occupation (525-401 BCE)	Date palm, olives, peanuts, fruits, wheat, rice	yes
46	E4	Douch	New Valley	Upper Egypt	Occupation from 4,000 BCE, ruins and qanâts from the 5th century BCE; temple from Roman time (1st -2nd century CE)	Date palm, olive, pomegranate, flax, wheat, barley, melon, grapes	yes

Appendix 2 ■ List of the main Saharan oases with their location, history, agricultural characteristics and presence of wheat (*continued*).

No	ID	Locality	Province	Region	History	Agricultural characteristics	Wheat
47	E5	Faiyum	Faiyum	Middle Egypt	Earliest evidence for farming in Egypt, during the 12th Dynasty of the Middle Kingdom (1,991-1,802 BCE); breadbasket of the Roman world	Figs, olives, grapes, vegetables, beans, maize, wheat, cotton, sorghum, fruits	yes
48	E6	Farafra	New Valley	Upper Egypt	Located between Bahariya and Dakhla oases, a stop on the road to Libya, Cairo and Alexandria	Date palm, olives, citrus, grapes, apricots, beans, medicinal plants, wheat, rice	yes
49	E7	Kharga	New Valley	Upper Egypt	During the Old Kingdom a stage on the Darb el-Arba'in trade road from Egypt to Sudan	Date palm, wheat, olives, clover, fruits, vegetables	yes
50	E8	Qara	Matrouh	Lower Egypt	Also called Qarat Umm el-Sugheir; population of 363 Berbers (census 2006)	Date palm	N/A
51	E9	Siwa	Matrouh	Lower Egypt	Inhabited since the Palaeolithic; temple from the 26th Dynasty (672 -525 BCE)	Date palm, olives, fruits, mulukhiyah (leaves of Corchorus species), wheat, barley	yes
					Libya		
52	L1	Al Fejeej	Wadi al Hayaa	Fezzan	On the crossroads between Sabha-Ubari road, and the south road to Murzuk	Date palm	N/A
53	L2	Al Jawf	Kufra	Cyrenaica	One of the most irrigated oases in Sahara	Date palm, forages (berseem or Egyptian clover), cereals (barley, wheat)	yes
54	L3	Al Wigh	Murzuk	Fezzan	N/A	N/A	N/A
55	L4	Awjila	Al Wahat	Cyrenaica	Mentioned by Herodotus (484-425 BCE); a stop on the Zwila - Cairo trading route	High quality date palm, tomato, wheat and barley (water from deep wells)	yes
56	L5	Buzaymah (Buzema)	Kufra	Cyrenaica	Around a salt lake; remains of a Tubu fortification system	Date palm (230 km^2), figs, tamarisk, acacia	N/A
57	L6	Gaberoum	Sabha	Fezzan	Old Bedouin settlement, abandoned in 1980	Date palm	N/A
58	L7	Ghadames	Nalut	Tripolitania	Known as Cydamus during the Roman period; important base for the trans-Saharan trade until the 19th century	Date palm, figs, apricots, peaches, almonds, pomegranate, citrus, onions, watermelon, tomato, cereals (barley, wheat)	yes

Appendix 2 ■ List of the main Saharan oases with their location, history, agricultural characteristics and presence of wheat (*continued*).

No	ID	Locality	Province	Region	History	Agricultural characteristics	Wheat
59	L8	Ghadduwah	Sabha	Fezzan	N/A	N/A	N/A
60	L9	Ghat	Ghat	Fezzan	Ancient Garamantian city, major terminal point on the trans-Saharan trade route	Date palm, cereals	yes
61	L10	Hun	Jufra	Fezzan	Several settlements, each built to replace an earlier village swallowed up by the desert	Date palm	N/A
62	L11	Jadid	Sabha	Fezzan	Also known as El-Gedid; closed to Sabha	Date palm, barley, wheat, vegetables	yes
63	L12	Jaghbub	Butnan	Cyrenaica	Stage on the East-West caravan route from Cairo to the Fezzan	Date palm, tomato, wheat, barley	yes
64	L13	Jakharrad (Jikharra)	Al Wahat	Cyrenaica	N/A	N/A	N/A
65	L14	Jalu	Al Wahat	Cyrenaica	Stage on the East-West caravan route from Cairo to the Fezzan	Date palm, tomato, cereals (salty water)	yes
66	L15	Kufra	Kufra	Cyrenaica	Described in 1154 by Al-Idrisi as a stop on the East-West trade road	Date palm, vegetables, alfalfa, wheat, barley	yes
67	L16	Marada	Al Wahat	Cyrenaica	N/A	N/A	N/A
68	L17	Ma'tan as-Sarra	Kufra	Cyrenaica	Allowed the creation in 1811 of the last trans-Saharan caravan route	Date palm	N/A
69	L18	Murzuk	Murzuk	Fezzan	Important warehouse and a stage of trans-Saharan trade	Vegetables (carrots, cucumbers, onions, garlic), maize, barley, wheat	yes
70	L19	Rebiana	Kufra	Cyrenaica	Originally named Muzui; the native inhabitants are Tubu	Date palm, mango trees	N/A
71	L20	Sabha	Sabha	Fezzan	Fortress from Ottoman times; the biggest camel market in Libya	Date palm, barley, wheat, vegetables	yes

Appendix 2 ■ List of the main Saharan oases with their location, history, agricultural characteristics and presence of wheat (*continued*).

No	ID	Locality	Province	Region	History	Agricultural characteristics	Wheat
72	L21	Sokna	Jufra	Fezzan	Sokna fortress, capital for three centuries of Turkish rule: from the early 17th century till 1929	Date palm; natural springs	N/A
73	L22	Tazirbu	Kufra	Cyrenaica	The name means «main seat» in Tubu language, as this was the seat of the Tubu Sultanate	Date palm, tamarisks, acacias, esparto, Juncus	N/A
74	L23	Ubari	Wadi al Hayaa	Fezzan	The second center for the Kel Ajjer Tuareg people, after Ghat	Date palm	N/A
75	L24	Waddan	Jufra	Fezzan	Oldest city in Jufra District, at the crossroads of the Sirte-Waddan Road and the Fezzan Road	Date palm	N/A
76	L25	Wadi Zighen	Kufra	Cyrenaica	There are five wells, the most important named Bir el Hárasc	Date palm	N/A
77	L26	Waw an Namus	Nurzuk	Fezzan	Prehistoric volcano; an important watering point for the caravans from Waw Al-Kabir to Rebiana	Scattered date palms	N/A
78	L27	Zella	Jufra	Fezzan	Ancient Berber castle	Date palm	N/A
79	L28	Zwila	Murzuk	Fezzan	One of the oldest inhabited places in Libya, town founded in 10th century; trade relations with Egypt and Sudan	Date palm, vegetables, wheat, barley	yes
					Mali		
80	Ml1	Araouane	Timbuktu	Timbuktu	Trade center and entrepôt (16th-19th centuries) on the caravan route Taoudenni - Timbuktu	N/A	N/A
81	Ml2	Bamba	Burem	Gao	Since Neolithic c. 2,500 BCE; town founded around 490 CE	Date palm, rice, millet, sorghum; livestock	yes

Appendix 2 ■ List of the main Saharan oases with their location, history, agricultural characteristics and presence of wheat (*continued*).

No	ID	Locality	Province	Region	History	Agricultural characteristics	Wheat
82	Ml3	Diré	Diré	Timbuktu	Situated on the Niger River, important agricultural and commercial activities	Wheat, rice, sorghum, maize, okra, tobacco, anise, cumin	yes
83	Ml4	Gao	Gao	Gao	Founded in c. 7th century; important commercial center of trans-Saharan trade from the 9th century	Wheat, rice, and sorghum grown by irrigation near the banks of the Niger	yes
84	Ml5	Kidal	Kidal	Kidal	A first military post established in 1908	Date palm, potato, tomato, tobacco, wheat, maize	yes
85	Ml6	Tadmekka (Essouk)	Kidal	Kidal	Rock carving c. 6,000 BCE; an important entrepôt for the trans-Saharan trade (9th -15th centuries)	Date palm, cotton, flax; wheat remains (10th century) suggesting exchanges with Sahara	yes
86	Ml7	Taghaza	Timbuktu	Timbuktu	First mentioned in c. 1275 by Al Qazwini, source of rock salt for West Africa, important trans-Saharan trade stage	Date palm, fruits	N/A
87	Ml8	Taoudenni	Timbuktu	Timbuktu	First mention in 1586 (Al-Sadi); the camel caravans (azalai) from Taoudenni are some of the last that still operate in the Sahara	Date palm, fruits, vegetables, wheat	yes
88	Ml9	Tessalit	Tessalit	Kidal	Rurale commune and village; stop on a trans-Saharan trade road	Date palm, tobacco, wheat, rice	yes
89	Ml10	Tinzaouaten	Abeïbara	Kidal	Rurale commune; stop on a trans-Saharan trade road	Date palm, fruit trees, figs, pastures	N/A
90	Ml11	Timbuktu	Timbuktu	Timbuktu	Founded in the 12th century by the Tuaregs; by the 14th century a major center for the trans-Saharan gold and salt trade	Wheat, pennisetum, tobacco, indigo, cotton, groundnut, vegetables, bean	yes

Appendix 2 ■ List of the main Saharan oases with their location, history, agricultural characteristics and presence of wheat (*continued*).

No	ID	Locality	Province	Region	History	Agricultural characteristics	Wheat
					Mauritania		
91	Mr1	Aoudaghost	Ayoun el Atrous	Hodh El Gharbi	Ruins from c. 7-9th centuries, important oasis town at the southern end of trans-Saharan caravan route	Date palm, wheat, cucumbers, figs, grapes and henna (11th century)	yes
92	Mr2	Ayoun el Atrous	Ayoun el Atrouss	Hodh El Gharbi	Founded in 17th century	Date palm, vegetables, cereals	yes
93	Mr3	Koumbi Saleh	Timbedra	Hodh Ech Chargui	Founded in c. 3rd century; capital of the Ghana Empire; in the11th century an important trade center	Wheat and grapes produced during the Ghana empire period	yes
94	Mr4	Lagueila	Chinguetti	Adrar	Inhabited since the Neolithic	Date palm, vegetables (in particular carrots), wheat and barley	yes
95	Mr5	Mhaïreth	Aoujeft	Adrar	Inhabited since the Neolithic	Date palm, vegetables, wheat , barley	yes
96	Mr6	Nbeika	N'Beika	Tagant	Inhabited since the Neolithic	Date palm, watermelon, bean, wheat, barley	yes
97	Mr7	Néma	Nema	Hodh Ech Chargui	Occupied since Neolithic c. 2,000 BCE; part of Ghana empire	Early millet cultivation	N/A
98	Mr8	Ouadane	Oudane	Adrar	From the 11th century, stop along the western trans-Saharan trade for caravans transporting salt from the mines at Idjil	First city to introduce date palm in Mauritania	N/A
99	Mr9	Oualata	Oualata	Hodh Ech Chargui	Among the oldest stone settlements on the African continent; built by the Soninke people; southern terminus of a trans-Saharan trade route	Date palms, watermelons	N/A
100	Mr10	Terjit	Aoujeft	Adrar	Inhabited since the Neolithic	Date palm; vegetables, wheat, barley, millet	yes

Appendix 2 ■ List of the main Saharan oases with their location, history, agricultural characteristics and presence of wheat (*continued*).

No	ID	Locality	Province	Region	History	Agricultural characteristics	Wheat
					Morocco		
101	Mo1	Erfoud	Errachidia	Meknès-Tafilalt	Founded as French military fort in 1913	Date palm, wheat	yes
102	Mo2	Er-Rich	Midelt	Meknès-Tafilalt	Developed around a ksar on a river bank of Oued Ziz; an important fortress in previous times	N/A	N/A
103	Mo3	Ferkla El Oulia	Errachidia	Meknès-Tafilalt	N/A	Date palm, almond trees, beans, wheat and alfalfa	yes
104	Mo4	Figuig	Figuig	Oriental	The town is built around an oasis called Tazdayt, meaning «palm tree» in Berber	Date palm, wheat	yes
105	Mo5	Fint	Ouarzazate	Souss-Massa-Drâa	Crossing point for African traders on their way to northern Morocco and Europe	Date palm, vegetables	N/A
106	Mo6	Hassilabied	Errachidia	Meknès-Tafilalt	Located on the bottom of Erg Chebbi, near the Algerian border	Date palm	yes
107	Mo7	Khamlia	Errachidia	Meknès-Tafilalt	Located near Erg Chebbi, 7km after Merzouga on the way to Taouz	Date palm, cereals, camels, goats	yes
108	Mo8	Merzouga	Errachidia	Meknès-Tafilalt	Rock graving in the area	Date palm, cereals (the largest natural underground body of water in Morocco)	yes
109	Mo9	M'Hamid El Ghizlane	Zagora	Souss-Massa-Draa	Since c. 3,000 BCE; stop for traveling nomads and caravans; due to the extension of the desert, the population is declining	Date palm, cereals, vegetables; due to reduced or even absent winter rains since the 1970s agriculture was almost abandoned	yes
110	Mo10	Tafilalt	Tafilalt	Meknès-Tafilalt	On the direct caravan route from the Niger to Tangier; Sijilmasa founded in the 8th century	Date palm, wheat, barley, clover	yes

Appendix 2 ■ List of the main Saharan oases with their location, history, agricultural characteristics and presence of wheat (*continued*).

No	ID	Locality	Province	Region	History	Agricultural characteristics	Wheat
111	Mo11	Tamegroute	Zagora	Souss-Massa-Drâa	A religious center since the 11th century (Nasiriyya Sufi order)	Date palm	N/A
112	Mo12	Tamdoult	Tata	Guelmim-Esmara	Founded in the 9th century; an important stop on the trans-Saharan trade route linking Nul (Asrir) and Ouadane to Sijilmasa, Massa and N'fis	Date palm	N/A
113	Mo13	Tinejdad	Errachidia	Meknès-Tafilalt	Tinejdad in Amazight (Berber) means "place of birds"; also known as Afrekla	Date palm, vegetables, fruits, wheat (bread and club), maize	yes
114	Mo14	Tinghir	Tinghir	Souss-Massa-Draa	Between the High Atlas in the North and the Little Atlas in the South; agricultural activities	Date palm, fruits, walnuts, almonds, figs, apricots, olives, alfalfa, wheat	yes
115	Mo15	Tisserdmine	Errachidia	Meknès-Tafilalt	Located on the bottom of Erg Chebbi, near the Algerian border	Date palm	N/A
116	Mo16	Tissint	Tata	Guelmim-Esmara	Very old oasis	Date palm	yes
117	Mo17	Zagora	Zagora	Souss-Massa-Draa	Almoravid fortress; town built in the 20th century	Date palm	N/A
					Niger		
118	N1	Agadez	Tchirozerine	Agadez	Founded during the 11th century; important stop on the trans-Saharan trade road through Ghat, Ghadames and Tripoli toward the Middle East	Date palm, medicinal plants	N/A
119	N2	Aouderas	Tchirozerine	Agadez	Inhabited since at least 10,000 years; Touareg settlement since 12th century	Date palm, vegetables, wheat, onions, maize, citrus	yes
120	N3	Bilma	Bilma	Agadez	Stop in trans-Saharan trade, destination of one of the last Saharan caravans (from Agadez)	Date palm, vegetables (known for its gardens); goats	N/A

Appendix 2 ■ List of the main Saharan oases with their location, history, agricultural characteristics and presence of wheat (*continued*).

No	ID	Locality	Province	Region	History	Agricultural characteristics	Wheat
121	N4	Dabaga	Tchirozerine	Agadez	In the Aïr; populated mainly by both sendentary and semi-nomadic Tuaregs and few Hausa	Pastoralism	N/A
122	N5	Dirkou	Bilma	Agadez	Oasis in the foot of Kaouar cliffs, on the Central Sudan to North Africa caravan route	Date palm, vegetables	N/A
123	N6	Fachi	Bilma	Agadez	Neolithic presence; a stopping point of the Taghlamt caravan (Agadez to Bilma)	Date palm, vegetables	N/A
124	N7	Iferouane	Arlit	Agadez	In the northern Aïr, in the Ighazar valley; military outpost in the French colony	Date palm, vegetables	N/A
125	N8	In-Gall	Tchirozerine	Agadez	Since c. 6,000 BCE; a stop on the main roads between Niamey and the mining town of Arlit	Date palm, fruits, vegetables	N/A
126	N9	Kaouar	Bilma	Agadez	Rock paintings c. 8,000 BCE; on the Bornu-Fezzan caravan route; major point of contact between the Sahel and the Mediterranean	Date palm	N/A
127	N10	Seguedine	Bilma	Agadez	Stop on the trans-Saharan route linking coastal Libya and the Fezzan to the Kanem-Bornu Empire near Lake Chad	Date palm	N/A
128	N11	Takedda (Azelik)	Tchirozerine	Agadez	Important stage on trans-Saharan trade routes; (visited by Ibn Battuta in 1353)	Agriculture flourishing in 14th century	N/A
129	N12	Timia	Arlit	Agadez	Nearby the ruined town of Assodé, founded c. 11th century, benefiting from trans-Saharan trade, and declining with it from 18th century	Date palm, lemons, oranges, pomegranates, grapes, vegetables (tomato, onions), maize, wheat, barley, millet; goats, cattle and camels	yes

Appendix 2 ■ List of the main Saharan oases with their location, history, agricultural characteristics and presence of wheat (*continued*).

No	ID	Locality	Province	Region	History	Agricultural characteristics	Wheat
				Sudan			
130	S1	Kerma (Dukki Gel)	Northern	Northern	Settled since at least 7,000 BCE; capital of the Kingdom of Kerma (c. 2,500 BCE to c. 1,500 BCE); trade center	Barley, wheat (emmer) consumed during the Kerma period; ancient pastoral culture (goats, sheeps and cattle)	yes
131	S2	Laqiya el-Arba'in	Northern	Northern	On the Darb el-Arba'in (Forty days') road, one of the oldest caravan routes connecting the Nile Valley to the savanna of central Sudan	N/A	N/A
132	S3	Laqiya' Umran	Northern	Northern	N/A	Date palm (few trees)	N/A
133	S4	Salima	Northern	Northern	Important point on Darb el-Arba'in trade route	Date palm	N/A
				Tunisia			
134	T1	Chebika	Kairouan	Central Tunisia	Mountain oasis, known as Qasr el-Shams («castle of the sun» in Arabic); Roman outpost, Ad Speculum; later a refuge of the Berber people	Date palm	N/A
135	T2	Degache	Tozeur	Djerid	Exploited since Roman antiquity; the ancient city of Thagis is situated a few kilometers away	Date palm (the high quality Deglet nour)	N/A
136	T3	Djemna	Kebili	Djerid	N/A	Date palm (the high quality Deglet nour)	N/A
137	T4	Douz	Kebili	Djerid	Known as the "gateway to the Sahara"; an important stop on trans-Saharan caravan routes	Date palm, fruits	N/A
138	T5	El Guettar	Gafsa	Central Tunisia	Occupated from the Mousterian period (c. 40,000 BCE)	Date palm, olives, figs, apricots, pistachios, grapes, vegetables	N/A
139	T6	El Hamma	Gabes	Fejej	Described from the 16th century	Date palm	N/A

Appendix 2 ■ List of the main Saharan oases with their location, history, agricultural characteristics and presence of wheat (*continued*).

No	ID	Locality	Province	Region	History	Agricultural characteristics	Wheat
140	T7	El Hamma du Djerid	Tozeur	Djerid	From Roman time	Date palm (saline water)	N/A
141	T8	Gabes	Gabes	Gulf of Gabes	The ancient Tacapae of the Roman province of Tripolitania	Date palm, figs, pomegranates, apricots, grapes, vegetables	N/A
142	T9	Gafsa	Gafsa	Central	Prosperous mesolithic civilization dating back more than 15,000 years	Date palm	N/A
143	T10	Ghannouch	Gabes	Gulf of Gabes	N/A	Date palm, fruits (pomegranates, apricots, plums), vegetables, forages	N/A
144	T11	Kebili	Kebili	Djerid	One of the oldest oases in Tunisia and North Africa; human occupation c. 200,000 years ago; part of Roman Empire after 146 BCE	Date palm (the high quality Deglet nour)	N/A
145	T12	Ksar Ghilane	Kebili	Southern Tunisia	Roman presence (ruins of the Roman fort Tisavar)	Date palm, wheat (less important today); goats, sheeps	yes
146	T13	Mareth	Gabes	Gulf of Gabes	On the territory of the Beni Zid tribe	Date palm (687 ha), fruits (pomegranates, apricots), alfalfa, wheat (marginal)	yes
147	T14	Metouia	Gabes	Gulf of Gabes	Roman remains	Date palm, vegetables (gardens)	N/A
148	T15	Mides	Tozeur	Gharsa	Small mountain oases in the Djerid region; called Madés by the Romans	Date palm, oranges, figs	N/A
149	T16	Nefta	Tozeur	Djerid	Settled originally by shepherds coming from Napata kingdom; occupied by Romans and Arabs (7th century); important staging-point for caravans	Date palm, wheat (marginal)	yes
150	T17	Oudhref	Gabes	Gulf of Gabes	On the territory of the Beni Zid tribe	N/A	N/A
151	T18	Souk Lahad	Kebili	Djerid	As suggested by its name meaning «sunday market» in Arabic, the town developed as an agricultural community	Date palm	N/A

Appendix 2 ■ List of the main Saharan oases with their location, history, agricultural characteristics and presence of wheat (*continued*).

No	ID	Locality	Province	Region	History	Agricultural characteristics	Wheat
152	T19	Tamerza	Tozeur	Gharsa	Known as Ad Turres by the Romans; the largest mountain oasis in Tunisia	Date palm	N/A
153	T20	Tozeur	Tozeur	Djerid	The name of the city in antiquity was Tusuros; important Roman outpost	Date palm, bananas, pomegranates, figs, citrus, abricot, grapes, wheat (marginal)	N/A
					Western Sahara		
154	WS1	El Aaiun (Laâyoune)	El Aaiun (Laâyoune)	Laâyoune-Boujdour-Sakia El Hamra	Founded by the Spanish colonists in 1938; administered since 1976 by Morocco	Nomadic pastoralism, fishing	N/A
155	WS2	Amgala		Sahrawi Republic (SADR)	Located between Tifariti and Smara, in the area controlled by the Polisario Front	N/A	N/A
156	WS3	Bir Lehlou	Smara	Sahrawi Republic (SADR)	In north-eastern of Western Sahara, near the Mauritanian border, in the area controlled by the Polisario Front	N/A	N/A
157	WS4	Guelta Zemmur	Boujdour	Laayoune-Boujdour-Sakia El Hamra	Around a guelta pool, retaining rain water for long periods; in the Moroccan-administered territory	N/A	N/A
158	WS5	Meharizze	Smara	Sahrawi Republic (SADR)	Between Tifariti and Amgala, in the area controlled by the Polisario Front, close to the Mauritanian border	N/A	N/A
159	WS6	Tifariti	Smara	Sahrawi Republic (SADR)	Since medieval times a nomadic encampment for the Sahrawis	N/A	N/A
160	WS7	Umm Dreiga		Río de Oro	In the Moroccan-administered territory	N/A	N/A

N/A : no information available