

Review

# Durum Wheat Breeding in the Mediterranean Region: Current Status and Future Prospects

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**Abstract:** This brief historical review focuses on durum wheat domestication and breeding in the Mediterranean region. Important milestones in durum wheat breeding programs across the countries of the Mediterranean basin before and after the Green Revolution are discussed. Additionally, the main achievements of the classical breeding methodology are presented using a comparison of old and new cultivars. Furthermore, current breeding goals and challenges are analyzed. An overview of classical breeding methods in combination with current molecular techniques and tools for cultivar development is presented. Important issues of seed quality are outlined, focusing on protein and characteristics that affect human health and are connected with the consumption of wheat end-products.

**Keywords:** Mediterranean basin; durum wheat; breeding; MAS; biochemical markers; quality

## 1. Introduction

Durum wheat (*Triticum turgidum* subsp. *durum* (Desf.) Husnot) is one of the most essential cereal species and is cultivated worldwide over almost 17 million ha, with a global production of 38.1 million tonnes in 2019 [1]. The largest producer is the European Union, with 9 million tonnes in 2018, followed by Canada, Turkey, United States, Algeria, Mexico, Kazakhstan, Syria, and India [2–6]. Durum wheat production and cultivation areas are concentrated in the Mediterranean. Moreover, the countries of the Mediterranean basin are the largest importers and the largest consumers of durum wheat products (flour, pasta, and semolina). Among European Union (EU) countries, Italy is considered the leader of durum wheat production, with an average production of 4.26 million tonnes in the last decade (1.28 million ha growing area), followed by France with 1.89 million tonnes (0.37 million ha), Greece with 1.07 million tonnes (0.37 million ha), and Spain with 0.98 million tonnes (0.38 million ha) (Table 1) [2]. Since durum wheat is mainly grown under rain-fed conditions in the Mediterranean basin, its productivity is profoundly affected by rainfall and biotic (pests and diseases) and abiotic (drought, sunlight, cold, and salinity) stresses.

**Table 1.** The world’s leading durum wheat producing countries (2010–2019) [2–4].

Country	Average Production (Millions of Tonnes)
Canada	5.2
Italy	4.3
Turkey	3.7
USA	2.3
Kazakhstan	2.2
Syria	2.2
Algeria	2.2
France	1.9
Morocco	1.8
Greece	1.1
Spain	1.0
Tunisia	1.0

## 2. A historical Review of Durum Wheat Breeding

### 2.1. Prehistory and Early History

Wheat cultivation and human civilization have evolved together for at least 10,000 years since humans first attempted to produce food during the “Neolithic Revolution” [7]. The first step in the improvement of durum wheat involved the domestication of its wild progenitors [8] in the hilly area of southwest Asia at the Tigris and Euphrates basin (ancient Mesopotamia) and in the mountains of Iran, Turkey, Syria, and Jordan, in the area often referred to as the “Fertile Crescent” [9,10].

According to Shewry [7], an early and primitive form of plant breeding was carried out with the first selections from wild populations of *T. turgidum* subsp. *dicoccoides* (Körn. ex Asch. and Graebner) Thell. based primarily on yield, but also considering other genetic characteristics; mainly non-brittle rachis and free-threshing naked kernels. It has been proven that the first trait is controlled by two major genes, *brittle rachis 2* (*Br-A2*) and *brittle rachis 3* (*Br-A3*), on the short arms of chromosomes 3A and 3B, respectively [11], while the free kernels originated from a dominant mutation at the Q locus [7,12].

The cultivated emmer (*T. turgidum* subsp. *dicoccum* (Schränk ex Schübler) Thell.) was the first dominant wheat in Asia, Africa, and Europe in the early years of agriculture, in the seventh millennium BC. Emmer grains were found in the tombs of the Egyptian Pyramids and were widespread in ancient Babylon and Central Europe [13]. Seeds of emmer were discovered in archaeological finds dating back to between 7500 and 6700 BC [10]. It remained a dominant cereal until the first millennium BC when it was replaced by free-threshing durum wheat [14]. Its grains have been found in eight archaeological sites of the Iron Age, dating from the end of the 2nd millennium BC to the end of the 4th century BC in Northern Greece [15]. The first agricultural book on wheat was written using cuneiform on a clay tablet around 1700 BC and was discovered in Israel in 1950 [13].

The written history of wheat science began 2500 years ago when the Greek botanist Theophrastus (371–287 BC) wrote the study “Enquiry into Plants”. Later, the famous Roman writers Columella, Varrone, Virgil, and Pliny the Elder described wheat as the primary agricultural food source in the Mediterranean region [16].

### 2.2. Modern History

The modern history of durum wheat breeding in the Mediterranean region began in the early 20th century and was affected by the global evolution of agricultural science. A high yield, good end-use traits, and resistance to abiotic and biotic stresses have always been targets for wheat breeders. The initial approach in durum wheat breeding focused on the exploitation of local genetic resources. Later, the Green Revolution resulted in the release of short, high-yielding durum wheat cultivars

from International research institutions, which are used extensively in crosses in almost all national breeding programs.

### 2.3. The Early Period, before the Green Revolution

At the dawn of the 20th century, the first systematic breeding efforts were made by public research institutes in the countries across the Mediterranean basin that pioneered plant breeding at that time. Initially, landraces were used as the starting materials in breeding programs (Table 2). Later, systematic breeding schemes were gradually applied using parent cultivars with different useful agronomic characteristics, such as high yield, good quality, and resistance to a range of disease.

**Table 2.** The main Mediterranean wheat landraces.

Country	Reference
<i>Italy</i>	
Biancuccia, Bivona, Castiglione, Ciciredda, Cotrone, Duro Lucano, Farro Lungo, Gioia, Regina, Ruscia, Sammartinara, Timilia	[17]
<i>Greece</i>	
Roussias, Asprostachys, Tsipoura, Asprostaro, Diminitis, Trimini, Gremmenia, Kondouzi, Mavragani, Zochovis, Deves, Rovaki, Arnaouti, Kokkinostaro, Floritsa, Mavrostaro	[18,19]
<i>Turkey</i>	
Uveyik, Sahman, Bagacak, Sorgul, Havrani, Menceki, Iskenderi, Kocabugday, Cambudayi, Kibris bugdayi, Amik, Akbasak, Karabasak, Karakilcik, Kunduru, Sari Bursa, Sari Basak	[20,21]
<i>Algeria</i>	
Tuzelle, Mahon, Biskri, Bidi 17	[22]
<i>Morocco</i>	
ML 19, ML 21, ML 22, ML 23, ML 24, ML 26, ML 28, ML 48, ML 49, ML 32, ML 33, ML 34, ML 35, ML 36, ML 37, ML 38, ML 39, ML 41, ML 42, ML 43, ML 44, ML 45	[23]
<i>Tunisia</i>	
Hamira, Richi, Mahmoudi, Jenah Khotifa	[24]

In Italy, breeding was initially done through public research institutes, universities, and departments from the Ministry of Agriculture [25]; later, private companies such as the Società Italiana Sementi and Società Produttori Sementi Bologna became involved [26]. The pioneer in the modern durum wheat breeding was the Italian Nazareno Strampelli (1866–1942). Strampelli began his efforts with selections of local landraces from southern Italy, the Italian islands, and the Mediterranean region. In 1923, Strampelli released the cultivar “Senatore Capelli”, which he had selected in 1915 from the local North African landrace “Jean Retifah”. This cultivar was a landmark for the cultivation of durum wheat in Italy, as it covered 60% of Italy’s durum wheat acreage for many decades, but also throughout the Mediterranean, where it has been widely used for crosses [16,27]. Casale, an Italian breeder, crossed cv. “S. Capelli” with Palestinian cv. “Eiti 6” in the 1940s and released the cultivar “Capeiti 8” which replaced “S. Capelli” in durum wheat cultivation in 56% of acreages due to its higher yield, although its seed quality was low. Another important breeder, Forlani, saw the possibility of improving durum wheat using interspecific crosses, particularly to introduce resistance to diseases [16,28].

In Greece, modern wheat breeding was started in 1923 by Ioannis (Juan) Papadakis (1903–1997), who founded the Institute of Plant Breeding, the first Research Center in the Balkan Peninsula. Papadakis introduced the new methods of the era, such as selection and crossbreeding, and conducted experiments in different locations using different controls and replications to evaluate the wheat’s genetic material. Papadakis started by inserting selections into local breads and durum wheat landraces. In 1924, he made the first crosses by selecting parents from both local and foreign landraces (Table 3) [29]. In 1929, Papadakis recorded and described in detail the genetic material of the wheat found in Greece, according to Professor Percival’s classification [30]. This study included 47 local cultivars or landraces of durum wheat cultivated in Greece [18]. The first durum wheat cultivars were released in 1932 [31].

The local durum wheat landraces were cultivated until 1930 were then replaced gradually by the new improved cultivars. The crosses of the plant breeding program of the Institute of Plant Breeding were produced in 1946, resulting in the cultivars “Methoni” and “Electra”, which had better quality and featured earlier maturation by one week compared to “Lemnos”. After 30 years, the new improved cultivars covered 60% of the durum wheat cultivated area in Greece, with the improved cv. “Lemnos” occupying 42% of the area [32].

**Table 3.** The main Mediterranean cultivars released before the Green Revolution.

Country	Name	Year of Release	Pedigree, Cross Name, Origin	Agronomic Characteristics	Reference
Italy	Senatore Capelli	1923	Selection from landrace “Jean Retifah”	Waxy, tall, rather late ripening, good quality	[16,17,27]
	Capeiti 8 (=Patrizio 6)	1955	S. Capelli × Eiti 6	Better yield and poorer quality than S. Capelli	[16,17,28,33]
	Sincap 9		Sinai × S. Capelli	Agronomical characteristics superior to S. Capelli	[16,28,33]
	Appulo	1964	(S. Cappelli × Grifoni 235) × Capeiti 8	Optimal grain quality and yield	[16,28,33]
	ISA-1	1971	Patrizio × Sassari 0130	Very early	[28]
Greece	Lemnos	1932	Selection from Landrace Akbasak	High yield, good quality for bread	[31]
	Methoni	1954	Lemnos × 7-B-1231	Better quality and earlier maturing than Lemnos	[32]
	Electra	1957	S. Capelli × [Lemnos × (Florence × Arditto) × Sinai2]	Better quality and earlier maturing than Lemnos	[32]
Spain	Andalucia 344	Before 1940	Selection from Manchón de Alcalá la Real		[34,35]
	Híbrido D	Before 1940	S. Capelli/Colorado dc Jerez		[34]
	Ledesma	Before 1940	S. Capelli/Rubio dc Belalázar		[34]
	Bidi 17	1950	Selection from Bidi or Blé Gounod, from Algeria	Tall, large grains and a weak yellow color index.	[34]
France	Bidi 17	1950	Selection from Algerian population “Oued Zenatti”	Tall, large grains and a weak yellow color index.	[26,36]
	Montferrier, Mandon			Better yield, very sensitive to leaf rust	[28,36]
	Agathe			Better yield, moderately sensitive to leaf rust	[36]
Turkey	Kundur 1149	1967	Selection from Landrace	Tall, drought tolerant, good winter hardiness	[20,21,37]
	Berkmen 469	1970	Selection from Landrace	Tall, drought tolerant, good winter hardiness	[21,37]
Morocco	Oued.Zenati	1949	Selection from landraces	Tall	[23,38]
	Zeramek	1949	Selection from landraces	Tall	[23,38]
	Kyperounda	1956	Selection from landraces	Tall	[23,38]
Tunisia	Chili 931	1953	France		[24]
	Kyperounda	1954	Cyprus		[24]
	INRAT 69	1970	Mahamoudi981/Kyperounda		[24,39]

At this initial stage of breeding, the classification of *Triticum* species was also the subject of extensive study by Spanish researchers. In the early 19th century, Spanish botanists Clemente and Lagasca compiled the “Ceres hispanica”, the first herbarium for *Triticum* species. Intensive work on the collection and conservation of durum wheat types in the Iberian Peninsula began in 1930 by Arana and was extended from 1950 to 1956 by Tellez, Prieto, and Garcia-Pozuelo. The first attempt to improve durum wheat in Spain was performed at the Agricultural Research Center of Jerez de la Frontera by Juan Bautista Camacho [40]. Based on the work that had been done in the previous years, selections were made in local durum wheat populations, and crossing programs were carried out, which resulted in the release of important cultivars, such as “Ledesma”, “Andalucia 344”, and “Híbrido D”, which, in 1963, covered 12%, 10%, and 6% of the durum wheat cropping area in Spain, respectively [34].

The characteristic resistance of local landraces to three types of rust has been studied at the Instituto Nacional de Investigaciones Agrarias since 1954 [40].

Concerning France, until the 1960s, production and research programs have mainly been conducted in Algeria, Morocco, and Tunisia. In 1930, breeding work was conducted in Algeria by Ducellier, who identified 29 local cultivars or populations of durum wheat. Wheat research was performed and coordinated by the Institut National de la Recherche Agronomique (INRA) in Montpellier until Algeria's independence in 1962, and then from The Algerian Center for Agronomic, Scientific, and Economic Research (CARASE), or INRA, in Algeria. In the early 1970s, the production of durum wheat increased drastically due to the release of the cultivars "Bidi 17", "Oued Zenati 368", "Hedba 3", and "Mohamed Ben Bachir", which resulted from selections among local landraces [22]. Accordingly, before the 1960s, breeding efforts in Morocco were focused on collecting local durum wheat landraces, from which, after the selection programs, the cultivars "Oued Zenati", "Zeramek", and "Kyperounda" were released (from 1949 to 1956). The latter cultivars were more productive than the local landraces, but their quality was inferior [23]. A similar approach was recorded in Tunisia, where local durum wheat landraces were mainly cultivated in the country until the 1940s. These were followed by cultivars produced from selections within the aforementioned landraces [24].

The Ministry of Agriculture started a breeding program in Libya in the 1950s. Durum wheat landraces, such as "Jlail-Dib" and "Hmira", were used to develop improved varieties. During the period of 1962–1965, nine durum wheat cultivars were collected and characterized [41]. Simultaneously, breeding work for durum wheat took place in Egypt, another important North African country. In 1914, Egyptian breeders released two cultivars with resistance to high temperatures, "Dakar 49" and "Dakar 52", which were selected from local durum wheat landraces. In the 1920s, these breeders released the cultivars "Hindi D", "Hindi 62", and "Tosson" using genetic material imported from India. Since 1942, this breeding program has focused on creating cultivars with resistance to the three aforementioned types of rust [42].

In Turkey, initial wheat research began in 1925 with the establishment of the first "Seed Improvement Station" in Eskisehir. The early durum wheat cultivars that were released resulted from selections within the local durum wheat populations and included "Kundurur 414/44", "Sari Bursa 7113", "Kundurur 1149", "Berkmen 496", "Akbasak 073/44", and "Karakilcik 1133" [20,43]. Finally, in Israel, the onset of genetic improvement in durum wheat was based on selections within local landraces. Local wheat landraces, mainly durum wheat that was previously cultivated in Palestine, were described as early as the 1920s. In 1948, Kostrinsky compiled a descriptive list of cultivars and landraces [44].

#### 2.4. Breeding Work in the Mediterranean during and after Green Revolution

A significant increase in yield was achieved in many national breeding programs through the second half of the 20th century [45]. The key to the dramatic increase in wheat yields during the 'Green Revolution' in the 1960s was the introduction of semi-dwarf genes into bread wheat, which resulted in the replacement of tall cultivars with semi-dwarf cultivars characterized by their responsiveness to inputs (e.g., fertilizers) and resistance to lodging. The primary donor of these genes was the semi-dwarf cultivar "Daruma" from Japan. Initially, the cultivar "Norin 10" was developed as a result of diallelic crosses between "Daruma" and some American cultivars. Norman Borlaug, at the Centro Internacional de Mejoramiento de Maiz y Trigo (CIMMYT), used the cross "Norin 10" x "Brevor 14" for the development of initial genetic material that was first shipped to Latin America and Southeast Asia, where it was rapidly adopted for cultivation with spectacular increases in yield [46]. The cultivar "Norin 10" has also been widely used in breeding programs around the world for the introduction of semi-dwarf genes in durum wheat, which has been recorded since 1956 [47]. This was an important milestone that affected durum wheat breeding efforts worldwide. The CIMMYT durum wheat germplasm continues to play an essential role in increasing the production and genetic gain of national agricultural research systems for developing countries. Indeed, 77% of the cultivars released



in developing countries in 1991–1997 originated from crosses between CIMMYT and indigenous genotypes. Moreover, 19% of these included at least one parent from the CIMMYT collection [48].

Another critical event in the evolution of plant breeding was the foundation of the International Center for Agricultural Research in the Dry Areas (ICARDA) in 1977 in Aleppo, Syria. Initially, this center was intended to control the CIMMYT's segregated wheat genetic material and pure lines. Since 1981, the ICARDA Improvement Program has worked on crosses, and, in 2003, this program became independent [49,50]. The first successful cultivar of durum wheat resulting from ICARDA's breeding program was "Waha" [syn. Cham1, Plc/Ruff/Gta/Rtte], which was enlisted in Algeria's National Variety Catalogue in 1984. Another successful cultivar was "Om Rabi 1" [syn. Cham 5, Jori/Haurani], which was released in Morocco in 1989. As of 2018, 130 cultivars that originated from the genetic material of ICARDA's breeding program have been released in 22 countries (Table 4) [50].

A comparison between old and new durum wheat cultivars bred in different periods is useful to understand which of the yield components and other associated traits contribute to the increased productivity of new cultivars. In ICARDA, the impact of 35 years (1977–2011) of public durum wheat breeding resulted in a 0.7 genetic gain per year, mostly based on earlier flowering and an increase in the spike density [50]. In Canada and Italy, durum wheat yield improvement is based on an increased number of grains [51,52]. Similarly, new high yield CIMMYT cultivars increased their numbers of grains per m<sup>2</sup> as a result of the increased number of spikes per m<sup>2</sup> and the grains per spike [48,53]. Royo et al. [54] studied the genetic changes in durum wheat yield components and their associated traits by comparing 24 old (<1945), intermediate (1950–1985), and modern (1988–2000) Italian and Spanish cultivars. As a result, it was found that the number of grains per m<sup>2</sup> increased by 39% and 55% in Italian and Spanish cultivars, respectively. This increase involves a 20% increase of plants per m<sup>2</sup>, a 29% increase of spikes per plant, and a 51% increase of grains per spike. The mean rate of increase in the yield per plant was 0.41% per year, 0.11% per year for plant density, 0.55% per year for the number of grains per m<sup>2</sup>, 0.48% per year for the harvest index, and 0.81% per year for the plant height [54]. The number of spikelets per spike did not change, so the increased numbers of grains per m<sup>2</sup> was due to the higher grain set in the modern cultivars. Similar results were found in a study on durum wheat cultivars released in Italy during the 20th century, where the genetic gain was mostly based on a higher kernel number per m<sup>2</sup> and spikes per m<sup>2</sup> [52].

Apart from yield, durum wheat breeding programs significantly affect grain quality [52,55]. The evaluation of durum wheat cultivars released during different breeding eras shows that genetic improvement reduces grain protein concentration as a result of improved yields, but without affecting pasta cooking quality [53]. The lower grain protein percentage of modern cultivars is based on the dilution effect caused by their heavier grains or increased amount of carbohydrates [55,56]. However, modern cultivars have increased gluten index, showing an improvement in pasta-making quality [32,52,55,57].

**Table 4.** The main Mediterranean cultivars released after the Green Revolution.

Country	Name	Year of Release	Pedigree, Cross Name Origin	Agronomic Characteristics	Reference
Italy	Trinakria	1973	(CpB144=Castelfusano) ×	Good quality	[16,26]
	Creso	1974	{[(Yaktana54-Norin10-Brevor) Capelli-63-4] Tehucan}	Good quality, resistance to <i>Fusarium graminearum</i> and brown rust	
	Simeto	1988	Capeiti 8 × Valnova	High yield, low tillering, excellent adaptability	[17,33]
	Svevo	1996	Sel. CIMMYT × Zenit sib	High quality for pasta	[16,26]
Greece	Mexicali-81	1981	Selection from Mexicali 75	High yield	[58]
	Selas	1982	Selection from Stork "S"	Good grain quality	[58]
	Elpida	2010	Sifnos × Mexicali-81	High quality and yield	[58,59]
	Thraki	2014	Simeto × Mexicali-81	High quality and yield	[58,60]

Table 4. Cont.

Country	Name	Year of Release	Pedigree, Cross Name Origin	Agronomic Characteristics	Reference
Spain	Claudio	1999	(Sel. Cimmyt × Durango) × (IS193B×Grazia)		[61]
	Mexa	1980	GERARDO-VZ-469/3/JORI(SIB)//ND-61-130/LEEDS		[35,61]
	Vitron	1983	TURCHIA-77/3/JORI-69(SIB)/(SIB)ANHINGA/(SIB)FLAMINGO		[35,61]
	Cocorit	1978	CIMMYT		[35]
France	Durtal	1972	<i>Triticum durum</i> × <i>T. aestivum</i>	High yield, short, good earliness, poor quality	[26,28,36]
Turkey	Dicle 74	1975	RAE/4×TC//STW63/3/AA“S” =Cocorit	Spring wheat	[20,37]
	Gediz 75	1976	LD357E/TC2//JO“S”	Spring wheat	[20,37]
	Cakmak 79	1979	UVY162/61.130	Winter wheat, good quality	[20,21,37]
	Kiziltan91	1991	UVY162/61.130	Winter wheat, good quality	[20,21,37]
	Altintac 95	1995	KND//68111/WARD	Irrigated winter wheat	[21,37]
	Selcuklu 97	1997	073/44×2/OVI/3/DF-72//61-130/ UVEYYK 162	Irrigated winter wheat	[21,37]
	Yilmaz98	1998		Irrigated winter wheat	[20,21,37]
	Ankara98	1998		Irrigated winter wheat	[20,21,37]
Algeria	Waha	1984	syn. Cham1, Plc/Ruff//Gta/Rtte	ICARDA genetic material	[50]
Morocco	Cocorit			Yield potential, wide adaptation, low quality	[62]
	Jori			Yield potential, wide adaptation, grain quality	[62]
	Haj-Mouline			Yield potential, wide adaptation, low quality	[62]
	Oum Rabia	1988	INRA 1718, Sel in “Cyprus 3”	High yield potential, better grain quality	[23,38,62]
	Karim	1985	Bittern ‘S’ or sel in « JO’S.AA”S”//FG’S’ »	High yield potential, better grain quality	[23,38,62]
Tunisia	Karim	1982	(Jori“S”/Anhinga“S”//Flamingo“S”) CIMMYT		[24,39]
	Khlar	1992	Chen“S”/Altar 84, CIMMYT		[24]
	Om Rabia	1987	Jori C69/Haurani, ICARDA		[24]
	Nasr	1990	GoVZ512/Cit//Ruff/Fg/3/Pin/Gre//Trob), ICARDA		[24]
	Maali	2003	CMH80A.1016/4/TTURA/CMH74A370/CMH77.774/3/ YAV79/5/Rassak/6/DACK“S”/YEL3“S”// Khlar, INRAT		[24]
	Salim	2010	ALTAR 84/FD8419-126-1-2/Razzak/3/Krf/ Baladia Hamra, INRAT		[24]

In tandem with the evolution of agricultural science occurring worldwide during the same time, in 1956 in Italy, Gian Tommaso Scarascia Mugnozza and Francesco D’Amato embarked on a pioneering durum wheat breeding program that included both fundamental genetic studies and applied mutation breeding and led to 22 registered varieties, six of which resulted from a direct selection of induced mutants [16,63]. An important cultivar that emerged from this program in 1974 was “Creso”. Considerable work has also been done at Italian universities, such as at Palermo University (cv. “Trinakria” in 1973 by G.P. Ballatore), at Sassari and Naples (cvs. “Maristella”, “Ichnusa” by R. Barbieri), and at Bari University [cvs. “Messapia”, “Salentino”, “Salizia” by G.T. Scarascia-Mugnozza, A. Blanco and coworkers]. J. Vallega and G. Zitelli, at the Experimental Institute for Cereal Research in Rome, used N. Borlaug’s selected genetic material in their crosses in their attempt to produce high-yielding cultivars resistant to lodging and diseases; this material had semi-dwarf genes of “Norin 10” [16]. In 1988, Calcagno released the successful cultivar “Simeto”, which was bred at the Experimental Station

for wheat at Caltagirone in Sicily. This cultivar was high yielding, low tillering, and had excellent adaptability across different environments. Thus, it has been widely cultivated in all the countries of the Mediterranean basin up to present with a large acreage [26] and is often used as a parent in crosses. In the private sector, seed companies have released many notable cultivars, including “Duilio” (Società Italiana Sementi, S.I.S.) and “Svevo” (Società Produttori Sementi), which are cultivated in several important durum wheat productive countries offering high-quality pasta products.

In Greece in the late 1960s, E. Skorda induced artificial mutations with gamma rays and thermal neutrons to increase genetic variability [64]. In the early 1980s, the breeder’s team from the Cereal Institute in Thessaloniki released cultivars that were bred from intra-cultivar selections of genetic material from the Mediterranean basin, including “Mexicali 81”, “Kallithea”, “Athos”, and “Selas”. Furthermore, new cultivars selected from CIMMYT segregating germplasm were made available to the farmers. Among the aforementioned released cultivars, “Selas” had an excellent grain quality and was used until 2015 by the pasta industry in Greece. The newest durum wheat cultivars released by the breeders from the Cereal Institute originated either from crossbreeding among different cultivars or from selections among CIMMYT segregating material included in the Greek National and the Common Catalogue of Cultivated Plants [58,60].

At the beginning of the 1960s in France, Pierre Grignac began the first durum wheat breeding program, in which the first crossings among Mediterranean landraces were developed at INRA in Montpellier. In the middle of the same decade, cultivars with good qualities, such as a good yellow-amber color, were imported from North Dakota for cultivation in northern France, and constituted a second genetic pool for the program [26]. Afterwards, Grignac used interspecific crosses with bread wheat to select new lines with improved characteristics [28,36].

In Algeria, the Field Crops Development Institute (IDGC) was founded in 1974. This institute was responsible for durum wheat breeding and has collaborated actively with CIMMYT and ICARDA since 1980. As a result, more than 60 modern durum wheat cultivars have been released, and the peak yields have been obtained with the cultivars “Hoggar” and “Sahel” [22]. In Tunisia, modern cultivars developed from CIMMYT and ICARDA genotypes prevailed during the 1970s and were replaced in the 1980s by more recent cultivars developed at INRAT [24].

In 1970, a result of the collaboration with CIMMYT and, later, with ICARDA was the introduction of foreign durum wheat germplasm into Morocco in an attempt to develop new high-yielding, early-maturing cultivars. The outcome of this program was the release of the cultivars “Marzak”, “Karim”, “Sebou”, and others after 1984 [23]. However, this new germplasm was inferior in quality.

Finally, in Turkey, the agreement between the Turkish government and the Rockefeller Foundation in 1967 resulted in the release of semi-dwarf, high-yielding, and disease-resistant cultivars [20,65].

### 3. Application of Classical Methodologies of Breeding

#### 3.1. Classical Approaches, New Perspectives, and Tools for Wheat Breeding

The main targets of a durum wheat breeding program established in the Mediterranean basin, where its cultivation is very well adapted, may focus on: (1) grain yield improvement; (2) yield stability and a better understanding of genotype  $\times$  environment interactions ( $G \times E$ ) and adaptation mechanisms; (3) responsiveness to inputs and the use efficiency of resources in different cultivation systems; (4) resistance to biotic stresses (pests and diseases), and tolerance to abiotic stresses (drought, salinity, etc.); or (5) improving grain quality.

The above parameters are taken into account by durum wheat breeders in the design of a breeding program for cultivar development. They use common classical breeding methods, such as pedigree, bulk, single-seed, backcross method, pure line selection, and recurrent selection, to develop cultivars with the desired characters mentioned above. These methods can be applied with some alterations to increase efficiency and reduce the duration of the breeding program. As an example, backcross (BC) is a very common method mainly used in durum wheat for the transfer of traits controlled by only one or



a few genes, such as resistance to diseases or quality parameters, from one donor parent to an elite line (recurrent parent) [66,67]. Molecular markers can significantly shorten the time needed, compared to the conventional backcross method, to identify the desired plants that have the target gene/genes and apply negative selection for the donor genome to ensure the maximum recovery of a recurrent-parent genome [68]. There are successful results in durum wheat breeding programs regarding the increased disease resistance or quality characteristics. Marker-assisted backcrossing (MABC) through simple sequence repeat (SSR) markers was shown to improve grain protein content in a wheat cultivar [69]; this method can assist the simultaneous selection of multiple stripe rust resistance genes and help avoid escapees during the selection process. In a previous study, the successful targeting of the gene transfer and reconstitution of the genome were completed in a period of four crop cycles, proving the practical application of MABC in developing high grain protein lines in the background of any popular cultivar [69]. In the single-seed descent method (SSD), only one seed from each  $F_2$  selected plant is kept and bulked with all the others to produce an  $F_3$  population. The same procedure is repeated until the  $F_5$ – $F_6$  generation. Two or more generations grow per year in the greenhouse, in winter nurseries, or in a growth chamber. The selection of lines takes place in the  $F_6$  lines, which have increased homozygosity, retaining a large part of the extensive genetic variability from the  $F_2$  generation. The single-seed descent method is considered a tool to exploit durum wheat genetic resources [70]. In the bulk breeding method, some plants are selected from the  $F_2$  population, and their seeds are bulked to form the  $F_3$  population. The same procedure is repeated until the  $F_5$  generation, where the evaluation of lines begins until the  $F_{10}$ – $F_{11}$  generation. This is an easy method to apply, thus saving breeders time and effort. Also, this method can increase the frequency of desirable genotypes in a population, but is not very effective for traits with low heritability. However, a modification of this method could be useful in wheat breeding when applied under salinity stress conditions [71]. In this case, using molecular markers through a bulk segregant analysis (BSA) will increase the effectiveness and shorten the needed time for all these processes [72].

Finally, the pedigree breeding method (and its modifications) is the most common method used in breeding programs for the release of durum wheat cultivars. Generally, pedigree breeding includes phenotypic selection in the early generations (until  $F_{3-4}$ ), and the normal yield test begins in the generations with increased homozygosity ( $\sim F_5$ ). The selection for yield during early generations was not very effective when the evaluation was done in normal plant density fields [73–76]; however, it was found to be effective when the evaluation was applied in low plant density fields and the experimental unit involved a single plant, as in the honeycomb methodology [77–80]. Finally, the selected lines from the experiments with replications will be evaluated in large plots (drill strips) over  $\sim 2$  years and  $\sim 5$ – $10$  locations to determine yield, stability across locations, maturity, plant height, semolina, pasta and important quality characteristics for cooking [81]. Following a classical approach, a period of 9–12 years is needed from the beginning to the end of a breeding program, but this time could be reduced significantly by using the Marker Assisted Selection (MAS) procedure [82].

It has been recorded that the effectiveness of breeding on durum wheat's yield potential has been remarkable in Spain, Morocco, Turkey, and Italy [20,35,62,83]. The improvement of grain yield (GY) during the past decade has been attributed mostly to the increased number of grains  $m^{-2}$  and to the increased number of spikes  $m^{-2}$  [83]. Thus, further improvements in these characteristics might improve yield [83]. Important increases in yield were also achieved by increasing the harvest index, which has almost doubled since the beginning of the 20th century [83,84]. Moreover, a further increase in yield was achieved through an increase in biomass and a subsequent increase in yield, which explains the stability of the harvest index over the last three decades [84]. Similarly, an increase in biomass could result in an increase in yield in the future. Other characteristics that contributed to the increased yield in the 20th century include a reduction in the heading date and physiological maturity and an increase in the grain filling period [83]. Similar changes in these characteristics in the future could result in an increase in yield, based on the results of the reduction of the effects of drought and

heat stress. Moreover, an increased yield could be achieved through the release of cultivars with higher water use efficiency [85].

Apart from the selection for increased yield potential, further improvements could be achieved through selection for increased tolerance to abiotic and biotic stresses. Moreover, the importance of traits that allow a plant to escape terminal drought and avoid critical stages of seed development (anthesis and seed filling), such as early vigor and an early heading date, has been well recognized [86,87]. All the above classical breeding methodologies have succeeded in making considerable progress in the yield and quality of durum wheat in the Mediterranean basin [24,57,88]. The main problem for the classical methods is that they are time-consuming, and phenotyping procedures are costly. In an effort to aid classical breeding methods, molecular genetics and associated technologies have been developed, and they offer important tools for plant breeders.

The parental selection of wheat lines can be based on phenotypic characterization and biochemical and DNA markers, which can estimate genetic variability even among phenotypically similar genotypes, as identified in several studies undertaken in Mediterranean countries [89–93]. By employing molecular markers in parental selection, the genetic diversity of wild and cultivated wheat can be exploited [94–98]. As an example, SSR markers were proven to be effective in the selection of genetically diverse genotypes with phenotypical similarities [90]. A combination of molecular markers and pedigree data could help in the exploitation of genetic diversity [91,99] and the selection of progenies, significantly increasing the efficiency and precision of plant breeding programs. Molecular markers supply various advantages over morphological markers in the linkage mapping of important agronomic traits. They are also unlimited in number, highly polymorphic, and can be used at any developmental stage without any environmental interference. Molecular markers can increase the precision and speed of selection in a durum wheat program through: (a) selection in the early stages or a simultaneous selection of multiple traits or traits that are difficult or expensive to evaluate; (b) the targeted introgression of useful genes in wide crosses; and (c) accelerated backcrossing. MAS or molecular breeding offers an opportunity to accelerate classical breeding approaches. MAS requires the establishment of a correlation between a desired trait, such as disease resistance, and molecular marker(s); this can be obtained by phenotyping a genetic mapping population followed by a quantitative trait locus (QTL) analysis [81]. For this purpose, several markers that are known to be associated with QTL/genes for some major economic traits are being deployed for MAS in wheat breeding programs. Several examples of the successful use of MAS are now available for wheat, and more examples will become available in the future [100–102]. Furthermore, molecular allele mining can help in broadening the reduced genetic diversity of cultivated wheat through the identification of allelic variation and the isolation of new rare alleles capable of improving tolerance to abiotic and biotic stresses [103,104]. According to Sehgal et al. [104], by using new technologies, unexploited genetic variation can further improve the drought and heat stress tolerance of the elite wheat pool and enrich it with novel drought and heat tolerance genes. This will contribute to achieve adaptability of the released cultivars to high temperature and drought that is for the most important emerging problems emerging in the Mediterranean due to climate change.

### 3.2. Participatory Plant Breeding

Today, it is recognized that agricultural production requires the adoption of environmentally friendly solutions, the preservation of crop biodiversity, and the release of varieties suitable for low input environments to set new goals for wheat breeding that align with the real needs of farmers and the market that are imprinted in the Mediterranean. Employing a participatory plant breeding (PPB) approach may have many benefits, including increased and more stable productivity, faster release and adoption of wheat varieties, better understanding of farmers' various criteria, enhanced biodiversity, the conservation of crop diversity on farms [105,106], increased cost-effectiveness, the ability to facilitate the learning of farmers, and the empowerment of farmers [107].

Participatory plant breeding (PPB) methods incorporate the involvement of end users in the breeding process [108] and the decentralization of selection sites into farmers' fields [109]. This has been

proposed as an alternative to formal plant breeding and is more likely to produce varieties acceptable to farmers in marginal environments [110]. Social studies concerning the related historical and cultural traditions can assess the needs of both farmers and the market for local products [111–113]. Usually, end users value different traits than plant breeders [114]. Plant breeders contribute their expertise in creating genetic variation, in population management, and in designing screening methods that can separate genetic from environmental effects [110]. Participation provides flexibility in the selection program. The objectives could be reoriented to ensure relevant end products in case some changes are necessary during the breeding procedure. Moreover, there is a mistrust of modern varieties among farmers, bakers, and consumers [81,115], and participatory plant breeding could rebuild client trust with improved varieties [116]. In many breeding programs where there are G × E interactions during evaluation, the lines selected under PPB have been found to perform better for farmer priority traits than those selected via formal plant breeding methods [117,118]. PPB programs can also reduce the costs of the breeding process. Cost savings primarily derive from the less frequent testing of advanced lines [119]. Many studies have shown that participatory variety selection (PVS) can improve the adoption of varieties [120–122], and thereby enhance productivity [123].

In Syria, decentralized participatory selection by farmers is significantly more efficient in identifying the highest yielding entries in farmers' fields than any other selection strategy [124]. Farmer-selected populations are not genetically homogenous, which may lead to higher yield stability in varying environments [125]. PPB projects including farmers have resulted in the wider and simpler adoption of new varieties [114,126,127]. Wheat populations after PPB will evolve by adapting gradually and continuously to climate change [128]. A wheat population developed at ICARDA [129] has been evolving for five years at a farm in Tuscany (using evolutionary participatory breeding principals); the name of this population is 'SOLIBAM Tenero Floriddia' [130]. Thanks to the EU Commission Implementing Decision (2014/150/EU), which provides specific derogations for the marketing of wheat populations, this genetically heterogeneous population is now, for the first time, being marketed as a certified seed [130].

### 3.3. The Application of Doubled-Haploid Techniques

The introduction of advanced in-vitro tissue culture techniques, such as androgenesis (anther or microspore culture), chromosome elimination techniques (wide hybridization), and ovule cultures (gynogenesis), in self-pollinating crop species, has helped breeders to accelerate trait fixation in segregating populations of durum wheat in research conducted in Tunisia and ICARDA [131,132]. Of the techniques mentioned above, androgenesis (more precisely, an anther culture) can only be incorporated into breeding programs if they ensure the production of a sufficient number of genetically stable doubled haploid plants from a wide range of genotypes [133]. An anther culture, despite its effectiveness and convenience, has the serious disadvantage of being firmly genotype dependent [134,135]. Furthermore, durum wheat hardly responds at all to this technique (i.e., its embryo production is deficient and most of the plants produced are albinos) [136,137]. For this reason, chromosome elimination techniques are an attractive alternative approach, since they are not genotype dependent [138] and are not influenced by the dominant Kr wheat crossover genes [139]. This technique is mainly used in producing new germplasm, not only in durum but also in bread wheat and triticale. The fourth technique, gynogenesis, is another alternative for producing new germplasm. In gynogenesis, haploid plant development is induced by an unpollinated ovary culture. However, the use of an ovary culture is practiced more rarely in wheat breeding programs [140]. In a recent study in Tunisia, Slama-Ayed et al. [132] compared three doubled haploid techniques and found that gynogenesis is an exciting approach that could be used to produce new durum wheat genotypes as a supplement to maize techniques.

#### 4. Breeding Challenges

Durum wheat breeding is considered to be one of the most cost effective and environmentally safe ways to meet the future challenges that durum wheat productivity will face due to climate change. The durum wheat is cultivated in rain-fed farming systems in Mediterranean basin. This is mainly connected with the high temperatures and drought that are expected to become more severe the next years and affect the cultivation across the Mediterranean [141]. In this context, investment in the productivity of rain-fed areas that cover a significant portion of Mediterranean countries could contribute to food security and rural growth. The UN reports several strategies for agronomic practices based on output and productivity in semi-arid areas, including the use of adaptable varieties, which is considered a very effective practice [142]. Breeding programs must be even more efficient due to the upcoming climate change effects and increased food demands. The identification of genetic resources and the study of genetic variability will provide further information regarding the increased tolerance of durum wheat under abiotic and biotic stresses. This could contribute to the increase and stability of production in future adverse climatic conditions. In this way, genetic studies for the identification of QTLs/genes that control important agronomic traits [82,143–145] and disease resistance [146] could also help. The identification of genomic regions that affect valuable target traits is known as quantitative trait locus (QTL) (or linkage) mapping, and it is a useful tool for the exploitation of loci that are co-segregating with traits of interest in a population [147]. QTL studies have been widely conducted on durum wheat for the genetic dissection of important breeding traits using diverse molecular markers and detailed genetic maps. Maps were used for the identification of QTLs controlling several characteristics, such as grain yield and kernel characters [82,148], grain-milling traits [149], and quality traits like endosperm color [150], grain protein content [151], and other pasta quality traits [152]. In extended experiments, including 249 recombinant inbred durum wheat lines evaluated in 16 environments, it was found that two major QTLs on chromosomes 2BL and 3BS have consistent effects across different environments [82]. Also, a QTL for plant height was identified on chromosomes 1BS, 3AL, and 7AS, and three QTLs for heading date were identified on chromosomes 2AS, 2BL, and 7BS. Moreover, 76 QTLs were identified for yield components along with several morpho-physiological traits (peduncle length, the Normalized Difference Vegetation Index (NDVI), and leaf greenness at the milk-grain stage expressed in Single-photon Avalanche Diode (SPAD) units) [143]. In a study under salinity conditions, four SSR markers were closely linked with grain yield, which could thus be used in the improvement of durum wheat through MAS under abiotic stress [144].

It is also expected that climate change will affect the vulnerability of durum wheat in different diseases [153,154]. Biotic resistance has also been investigated for the identification of QTLs that confer resistance to fungi [155] or pests [156]. Additional QTL studies use even greater genetic diversity, such as multiparental crosses for the identification of yield-related QTLs [157]. Abiotic resistance has also been under investigation for the identification of QTLs. A genome-wide association study of a durum wheat core set using 7652 Single Nucleotide Polymorphism (SNP) markers allowed the identification of major QTLs controlling the adaptation to heat stress [145]. Additionally, 12 loci were found to control the main heat tolerance traits; among these loci, three activated only when heat stress occurred. Moreover, two loci validated in a Kompetitive Allele Specific PCR (KASP) marker, are ready for deployment via MAS and could result in increased productivity in heat-stressed areas and improved resilience to climate change. A haplotype analysis of 208 elite lines confirmed that those with positive allele at all three QTLs had an 8% higher yield in a heat-stressed field environment [145].

Another important parameter is the durum wheat quality in terms of its protein content, endosperm texture, and glutenin content, which cannot be easily measured phenotypically. However, the methods for testing quality are typically costly, time-consuming, and need relatively large amounts of grain, which are available only in the late stages of breeding programs. Thus, markers for wheat quality traits can be very useful to enable the screening of a high number of lines and can be used early in breeding programs [158,159]. The durum wheat breeding programs carried out over the 20th century have focused on an increase of yield in combination with quality characteristics for pasta

products [52,160–162] and the achievement of better adaptability under Mediterranean conditions [52]. Little attention has been given to increasing other grain health-promoting components and nutritive constituents of durum wheat, such as dietary fibre (DF), total and soluble arabinoxylan content, and beta-glycan in semolina. There are indications that intense breeding either increases or does not affect these parameters in modern cultivars compared to old cultivars [88], indicating that the breeding process may contribute to a further improvement of durum wheat's nutritive characteristics.

Thus, markers for wheat quality traits can be very useful to enable the screening of a high number of lines and can be used early in breeding programs [158,159]. Six QTLs explained 49%–56% of grain protein variations [163], and seven QTLs explain 62%–91% of the sodium dodecyl sulfate (SDS) volume [160] in durum wheat germplasm. A number of markers targeting different glutenin alleles have been referenced, including markers for *Glu-B1* alleles, based on the sequence variations of Bx type genes [161]. Further, MAS succeeded in increasing pasta-quality-associated properties through the transfer of significant QTLs, such as the *Gli-B1* locus containing  $\gamma$ -gliadin 45 and the *Glu-B3* locus containing Low Molecular Weight (LMW)-2 type glutenins [162].

#### 4.1. Seed Storage Proteins and Quality

Seed storage proteins are prolamins that account for 80% of total grain proteins, and their role is crucial in determining the technological properties of durum wheat end products [57]. Prolamins are alcohol-soluble and can be classified according to their electrophoretic mobility in two classes: monomeric gliadins and polymeric glutenins. The former can be further classified as  $\alpha$ ,  $\beta$ ,  $\gamma$ , and  $\omega$  gliadins or as the high and low molecular weight glutenin subunits (HMW-GS and LMW-GS respectively) [57]. Many reports have discussed the effects of gluten protein composition on durum's end products [164,165]. These effects are either genotypic or environmentally dependent [166,167]. It is well established that certain HMW and LMW glutenin subunits affect the end product quality differently in durum wheat. For example, HMW GS 7+8 alleles are associated with better quality compared to allelic HMW-GS 20 [110]. For LMW-GS, it has also been demonstrated that certain subunits encoded by the loci located on chromosome 1B (*Glu*-) positively (LMW -2 group of subunits) or negatively (LMW-1 group of subunits) affect pasta-making properties [168].

Wheat gliadin is also characterized by high intervarietal polymorphism, and most individual cultivars show unique electrophoretic patterns [169–171]. In durum wheat, the presence of components  $\gamma$ -42 and  $\gamma$ -45 encoded by allelic genes on chromosome 1B is reported to affect the viscoelastic properties of gluten [172]. Gliadin  $\gamma$ -45 is associated with a group of LMW-GS subunits termed LMW-2, and  $\gamma$ -42 is associated with LMW-1 glutenin subunits. Gliadin  $\gamma$ -45 could be used as a genetic marker for high gluten quality, whereas gliadin's  $\gamma$ -42 component could serve as a genetic marker for poor gluten quality. Also, gliadin alleles were found to be correlated with resistance to cold and stem rust [173]. Finally, in breeding programs, knowledge of the allelic composition at each locus is beneficial in identifying and using the genotypes that carry the most promising qualitative traits.

#### 4.2. Seed Quality Characteristics Connected with Human Health

The durum wheat breeding programs carried out over the 20th century mainly focused on increasing yield in combination with quality characteristics for pasta products [52,174–176] and the achievement of better adaptability to Mediterranean conditions [52]. Little attention was given to other grain health-promoting components. It has been suggested that intensive breeding has led to decreased contents of health-promoting components in modern wheat cultivars [177]. Recently, several researchers have investigated, in detail, the other nutritive constituents of durum wheat, such as dietary fiber (DF), that have many health benefits; it was found that intense breeding has not decreased DF in the modern cultivars compared to the old ones [88]. It was also observed that the total arabinoxylan content in wholemeal or semolina is not differentiated between recent and old genotypes, while modern cultivars have higher proportions of soluble arabinoxylan in wholemeals and



of beta-glycan in semolina compared to the old genotypes [88]. These results show that the breeding process could contribute to further improvements in durum wheat's nutritive characteristics.

Apart from its value as a source of nutrients, wheat may cause inflammatory immune reactions and disorders like wheat allergies, celiac disease and non-celiac wheat sensitivity (NCWS), fructose malabsorption, and irritable bowel syndrome (IBS), highlighting the need for less-reactive wheat products that can contribute to quality of life improvements [81,178]. Wheat proteins, including gluten and non-gluten proteins like amylase/trypsin inhibitors (ATI) and others, are characterized as triggering factors. Recent studies have sought to investigate the underlying causes of these immune reactions [178]. According to the types of reactions caused, wheat-related disorders are classified as: (a) allergies, including immunoglobulin E (IgE) and non-IgE mediated allergic reactions; and (b) autoimmune, including celiac disease and herpetiform dermatitis [179]. Several studies have focused on the factors that affect the immunostimulatory capacity of allergic factors present in cereals, since it has been reported that short immunotherapy may represent a valid way to treat the disease [179,180].

Recent comparative studies on the nutritional characteristics of old and modern durum wheat genotypes have found that the breeding process improves durum wheat's gluten quality both in terms of its technological performance in producing high-quality pasta products and its allergenic potential [57]. More specifically, in modern cultivars, a higher gluten index was found to be connected to increased glutenin content. Further, the breeding process contributed to the drastic reduction of a significant allergen in wheat-dependent exercise-induced anaphylaxis (WDEIA), while the old and modern durum cultivars were not different in their  $\alpha$ -type and  $\gamma$ -type gliadin content, the former being considered a factor associated with celiac disease toxicity [57]. Despite the existence of allergens in wheat grain, there is genetic variability within wheat's genetic resources, and further research is necessary for the identification and the development of cultivars with lower reactivity and/or higher secondary health-promoting ingredients to meet the different needs of consumers [81,174].

## 5. Future Prospects

Modern genome-wide association studies (GWASs) offer the advantage of performing association analyses using the association of each marker and the phenotype of interest that has been scored across a large number of unrelated genetic materials. Furthermore, GWASs take advantage of the higher number of gene recombinations used within the panel compared to linkage mapping where meiotic recombinations are limited. As a consequence, the aim of a GWAS is to locate important QTLs for complex characteristics by employing diverse germplasm collections and modern molecular markers. GWASs are complementary to QTL mapping [181]. GWAS studies have been conducted on bread wheat to analyze important characteristics. A genome-wide association study of a durum wheat core set using 7,652 single nucleotide polymorphism (SNP) markers facilitated the identification of a major QTL controlling adaptation to heat stress [145]. Additionally, 12 loci were found to control the main heat tolerance traits; among them, three were activated only when heat stress occurred. Twenty-nine QTLs for three different yield components were identified by a GWAS in a panel of 233 tetraploid wheat accessions, including durum wheat accessions, using SNP markers [182]. GWAS is a valuable tool for breeders since broad genetic resources can be screened for market-trait associations. Germplasm collections that contain a wealth of useful genes for valuable traits such as disease resistance could be used to identify possible sources of resistance.

A GWAS that focuses on drought tolerance and 17 other agronomical traits was conducted for 493 durum wheat accessions; this study identified a putative QTL that controls drought tolerance [183]. Two QTL hotspots related to stress tolerance and yield were identified on chromosomes 2A and 2B using 6211 diversity array technology (DARtseq) SNPs on a panel consisting of 208 durum wheat lines [184]. Other GWAS studies have focused on other traits, such as disease resistance [185–188] and important quality traits. Marcotuli et al. [189] identified 37 marker-trait associations and 19 QTLs, possibly underlining arabinoxylan content in the grains of 104 tetraploid wheat genotypes. Arabinoxylans have been shown to have various health benefits. Furthermore, the co-migration of

QTLs for grain protein content and the candidate genes related to nitrogen metabolism found in a study of a durum wheat germplasm collection show that such approaches can be applied to MAS breeding schemes [190].

The rapid development of next-generation sequencing (NGS) technologies has facilitated the discovery of vast numbers of SNPs across genomes. SNP markers are now popular molecular markers because they are ubiquitous in plant genomes and are very easy and cheap to score. The high-throughput genotyping of wheat varieties is now applied routinely, especially after the construction of specific genotyping arrays and the sequencing of wheat genomes. A recently-developed genotyping array for wheat that includes 90,000 gene-associated SNPs is aiding the fast identification of genetic variation that underlines trait variation in wheat genetic materials [191]. This genotyping array contains mostly bread wheat SNPs, but also includes a large number of durum wheat SNPs. A total of 90 k genotyping wheat arrays have also helped in the construction of a detailed SNP-based genetic map based on 140 RILs developed from a cross between a wild emmer wheat population and a durum wheat cultivar [192]. More genetic maps are available today for durum wheat [193]. The durum wheat genome was only recently sequenced, revealing more valuable information about the crop's genome evolution during domestication and selection [194]. It is expected that this genome will aid in clarifying marker–trait associations and facilitate exploration of the genes underlying important characters. Durum wheat transcriptomes have also become increasingly available, thus aiding MAS breeding [195,196]. Genome sequencing is providing breeders with precise info about the nature of the genome changes in their breeding lines. Furthermore, genetic information obtained by DNA sequencing and extracted with the use of advanced bioinformatics tools will help in the application of new DNA-marker platforms and is expected to help enormously in genomics-assisted breeding for yield and quality. NGS has made possible the development of the first mutant library for wheat, which is now available publicly [197] while plenty of DNA information has been deposited in public databases accessible to scientists working on wheat all over the world.

Genotyping-by-sequencing (GBS) identifies genome polymorphism (SNP) NGS technologies, which facilitate the discovery of genetic variation in natural populations of many plants, including wheat. GBS is a useful tool and has revealed that winter durum wheat lines have significant genetic diversity, which is crucial for breeding [198]. DArTseq and SNP markers based on GBS technology were used to survey the genetic variation and the genomic characterization of 91 durum wheat landraces from Turkey and Syria, revealing extensive mixing of landraces between the two geographical regions [199]. The use of GBS in a large wheat accession collection resulted in the discovery of thousands of new SNP variations for drought and heat stress tolerance [104], which is useful for improving the elite wheat pool and enriching it with novel drought and heat tolerance genes. According to Sehgal et al. [104], this unexploited genetic variation can further improve the drought and heat stress tolerance of the elite wheat pool and enrich it with novel drought and heat tolerance genes. As the ultimate MAS tool, GBS can effectively facilitate breeding.

Furthermore, a very promising modern tool in plant breeding is genomic selection (GS). GS is a strategy used to predict the genetic value of selection candidates based on the estimated genomic breeding value, which is predicted using high-density molecular markers that are dispersed across the genome [200]. GS bases its success on the use of genome-wide markers to ensure that minor to medium effect QTLs cannot be left uncaptured unlike MAS, which focuses on the few markers linked to major genes [201]. GS models have shown high forward prediction accuracies and an enhanced genetic gain for semolina, as well as grain quality characteristics revealing that a combination of MAS and GS can be used effectively to select for quality traits [202].

The development of speed breeding is a very promising technique that could substantially help in this area. Speed breeding entails the use of specifically controlled-environment plant growth conditions and extended photoperiods of 22 h light/2 h dark that accelerates plant development. As a result, plant breeding speeds can reach up to 6–8 generations/year for wheat. Therefore, speed breeding accelerates genetic gain and significantly reduces the length of breeding cycles [203]. Specifically,

studies on durum wheat [204] have recently shown that the application of constant light and controlled temperature greenhouse conditions allow the rapid growth of durum wheat seedlings and the quick phenotyping for five important traits. Early selection in the F2 generation of a bi-parental cross has led to the significant improvement of traits like crown rot tolerance, root angle, and root number, thereby proving that a combination of speed breeding with early selection can facilitate the time and efficiency of breeding programs, as recombinant inbred lines can be provided with the desirable alleles [204]. For GWAS, using speed breeding, 393 durum Recombinant Inbred Lines (RILs) and DArT-seq markers have identified a major QTL for the seminal root angle on chromosome 6A [204]. Speed breeding coupled with genomics-based technologies and other advances in phenomics could yield significant progress in the rate of genetic gain in breeding schemes.

Genetically modified wheat has been developed previously [205,206], but today no GMO wheat is cultivated officially in any part of the world. However, new technologies like genome editing and its relevant protocols provide promising tools for the future. Transcription activator-like effector nucleases (TALENs) and clustered regularly interspaced short palindromic repeat (CRISPR)–associated protein 9 (Cas9) systems have been used on bread wheat to modify three homoalleles that code for mildew-resistance locus (MLO) proteins and a TaMLO-A1 allele, respectively, to make the wheat resistant to powdery mildew [207]. Detailed improved protocols for the application of CRISPR/Cas9-mediated mutagenesis are emerging; these protocols would help achieve fast and efficient gene targeting in wheat [208–210]. Furthermore, gene editing could be used in studying gene function. Resequencing of 1526 tetraploid and 1200 hexaploid wheat mutants created a database of 10 million sequenced mutations which, by more than 90%, result in truncations or deleterious amino acid changes [211]. More precise mutations can be introduced in wheat by gene editing and this, coupled with improved transformation technologies now evolving in wheat, would mean that researchers could be further helped in their efforts to introduce novel allelic diversity for breeding durum wheat and better understand basic gene function. However, since genetic modification in Europe is legally tightly regulated and gene editing has recently been ruled out as a form of genetic modification, the production of wheat cultivars based on these techniques has to be carefully considered in the future. Nevertheless, all modern biotechnological approaches (high throughput genome analysis, gene editing, genetic engineering, and proteomics and transcriptomics) are powerful tools to complement the classical methods of breeding. It is now proposed that genome assembly, germplasm characterization, gene function identification, genomic breeding, and gene editing constitute a comprehensive 5G approach in modern breeding that could help develop new varieties with a high yield, good quality, and strong resilience to changing climate conditions [212].

## 6. Conclusions

Classical breeding approaches will continue to play an important role in durum wheat improvement for the release of cultivars. Advances in DNA sequencing and other technologies, such as bioinformatics, statistics, and other scientific areas, could help breeders increase the efficiency and speed of a breeding program to meet humankind's growing demands for more food that is nutritious and sustainably produced. Ultimately, the use of new molecular biology technologies is essential, but also inexorably coupled with reliable and extensive testing under real field conditions.

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