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RESEARCH ARTICLE

Durum wheat in the Mediterranean Rim: historical evolution and genetic resources

Fernando Martínez-Moreno · Ignacio Solís · Dolores Noguero · Antonio Blanco · İrfan Özberk · Nasserlehaq Nsarellah · Elias Elias · Ioannis Mylonas · Jose Miguel Soriano

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Abstract Durum wheat (*Triticum turgidum* L. subsp. *durum* (Desf.) van Slageren) is an important crop in the Mediterranean Rim, and it is deeply rooted in the history and tradition of this region. Recently, several studies that examined DNA markers on Mediterranean landrace collections have successfully elucidated the pathways of this crop across the Mediterranean Rim, but the historical frame is still rather diffuse. This paper aims at tracing the historical evolution of durum wheat throughout the Mediterranean Rim since its commencement as a crop until present times. A search was carried out through archaeological references where durum wheat remains were found. Historical descriptions about cultivation of this crop, references to products

made from its grain, and articles interpreting DNA marker information from Mediterranean landraces were also consulted. The present article also examines the currently available durum wheat genetic resources. Durum wheat was domesticated in the Levant area. Phoenicians, Greeks, and above all Romans were active in the expansion and success of durum cultivation in all Mediterranean Rim that started displaced emmer by the mid first millennium BCE. Early Arab empire expanded in the area of durum wheat cultivation promoting food types based on semolina (dry pasta and couscous). Up to 1955 most durum areas in this area were planted with landraces, but several breeding programs were initiated in Italy, and later at CIMMYT and at ICARDA. Landrace collection and conservation efforts were

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carried out along the Mediterranean Rim countries to preserve the legacy of this crop.

Keywords *Triticum* · *Triticum turgidum* · Landraces · Gene bank

Introduction

Durum wheat (DW), *Triticum turgidum* L. subsp. *durum* (Desf.) van Slageren, ($2n=4x=28$, AABB), is an important worldwide crop with approximately 16.1 million ha sown annually and a production of 39.9 million t in 2017 (Dahl 2017). Currently, eight Mediterranean countries are the main producers: four in southern Europe (Spain, France, Italy, and Greece), three in northern Africa (Morocco, Algeria and Tunisia), and two in south west Asia (Turkey and Syria). In the Americas, new producers are Canada, the USA, and Mexico. Since the USA and Canada have enormous production potential, especially in terms of land acreage, these could greatly impact DW trade within the Mediterranean Rim (MR) (Dahl 2017). Regarding global trade, many Mediterranean countries are also importers since DW products are deeply connected with the tradition in these countries, such as Italy, Algeria and Tunisia (FranceAgriMer 2011). DW is well adapted to the Mediterranean climate since it has good heat and drought tolerance and performs well in poor soils (Mastrangelo et al. 2005). The milling of DW kernel produces semolina, the raw material for pasta, couscous, as well as various kinds of unleavened and leavened breads. Whole kernels are also used to make bourghul and freekeh. All these foods have historically been a fundamental part of Mediterranean cuisine (Elias and Manthey 2005).

There are several articles dealing with DNA markers identified in DW landraces, leading to a population structure, genetic distances and dendrogram construction that shows how the crop evolved and spread westwards throughout the MR (Moragues et al. 2007; Soriano et al. 2016). However, in many of these articles the historical frame is rather diffuse or absent. The objective of this work was to carry out a historical review of this crop in the MR and to trace the evolution since its domestication to the changes during the twentieth century.

Making of tables and figures

Tables 1, 2 and 3 were produced by literature searching of: (1) archaeological references where DW remains were found; (2) literature referring to locations where DW was cultivated in antiquity; and (3) references where products derived from DW were identified in antiquity. In Table 4 the names of selection of popular DW landraces (and the meaning of many of them) along de MR are mentioned. Table 5 resulted from a searching of genes frequently found in DW whose origin was either DW landraces or other tetraploid wheats. The last table (Table 6) referred to the most important gene banks preserving DW and the number of accessions they contain.

Figures 1 and 2 are maps made with QGIS free software program. In Fig. 1 main climatic areas were represented (Kottek et al. 2006), as well as main sea currents and winds in the MR. In the Fig. 2, all locations mentioned in Tables 1, 2 and 3 are represented in a georeferenced map.

Figure 3 represents the DW acreage evolution in eight countries of the MR in the period 1920-2017 whereas Fig. 4 depicts the durum to bread wheat acreage percentage in those countries in the same period. Numerous sources have been consulted for the making of these two figures, including FAO-STAT, and IGC (International Grain Council). All sources are mentioned in the footnote of Fig. 3.

DW domestication and first expansion

Wild emmer, *Triticum turgidum* subsp. *dicoccoides* (Körn. ex Asch. & Graebn.) Thell., is a tetraploid wheat that settled mainly in the west part of the so-called Fertile Crescent (Israel, Jordan, Lebanon, Syria, south-eastern Turkey, northern Iraq, and western Iran). This species was domesticated around the Karacadag mountains of south east Turkey (Özkan et al. 2002) about 8000 BCE (Before Common Era) by selecting plants with non-brittle rachis (due to recessive mutations in the locus *Br* located on chromosomes 3A and 3B) and non-latent seed giving rise to (cultivated) emmer, *T. turgidum* L. subsp. *dicoccon* (Schrank) Thell. Schübl (Faris 2014). Emmer was the main cereal of the Neolithic period, even more important in the Bronze Age, ahead of einkorn and barley, though often found in company

Table 1 Archeological references to places where remains of durum wheat have been found

Year ^a	Place	Historical region	Current country	Literature source	Original literature source
7000-6500	Cafer Höyük ^b	Neolithic Levant	Turkey	Feldman and Kislev (2007)	De Moulins (1997)
6900-6600	Tell Aswad ^b	Neolithic Levant	Syria	Feldman and Kislev (2007)	van Zeist and Bakker-Heeres (1985)
6400-5900 BCE	Tell Bouqras ^b	Neolithic Levant	Syria	Zohary et al. (2012)	van Zeist and van Rooijen (1985)
6400-5700 BCE	Can Hasan III ^b	Neolithic Levant	Turkey	Feldman and Kislev (2007)	Hillman (1978)
6300-6000	Abu Hureyra ^b	Neolithic Levant	Syria	Feldman and Kislev (2007)	Hillman (1978)
4600-3200 BCE	Arkadiko ^b	Neolithic Greece	Greece	Valamoti (2009)	Valamoti (2004)
5500-4200 BCE	Can Hasan III	Neolithic Levant	Turkey	Feldman and Kislev (2007)	Hillman (1978)
5450-4600 BCE	Tell Bouqras	Neolithic Levant	Syria	Zohary et al. (2012)	van Zeist and van Rooijen (1985)
5350-4950 BCE	Çatalhöyük	Neolithic Levant	Turkey	Zohary et al. (2012)	Fairbairn (2005)
5350-4950 BCE	Tell Ramad	Neolithic Levant	Syria	Zohary et al. (2012)	van Zeist and Bakker-Heeres (1985)
2250-1600 BCE	Argissa, Peukakia	Bronze Age	Greece	Valamoti (2009)	Kroll (1981)
1120 BCE	Balikh Valley	Bronze Age	Syria	Decker (2009)	van Zeist (1999)
1100 BCE	Tell Keisan	Canaan-Phoenicia	Israel	Decker (2009)	Kislev (1980)
~ 0 ACE	Mons Claudianus	Roman Empire	Egypt	Decker (2009)	van der Veen (1996, 1998)
~ 0 ACE	Karanis, Fayum	Roman Empire	Egypt	Decker (2009)	Leighty (1933)
~ 0 ACE	Quseir al - Qadim	Roman Empire	Egypt	Decker (2009)	Cappers (1996)
~ 0 ACE	Berenike	Roman Empire	Egypt	Decker (2009)	Cappers (1996)
~ 0 ACE	Ghirza	Roman Empire	Libya	Decker (2009)	van der Veen (1984)
~ 0 ACE	Cirenaica	Roman Empire	Libya	Decker (2009)	Barker (2002)

^a BCE (Before Common Era); ACE (After Common Era)

^b Remains corresponding to free threshing tetraploid wheat but most likely not DW (probably *T. turgidum* ssp. *parvicoccum*)

of these two cereals, with which it spread east and west. Apart from the countries already mentioned, remains of charred emmer seed have been found in several countries of the MR (Greece, Egypt, Italy, and Spain), all around 4500 BCE (Zohary et al. 2012). In the west, emmer followed the Balkans land route: from Greece and the Balkans Peninsula through the Danube River Valley at a pace of about

a mile a year. Emmer also spread via maritime routes along the coast of the Mediterranean Sea into southern Italy and from there it moved to Maghreb and Spain (Mac Key 2005). Emmer also entered Egypt, where it was widely adopted along with barley. Remains of this cereal were found in Tutankhamun's tomb with an estimated age of 3400 years. It was an important cereal until the end

Table 2 References in ancient literature to places in the Mediterranean Rim where durum wheat was cultivated

Year	Place	Historical region	Current country	Literature source	Original literature source
245 BCE	Fayum	Egypt, Ptolomeum I-II	Egypt	Decker (2009)	Westermann et al. (1940).
~ 150 BCE	Oudna	Roman Republic	Tunisia	Gharbi (2017) (p.c.)	Roman mosaic
~ 0 CE	Africa Proconsularis	Rome	Libya, Tunisia, Algeria	Decker (2009)	van der Veen (1984)
~42 ACE	Betica	Roman Hispania	Spain (Andalusia)	Decker (2009)	Columella, Ash (1941)
~50-70 ACE	Anazarbus	Roman Empire	Turkey	Decker (2009)	Dioscorides, Beck (2005)
200 ACE	Alexandria	Roman Empire	Egypt	Decker (2009)	Athenaeus of Alexandria (1941/~200)
380 ACE	Pergamus (Anatolia)	Roman Empire	Turkey	Decker (2009)	Oribasius of Pergamus Grant (1997)
320-620 ACE	Alexandria	Byzantine	Egypt	Decker (2009)	Casianus Baso, Beckh (1994)
~600-800 ACE	Jordan, Syria, Irak	Arab Empire	Jordan, Syria, Irak	Watson (1983)	<i>Nabatean Agriculture</i> (anonymous), Fahd (1998)
~930 ACE	Toledo	Arab Empire	Spain	Watson (1983)	Al Razi (Lévi Provençal. 1953)
~1060 ACE	Sijilmasa	Arab Empire	Morocco	Watson (1983)	Al-Bakri (1913/1094)
~1200 ACE	Seville	Almohad Kingdom	Spain	Cubero (2003)	Al-Awwam, Cubero (2003)
~1280 ACE	Morocco	Arab Empire	Morocco	Watson (1983)	Al-Umari (1928/1301-1349)
1513	Spain (South and east, Granada)	Kingdom of Spain	Spain	Alonso de Herrera (1818)	Alonso de Herrera (1818)
1566	Algeria	Ottoman Empire	Algeria	Abdelkader (2014)	Kornicke and Werner (1885)
1767	Apulia, Sicilia, Naples, Sardinia	Independent kingdoms	Italy	Serventi and Sabban (2002)	–
1767	Morocco	Morocco	Morocco	Serventi and Sabban (2002)	–
1771-93	Tunisia, Algeria	Ottoman Empire	Tunisia, Algeria	Abdelkader (2014)	Desfontaines (1798)

Table 3 References in ancient literature to places in the Mediterranean Rim where products from durum wheat were identified

Year	Place	Historical región	Current country	Broad literature source	Original literature source	Product
40 ACE	Apulia, Rome	Roman Empire	Italy	Serventi and Sabban (2002)	Horace	<i>Lagana</i> (lasagne)
~60 ACE	Italy	Roman Empire	Italy	Thurmond (2006)	Pliny the Elder	Gruel, oatmeal
~60 ACE	Italy	Roman Empire	Italy	Thurmond (2006)	Pliny the Elder	<i>Triticum</i> (durum) flour
~100 ACE	Tyana	Roman Empire	Turkey	Serventi and Sabban (2002)	Athenaeus of Naucratis	<i>Lagana</i> (lasagna)
~170 ACE	Pergamus/Rome	Roman Empire	Turkey/Italy	Serventi and Sabban (2002)	Galen (<i>de alimentorum facultatibus</i>)	<i>Itryon</i> (pasta)
~400 ACE	Jerusalem	Byzantine Empire	Israel	Serventi and Sabban (2002)	Talmud of Jerusalem	<i>Itrium</i>
(pasta)						
~630 ACE	Seville	Visigothic Hispania	Spain	Serventi and Sabban (2002)	Isidore of Seville (<i>Etymologiae</i>)	<i>Lagana</i> (lasagna)
~870 ACE	Tunisia	Arab Empire	Tunisia	Wikipedia, pasta	Isho Bar Ali; Dickie (2008)	<i>Itriyya</i> (pasta)
1154 ACE	Palermo	Norman Sicily (Roger II)	Italy	Serventi and Sabban (2002)	Al-Idrisi Rizzitano (1966)	<i>Itriyya</i> (pasta)
~1200 ACE	Marrakech/Seville	Arab Empire	Morocco/Spain	Watson (1983)	Anonymous (1250/2012)	Couscous, noodles, pasta sheets
1273 ACE	Genoa	Genoa Republic	Italy	Alessio (1959)		Macaroni
1284 ACE	Pisa	Pisa Republic	Italy	Serventi and Sabban (2002)		<i>Vermicelli</i> (spaguetti)
~1300 ACE	Valencia	Aragon Kingdom	Spain	Watson (1983)	Anonymous (1324/2008)	<i>Aletria</i> (noodles)
1351 ACE	Cagliari (Sardinia)	Aragon Kingdom	Italy	Serventi and Sabban (2002)		Pasta
~1390 ACE	Lombardy	Lombardy	Italy	Watson (1983)	Cogliati Arano (1976) (<i>Tacuinum sanitatis</i>)	Pasta
~1400 ACE	Tunisia	Arab Empire	Tunisia	Watson (1983)	Brunschvig (1940)	Couscous
~1600 ACE	Gragnano	Naples Kingdom	Italy	Serventi and Sabban (2002)	Gargiulo and Quintavalle (1983)	Macaroni

of the Bronze Age (1500-1000 BCE), where it was progressively replaced by the naked wheat DW. In Egypt, emmer (named *olyra* o *pistikion*) is mentioned in the Ptolemaic Age (300 BCE) where it was the main cereal (Decker 2009). In Greece charred archaeobotanical emmer remains were found at Sesklo (6600-5700 BCE) (Kroll 1981) and at Arkadiko (4600-3200 BCE) (Valamoti 2004).

DW originated from a selection of hulled tetraploid wheat genotypes (similar to, but not emmer) (Oliveira et al. 2012; Kabbaj et al. 2017) with a dominant mutation of the *q* locus, located on chromosome 5A, that produces free threshing plants and naked seed (Faris 2014). Free-threshing wheat

was found in archaeological excavations along the Levantine Corridor several hundred years after the origin of cultivated emmer, about 6500 BCE, but it became a major crop in the Greek time. Nonetheless, it is possible that these early free-threshing wheat were not DW, but the extinct tetraploid *T. turgidum* subsp. *parvicoccum*, a small grain wheat that was widely cultivated in the Levant and the Mediterranean region over several millennia (up to Hellenistic times and locally up to the first century CE (Feldman and Kislev 2007). Other free threshing tetraploid wheat but of more recent origin compared to DW is the rivet wheat (*T. turgidum* L. subsp. *turgidum*), similar to DW but with softer kernels and

Table 4 Name, origin, and meaning of a selection of landraces along the Mediterranean Rim

Name	Country	Meaning
Adjini	Algeria	Family name
Dur de Medeah	Algeria	Toponym
Hamra	Algeria	Red ear
Kahla	Algeria	Black ear
Mahmoudi	Algeria	Synonym of prophet Muhammad's name
Baladi bouhi	Egypt	Local (landrace)
Kazouria taliani	Egypt	Italian
Mavragani	Greece	Black awns
Ak basak	Greece	White ear
Asprostaro	Greece	White seed
Kokkinostaro	Greece	Red seed
Cicirello	Italy	Mediterranean sand eel (fish)
Razza	Italy	Race
Realforte	Italy	Very hard and royal wheat
Russello	Italy	Reddish ear
Saragolla	Italy	Yellow kernel
Scorsonera	Italy	Black glume
Trigo murru	Italy	Snout wheat
Triminia	Italy	Three month wheat
Trinakria	Italy	Triangle (island), i.e. Sicily
Guemh di Abbou	Morocco	Wheat of Abdallah
Krifla beda	Morocco	White of Krifla (toponym)
Maghroussa	Morocco	Planted
Fanfarrón	Spain	Boastful
Moruno	Spain	Moorish
Raspinegro de Águilas	Spain	Black awns/toponym
Recio	Spain	Sturdy, hard
Rubio de Montijo	Spain	Blond/toponym
Haurani	Syria/ Jordan	Toponym (from Hauran plateau)
Aoudj	Tunisia	Twisted
Bidi	Tunisia	–
Souri	Tunisia	Syrian
Hamira	Tunisia	Red ear
Biskri	Tunisia	Toponym
Jenah Khotifa	Tunisia	Sparrow wing
Akbasak	Turkey	White spike
Karakilçik	Turkey	Black awns
Kibris bugdayi	Turkey	Cyprus wheat
Iskenderi	Turkey	Toponym (from Alexandria)

more cold tolerance. DW (always in a low proportion compared to the other cereals) expanded to several areas of Turkey such as Can Hassan III where the first DW remains of their naked and large kernels were found 5500-4200 BCE (Hillman 1978), and to Syria (Tell Bouqras). Archaeological references to DW remains are represented in Table 1 and Fig. 2. As these wheat lines have naked seed it is also difficult to distinguish them from free threshing hexaploid wheat that came later, though differentiation can be made through the rachis (Hillman et al. 1996). From its area of origin, DW spread in all directions following a similar route as emmer, einkorn and barley to the MR: by land through the Balkans and the maritime route through the Mediterranean Sea, although it was a minor crop and it was not a prominent crop until about 300 BCE during the Hellenistic period. Perhaps the early DW types were less adapted to local conditions than the two main tetraploid wheats (emmer and subsp. *parvicoccum*) (Feldman 2000). Sea currents in the MR follow a general counter clockwise sense, while the main winds blow from north to south (Mistral, Bora, Etesian) or from south to north (Scirocco, Khamsin), though Levanter and Vendaval blow east to west and reverse respectively along the Strait of Gibraltar (see Fig. 1).

DW in pre-classical times and Roman epoch (~1000 BCE-~476ACE)

Durum cultivation and routes of expansion

DW kernels were found at Tell Keisan (Israel), a Phoenician and Cananean town, and they were dated to around 1100 BCE. At this time, between Bronze and Iron Age, DW started to slowly replace emmer in many regions of the east MR, except in Egypt where emmer was the predominant wheat species.

From 1000 BCE on, first the Phoenician and then the Greeks began to establish coastal colonies throughout the MR initiating a market of DW seeds brought from their regions of origin. Main maritime routes are depicted in Fig. 1. By the fourth century BCE, DW was gaining ground over emmer (Lupton 1987) although the latter was quite common in Rome until the first century BCE. Jasny (1944) reported how DW was well established in North Africa in the

Table 5 Characteristics of a selection of genes present in durum wheat landraces and cultivars

Gene	Trait	Origin	Species	Chr	Reference
<i>Lr14a</i>	Leaf rust	Yaroslav	Emmer	7BL	McIntosh et al. (2003)
<i>Lr23</i>	Leaf rust	Gaza	Durum	2BS	McIntosh et al. (2003)
<i>Lr61</i>	Leaf rust	Camayo	Durum	6BS	Herrera-Foessel et al. (2008)
<i>Lr72</i>	Leaf rust	Atil	Durum	7BS	Herrera-Foessel et al. (2014)
<i>Sr2</i>	Stem rust	Yaroslav	Emmer	3BS	Nelson et al. (1997)
<i>Sr7a</i>	Stem rust	Khapli	Emmer	4AL	Singh and McIntosh (1987)
<i>Sr9e</i>	Stem rust	Vernal	Emmer	2BL	Singh et al. (1992)
<i>Sr9g, Sr12</i>	Stem rust	Iumillo	Durum	2BL/3BS	Nazareno and Roelfs (1981)
<i>Sr13</i>	Stem rust	Khapli	Emmer	6AL	Zhang et al. (2017)
<i>Sr14</i>	Stem rust	Khapli	Emmer	1BL	Yu et al. (2014)
<i>Yr7</i>	Yellow rust	Iumillo	Durum	2BL	Zhang et al. (2009)
<i>Yr26</i>	Yellow rust	γ 80-1	Rivet	1BL	Ma et al. (2001)
<i>Pm4</i>	Powdery mildew	Khapli	Emmer	2AL	Ma et al. (1994)
<i>Pm6</i>	Powdery mildew	<i>T. timopheevi</i>	Timopheevi	2BL	Wang et al. (2000)
<i>Qfhs.ndsu-3AS</i>	Fusarium Head Blight	Langdon	Durum	3AS	Otto et al. (2002)
<i>QGpc.ndsu.6Bb</i>	Grain protein	Langdon	Durum	6BS	Olmos et al. (2003)
<i>QLr.ubo-7B.2</i>	Leaf rust	Creso	Durum	7BL	Maccaferri et al. (2008)
<i>Ppd-A1</i>	Photoperiod response	Kofa \times Svevo	Durum	2A	Maccaferri et al. (2008)
<i>Ppd-B1</i>	Photoperiod response	Kofa \times Svevo	Durum	2B	Maccaferri et al. (2008)
<i>PSY-B1</i>	Grain yellow pigment content	Kofa	Durum	7AL	Zhang and Dubcovsky (2008)
<i>Cdu-B1</i>	Grain cadmium content	Svevo	Durum	5BL	Wiebe et al. (2010)

classical times, including Egypt, where emmer relevance lasted longer (Loret 1892).

Around this time BW was already cultivated in the Roman Empire, especially in the northern part since it is better adapted to cooler conditions (main BW varieties were winter type while most DW varieties were spring type), and it slowly expanded towards the northern parts of the MR. The flour it provides allows the production of leavened and spongy bread. Hispanic-Roman agronomist and writer L.J.M. Columella (4 BCE–40 ACE, After Common Era) classified naked wheats (named *triticum* in Latin) into three types namely, *robustus* (meaning blond kernel wheat, i.e. DW), *siligo* (meaning good quality flour, i.e. BW), and *trimestre* (spring and early heading wheat) (Columella ~42 ACE/1941). Table 2 and Fig. 2 shows historical references to DW cultivation. Nevertheless, DW was the main wheat species in the Roman Republic and Empire and writers of the time

often used the word *triticum* to refer to DW (Serventi and Sabban 2002).

In Roman Italy there are references citing that *triticum* was imported from Sicily and Northern Africa, whereas *siligo* was cultivated in central and northern Italy (Serventi and Sabban 2002). Wheat in Spain was mainly located in the southern part (*Betica* province). It must have been mainly DW since the access to Spain from northern Africa (Strait of Gibraltar) and southern Italy was easier and these regions share a common climate (warm Mediterranean climate, *Csa*) (Kottek et al. 2006). Roman historian Strabo reported that the *Betica* (along with north Africa and Sicily) was one of the Roman Empire's granaries (Schulten 2004). The main climates of the MR are represented in Fig. 1. *Csa* is the most common climate in the MR, especially in the southern side. *Cfa* and *Cfb* are colder and more humid prevailing in the northern side of the MR. *BSk* and *BWk* are arid and desert type of climates respectively,

Table 6 Most important Gene Banks of durum wheat around the world based on the number of accessions they preserve and their origin

Centre ¹	Country	N entries	Biological status			Most representative countries					
			Breeder line	Cultivar	Landrace	Other/unspecified	(N entries)				
CIMMYT	Mexico	20,779	7971	5173	4006	3629	Mexico (5822)	Ethiopia (847)	Iran (683)	Turkey (613)	Spain (170)
ICARDA	Lebanon	18,276	3288	–	12,486	2502	Turkey (2164)	Tunisia (1451)	Ethiopia (1409)	Algeria (1207)	Jordan (928)
NSGC	USA	10,690	1269	678	6660	2083	Ethiopia (1875)	Turkey (1445)	Iran (1073)	Israel (666)	Portugal (456)
AGG	Australia	9966	–	–	–	9966	Turkey (1385)	Ethiopia (591)	Portugal (584)	Mexico (524)	Italy (429)
IBBR	Italy	1216	–	–	–	1216	Greece (262)	Italy (191)	Turkey (71)	Spain (63)	Tunisia (19)

¹ Source: (Genesys 2019; 2019)

² In bold letter number of accessions of Mediterranean countries

with a cold winter, being the former present in the interior of Spain, Morocco, and Turkey, and the latter in Morocco, Libya, and Syria.

The first archaeological remains of DW in classical times are recorded in Egypt (Nesbitt and Samuel 1996). In the fourth century BCE Oribasius of Pergamon described the ‘semidalit’ wheat, a type of wheat which kernels were heavier, yellow and transparent, and that the ‘doctor considered it superior to other cereals’ (Grant 1997). Around the Common Era, importation of DW from the Nile Valley to the mines near Mons Claudianus (close to Red Sea) is mentioned (Decker 2009). By the fourth century ACE DW had fully replaced emmer, even in Egypt. The so called ‘Alexandrian wheat’ might be DW (320-620 ACE) (Decker 2009). According to the Swedish botanist Vivi Laurent-Täckholm, “*T. pyramidale* Perc. was the most widely cultivated wheat throughout Egypt” (Täckholm et al. 1941). *T. pyramidale* represents a DW wheat type with compact ear and plump grains, possibly as a result of spontaneous crosses between DW and *T. turgidum* subsp. *parvicoccum* in Egypt (Feldman and Kislev 2007).

Emmer and DW products

Emmer products were common during the Roman Republic. Emmer gruels named *puls* were a typical food among the population. Wedding cake name was *confarreatio*, that derives from *far* (Latin word for emmer). Table 3 and Fig. 2 shows historical references on DW based food. Regarding milling, DW flour or semolina was divided into four categories: *pollen* (the highest quality), *similago* (good quality), *secundarium* (standard product), and *furfur* (bran). *Siligo* flour was likewise graded into *flos*, *siligo*, *cibarium*, and *furfur* (Thurmond 2006).

In the first century ACE writer Horace mentioned *lagana* (singular, *laganum*), which involved fresh pasta sheets that were fried and that might be a progenitor of current lasagne. Athenaeus of Naucratis also reports a *lagana* recipe in the second century (Serventi and Sabban 2002). Another historical food likely created with DW was the *itrion*, similar to pasta (170 ACE). In the Talmud of Jerusalem the use of *itrium* was mentioned around 300-400 ACE (Serventi and Sabban 2002).

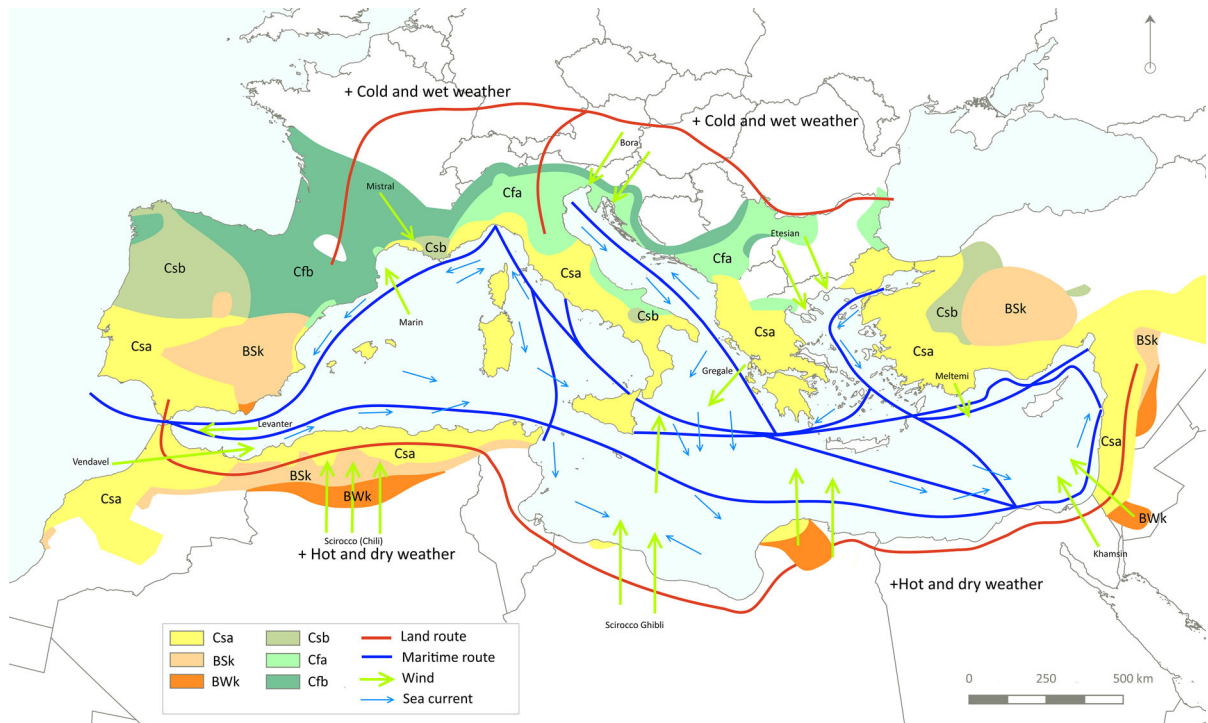


Fig. 1 Map of the Mediterranean Rim where sea currents, main winds and climatic areas are located. Climate nomenclature follows Köppen-Geiger classification (Kottek et al. 2006). *Csa* (warm climate, dry and hot summers, mild wet winters); *BSk* (arid climate, cold winters); *BWk* (desert climate, cold

winters); *Csb* (warm climate, dry and warm summer, mild wet winter); *Cfb* (temperate oceanic climate); *Cfa* (warm climate, fully humid, hot summer), and *Cfb* (warm climate, fully humid, warm summer)

DW during the early Islamic world (~622 ACE - ~1300 ACE)

DW cultivation and routes of movement

It seems clear that DW was well settled in the MR at the end of the Roman Empire, especially in northern Africa and west Asia, but also in southern Europe (south regions of Spain, Italy, and Greece). Some authors have rebutted this argument stating that DW was brought to most of the MR at the time of the early Islamic world. Thus French ethnobotanist Roland Porteres wrote that DW replaced BW with the arrival of the Arabs to Algeria (Porteres 1958) and the Canadian economist Andrew Watson stated that DW was little known in the MR before the Arab invasion, although he later casted doubts about this assertion (Watson 1983). The basis of this argument is that the first Arab Empire stretched through the southern MR where DW was the common wheat, and with many information sources of Arab origin during

ninth-twelfth centuries ACE describing DW cultivation (not always clear if referring to wheat in general or to DW), and, above all, a multitude of food products based on this crop. As the Arab Empire grew larger, DW varieties might have easily circulated between the Levant, northern Africa, southern Turkey, Sicily, and Spain. The caravans' routes along the North African coasts and the Sahara Desert were common pathways at this time (Fig. 1), first reaching Sicily and Spain, and from there moving to Europe (Bozzini 1988).

There are several descriptions of DW reported at the time of the early Islamic world by Watson (1983) (Table 2): Ibn Wahshiya in the tenth century pictured DW when he detailed a kind of wheat 'viscous and with a high gluten content that allows the making of pasta'. In the eleventh century Andalusian historian Al-Bakri reported on a dry wheat seed in the region of Sijilmasa (Morocco) that may seed itself for three consecutive years. There are several other descriptions mentioning an alleged durability of the grain of

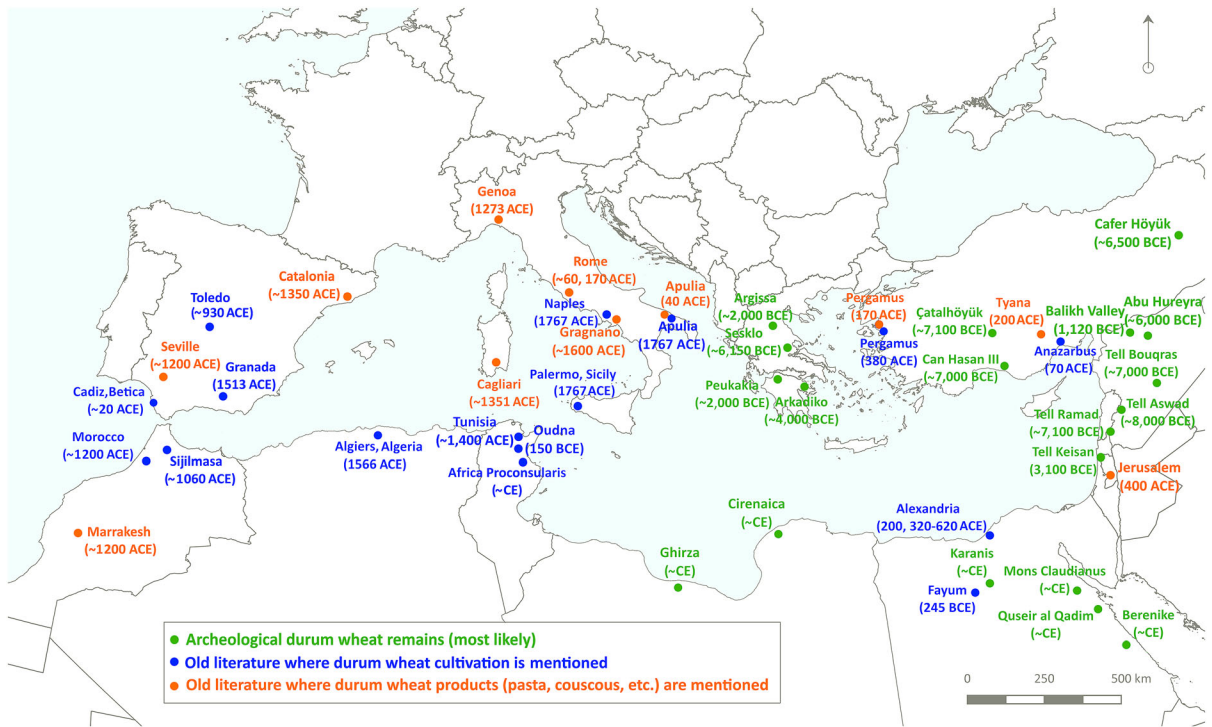


Fig. 2 Map of the Mediterranean Rim where (georeferenced) places related to archaeological remains of durum wheat, historical references to durum wheat cultivation, or food based on durum wheat are reported

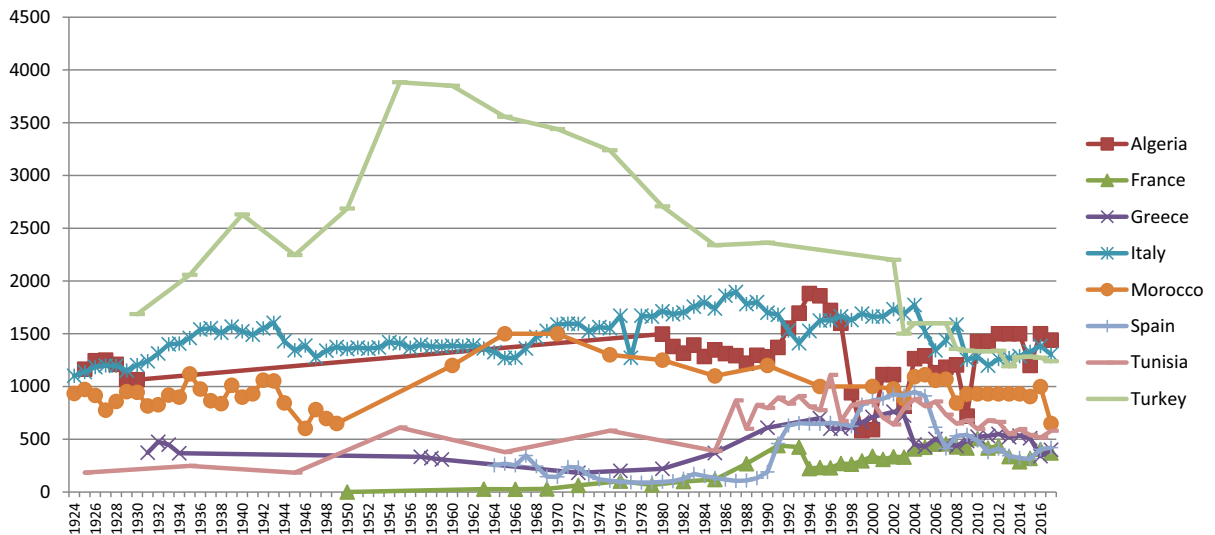


Fig. 3 Graph representing the durum wheat acreage (\times 1000 ha) in eight countries of the Mediterranean basin in the period 1924–2017. Sources: Algeria, Miège (1950), Bourihane and Mekkaoui (2013); France, FranceAgriMer (2011); Greece, Kokolios (1962), Koutsika-Sotiriou et al. (2011); Italy, Annuario di Statistica Agraria (1924–2018); Morocco, Tinthoin

(1947), Miège (1950), Jlibene and Nsarellah (2011); Spain, Ministerio de Agricultura, Alimentación y Pesca (Estadística 1964–2018); Statistiques financières Tunisie (2019); Turkey, Tarım ve Orman Bakanlığı (2018); General, FAOSTAT, IGC (International Grain Council)

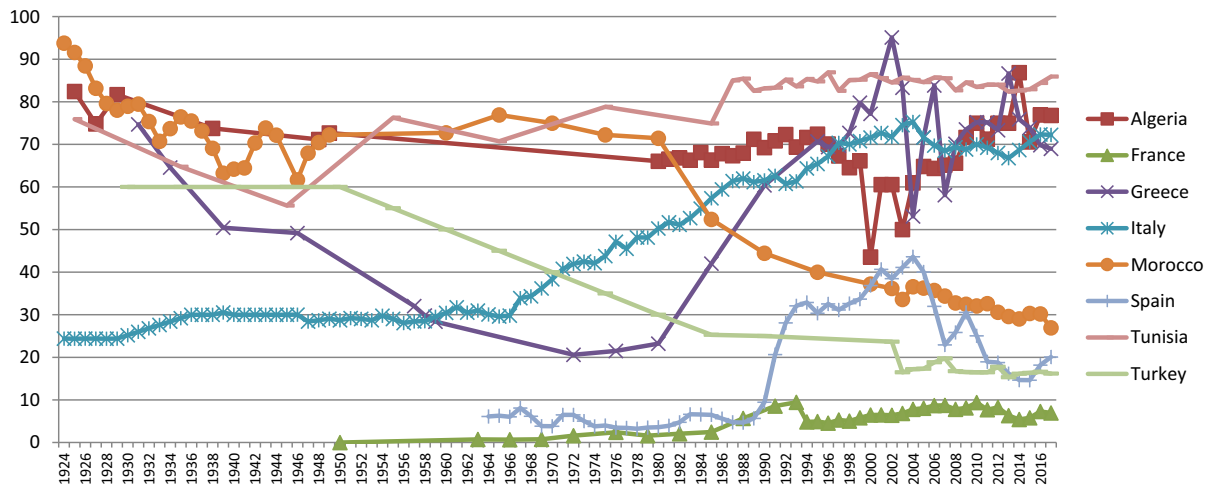


Fig. 4 Graph representing the percentage of durum to bread wheat acreage in eight countries of the Mediterranean basin in the period 1924–2017 Sources: The same used to make the previous Figure

this wheat, for instance ‘Toledo’s (Spain) wheat may be stored for 66 years in a silo without rotting’ (Watson 1983).

DW products

Many products known as *itriya* are mentioned at this time mainly referring to noodles. *Itriya* is mentioned in Tunisia (870 ACE) and its exportation is reported from 1154 ACE (Serventi and Sabban 2002) (Table 3). Although 4000 year old noodle remains have been found in China (Lu et al. 2005) and by the Han dynasty (third century BCE) fresh wheat noodles became a staple food in China (Sinclair and Sinclair 2010), noodles in the MR were first described in *kitab al tabikh fi-l-Maghrib wa-l-Andalus* (The book of cooking in Maghreb and Al-Andalus) (Anonymous 2012/~1250). This anonymous book was released in Andalusia (Spain) around the thirteenth century and mentions the word *al-fidawsh*, from which it comes the Spanish word *fideos* (short kind of noodles) and the Italian word *fidellini* (Watson 1983). That book also has the first reference to couscous. A fourteenth century Catalan book also uses the word *aletria* when speaking of noodles (Anonymous 2008/1324). Dry pasta was described for the first time in the Arab Sicily, and then it moves to Naples and Genoa (Watson 1983). The first description of macaroni is reported a little bit later in Genoa (1273 DC) (Alesio 1966).

DW in Modern Epoch (1453-1900)

DW cultivation and routes of movement

There is not much information about this period. DW is well settled in northern Africa, but also in the south and coastal areas of several countries such as Spain (Andalusia, Valencia, and Balearic Islands), Italy (southern side, Sardinia, Sicily), Greece, the Balkans, Turkey (South east Anatolia and Trance), and Syria. In this period northern Africa (except Morocco) and the east of the MR were controlled by the Ottoman Turks. It is likely that DW varieties moved between and within the provinces or *eyalets* of the Ottoman Empire (Fleet 2013).

DW descriptions by travelers and botanists

Flemish botanist Rembert Dodoens made the first description of DW in 1566 in northern Africa (Kornicke and Werner 1885). But it was the French botanist René Desfontaines who first described DW as a different species in 1798 in his *Flora Atlantica*, with some of its genuine traits (solid stem, pubescent lemma, long awns, and long vitreous kernels). In fact, the sole wheat species Desfontaines saw in his voyages to Tunisia and Algeria (1773-86) was DW (Abdelkader 2014). The Danish botanist Peter Schousboe also reported that all wheat cultivated in Morocco in 1771-93 was DW (Ducellier 1921).

Before the French colonization of Tunisia (1880s) almost all cultivated wheat was durum. *Zrea* was a landrace of long ears and large kernels, *Trikia*, had a compact ear and small kernels, and *Maizza* presented a black spike (Table 4). BW was found as mixtures in DW fields. Those mixtures were either undesirable or used to improve the bread making quality of the semolina. Interestingly BW was also found in the oasis of Morocco, Algeria, and Libya (Zaharieva et al. 2014). The Arab word for DW was *gamh*. In the local language, *farina* was the word that referred to BW and was taken from the French word *farine* meaning ‘flour’. Even by 1930 only DW was cultivated on Tunisia’s plains. French settlers introduced BW varieties *Tuzelle* (from south west France) and *Mahon* (from Balearic Islands) in their colonies in Northern Africa. A main reason for this introduction was that they wanted to eat *baguette* bread type and they needed BW flour (Ammar et al. 2011).

The book *Agricultura General* of the sixteenth century by Spaniard writer Gabriel Alonso de Herrera mentions the wheats *Trechel* and *Rubion* (two kinds of DW, probably synonyms) that are opposed to *Candeal* wheat (the main BW type in Spain) wheat (Alonso de Herrera 1818). In the nineteenth century, Spaniard botanists Simón de Rojas Clemente and Mariano Lagasca reported the presence of many DW *castas* (breeds) in southern and eastern Spain, the most common being the landraces *Fanfarrón*, *Recio*, and *Moruno*. All this new information was added to the 1818 edition of the book by Alonso de Herrera (Table 4) (Alonso de Herrera 1818).

There are references regarding the DW landraces cultivated in Greece since nineteenth century. According to Palaiologos (1833) two main wheat types were cultivated in Greece: a) *Kokkinostaro*, *Hondrositaro*, and *Mavragani* cultivated mainly in lowland areas, and b) *Asprostaro* and *Rapsani* cultivated mainly in mountain areas.

Interestingly, there is not much information about DW in Egypt, during that time under Ottoman administration. Täckholm stated that DW ‘was commonly grown in Upper Egypt and such distant places as Kharga, Dakhla and Sinai’ up to the beginning of the twentieth century. However in the beginning of the twentieth century, BW quickly spread in the Delta region, and gradually replaced DW in Giza, Fayum, Minia, and Upper Egypt (Täckholm et al. 1941). Apparently BW had better baking qualities for

Egyptian bread. In Upper Egypt there were still DW landraces cultivated, whose selection in the 1920s by the Agriculture Research Center (Wheat Research Section) gave rise to cultivars *Baladi 166*, *Dakar 49*, and *Dakar 52*, but it was already a declining crop (Gowayed 2009). Currently Egypt had an annual DW average acreage of just 37,600 ha during 2002–2017, about 3% of total wheat acreage (IGC, 2019).

DW from the twentieth century (1901-present day)

In the last decades of the nineteenth century a few breeding programs started in Europe, mainly using the bulk selection method, but in 1900 Mendel’s Laws were rediscovered, setting up the practice of scientific breeding based on the crossing of two or more varieties with contrasting traits and selection of the best individuals from the segregating population.

There were wheat breeding programs in many countries (United Kingdom, France, The Netherlands, Sweden United States, Australia, etc.), but most of them focused on BW, almost none on DW, a minor (if not non-existent) crop in those countries. Many of these breeding programs were successful and improved varieties were released regularly. Furthermore, some of these new BW varieties (especially from France and Italy) gained ground in the MR, occupying many areas previously cultivated with DW (Ammar et al. 2011).

The most important DW breeding at this time was performed at *Centro di Ricerca per la Cerealicoltura*, Foggia (Italy) by Italian breeder Nazareno Strampelli (Di Fonzo et al. 2005). *Senatore Cappelli* (or simply *Cappelli*) was the most successful variety, selected from a line of the Tunisian landrace *Jenah Khotifah* in 1915. This variety was highly productive and had high quality; its yield was not surpassed until 1960 and was planted on up to 60% of the Italian DW growing area from the 1920s to the 1950s. It should be noted that *Senatore Cappelli*, after more than a century, is still registered in the Italian Variety List and is grown nowadays for specific final products, such as the monovarietal pastas. It spread to other Mediterranean countries including Spain, Morocco, Turkey and Greece, where it was widely cultivated for more than 20 years (Kokolios 1962; Porceddu and Blanco 2014; Martínez-Moreno and Solís 2017).

In general, DW breeding programs were scarce in the MR and they usually employed the selection technique exploiting the genetic variation present within the landraces. Up to 1955, DW could be defined as an “orphan” crop regarding plant breeding and scientific research on crop physiology, technological quality, genetics, and plant breeding. That year cultivar *Capeiti 8* was released at the *Stazione di Granicoltura di Sicilia* (Italy) by crossing *Senatore Cappelli* and *syriacum* DW type *Eiti 6*. The *syriacum* landraces had a reduced height and increased earliness compared to *mediterraneum* type landraces that were more common in the west MR (*Senatore Cappelli* belongs to the *mediterraneum* type). *Capeiti 8* represents a landmark in DW breeding and slowly but steadily replaced *Senatore Cappelli*, respect to which it was superior in terms of yield, earliness, and lodging resistance, while preserving the grain quality of the latter (Bozzini 1970). In 1958, F. D’Amato and G.T. Scarascia-Mugnoza began an innovative research project on DW in the new Laboratory of Plant Genetics and Mutagenesis at the Research Centre of Rome. This project had the objectives to use DW as a model plant and to increase the variability of the species through induction and selection of useful mutations. Hundreds of morphological and physiological mutations were isolated after several experiments with radiation and chemical agents: they made up the materials used for extensive genetic, cytogenetic, and physiological researches at Casaccia Center and elsewhere (D’Amato 1992). While studying the effects of radioactive mutagens on DW, some lines with short height, lodging resistance, and early ripening were isolated. One of these lines, Castelporziano, thanks to its erectoid genes, was able to stand in the most adverse lodging conditions (Scarascia-Mugnoza et al. 1993).

The Green Revolution was engineered at CIMMYT (International Center for Maize and Wheat Improvement) in Mexico, first depending on USDA (United States Department of Agriculture) and private funding, and later from CGIAR (Consultative Group for International Agricultural Research). Efforts started with BW breeding with incredible success. New semi-dwarf high yielding varieties were released for developing countries in the 1960s. However, the CIMMYT DW breeding program had at least a 10-year delay compared to the BW program due to the lower global importance of this crop, but

DW was important in northern Africa, one of the targeted CIMMYT areas. Successful varieties were released by CIMMYT in the 1970s (*Cocorit C71*, *Mexicali C75*, *Yavaros C79*). Many of the traits responsible for BW success (dwarfing, day length insensitivity, rusts resistance, high yield potential, etc.) were brought to DW. The cultivar *Yavaros C79* (released in 1979) achieved popularity in the Mediterranean countries similar to *Senatore Cappelli* 60 years before. It had a high and stable yield and displayed a wide adaptation to different soil and climatic conditions. For a period stretching 30 years (from 1980s to the 2000s) it was an important cultivar in the Maghreb countries (where it was known as *Karim*), and in Spain (known as *Vitrón* or *Nuño*) (Nsarellah and Amri 2005; Martínez-Moreno and Solís 2017). In Italy, from the progeny of a cross between a *Senatore Cappelli* short-straw mutant (*CpB144*) and a dwarf CIMMYT line, the cultivar *Creso* was released in 1974 and enjoyed an immediate success, reaching yields levels of many BW cultivars planted at that time (Bozzini and Bagnara 1974).

In Greece, DW breeding program began officially in 1923 when Juan Papadakis started crossing foreign cultivars with Greek landraces. This resulted in the gradual replacement of DW landraces with improved cultivars. In 1931 DW improved cultivars occupied 4.4% of DW cultivated area, in 1939 31.4%, in 1946 47.2%, and by 1959 occupied 76.7% (Papadakis 1934; Kokolios 1962). In Turkey, wheat breeding started in the Dry farming Research Station at Eskisehir in 1925. The first DW cultivar developed by selection from landraces was *Sarı Buğday 710*. It had good tolerance to winter hardiness (Anonymous 1929-1950).

ICARDA (International Center for Agricultural Research in Dry Areas), another international center from CGIAR that settled in Aleppo (Syria), also started a durum breeding program from which the successful cultivars *Om Rabi* (also named *Cham 5*) were obtained in 1981. *Om Rabi* derived from a cross between the CIMMYT cultivar *Jori 69* and the Jordanian landrace *Haurani* (Kabbaj et al. 2017). There were also national breeding programs in Spain, Turkey, Morocco, Algeria, and Tunisia. As a result, new DW cultivars were released that could compete with BW in good conditions. As a drawback, many landraces ceased to be cultivated by farmers as they

were replaced by these elite DW cultivars (ICARDA 2019).

The last decades of the twentieth century saw a high world demand for pasta. In 1992 the European Union launched a regulation aimed at encouraging the production of high quality DW through a premium for using appropriate varieties and agricultural practices. Acreage increased in all DW growing areas in Europe (Royo 2005). The success was limited since much of the DW grain did not achieve the required quality and was used as animal feed. In 2007 the subsidies were cut off. Around the last two decades of the previous century, France emerged as a new power regarding DW production. The DW acreage in France was negligible up to the 1950s, when a small production set up in the south west. Interestingly, France was a great pasta producer at least since the seventeenth century (with many factories in Marseilles), but the majority of DW was imported, since most varieties did not adapt and performed poorly (Serventi and Sabban 2002). DW steadily increased, with new varieties adapting to the climates of south west and central France, reaching 450,000 ha in 1991. By the beginning of the twenty-first century, there were more than 400,000 ha (reaching a peak of 507,000 ha in 2010) resulting in an annual production of more than two million t, making France the third largest producer in the MR after Italy and Turkey (FranceAgriMer 2011). Currently the annual acreage ranges around 300,000 ha (GIE Blé dur 2019). International demand of high quality pasta and the popularity of couscous in the Maghrebi community might explain the acreage increase of DW in France.

In the Maghreb countries, DW research efforts started in the early years of the twentieth century. These countries were French colonies and the agricultural development authorities comprised an administrative branch that took care of research. The first efforts were to round up existing landraces, evaluate their production potential, and then use the best entries for production. Success was obvious regarding the numerous varieties that were released by pure line selection from landraces *Hamira*, *Mahmoudi*, and *Jenah Khotifa* in Tunisia. In Algeria the cultivars *Bidi17*, *Zenati 368*, *Hedba3*, and *Mohammed ben Bachir* were also obtained by landrace selection. In Morocco cultivar *Selbera* was obtained by selection whereas *Zeramek* where

obtained from a cross (Ammar et al. 2011; Jlibene and Nsarellah 2011; Abdelkader 2014; Hammami and Gharbi 2018). Another positive impact of this research was the acquisition, storage, and use of valuable genetic resources from Mediterranean DW. Starting from the 1970s, genetic materials obtained from CIMMYT and then from ICARDA led to the registration of new high yielding cultivars with better adaptation. During the last decade of the twentieth century until today, it is obvious that the quality of North African DW varieties is lagging behind the French, Canadian, and USA varieties. With the liberalisation of international trade these countries are importing good quality DW for the purpose of their modern mills, and leaving their national production for the small or traditional mills.

Acreage evolution during the twentieth century

Figure 3 represents DW acreage changes from 1924 to 2017. DW acreage dropped in Turkey (from almost 2.5 million ha up to the early 1980s to 1.2 million ha in the 2017), while Italy, Tunisia, and Algeria maintained their high acreage. The only acreage drop in Algeria occurred in the 1990s, possibly because of the civil war (1991-2002), whereas Morocco seems to lose acreage of this crop in the last 30 years. Spain, Greece and France increased their acreage in the 1990s and early 2000s (due to EU subsidies) and currently are stabilized at approximately 300–400,000 ha.

The DW acreage share (from total wheat) evolution in eight countries of the MR (1924-2017) is presented in Fig. 4. In general, there was a decreasing tendency up to the 1970s and then it increases slightly to the present, although DW percentage (from total wheat) is variable among countries.

Turkey and Morocco are countries with a great DW tradition but their acreage steadily decreased in favor of BW, especially in Turkey, where DW area was about 60% up to the 1960s, then it was 25% in the 1980s and 1990s, and currently it is about 16%. However, in Algeria and Tunisia the DW proportion respect to all wheat area has been maintained as 70–90%. Italy increased its DW acreage percentage during the twentieth century and the beginning of the twenty-first century from 25 to 70%. Spain had a small DW acreage (around 6%) that increased in the

1990s to currently nearly 20%. The case of Greece is special. It had a DW share of about 70% up to the early 1930s, which steadily decreased from the 1940s to 1980s. There was a minimum of 20.6% in 1971/72. Nevertheless, the situation reversed in the 1990s reaching a 70.7% in 1995, a figure similar to today's DW share.

There are several factors influencing DW acreage shifting:

- Time lapse between BW and DW breeding. Improved DW cultivars that competed with modern BW cultivars just arrived by the 1970s. But BW cultivars obtained by breeding are available since the early 1900s, although Green Revolution brought still better BW cultivars by the 1960s.
- DW cultivars with cold tolerance permitted their cultivation in new regions of Italy and France.
- Local, national or international demand for products derived from DW. It is the case of couscous in the Maghreb, bourghul in Turkey or pasta in Italy, the latter with a high international demand.
- Low prices of DW. DW grain usually has a slightly higher price than BW. However when prices (that are global) tend to equalize, many farmers prefer to sow BW that has a higher yield potential. Low prices also prompts DW imports (mainly from Canada and the USA), as this is the case of Algeria, Morocco, and Tunisia.
- Subsidies to DW, such as the 1990s of the European Union, which boosted cultivation of this crop.

DW genetic resources

Landraces collection efforts

The Green Revolution led to the development of a new generation of high yielding semi-dwarf and disease resistant wheat cultivars adapted to the major wheat production areas around the world, making it one of the most important events in agriculture of the last century. The introduction of the new cultivars displaced the cultivation of wild relatives and landraces, resulting in a reduction of genetic diversity (genetic erosion) as reported by Tanksley and McCouch (1997). Conservation of the genetic

diversity plays an important role for sustainability and the ability to overcome new challenges for agriculture due to climate change. The FAO/IBP Technical Conference in Rome (1967) on the exploration, utilization and conservation of plant genetic resources highlighted the urgent need to protect the plant genetic resources of the world. This conference can be considered the starting point of the worldwide coordinated efforts to collect and conserve plant genetic resources, i.e. the creation of gene banks (Carrillo et al. 2010). The genetic diversity present in the gene banks is the key to recover the allelic diversity lost through plant breeding.

A detailed description of the origin and morpho-physiological characteristics of wheat germplasm in Italy in the first half of the twentieth century is reported by Emanuele De Cillis (1927). In Turkey the first collection was made in 1925–1927 by Russian scientist Peter Zhukovsky, who by Nicolai Vavilov's advice, conducted three collecting missions. He was accompanied by Turkish scientist Mirza Gökgöl and both teams collected 18,000 wheat samples from all over Turkey, evaluated them for many traits, and Gökgöl published a two-volume book named *Türkiye Buğdayları* (Wheats of Turkey, 1935, 1939) (Zencirci et al. 2018). In 1929 Papadakis collected all the wheat types cultivated in Greece and classified them based on their morphological characteristics but unfortunately a big part of that collection was lost during the Second World War (Papadakis 1929; Koutsika-Sotiriou et al. 2016). Between 1978 and 1981 new expeditions for collections were implemented by FAO and Greek authorities. In Spain, several wheat collection expeditions were carried out in the first half of the twentieth century. Spaniard agronomists Enrique Sánchez-Monge (1957) and Manuel Gadea (1958) described the diversity of the Spanish wheat landraces, including DW. Several wheat collection missions were conducted by FAO and IBPGR in Morocco in the 1980s and lately in the 2010s. These collections were shared with international gene banks for safekeeping (INRA Morocco 2019).

Main gene banks

In gene banks, the germplasm collections are characterized to study their genetic diversity and phenotypic performance. Advances in next generation sequencing (NGS) technologies provided a rapid

and high-throughput whole genome fingerprinting (Elshire et al. 2011; Wang et al. 2014). The phenotypic characterization of the accessions allows identification of alleles for introgression into breeding programs.

Around the world there are several gene banks where DW landraces, wild accessions, breeding lines from crosses, obsolete cultivars and modern cultivars are preserved. Among the most important banks (based on the number and origin of accessions) are those hosted at CIMMYT, ICARDA, USDA-ARS, and Australian Seed Bank Partnership.

The gene bank at CIMMYT in El Batán (Mexico) preserves more than 150,000 seed samples of wheat from more than 100 countries (CIMMYT 2019). DW is represented with 20,779 accessions (Genesys 2019). The ICARDA gene bank keeps accessions at three locations: Tel Hadya (Syria), Terbol (Lebanon), and Rabat (Morocco). Wheat is represented by about 35,000 accessions, including 18,276 from DW (Genesys 2019). Eighty percent of the ICARDA accessions are duplicated in the Svalbard Global Seed Vault in Norway (ICARDA 2019). The NSGC (National Small Grains Collection) at the USDA-ARS in Aberdeen (ID, USA) holds more than 63,000 accessions corresponding to *Triticum* species (USDA 2019) including 10,690 accessions of DW (Genesys 2019). The AGG (Australian Grains GeneBank) in Canberra (Australia) takes part of the Australian Seed Bank Partnership. This gene bank hosts nearly 42,000 wheat accessions (AGG 2019) which 9966 are DW (Genesys 2019). The IBBR (Institute of Biosciences and Bioresources) gene bank at Bari (Italy) contains over 29,650 accessions of *Triticum* spp., including wild and cultivated diploid, tetraploid and hexaploid species, and 1216 DW entries (IBBR 2019).

More detailed information about number of DW accessions and the main countries of origin for these gene banks is reported in Table 6. Other gene banks with an important presence of DW accessions are VIR (Vavilov Institute of Plant Industry, St Petersburg, Russia) with 5897 accessions (Liapounova 2000); the ICAR-NBPGR (National Bureau of Plant Genetic Resources) at New Delhi (India) with 31,007 *Triticum* spp. accessions, including 3871 of DW (Dutta et al. 2015); CRF-INIA (National Center of Plant Genetic Resources) at Alcalá de Henares (Spain) with 1164 accessions (CRF 2019); and PGRC (Plant Gene Resources of Canada, Saskatoon,

Canada) having 899 accessions (PGRC 2019). The Greek Gene Bank (GGB) at Thessaloniki (Greece) holds 1190 accessions of wheat landraces and wild relatives, including 109 DW accessions (Xepapadeas et al. 2014) and the gene bank of the Aegean Agricultural Research Institute (Izmir, Turkey) keeps 1568 DW accessions.

Gene banks are valuable resources for plant breeders due to the high diversity they preserve. However, managing these large collections is a challenging task for breeders and complete phenotypic and genetic characterization becomes costly and time consuming. To increase the efficacy and use of the germplasm resources maximizing genetic diversity, Frankel (1984) introduced the concept of core collection. A core collection is a small collection ranging from 5 to 30% of the original germplasm that represent the maximum genetic diversity with a manageable number of accessions (Yonezawa et al. 1995). The National Gene Bank of India hosts a DW core collection of 489 accessions from an entire collection of 3871 accessions (Dutta et al. 2015). In Spain a DW core collection is maintained at INIA-CRF comprising 190 tetraploid entries (139 DW accessions) from an entire collection of 555 Spanish landraces and old cultivars. That core collection was later reduced to 94 genotypes (52 DW entries) (Ruiz et al. 2013). A core collection is preserved in the NSGC at USDA-ARS (Aberdeen, ID, USA) as a resource for the identification and characterization of wheat lines with preventive activity against chronic diseases is composed of 63 accessions (Santra et al. 2013). More recently, since DW can act as a bridge between tetraploid wild relatives and BW, a DW reference collection, the Global Durum Panel (GDP) was established in 2015 by the Expert Working Group “DW Genomics and Breeding” of the Wheat Initiative in order to explore the wild relatives of tetraploid wheat to harness novel beneficial allelic diversity (BBSRC 2019). The GDP with 2500 accessions includes 2130 worldwide DW accessions and 385 accessions of other related tetraploid species. Six sub-panels comprising 1000 accessions are currently used for genome-wide association study and/or allele mining in order to better exploit the available biodiversity for improving yield per se and adaptation to abiotic and biotic stresses in cultivated wheat.

DW evolution in the MR by landraces, molecular analysis, and agronomic traits

Some studies on DW evolution by DNA markers have been performed in the last few years. In a work with AFLP and SSR markers Moragues et al. (2007) found two dispersal patterns of DW in the MR from its eastern origin. One dispersal route runs through the north (Syria, Turkey, Bulgaria, Balkans, Cyprus, Greece, and Italy). The second route involved landraces from northern Africa (Egypt, Algeria, and Morocco) and the Iberian Peninsula (Spain and Portugal). In a broader SSR study from the same research group with 172 DW landraces from 21 Mediterranean countries, Soriano et al. (2016) could classify most landraces into four populations: eastern Mediterranean, eastern Balkans and Turkey, western Balkans and Egypt, and western Mediterranean, with gene diversity increasing towards the west. In another global study of 1856 tetraploid wheat accessions with 5775 SNPs (which also include the fully assembled genome of the Italian DW cultivar Svevo) Maccaferri et al. (2019) again described the dispersal pattern of DW from its origin area (western Fertile Crescent) to Greece, Balkans, and the rest of MR. The east to west dispersal pattern is again clear, and it was caused by successive waves of migrations (Phoenicians, Greeks, Romans, early Arab Empire, Ottoman Empire, etc.).

During the process of migration from the east to the west of the Mediterranean Basin, DW underwent an adaptation process to different climates and environments (all variations of the Mediterranean climate). Those environments could roughly be divided in two, the warmer and drier climate of southern MR (northern Africa and southern Levant) and the colder and wetter climate of the northern MR (Turkey, Balkans, and most Italy). Southern Italy, southern and eastern Spain, southern Turkey, and Greece represent areas with an intermediate climate. Thus, the harvest index from southern landraces (warmer and drier areas) was higher, suggesting a better ability to move biomass into grains using less water (Moragues et al. 2006).

Royo et al. (2014) also studied the adaptation processes DW underwent through dispersion across the MR. The climatic zone of the origin of landraces could explain 32.8, 28.3, and 14.5% of the variance for days to anthesis, plant height, and grain filling rate, respectively. The number of days to heading

increased when moving from southern to northern MR (colder places with more rainfall) which is an adaptation to escape drought and fill grain in a more favourable timespan. Landraces from the southern MR had more spikes, but lighter kernels, and lower biomass and yield compared to northern MR landraces.

Conclusions

The main historical milestones on DW evolution in the MR may be summarized in the following statements:

1. DW was domesticated in the Levant area, where it was accompanied by other tetraploid species, among which emmer stands out. From this region, DW slowly expands just within the Levant, being restricted to this area for a long period.
2. Phoenicians, Greeks, and above all Romans were active in the expansion and success of DW cultivation in all MR that started displaced emmer by the mid first millennium BCE. By the time of the Roman Empire BW started to strongly compete with DW in the northern MR, but not in the south.
3. Early Arab empire expanded in an area of DW cultivation (Levant, northern Africa) introducing or promoting food types based on DW semolina, such as dry pasta (especially the thread pasta, spaghetti and noodles), and couscous.
4. In the period 1850–1950 BW displaced DW in a portion of land in the northern MR but also in northern Africa that had been cultivated with DW for centuries due to the French colonization in the Maghreb and later, to the release of new BW varieties in France and Italy.
5. Up to 1955 most DW areas in the MR were planted with landraces and remained in an “orphan crop” situation, with just a few breeding programs (mainly by selection and in Italy), from which the variety *Senatore Cappelli* stood out.
6. After 1955 (year of *Capeiti 8* release) several well established and funded breeding programs were initiated in Italy, and a bit later in the international research centers such as CIMMYT (Mexico) and ICARDA (Syria). From those

programs, new high yielding varieties were obtained that competed well with the BW varieties but also replaced a multitude of DW landraces planted for centuries. Landrace collection and conservation efforts were carried out along the MR countries to preserve the diversity and legacy of this crop.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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