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Wheat: A Crop in the Bottom of the Mediterranean Diet Pyramid

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Abstract

Wheat currently provides 18% of the daily intake of calories and 20% of proteins for humans. Since its domestication in the Fertile Crescent, wheat has been the basic staple food of the major civilizations of Europe, West Asia and North Africa. The wheat-growing area within the Mediterranean Basin represents 27% of the arable land, and the region represents 60% of the world's growing area for durum wheat, the species used for pasta manufacturing. Many changes have occurred from the low-productive plants cultivated in prehistoric times to the modern varieties that are now grown, which offer high productivity and quality standards. During the migration process of ancient forms of wheat from the east to the west of the Mediterranean Basin, both natural and human selections occurred, resulting in the development of local landraces characterized by their huge genetic diversity and their documented resilience to abiotic stresses. Wheat breeding activities conducted in the Mediterranean Basin during the twentieth century resulted in large genetic gains in yield and quality. New wheat varieties to be grown in the Mediterranean Basin will need to be resilient to climate change because more frequent episodes of higher temperatures and water scarcity are to be expected.

Keywords: wheat origin, wheat domestication, landrace, population structure, core collection, adaptation, productivity, grain quality, wheat breeding, genetic gains, yield, yield components

1. Introduction

Wheat is currently the most widespread crop. It is grown on about 219 million hectares all over the world (**Figure 1**) and is the basic staple food of mankind, providing humans with 18% of their daily intake of calories and 20% of their protein (<http://faostat.fao.org/>). The

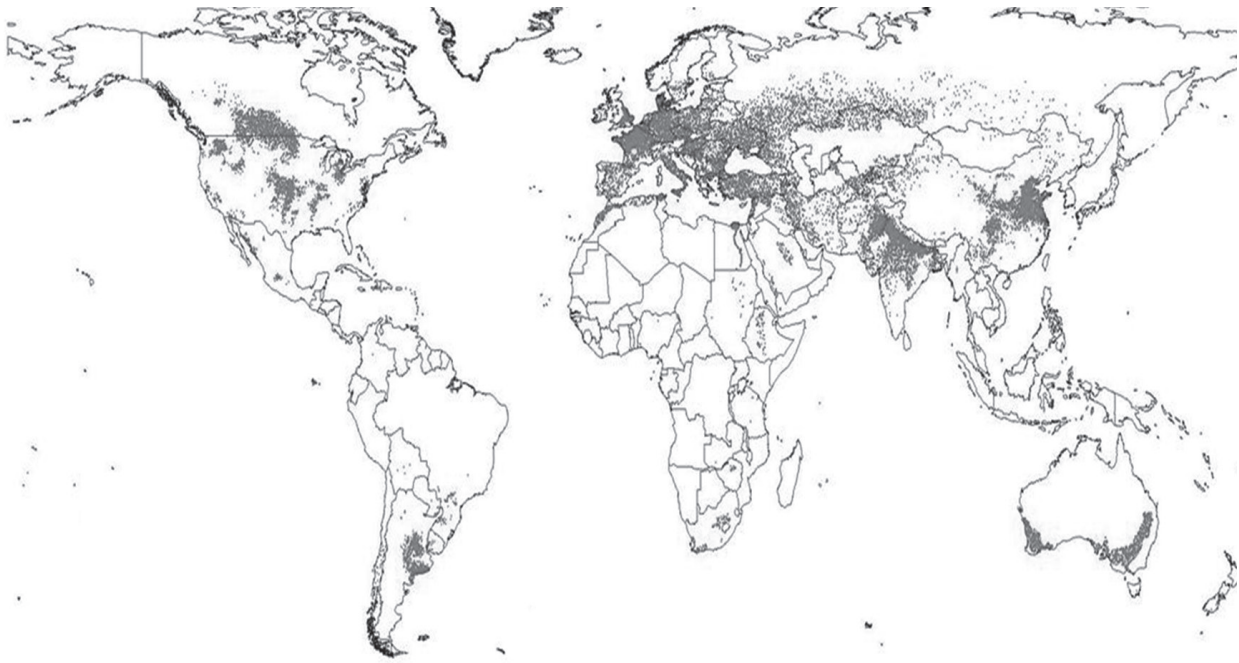


Figure 1. Global wheat distribution. Each point represents 20,000 t of grain production (modified from CIMMYT).

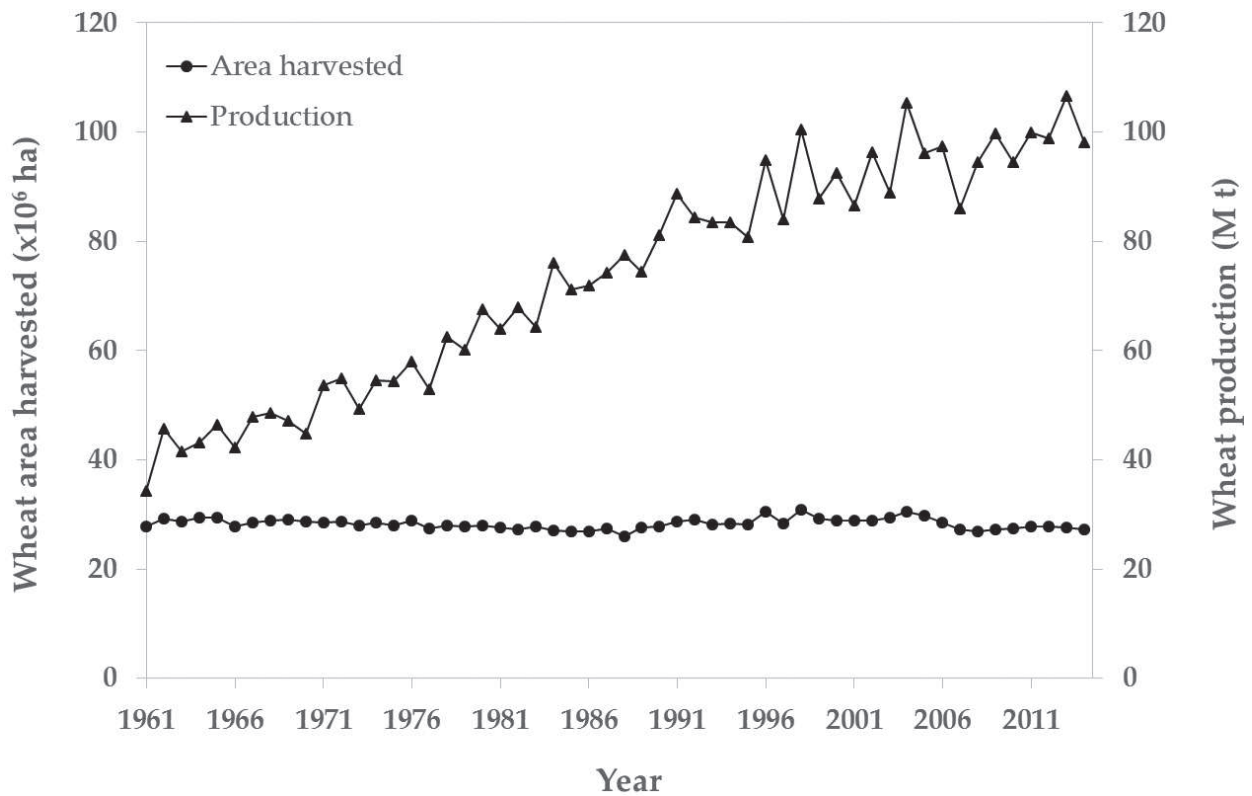


Figure 2. Total wheat harvested area and wheat production in coastal countries to the Mediterranean Sea from 1961 until 2014 (own elaboration from FAOSTAT data; www.fao.org/faostat).

wheat-growing area within the Mediterranean Basin represents 27% of the arable land (Figure 2), and the region represents 60% of the world's growing area for durum wheat, the species used for pasta manufacturing. The Mediterranean dietary traditions have often been related to health benefits and the prevention of cardiovascular disease [1]. The Mediterranean diet is the heritage of millennia of exchanges between people, cultures and foods of all countries around the Mediterranean Basin, and during the twentieth century, it has been the basis of food habits in all countries of the region, originally based on Mediterranean agricultural and rural models [2]. Cereals, and mostly wheat in the form of bread, pasta or couscous, form the base of the pyramid and are daily included as part of the main meals [3].

There are several species of the wheat genus (*Triticum*). The most widespread is common or bread wheat (*Triticum aestivum* L.), which occupies 94% of the total area cultivated with wheat, is mainly used for manufacturing bread and biscuits. Durum wheat (*Triticum turgidum* L. var. *durum*) is grown on about 13 million hectares, about 60% of them located in the Mediterranean Basin, where it is considered a typical crop. Durum wheat is mostly used for pasta making, but it is also the raw material for producing other traditional goods of Mediterranean countries such as flat breads, couscous and bulgur. The genetic differences between the two species lie in the number of chromosomes, as durum wheat is a tetraploid species (with 28 chromosomes in four sets), while bread wheat is a hexaploid species (with 42 chromosomes in 6 sets).

2. The origin of wheat and its spreading through the Mediterranean Basin

Wheat was one of the first domesticated food crops and its history is that of humanity. The domestication of wheat and the beginning of agriculture go hand in hand. Kislev [4] classified the data of wheat husbandry into three major phases: (i) the agro-technical revolution, which occurred within a still hunting-gathering society during the Natufian period (Epipalaeolithic, 13,000–10,300 BP); (ii) the domestication revolution (Pre-Pottery Neolithic 10,300–7500 BP); and (iii) the expansion of agriculture, mostly during the Ceramic or Pottery Neolithic (7500–6200 BP).

The crucial separation of individuals of the *Triticeae* tribe that resulted in the different cereal species (wheat, barley, rye, etc.) is believed to have occurred during the Pleistocene, a glacial epoch. The major climate changes that started on the eastern Mediterranean coast about 15,000 BP replaced the original cold and arid conditions with warmer and moister ones, thus allowing the expansion of grasses [5, 6]. Palaeobotanical investigations and other indications show that, from about 11,500 BP, the climate of the eastern Mediterranean region (Levant) became dry and cold [7] and the large variations in rainfall and temperature between years and seasons forced vegetation to make important changes in order to adapt to the new environmental conditions. It is believed that at that time, self-fertilization (autogamy) increased as a mechanism of reproductive assurance [8]. The growth habit of vegetation became annual and seed dormancy augmented, allowing seeds to overcome periods of harsh environmental conditions by remaining in the soil until conditions were suitable for germination [6]. It was

probably during this time that, somewhere along the Fertile Crescent, the hunter-gatherers who were accustomed to collecting grains of wild cereals, fruits and roots of other plants started to cultivate grasses [9]. It has been suggested that the Natufian tribe, who lived around Mount Carmel in present-day Israel and showed advanced preadaptive traits, or the dwellers in the Karacadağ Mountains in southeast Turkey may have been the first [4, 10]. This assumption is supported by genetic studies demonstrating that in this area, wild einkorn grass (a diploid ancestor species of wheat) contains an identical genetic fingerprint to modern domesticated wheat. As women had the primary responsibilities for plant gathering in hunter-gatherer societies, it is believed that they probably planted the first seeds. Einkorn (diploid), emmer (tetraploid) and spelt (hexaploid) are among the earliest cultivated wheats and are commonly referred to as 'ancient' wheats [11].

The first signs of cultivation of the so-called emmer (an awned wild wheat) correspond to the Pre-Pottery Neolithic A period (10,300–9500 BP), at the end of which all basic agricultural practices had already been established [6]. The transformation of some wild cultivated forms into domesticated wheats proceeded very rapidly from this stage. From the Karacadağ Mountains, emmer spread first northward and then southward. There is a general agreement that domestication occurred at the beginning of the Pre-Pottery Neolithic B (9500–7500 BP) [7, 12], when the spontaneous crosses between grasses that led to the appearance of bread wheat probably took place. Plant domestication was driven by humans' need to secure the greatest possible amount of food with the least possible labour.

Wheat domestication involved major morphological, physiological and adaptive changes in plants, most of them induced by humans. One of the clearest examples of the contribution of humans to domestication was the transformation of the spike axis from brittle to tough. In wheat ancestors, the spike became brittle at maturity, falling apart into small pieces (spikelets) containing the seeds, which were spread by wind and animals as an essential mechanism of propagation and survival. However, a small number of plants (those carrying a recessive allele conferring axis robustness) tended to develop robust spike axes, and this caused the seeds to remain together in the spike at ripeness without falling down. This feature was very beneficial for humans, as it allowed them to harvest complete spikes at ripening instead of unripe spikes. It is likely that seed collectors gradually increased the proportion of tough-axis spikes gathered, thus unconsciously favouring the tough-axis genes in the harvested grains, which led to a suppression of the brittle axis in domesticated wheats [13]. Thus, due to the loss of the seed-dispersal mechanism, wheat started to depend on humans for survival. Other important changes that occurred during domestication were the reduction of grain self-protection (due to the loss of the leaf-like glumes that covered each seed), which made the grains free-threshing, and the loss of seed dormancy, which favoured a uniform and rapid seed germination.

The establishment of agriculture in the Levant and the neighbouring regions was a very gradual evolutionary process that took place over a period of several hundred years [7, 12]. Studies conducted today to imitate different harvest techniques of wild wheats grown in a dense stand suggest that at that time, it was possible to obtain about 0.5–1 kg of pure grain per hour or 300–700 kg of grain per hectare or even more [14, 15]. This significant improvement led to a substantial population growth.

In the Ceramic or Pottery Neolithic, the wheat culture spreads from the western flank of the Fertile Crescent to southeast Europe through Transcaucasia, reaching the Balkan Peninsula and Greece in about 8000 years BP. Primitive wheat was transported by ships along the coast of the Mediterranean Sea to Italy and Spain (7000 BP) [5, 16] and south of Gibraltar. Two possible ways have been proposed for the introduction of durum wheat into the Iberian Peninsula: North Africa and south-eastern Europe [6, 17]. Wheat reached Egypt through Israel and Jordan [5].

After arriving in a given territory, wheat underwent a progressive adaptation to the varying conditions of the new area and gradually established new strategies for yield formation, which likely conferred adaptive advantages under the new environmental conditions [18]. During the dispersal of wheat along the Mediterranean Basin, the farmers took their habits wherever they went, not just sowing, reaping and threshing but also other well-established technologies such as baking and fermenting. This process of migration and natural and human selection resulted in the establishment of a wide diversity of local landraces specifically adapted to different agro-ecological zones. These dynamic populations with distinct identities are considered to be genetically more diverse than currently cultivated varieties (**Figure 3**); they show local adaptation and are associated with traditional farming systems [19].

The Mediterranean Basin comprises countries between 27° and 47°N and between 10°W and 37°E, including three continents with a coastline of 46,000 km. In this region, wheat is grown in a range of environmental conditions varying from favourable to dry land areas. In the Mediterranean



Figure 3. Variability in spike morphology in durum wheat Mediterranean landraces.

climate, most rain falls in autumn and winter, and a water deficit appears in spring, resulting in moderate stress for wheat around anthesis that increases in severity throughout the grain-filling period. However, the climatic conditions of the north and the south of the Mediterranean Basin have great differences. While the north has temperate and cold climates (classes C and D, respectively, according to the Koppen climate classification), the south has a dry climate (class B according to the same classification) [20]. Scientific evidence has shown that contrasting adaptation strategies occurred during the spread of wheat over the north (via Turkey, Greece and Italy) and south (via North Africa) of the Mediterranean Basin. The different climates prevalent in the zones of adaptation may have induced gradual changes in crop phenology and in the strategies used by wheat to form its yield during its dispersal from the east to the west of the Mediterranean Basin [21]. Royo et al. [18] demonstrated that the number of days to heading and flowering of traditional durum wheat varieties (landraces) increased from the warmest and driest zone of the Mediterranean Basin to the coldest and wettest one. Durum wheat landraces collected in the north of the Mediterranean Basin have been found to have more stems per unit area, more biomass, a higher proportion of biomass and leaf area allocated on tillers at flowering and heavier grains than those collected in the south [18, 21, 22]. African landraces of diploid, tetraploid and hexaploid wheats have been reported to carry genes for tolerance to physical environmental stresses [23] and are therefore better adapted to drought environments than those of northern countries [22]. Durum wheat landraces from southern Mediterranean countries allocate more biomass to the main stem, produce more grains per spike and per unit area and have higher harvest index than those from northern countries [21, 22]. These differences mean that grain yield of landraces collected in northern Mediterranean countries is mainly related to variations in grain weight, whereas grain yield of landraces collected in the drier and warmer southern countries is mainly related to the number of spikes per unit area [21].

3. Mediterranean wheat landraces

During the first few decades of the twentieth century, the wheat varieties grown in the Mediterranean were the so-called traditional varieties or landraces. Landraces resulted jointly from the evolution of wheat during its dispersal to new territories and from the role of humans in selecting large spikes for planting the next generation after the advent of agriculture. Landraces are heterogeneous in their shape because they are populations formed by sets of plants with different genetic constitutions. Their huge genetic diversity makes them a particularly important group of genetic resources. Knowledge of the genetic diversity and population structure of landraces is essential for their conservation and efficient use in breeding programmes. The first diversity studies used phenotypic markers of morphological and physiological traits, but DNA-based markers are currently extensively used as they are not affected by the environment and can be detected in all tissues at all developmental stages. Among them, microsatellites or simple sequence repeats (SSRs) have proven to be very useful for evaluating the genetic diversity and population structure of Mediterranean wheat collections [17, 24–29].

A number of studies have been conducted by our team to assess the genetic diversity and population structure of Mediterranean durum wheat germplasm. In all cases, the genetic structure of the landrace populations proved to be associated with the geographical origin of accessions. The study of Moragues et al. [17], which used a set of 63 durum wheat landraces from 12 Mediterranean countries, grouped the accessions in two clusters: (i) landraces from north and east of the Mediterranean Basin and (ii) landraces from North Africa and the Iberian Peninsula. These results support the hypothesis of two dispersal patterns of durum wheat in the Mediterranean Basin previously proposed by MacKey [6], one through the north side and one through the south side.

A recent study by Soriano et al. [29] classified a collection of 152 durum wheat landraces and old varieties from 21 Mediterranean countries into four subpopulations that showed an eastern-western geographical pattern (**Figure 4**): eastern Mediterranean, eastern Balkans and Turkey, western Balkans and Egypt and western Mediterranean. The genetic diversity found by Soriano et al. [29] was lower in the eastern Mediterranean group, indicating that the diversity of wheat increased during the dispersal from its area of domestication to the western Mediterranean Basin.

A study was carried out by Ruiz et al. [26] on a collection of 190 durum wheat Spanish landraces. The results showed that the diversity and agro-morphological traits were correlated with geographic and climatic features. The distribution of the collection in nine clusters was largely determined by the three subspecies, *dicoccon*, *turgidum* and *durum*, which were present on it, with an east-west geographic structure for *dicoccon* and a northeast-southwest structure

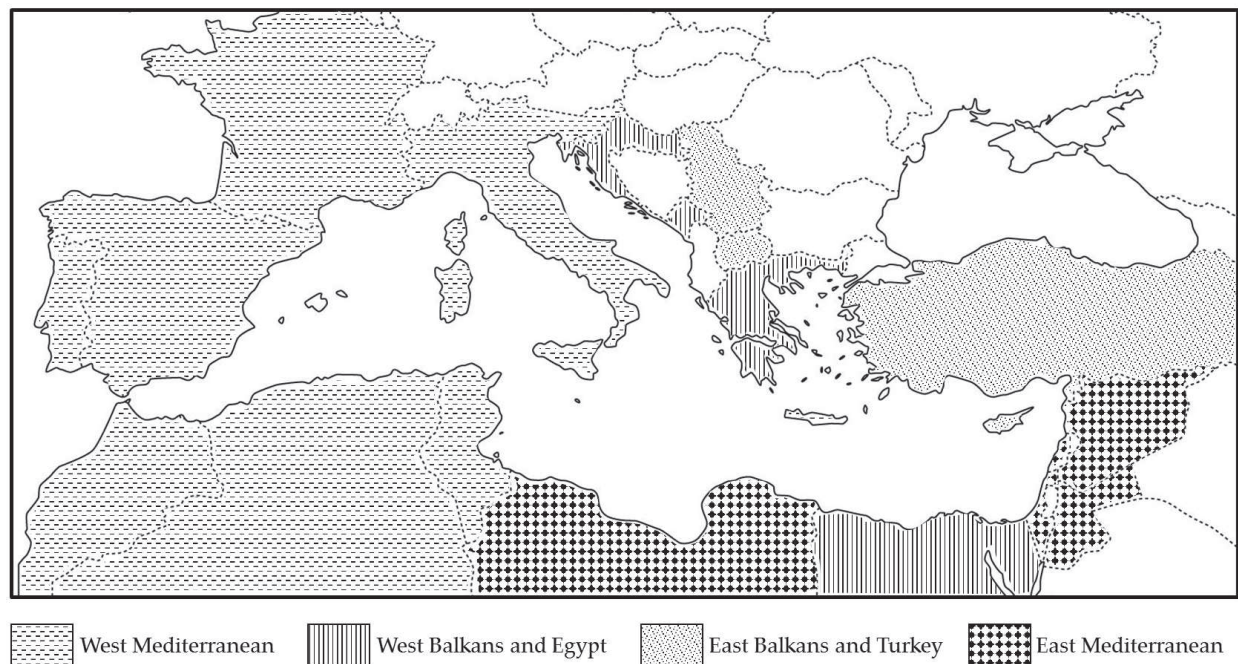


Figure 4. Genetic structure of the Mediterranean durum wheat landraces and old varieties reported by Soriano et al. [29] according to their countries of origin.

for *turgidum*. The results of the phylogenetic study showed that some *durum* accessions were more related to *ssp. turgidum* from northern Spain, while others were more related to *durum* wheats from North Africa [26]. These results also support the hypothesis of two possible forms of introduction of durum wheat in the Iberian Peninsula, South-East Europe and North Africa, as suggested by Moragues et al. [17].

During the last century, a large number of wheat germplasm accessions have been collected by Mediterranean gene banks. Western Mediterranean countries (Portugal, Spain, southern France, Morocco, Algeria and Tunisia) have been identified as one of the principal regions for collecting tetraploid wheats due to the variability gathered by local germplasm [23]. As the management of the whole collections is costly and inefficient, if the collection shows a significant level of redundancy, core collections consisting of a limited set of accessions that maximize the genetic variation contained in the whole collection with a minimum of repetitiveness [30] have been created. The bread wheat worldwide core collection formed by Balfourier et al. [31] from 3942 cultivars included 372 accessions, 149 of which came from 18 countries around the Mediterranean Basin. The accessions were grouped using molecular markers according to their geographical distribution—western and southern Europe, the eastern Mediterranean Basin, North Africa, Turkey, the Balkans and finally France—which was grouped with cultivars from central and northern European countries. The Spanish durum wheat core collection created by Ruiz et al. [26] includes 94 accessions representative of a collection of 555 Spanish landraces and old cultivars and contains a wide range of genotypes adapted to Mediterranean environments.

Mediterranean landraces have a good adaptation to Mediterranean environments. They can be considered as likely sources of putatively lost variability and may provide favourable alleles for the improvement of commercially valuable traits, especially in breeding for suboptimal environments. However, their plant height, general lateness and low harvest index limit the attainment of high yields, particularly when they are grown in intensive agricultural systems. A study by our team conducted on 154 durum landraces from 20 Mediterranean countries revealed that landraces from western Mediterranean countries had greater grain-filling rates and heavier grains than those of eastern ones [32]. The contribution of landraces in wheat breeding programmes also seems possible in terms of end-product quality, given the high level of polymorphism of key quality genes and the large genetic diversity found for quality traits between and within landrace populations [33–35]. It has been reported that specific Mediterranean durum wheat landraces may be used as sources of quality improvement for grain protein content, gluten strength, grain weight, test weight and general quality [32]. In order to identify durum wheat landraces as potential parents in breeding programmes for gluten strength enhancement, Nazco et al. [35, 36] analysed the allelic composition at five glutenin loci on a collection of 155 durum wheat landraces and old varieties from 21 Mediterranean countries and 18 representative modern cultivars. The results indicated that landraces with outstanding gluten strength were more frequent in eastern than in western Mediterranean countries. Only 9 different allelic combinations were identified in modern cultivars, but 126 in the landraces, 3 of them new with a positive effect on gluten strength [36]. Twelve banding patterns positively affecting gluten strength were identified in the landraces [35].

4. From local landraces to modern Mediterranean wheat cultivars

The pioneer breeders or entrepreneurial Mediterranean agriculturalists started selecting from within landrace populations (sometimes from foreign countries) the plants with the most favourable characteristics in terms of vigour, phenological adaptation, spike length and yield in order to produce superior lines. This pure-line selection did not entail the development of new genotypes as the improvement was only achieved by identifying and isolating the best lines already existing within the original landrace. This methodology was used by Nazareno Strampelli in Italy to release the durum wheat cultivar 'Senatore Cappelli' in 1915 from the Algerian population 'Jean Retifah' [37], by Enrique Sánchez-Monge Parellada in Spain to release the barley variety 'Albacete' from a selection within a local population, the bread wheat 'Aragón 03' selected by Manuel Gadea from a selection within the local variety 'Catalán de Monte' and the durum wheat varieties 'Andalucía 344' and 'Jerez 36' obtained in Spain by Juan Bautista Camacho from 'Manchón de Alcalá la Real' and 'Raspinegro de Alcolea', respectively [38].

The first organized wheat programme in France was implemented by the Vilmorin family in the eighteenth century [39]. When Mendel's laws were rediscovered at the beginning of the twentieth century plant breeding was established as a science, making crosses between varieties or breeding lines selected in the previous phase of breeding. The Italian breeder Nazareno Strampelli, considered the local promotor of the Mendelian findings, started to make crosses around 1900 [40]. In parallel, breeders started to interchange germplasm and to use foreign varieties or lines developed by their colleagues in other countries, for crossing with their best types. Farmer breeding was also encouraged by the collection and distribution of wheat seed from all over the world. In the 1850s, the harvest index (the partitioning of photosynthates between the grain and the vegetative plant) of most wheats was about 0.3 or less [41].

From around 1940, breeding programmes based on scientific findings were created in a number of countries. One of the most famous was the Rockefeller-Mexico programme, led by Dr. Norman Borlaug, which started in 1945, which used germplasm from different origins in his crosses. The particularities of Mexico allowed Borlaug's programme to grow two cropping seasons every year, thus speeding the breeding process. Using Norin 10, a Japanese variety, and the cross Norin/Brevor as a parental, Borlaug obtained 'semi-dwarf wheats' that yielded far better than the taller wheats grown in most parts of the world at that time. The incorporation of the dwarfing genes designated as *Rht-B1b* (formerly *Rht1*) and *Rht-D1b* (formerly *Rht2*) resulted in an increased earliness, a reduction in plant height and lodging without significant decreases in total plant dry weight and a larger allocation of resources in grains, thus improving the harvest index [41–44]. In addition, the incorporation of photoperiod insensitivity in the wheats developed in Mexico, as consequence of the shuttle breeding between contrasting environments, allowed them to be adapted to a wide range of environments all around the world, showing good adaptation to a number of environmental conditions. Semi-dwarf varieties have the capacity to redistribute the plant weight so as to allocate a higher percentage of it to the grain than in unimproved varieties. As a result, plant height decreased (**Figure 5**), but harvest index increased.



Figure 5. Field plots of a durum wheat landrace (left) and a semi-dwarf improved variety (right).

The semi-dwarf varieties developed in Mexico were rapidly adopted by Mediterranean countries, leading to the progressive abandonment of the cultivation of landraces. The adoption of improved semi-dwarf varieties was accompanied by the intensification of management practices to allow the semi-dwarf wheats to express their potentiality. The progress achieved for grain yield until 1982 was the result of combining improved varieties with appropriate crop management strategies. Sowing densities, application of fertilizers (particularly nitrogen), irrigation and the use of pesticides to control weeds and diseases increased resulting in yield rises in many countries. International Maize and Wheat Improvement Center (CIMMYT) was formally launched in 1966, and Norman Borlaug was honoured with the Nobel Peace prize in 1970 for his contribution to the Green Revolution.

Advances in yield during the twentieth century in Mediterranean countries due to variety improvement have been widely reported in the literature for bread wheat [43–45] and durum wheat ([42, 46] and references therein). The role played by the variety is generally ascertained by growing historical series of cultivars in a common environment. Following this approach, our group quantified yield increases during the last century in $35.1 \text{ kg ha}^{-1} \text{ y}^{-1}$, or $0.88\% \text{ y}^{-1}$ in relative terms, for bread wheat in Spain [43] and in 16.9 and $23.6 \text{ kg ha}^{-1} \text{ y}^{-1}$ (0.51 and $0.72\% \text{ y}^{-1}$ in relative terms) for durum wheat in Italy and Spain, respectively [47]. For both species, the modification of plant architecture by the introduction of dwarfing alleles played a major role in the achieved gains [42, 43], by reducing plant height and reallocating photosynthates in reproductive organs of plants with more grains per spike and improved tillering capacity [42, 43]. In Spain, changes of harvest index during the twentieth century have been estimated by our team to be from 0.25 to 0.40 in bread wheat [44] and from 0.36 to 0.44 in durum wheat [42, 48].

However, the GA insensitivity conferred by the dwarfing genes *Rht-B1b* and *Rht-D1b* resulted in grains of similar weight.

The effect of dwarfism was greater on the root system than on aerial biomass, reducing the aerial biomass of each plant at anthesis by 7.6% and the root by 28.1% [49]. However, despite their reduced root biomass, modern cultivars are more responsive in terms of yield and number of grains per spike to environments with high water input after anthesis [50]. Breeding also improved adaptation to Mediterranean conditions by reducing cycle length to flowering [44, 51], thus benefiting grain setting [46] and improving photosynthesis during grain filling [44] in environments characterized by terminal stresses. The adaptation pattern of bread wheat changed towards varieties with a wider adaptation to variable environmental conditions and spring types that performed better than landraces in environments with high temperatures before heading [52]. However, our results also evidenced a slowdown in bread wheat yield increases since 1970 [43]. Breeding activities improved the overall processing quality of wheat for making bread and pasta. Although most modern cultivars have less grain protein content than traditional varieties, breeding activities during the twentieth century in Mediterranean countries resulted in an improvement of global grain quality in both bread and durum wheat [44, 53].

Comprehensive information about the history of wheat breeding in Mediterranean countries may be found in Bonjean et al. [39, 54] and Royo et al. [55].

Although the Green Revolution was critical for raising wheat production enough to mitigate the effect of rapid demographic growth, it affected the natural habitat of wheat. Landraces and pure-line cultivars obtained through mass selection from them during the first decades of the twentieth century were widely grown until the late 1960s, but due to the massive introduction of the homogeneous and more productive semi-dwarf cultivars released since the Green Revolution, they practically disappeared from farmer's fields. Particularly, in the domestication area of wheat and the Mediterranean regions, which are the reservoir of the greatest genetic variability of the species, wild relatives and landraces were displaced by improved varieties. In consequence, the variability present on farmer fields due to the cultivation of old unimproved varieties (landraces) gave way to the genetic uniformity of the most productive modern cultivars. The decrease in cultivar diversity and the loss of the natural variation present in landraces increased the genetic vulnerability of wheat crops [23] and led to a loss of the diversity exploitable by plant breeders, the so-called genetic erosion. Among the factors that have been reported to contribute to the narrow genetic background underlying successful modern wheat varieties, the reduced number of ancestors and the relatively small number of varieties cultivated at present are among the most significant [56, 57].

Another important change derived from the advent of modern cereal culture was the requirement of field uniformity, which led to the planting of large extensions of a single variety or a small number of varieties, managed under similar cultural practices. This homogeneity is very convenient from the industrial and commercial viewpoints as it allows sets of tons of wheat grains with similar quality characteristics to be obtained. However, it most likely increases the vulnerability to diseases as the pressure exerted by large extensions of uniform varieties pushes the races of fungal species to mutate, and to very rapidly overcome the genetic resistance of cultivars [58].

5. Future prospects

Several global and regional climate models suggest that the Mediterranean Basin might be an especially vulnerable region to global change [59]. A pronounced decrease in precipitation and warming are projected, particularly in the summer season, with large interannual variability leading to a greater occurrence of extremely high-temperature events [59, 60]. The impact of agricultural practices on climate change has redesigned the breeding paradigm. While past yield improvements relied on the development of improved varieties that needed the intensification of agricultural practices to maximize yields, the new released varieties have to be able to produce with the minimum environmental impact, that is, they must fit into the concept of 'sustainable agricultural ecosystems'. This entails their genetic adaptation to environmental conditions, making it unnecessary to modify the environment through the use of non-sustainable practices to cover the variety requirements, as was the case in the past. This is a huge challenge for breeders, as wheat breeding today largely depends on the incorporation in improved varieties of adaptive traits for specific environments.

Given that most traits useful for improving the adaptation of modern cultivars to abiotic or biotic constraints cannot be found in modern cultivars, in many cases the enlargement of the genetic variability has to be sought in local landraces and close-related species. The high genetic diversity of landraces buffers them against spatial and temporal variability and upgrades the resilience to abiotic and biotic stresses in comparison with modern varieties [61, 62]. The essential role of landraces as likely sources of highly beneficial untapped diversity has led them to be considered essential for food security because they are potential providers of new favourable genes to be incorporated into modern cultivars. However, as the genetic variation contained in them is usually unknown, the effective use of landraces in breeding programmes will make necessary to evaluate the existing diversity in the gene pool and to characterize the available accessions [62]. Detecting the presence of variants of potential interest for breeding purposes in landraces may be particularly useful in situations of breeding for suboptimal environments.

Among the set of wheat landraces, the ones coming from the Mediterranean Basin are considered to hold the largest genetic variability within the species as shown by the genetic variability found in Portuguese [63] and Spanish [34] wheats. Mediterranean wheat landraces are considered as a potential genetic resource of drought resistance, frost tolerance and biotic and abiotic stresses in general. In addition, as mentioned above, an increase in the available genetic variation through the use of landraces in breeding programmes seems possible in terms of yield component enhancement and end-product quality.

The enormously expanding potential of recently developed technologies offers opportunities for improvement of plant traits and agricultural management that were inconceivable few decades ago. Genomics offers new opportunities to dissect traits of quantitative inheritance and chromosomal regions whose allelic variation may be statistically associated with a specific trait. During the last few decades, several types of molecular markers have been used for wheat genetic studies, providing effective genotyping but resulting costly and time-consuming due to the low number of markers to be screened in a single reaction. In the last few years, the advances in next-generation sequencing (NGS) technologies has reduced the costs of DNA

sequencing to the point that genotyping based on sequence data is now feasible for high-diversity and large-genome species. New high-throughput platforms have been developed in bread wheat, such as single nucleotide polymorphism (SNP) arrays [64, 65] and genotyping by sequencing (GBS) platforms, e.g., DArT-seq, developed by Diversity Arrays Technology Pty Ltd (Canberra, Australia). In early 2017 the bread wheat genome sequence was released providing wheat researchers with a new resource to identify the most influential genes that are important to wheat adaptation, stress response, pest resistance and improved yield. Recent scientific breakthroughs in genome-editing technologies, such as the clustered regularly interspaced short palindromic repeat (CRISPR), have opened new avenues for accelerating basic research and plant breeding by providing the means to modify genomes rapidly in a precise and predictable manner [66]. With recent biotechnology developments, advances in statistics, precision agriculture and information technologies such as geographic information system (GIS), remote sensing and the exploitation of big data among other new tools will hopefully help to meet the challenges of breeders and agronomists in the next few decades.

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