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Genetic approaches to exploit landraces for improvement of *Triticum turgidum* ssp. *durum* in the age of climate change

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Addressing the challenges of climate change and durum wheat production is becoming an important driver for food and nutrition security in the Mediterranean area, where are located the major producing countries (Italy, Spain, France, Greece, Morocco, Algeria, Tunisia, Turkey, and Syria). One of the emergent strategies, to cope with durum wheat adaptation, is the exploration and exploitation of the existing genetic variability in landrace populations. In this context, this review aims to highlight the important role of durum wheat landraces as a useful genetic resource to improve the sustainability of Mediterranean agroecosystems, with a focus on adaptation to environmental stresses. We described the most recent molecular techniques and statistical approaches suitable for the identification of beneficial genes/alleles related to the most important traits in landraces and the development of molecular markers for marker-assisted selection. Finally, we outline the state of the art about landraces genetic diversity and signature of selection, already identified from these accessions, for adaptability to the environment.

KEYWORDS

triticum turgidum ssp. *durum*, landraces, genotyping, breeding, molecular markers, climate change, abiotic stress

Introduction

Durum wheat (DW) (*Triticum turgidum* L. ssp. *durum*) (Desf.) is the 10th most cultivated cereal worldwide, with a total production of about 38 million tons (Xynias et al., 2020). DW is grown primarily in the Mediterranean basin, accounting for 75% of global production, supported mainly by Italy, Spain, France, Greece, Morocco, Algeria, Tunisia, Turkey and Syria (Table 1). In addition, outside the Mediterranean basin, the major producers are Canada, Mexico, the USA, Russia, Kazakhstan, Azerbaijan, and India (De Vita and Taranto, 2019; Martínez-Moreno et al., 2022). Although DW production constitutes only 7% of total wheat production, the rest is produced from bread wheat (*Triticum aestivum*), its importance for the countries of the Mediterranean basin is pivotal. DW is considered a staple food as it

TABLE 1 Durum wheat of the major producer countries in European Union: area, production, yield and growing seasons (source: DG Agriculture and Rural Development based on Eurostat crop production annual data).

Country	Durum wheat area (thousand hectares)			Durum wheat production (thousand tonnes)			Durum wheat yield (tonnes/hectare)			Growing seasons
	2019	2020	2021	2019	2020	2021	2019	2020	2021	
EU	2,145	2,112	2,206	7,476	7,420	7,822	3	4	4	
Italy	1,224	1,210	1,229	3,849	3,885	4,065	3	3	3	July and August
Spain	267	251	298	704	787	744	3	3	2	June and July
Greece	254	263	220	684	794	573	3	3	3	From June to August
France	246	252	294	1,566	1,321	1,581	6	5	5	From June to August
Slovakia	44	34	49	188	174	292	4	5	6	From June to August
Hungary	37	27	30	162	121	160	4	4	5	From June to August
Germany	32	34	38	155	183	207	5	5	6	From June to August
Austria	17	17	19	81	79	88	5	5	5	From June to August
Others EU	26	25	29	86	75	113	n.a.	n.a.	n.a.	

constitutes the dominant part of the diet for many populations in this area. The main products derived from DW include pasta, cous cous, burghul, and bakery products. Durum wheat-based products have a low glycemic index which makes them healthy products that can be recommended for low-carb diets (Di Pede et al., 2021). Furthermore, DW constitutes the main food source for 1.2 billion poor people, providing 20/50% of daily calories, 20% of protein, and is considered a strategic crop for food security. Regarding the economic importance of DW, Italy is the world's largest producer of pasta with over 3.36 million tons/year of pasta produced, and the leading country for exports with 1.9 million tons/year (Altamore et al., 2020). On a cultural level, DW and its ancestor wild emmer (*Triticum turgidum* ssp. *dicoccoides*) have been at the foundations of food, from the Neolithic period to the Greeks and the Roman Empire, up to the present day (Martínez-Moreno et al., 2020). Its cultivation and processing constitutes a cultural heritage.

However, the on-going climate change threatens DW production and is subjecting this crop to stresses rarely experienced. In the Mediterranean area and western Europe, climate projections for the 2040-2070 interval warn that extreme drought events will become more frequent and severe due to decreased winter precipitation and increasingly dry springs (Spinoni et al., 2018). In a recent study, it was estimated that global warming may reduce the world's suitable areas for DW cultivation by 19% in 2050 and by 48% in 2100, with the greatest losses occurring in the Mediterranean basin which is recognized as a climate change hotspot (Shayanmehr et al., 2020; Martínez-Moreno et al., 2022). The main environmental constraints influencing the yield of DW in this area are drought, high temperatures, and salinity (De Vita and Taranto, 2019). These stresses, if occurring in growth stages such as flowering, pollination, and grain-filling, can strongly affect crop productivity.

This review aims to highlight the important role of durum wheat landraces as a useful genetic resource to improve the sustainability of Mediterranean agroecosystems, with a focus on adaptation to environmental stresses (Figure 1). We described the most recent molecular techniques and statistical approaches suitable for the

identification of beneficial genes/alleles related to the most important traits in landraces and the development of molecular markers for marker-assisted selection. Finally, we outline the state of the art about landraces genetic diversity and signature of selection, already identified from these accessions, for adaptability to the environment.

Durum wheat cultivation: An historical overview

Durum wheat (tetraploid, genome AABB, $2n=4x=48$) is a cereal grain evolved from the tetraploid domesticated emmer wheat *Triticum turgidum* ssp. *dicoccum* (Schrank ex Schübl.) Thell (Özkan et al., 2002). Domestication of wild emmer (*Triticum turgidum* L. ssp. *dicoccoides*) occurred in the Fertile Crescent (Israel, Jordan, Lebanon, Syria, south-eastern Turkey, northern Iraq, and western Iran) about 8000 years BCE (Before Common Era) from limited founder lineages (Özkan et al., 2002; Wang et al., 2022). Emmer wheat has been the main cereal together with einkorn and barley during the Neolithic period and the Bronze age. Then, it was progressively replaced by the tetraploid naked DW, spread by land through the Balkans and the maritime routes to the Mediterranean regions of Southern Italy, France, Spain, and Greece (Martínez-Moreno et al., 2020). Finally, DW became a prominent crop at about 300 BCE during the Hellenistic period. DW was commonly cultivated in the Roman Republic where the writers started to call it *Triticum* in Latin. Later, the early Islamic world and then the Arab empire further promoted the spread of the cultivation of DW through the Mediterranean areas by introducing several food types based on semolina (dry pasta and couscous). Until 1950-1955 most of the DW Mediterranean areas were cultivated with DW landraces, local accessions adapted to their place of origin (Martínez-Moreno et al., 2020). However, the first breeding activities were started in Italy in the early 1900s, resulting in the release of the most renowned cultivar Senatore Cappelli in 1915, by the breeder Nazareno Strampelli (Scarascia Mugnozza, 2005).

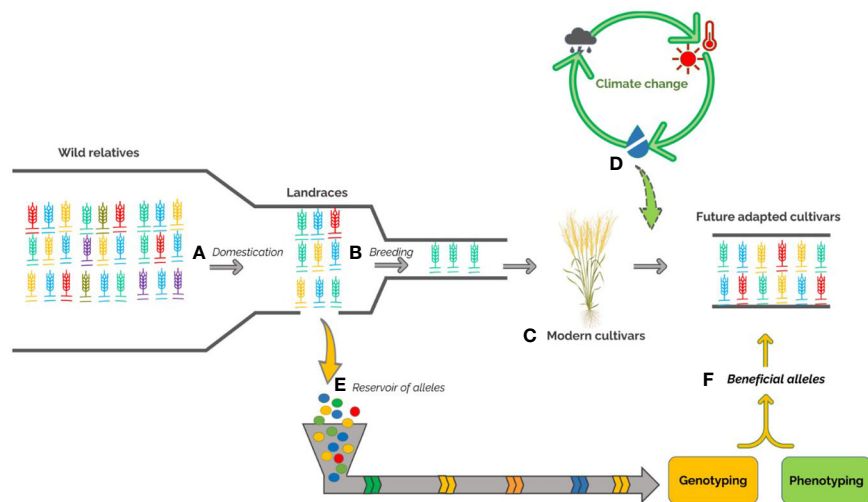


FIGURE 1

Development of durum wheat over time, including the loss of the diversity through the genetic bottlenecks of domestication (A) from wild relatives to the selection of landraces and plant breeding activities (B) moving from landraces to modern cultivars (C). The emergence of climate change (D) requires to broaden the genetic basis of modern cultivars. The exploration and exploitation of genetic variability within landrace germplasm (E) coupled to -omics approaches will be useful to discover beneficial alleles (F) and develop new modern cultivars best adapted to environmental changes.

Since then, the cv. Senatore Cappelli appeared in the pedigree of almost all new DW varieties due to its repeated use in DW programs until the end of the 1960s (Laidò et al., 2013). Afterward, the introduction of the law n. 580/67 for Pasta Purity gave the impulse to start the development of private seed companies and international research centers, such as CIMMYT and ICARDA. In particular, the development of the CIMMYT-derived semi-dwarf wheat varieties led to the Green Revolution in several countries. During the period between 1960'-90', breeding activities coupled with mutagenesis generated new genetic variability (Xynias et al., 2020) and efforts were made to release every year improved varieties with high yield potential and other interesting traits. Such more productive cultivars were preferred for cultivation over large areas. Therefore, the multitude of DW landraces planted for centuries was progressively replaced. This replacement has led to an important erosion of the environmental adaptation traits evolved during the years by the landraces.

Environmental challenges for durum wheat cultivation

The climate characteristics of the Mediterranean region have played a significant role in shaping the phenotypic (and the genotypic) configuration of both DW wild relatives and cultivated varieties. This basin is characterized by hot and dry summers, followed by cold and wet winters. Climate change, particularly important in the last decades, points to an increased variability, in which drought events, often coupled with heat waves, can hamper growth and development, eventually affecting crop yield. For example, yield is reduced of about 5% per Celsius degree of increase in temperature, with a gross loss reaching 24% under a growth temperature of 31°C during flowering (Liu et al., 2016). Clearly, the negative effect of the abiotic stress depends on its

duration and the phenological phase of the plant. For instance, sudden and extremely high temperature ($T > 32^{\circ}\text{C}$) for a short duration (3 to 5 days) is referred to as a *heat shock*, while moderately high maximum temperature (20 to 30°C) for a longer duration is known as *chronic heat stress* (Li et al., 2013). In DW, the most sensitive stages to heat stress are anthesis and grain filling (Chaparro-Encinas et al., 2021). Heat stress alters membrane fluidity and enzyme activity which in turn hamper respiration and photosynthesis, and related processes (e.g. electron flow and carbon fixation metabolism, starch accumulation and stability, architecture and functioning of thylakoids), as well as water assimilation and nutrient absorption and allocation in the plant body. After phase transition, this results in compromised pollen viability, aberrant macrosporogenesis, starch synthesis, and grain filling, responsible for the reduction in yield. Reduced water availability, due to both erratic or deficient rainfall and limited irrigation, worsens the negative effect of heat stress, hindering grain yield (in terms of seed number and weight) and technological quality and protein composition (Flagella et al., 2010). Drought stress is induced also by soil physical characteristics, which significantly affect water holding capacity and supply, influencing water and nutrient absorption by roots. Plants respond to drought and heat stress by enacting similar physiological mechanisms. Transcriptome analysis of heat susceptible and tolerant wheat revealed the involvement of multiple processes associated with tolerance to heat shock and drought stress, including the formation of deeper roots, synthesis of heat shock proteins, stomatal control, coordination of transpiration rate, and enhancement of osmoprotective response (Kulkarni et al., 2017). Also, the use of genome wide mapping approaches is providing abundant information about genomic regions associated to heat tolerance (Sukumaran et al., 2018).

Soil geo-biochemistry, geographical localization (sea proximity, with seawater intrusion into freshwater aquifers), and events of rising groundwater table can increase the amount of salts in soils. Moreover,

anthropogenic activities, such as inappropriate irrigation and drainage practices or irrigation with brackish water, determine salt accumulation in the soil surface or within the solum, causing salinity stress in plants (Annunziata et al., 2017). Soil salinity is usually referred to the increased amount of Na^+/Cl^- in the soil upper layer, but a variety of ions, mainly K^+ , Ca^{2+} , Mg^{2+} , and SO_4^{2-} , HCO_3^- , NO_3^- , can also accumulate. On one hand, salinity leads to permanent modifications of the soil structure by decreasing soil aeration, leaching, and infiltration rate, and increasing runoff and soil erosion (Edelstein et al., 2010). On the other hand, salinity affects plant physiology and growth. Stress effects harbored by salinity are usually due to both (i) cell toxicity of the accumulated ions, which often results in nutrient imbalance and enhanced oxidative stress, and (ii) osmotic stress, due to the extremely low water potential of soil along with a reduction in water assimilation. Therefore, cellular, and metabolic processes involved to counteract salt stress are comparable to those induced by drought (Munns et al., 2006). Interestingly, DW is conventionally considered a tolerant crop enduring up to 5.9 dS/m (De Santis et al., 2021). In field conditions with 10 dS/m NaCl, DW produced a reduced yield, compared with rice that died before maturity (Munns et al., 2006). Lower level of salinity reduces the leaf area and shoot biomass, while grain yield is not affected. Tolerance to salinity is associated with low rate of Na^+ root-to-shoot transport and higher selectivity for K^+ than for Na^+ . Indeed, a correlation between grain yield and Na^+ exclusion from the vegetative organs, together with the enhanced K^+/Na^+ discrimination in root absorption and xylem loading has been identified in tolerant genotypes (Munns et al., 2000), which confirmed xylem transport, as one of the main discriminants between sensitive and tolerant species (Davenport et al., 2005). Tolerance to salinity is a quantitative trait controlled by many genes. Moreover, it appears that the expression of genes responsible for salt tolerance depends on plant age and ontogeny. Also, environmental factors contribute to the large phenotypic variation reported, enhancing the difficulty of breeding programs aimed to improve salt tolerance (De Santis et al., 2021). In wheat, a QTL mapping approach has identified the locus *Nax1* (involved in limiting Na^+ translocation to the above-ground tissues and inducing salt tolerance), mapped to the long arm of chromosome 2A, responsible for almost 38% of phenotypic variation in low Na accumulation in the mapping population, and this locus, together with closely linked markers, are commonly adopted to select salt tolerant durum genotypes (Lindsay et al., 2004). Other characteristics of salt-tolerant genotypes include differential ion partitioning between aged and young leaves, cell osmotic adjustment contrasting osmotic stress, and early phase-transition, leading to a shorter growing season (Colmer et al., 2005).

Drought, heat, and salt stress, being linked to each other, induce the generation of reactive oxygen species (ROS), including hydrogen peroxide, superoxide, or hydroxyl radicals, which are continuously formed mainly in the cytosol, chloroplasts, and mitochondria (Laus et al., 2022). ROS have a significant role in signaling but, under stress conditions, their over-accumulation may be responsible for the oxidative stress characterized by membrane peroxidation, protein degradation, and DNA mutation, eventually leading to the death of the plant cell. Plant cells are usually equipped with a great variety of ROS scavenging enzymes including superoxide dismutase, catalase, and glutathione peroxidase, and antioxidants, such as ascorbic acid,

tocopherol or glutathione, which also contribute to ROS detoxification (Dvorak et al., 2021). Interestingly, the tolerance of DW genotypes to environmental stresses leading to ROS production has been widely associated with higher activities of scavenging enzymes, pointing to a role of these mechanisms in the drought and salt tolerance in particular genotypes (Laus et al., 2022). Therefore, they are a good candidate to be considered in DW breeding programs. Anyway, it should be stressed that as the DW sensitivity to stress is influenced by the phenology, also the antioxidant performance depends on the stress characteristics (severity and duration), on the stage of development at which the stress acts, and on the plant organs targeted. Finally, (as shown by the increasing literature on the topic, Li et al., 2013; De Santis et al., 2021), breeding programs should also keep the attention on the stress effect on quality traits of DW grains. Indeed, changes in grain content and composition, affecting technological and health quality (e.g. protein, starch and dietary fiber accumulation and composition, phytochemical, and health-related micronutrient accumulation), are incredibly susceptible to environmental clues and stress and must be taken into account when implementing the breeding programs.

Durum wheat landraces: An endless treasure

Many efforts are made by researchers and breeders to constantly look for new sources of genetic variability to improve the elite varieties for adaptation traits, to face climate change. The exploitation of the existing genetic variability, still available in landraces, is one of the best approaches to adopt. According to Camacho Villa et al. (2005), a landrace is “a dynamic population of a cultivated plant that has a historical origin, distinct identity, and lacks formal crop improvement, as well as often being genetically diverse, locally adapted, and associated with traditional farming systems”. It is the result of natural and/or farmer-mediated evolutionary forces that generated plants better adapted to the local climate/environmental conditions (Zeven, 1999).

They are considered a reservoir of useful alleles that can be exploited to broaden the genetic basis of important adaptation traits. Landraces are rich in micronutrients and have high concentrations in total phenol and antioxidant content, as well as in tocopherols, carotenoids, and lutein (Azeez et al., 2018). Since the landraces can tolerate abiotic and biotic stresses, their yield is lower than modern varieties (Tan, 2002). For this reason, landraces are no longer cultivated over large areas where the more productive cultivars are preferred. Anyhow, several landraces have been rediscovered and reused thanks to their adaptation to sustainable and low-input cropping systems. They produce a great amount of straw, which, when used for animals, can make them economically more convenient than modern varieties, or preferable for organic farming because of their greater competitive ability against weeds (Lemerle et al., 2001; Annicchiarico et al., 2005).

Indeed, thanks to the efforts of farmers and scientists, wheat landraces and old cultivars have been collected and conserved by *in-situ* or *ex-situ* strategies. The *in-situ* strategy relies on individual farmers who traditionally cultivate landraces for their production or are sponsored by the government or private companies. The *ex-situ*

conservation is managed by international institutions such as CIMMYT, ICARDA, and USDA or by national projects led by local universities (Adhikari et al., 2022). With the advance of modern technologies, phenotyping and genotyping are extremely affordable, and the landraces can be studied both for their conservation and for molecular markers development (Nazco et al., 2012; Marone et al., 2021). The exploration of genetic variability in landrace germplasm has become an issue of great global interest, mainly during the last two decades. Figure 2 shows how the number of publications related both to “plant breeding” and “landraces”, and “plant breeding” and “climate change”, have had a strong increase since 2005, when “The 2005 United Nations Climate Change Conference” took place and marked the entry into force of the Kyoto Protocol. From 2005 to 2021 the number of publications related to the plant breeding strategies, to cope with climate change, has grown exponentially. Also for “durum wheat” and “landraces”, it can be noted a similar trend, although the number of publications is scarce. Some works aimed to characterize specific DW landraces are reported in Table 2, which includes a list of the most important European landraces specially studied both for stresses and quality related traits.

Because of the genetically heterogeneous nature of landraces, which are in a constant state of evolution due to different factors such as ecogeographical area and conventional or modern breeding techniques (Casañas et al., 2017), the establishment of core collections represents an affordable cost approach to reduce the degree of co-ancestry redundancy and the genetic stratification in the landraces whole collections. The goal of creating core collections is to maximize the allelic richness at molecular markers and best represent variation at phenotypic traits, in order to define the smallest possible number of individuals that represents a more compact and manageable population. Core collections were made for Spanish, Indian, Iranian, and Israeli-Palestinian landraces (Etminan et al., 2017; Ruiz et al., 2012 and 2013; Frankin et al., 2021; Phogat et al., 2019; Chacón et al., 2020). In addition, a core set of landraces was developed starting from the Global Panel of Durum Wheat (GPD), reducing their number from 416 to 192 (Mazzucotelli et al., 2020 and Kabbaj et al., 2017). This approach is useful not only to represent whole

genetic diversity but also to enquire and identify new sources for interesting traits. For example, SNP markers associated to resistance to leaf rust, tan spot and *Stagonospora nodorum* blotch were identified using the core collection created from the Watkins collection (Martínez-Moreno et al., 2021, Halder et al., 2019). Moreover, the core collections have also been used for unlocking the genetic and morpho-physiological adaptation traits to semi-arid environments (Abu-Zaitoun et al., 2018) and to study agronomic and quality traits, such as root architecture, stem cross section, height, heading date and carotenoid content (Ruiz et al., 2018; Ávila et al., 2021; Requena-Ramírez et al., 2021).

Durum wheat genome and pangenome assemblies

The DW sequencing project has been carried out by Maccaferri et al. (2019) using the modern cultivar Svevo. The annotation led to the identification of 66,559 genes, where the gene density distribution reflects the QTL density distribution. The comparison between wild emmer Zavitan and Svevo genomes identified putative loci under domestication and selection, and localized the reduction in diversity mainly in the pericentromeric regions of the chromosomes (Maccaferri et al., 2019). However, in the evolution of DW landraces, the reduction of diversity was more spread along the genome as a consequence of breeding programs.

Resequencing techniques, such as whole genome resequencing, are not suitable for species with complex genomes, for which a reduction of genomic complexity prior to NGS-based SNP discovery is preferred (Borrill et al., 2019). In polyploid species such as DW, with a large genome size (about 10.45Gb) and a large proportion of repetitive sequences (> 85%), the presence of paralogous and multi-copy sequences adds complexity in classifying the correct scoring of SNPs at a single locus for SNP discovery (Sandve et al., 2010).

In the last decades, the number of sequenced genomes in crop species has continued to increase exponentially, highlighting the

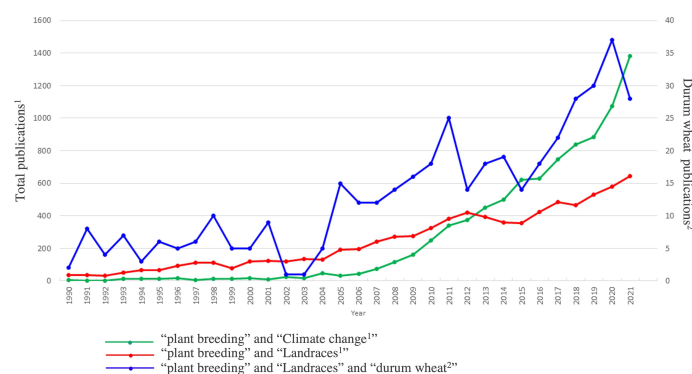


FIGURE 2

Number of publications in which climate change, landraces, and durum wheat are associated to plant breeding. The scale of the primary vertical axis shows the values for the associated data series in green: complete query = (“plant breeding” AND “climate change”) and red: complete query = (“plant breeding” AND “landraces”); the scale of the secondary vertical axis shows the values for the associated data series in blue: (“plant breeding” AND “landraces” AND “durum wheat”). The analysis is based on the information available in the Web of Science database (www.webofknowledge.com), category “Plant science”, considering the time interval of 1990–2021. Different keywords (i.e., “plant breeding”, “landraces”, “climate change” and “durum wheat”) and Boolean operators were used to query the database.

TABLE 2 List of the most important durum wheat landraces.

Country	Common name/Accession	Trait	References
Italy	Tumminia SG3	polyphenols profile and content	Lo Bianco et al., 2017
Italy	Scavuzza	polyphenols profile and content	Lo Bianco et al., 2017
Italy	Russello SG8	polyphenols profile and content	Lo Bianco et al., 2017
Italy	Ruscia	polyphenols profile and content	Lo Bianco et al., 2017
Italy	Manto di Maria	polyphenols profile and content	Lo Bianco et al., 2017
Italy	Margherito	polyphenols profile and content	Lo Bianco et al., 2017
Italy	Biancuccia	polyphenols profile and content	Lo Bianco et al., 2017
Italy	Bidi	suitable characteristics for malting and brewing	Alfeo et al., 2018
Italy	Francesca	suitable characteristics for malting and brewing	Alfeo et al., 2018
Italy	Gioia	suitable characteristics for malting and brewing	Alfeo et al., 2018
Italy	Giustalisa	suitable characteristics for malting and brewing	Alfeo et al., 2018
Italy	Inglesa	suitable characteristics for malting and brewing	Alfeo et al., 2018
Italy	Martinella	suitable characteristics for malting and brewing	Alfeo et al., 2018
Italy	Bufala Bianca	malt characteristics suitable for brewing	Alfeo et al., 2021
Italy	Bufala nera corta	malt characteristics suitable for brewing	Alfeo et al., 2021
Italy	Bufala rossa lunga	malt characteristics suitable for brewing	Alfeo et al., 2021
Italy	Russello	high content of antioxidant phenolic compounds	Visioli et al., 2021
Italy	Trentino	suitable characteristics for malting and brewing; polyphenols profile and content	Alfeo et al., 2018; Lo Bianco et al., 2017
Italy	Tripolino	polyphenols profile and content	Alfeo et al., 2018; Lo Bianco et al., 2017
Italy	Urria	polyphenols profile and content	Alfeo et al., 2018; Lo Bianco et al., 2017
Italy	Timilia	high content of antioxidant phenolic compounds	Taranto et al., 2022
Portugal	PI 192051	stem rust resistance sources	Aoun et al., 2019
Portugal	Aus26582	leaf rust resistance	Qureshi et al., 2018
Portugal	Aus26579	leaf rust resistance	Qureshi et al., 2018
Cyprus	IG-82549	glutenin protein composition	Moragues et al., 2006
Portugal	Lobeiro de Grao Escuro	having high EU quality index and high protein quality	Nazco et al., 2014a
France	Trigo Glutinoso	having high EU quality index and a high sedimentation index	Nazco et al., 2014b
Spain	BGE-013614	glutenin protein composition	Moragues et al., 2006
Spain	BGE018675	higher zeaxanthin relative content	Requena-Ramírez et al., 2021
Spain	BGE045643	higher zeaxanthin relative content	Requena-Ramírez et al., 2021
Spain	BGE045657	higher zeaxanthin relative content	Requena-Ramírez et al., 2021
Spain	BGE018321	higher relative β -carotene content	Requena-Ramírez et al., 2021
Spain	BGE045628	higher relative β -carotene content	Requena-Ramírez et al., 2021
Spain	BGE045633	higher relative β -carotene content	Requena-Ramírez et al., 2021
Spain	BGE030921	highest α -carotene content	Requena-Ramírez et al., 2021

presence of large structural variations between individuals of the same species. Therefore, relying on the single reference genome cannot represent the entire sequence diversity present in a population (Golicz et al., 2016). This observation led to the concept of “pangenome”, that

describes the landscape of genetic variation within a species, in order to capture a comprehensive view of genetic diversity that include the entire crop gene pool (Bayer et al., 2020; Khan et al., 2020). In the pangenome development, it is pivotal to consider the genetic variation

brought by the crop wild relatives, in order to include as much genetic variability as possible (Khan et al., 2020). In fact, wild species preserve important genes related to tolerance to various types of stress that were lost during the domestication process. The increasingly less expensive sequencing approaches have allowed to deepen the genetic architecture of the crop wild relatives leading, in the past decade, to several *de novo* sequencing projects developed also in crop wild relatives. In soybean, 14 cultivated and 17 wild accessions were resequenced, confirming the great allele diversity present in wild accessions (Zhou et al., 2015). In maize, 75 lines including cultivated, wild and landrace accessions were resequenced, highlighting the genes linked to selection and providing evidence for introgression from wild relatives (Hufford et al., 2012).

In wheat, the first pangenome has been constructed using the bread cv. Chinese Spring as suitable reference assembly, followed by the expansion of this reference with 16 additional sequences from other bread wheat varieties (Montenegro et al., 2017). Graph pangenomes based on 16 public assemblies (Wheat Panache) was developed with the aim to discover genome variation between cultivars and to mine the diversity present in the large and complex wheat genome (Bayer et al., 2022). However, the mathematical modeling of pangenome expansion revealed that all these wheat varieties have a closed pangenome; therefore, the inclusion of more distant accessions such as wild relatives and landraces could harbor yet unexplored sequence variants that may further increase the gene content of the pangenome. The use of divergent individuals may increase the number of novel gene variants as well as improve the accuracy of the read mapping for SNP discovery. The use of landraces can support the breeding of cultivars better adapted to diverse environments and more resilient to climate change; indeed, plant pangenome assemblies have shown that genetic variations are often associated with biotic or abiotic stress.

No pangenome has yet been assembled for durum wheat, although several projects are underway. Indeed, the use of Svevo genome as suitable reference may accelerate the sequencing of new durum cultivars enabling the pangenome construction. As far as is known, at the moment the only reference genome for durum wheat remains Svevo. Given the growing interest in some European landraces (Table 2), the release of new genome assemblies from landraces is expected in the next few years.

High-throughput genotyping techniques

Exome and RNA sequencing

A widely employed method for *de novo* SNP discovery and genotyping in large genome-size species is the exome sequencing. The workflow involves the fragmentation of high-quality genomic DNA, repair ends, adenylation, adapter ligation, and the selective hybridization of probes for target enrichment. Then two consecutive captures of the hybridization probes ensure high specificity of target region before the sequencing step (Kaur and Gaikwad, 2017). Ready to use exome kits and their customization are available for many crop species such as wheat (Harrington et al., 2019). Exome sequencing techniques have been used to identify polymorphisms and genes in the tetraploid wheat genome, also in combination with bulk segregant

analysis (Saintenac et al., 2011; Mo et al., 2018). In the last few years, thanks to the release of wheat reference genomes and annotations, this approach is increasingly used.

An alternative to exome capture is the high-throughput RNA sequencing which analyzes sequence variations in the transcribed portion of the genome. RNA-seq is the technique of choice for the identification of new genes and isoforms, and for the detection of variants including expressed SNPs and INDELS. Furthermore, this approach allows the identification of differentially expressed genes in plants under stress conditions. However, this technique is expensive since the reagents for the sequencing of the entire transcriptome are required. To overcome this problem, a new technique that is emerging also in plants (it is already widely used in human genetics) is the target RNA sequencing. This technique allows very high precision in the discovery and quantification of genes because it sequences only those of interest. The most important step of target RNA-seq is the design of the specific probes that can be customized to meet the specific needs of each experiment. Since only the genes of interest are sequenced, the coverage can also be very high, allowing to increase the power to assemble low expression transcripts (Ostezan et al., 2021).

Reduced representation sequencing (RRS)

With the decrease in the NGS cost, sequencing techniques are increasingly used as genotyping tools. However, to afford sequencing in large genome size species, reduced representation sequencing (RRS) approaches can be considered (Davey et al., 2011). Genotyping-by-Sequencing (GBS) is the most used technique to greatly reduce genome complexity using restriction enzyme(s) digestion (Elshire et al., 2011; Rasheed and Xia, 2019). The digestion occurs in the presence of a specific combination of enzymes recognizing rare-rare, frequent-rare, or frequent-frequent restriction sites. In wheat, since the complexity of the genome is very high, it is normally used a double enzyme digestion (Poland et al., 2012). The digested DNA is then ligated with adapters, amplified through PCR, and sequenced. The generated data are directly used for genotyping (Deschamps et al., 2012). Typically, the sequencing involves 100-150 bp. This technique has a simple protocol, specific and reproducible, with a reduced sample handling, without the need of a reference genome (Davey et al., 2011). These properties make GBS a genotyping technique suitable for a number of species and genetic studies (Chung et al., 2017), such as genomic selection (Poland et al., 2012), SNP marker development (Forrest et al., 2014), and genetic diversity (Alipour et al., 2017). Diversity Array Technology (DArT), developed by Diversity Arrays Technology Pty Ltd. (Canberra, Australia) originally with the microarray technology platform, is one of the GBS-based techniques widely adopted in wheat, thanks to its versatility, accuracy, and low cost (Colasuonno et al., 2021).

SNP Array

NGS technology has also created the basis for the establishment of high-density SNP arrays and the related high-throughput platforms capable of genotyping large numbers of samples (Ganal et al., 2012).

Currently, the most widely used genotyping platforms for large scale genotyping are the Infinium platform from Illumina (San Diego,

CA, USA) and the Axiom technology from Thermo Fisher Scientific (Waltham, MA, USA) (Scheben et al., 2018). Technically, the Illumina technology is based on spheres covered with specific oligos adapted to the microwells and the amplification takes place on a single-base two-color extension with a single probe SNP marker (Steemers and Gunderson 2007). On the other side, the GeneChip[®] array of Affymetrix uses photolithographic oligos on an array and the target SNP amplification involves assays with 30-mer probes (Thomson, 2014).

In wheat, the first SNP array developed was the 9K Infinium SNP Array by Cavanagh et al. (2013) used for genotyping 2,994 lines of bread wheat. Later, the array with 90K SNPs was fine-tuned (Wang et al., 2014). However, both of these chip had a greater representation in cultivated varieties, thus their use was very limited in the study of landraces (Rasheed et al., 2018). This problem was overcome by the development of the 820K Affymetrix Axiom SNP array which relied on exomes sequencing of 43 bread wheat and wild species accessions (Winfield et al., 2016). Axiom 35K SNP was then developed from this array, capable of analyzing even wild accessions at a more limited cost (Allen et al., 2017). In parallel, the Chinese Academy of Agricultural Sciences (CAAS) also developed an array containing 660K SNPs (Jin et al., 2016). More recently, in 2019, Wheat 50K (Triticum TraitBreed array, Rasheed and Xia, 2019) and 15K SNP arrays were developed (Muqaddasi, 2017) containing a selection of SNPs from Wheat 35K, 90K, and 660K SNP arrays.

SNP arrays have the advantage of facilitating high-density SNP scanning, have a high call rate, and are also cost effective when there is a need to genotype a high number of markers on many samples. However, a disadvantage, is that the set of SNPs is fixed and cannot be changed; they are also developed in hexaploid wheat, thus the SNPs present in the D genome will be unknown if it is applied in DW.

Genotyping for marker assisted breeding

Among the most competitive technologies used for marker assisted breeding, with a medium/low throughput, there are TaqMan (Applied Biosystems, Foster City, CA), KASP (Kompetitive allele specific PCR, Hoddesdon, UK), and rhAmp (Integrated DNA Technology technologies, Redwood City, CA), widely used in many plant species such as wheat and sugar beet (Broccanello et al., 2018; Ayalew et al., 2019). TaqMan chemistry is based on fluorescently-tagged, allele-specific probes detected using real-time PCR-based assays, while KASP technology adopts an endpoint fluorescence detection to discriminate tagged SNP alleles. The most recent method is rhAMP, that uses RNase H2 to activate primers after successful binding to their target site. All these chemistries are suitable for use on a variety of real-time PCR instruments with different throughputs. For example, the TaqMan assays can be applied in Real-Time PCR, but also can be used with the Open Array technology (Thermo Fisher Scientific, Carlsbad, CA) which allows the simultaneous analysis of 4 OpenArray plates, each composed of 3,072 through-holes allowing the genotyping analysis of 16, 32, 64, 128, 192, 256 SNPs at a time (Broccanello et al., 2020). Perry and Lee, (2017) developed an OpenArray plate composed of 16 SNP markers able to discriminate 47 DW varieties registered for production in Canada.

These chemistries have the advantage of being highly reproducible, sensitive, and cost effective; moreover, they can be freely customized both for the number of samples and SNPs that can be analyzed, adapting perfectly to marker assisted selection for crop improvement (Broccanello et al., 2018).

Advancements in trait genetic dissection and breeding

Genome wide association study (GWAS)

Genome wide association study is a powerful tool to study the genetic base of complex traits and detect relationships between phenotypic variations and the associated genetic polymorphisms (Taranto et al., 2018). The statistical methods for the analysis of associations have improved over the years, going from a classic ANOVA, that generates many false positives to the development of the mixed model framework, which increases computational speed and improves statistical power (Pavan et al., 2020; Tibbs Cortes et al., 2021). Subsequent advancement in statistical analysis methods led the association analysis of all markers simultaneously. This approach is based on Bayesian methods which are normally used in genomic prediction (Fernando and Garrick, 2013). However, the most common actual methods include TASSEL (Bradbury et al., 2007), GAPIT (Lipka et al., 2012), and GEMMA (Zhou and Stephens, 2012). 58 candidate genes associated with salt tolerance have been found, in bread wheat, performing 5 multi locus GWAS models that include mrMLM, FASTmrMLM, FASTmrEMMA, pLARM EB, and ISIS EMBLASSO (Chaurasia et al., 2020; Esposito et al., 2022). In DW genome wide association studies often involve the use of landraces to identify new causative SNPs. Moreover, the genomic regions linked to wheat blast resistance were identified in Indian genotypes with a MLM (mixed linear mode) in TASSEL. A novel GWAS approach is the environmental GWAS (envGWAS) that associates the single nucleotide polymorphisms with the geographic information system (GIS) of the original samples collection sites. In this context, the genome wide association was performed to study the local adaptation of Iranian and Pakistani bread wheat landraces using an EigenGWAS approach and a fixed and random model circulating probability unification (FarmCPU) (Hanif et al., 2021).

Genomic selection

In a context of climate change, a technique developed to accelerate breeding procedures and speed up the selection of superior genotypes is genomic selection (GS) (Crossa et al., 2017). This statistical model uses SNP molecular markers for a genomic prediction of genotype performance. The aim of GS is to predict breeding and/or genetic values. GS uses genotypic and phenotypic data for the constitution of a training population and then the predictive equation is used to select candidates that have been genotyped but not phenotyped. GS has the advantage of being able to rapidly improve complex and low heritability traits and reduce the cost of hybrid development. This technique can also be used for less complex traits with high inheritance and, for this scenario, high

genomic prediction (GP) accuracy is expected. However, when a trait is controlled by a high number of loci there are several factors influencing the prediction accuracy such as the size and genetic diversity and how distant is the training from the testing population. Moreover, for complex traits with large numbers of markers that are not in linkage disequilibrium (LD) with the QTL, GP accuracy is lower (Daetwyler et al., 2010).

In general, the statistical models developed for GP are based on single-environment assessments. However, in plant breeding the presence of a Genotype x Environment (G x E) interaction may complicate the selection of stable lines. Hence, some genomic prediction models, considering the G x E interaction, help breeder select lines with optimal overall performance across different environments and in a specific target environment. Specifically, a reaction norm model, which is an extension of the random effect Genomic Best Linear Unbiased Predictor (GBLUP) model, was developed by Jarquín et al., 2014. In this model, the main effect of lines, the main effect of environments, the main effect of markers, the main effect of pedigree, and their interactions with environments, are modeled using random covariance structures that are functions of marker or pedigree genotypes and environmental covariates (Jarquín et al., 2014). Appropriate cross-validation schemes are designed to obtain valid and unbiased estimates of the predictive ability obtainable from the developed genomic prediction models (Roberts et al., 2017). The reaction norm model has already been applied for the genomic prediction of 8,416 Mexican wheat landrace accessions and 2,403 Iranian wheat landrace accessions from the CIMMYT by Cossa et al. (2016). In this work, the authors evaluated two traits in two different environments and some heritable traits in a single optimal environment. The accuracy of the prediction for some traits such as maturity, quality traits, and grain yield and yield components was around 50-70%. The most used traits of study in genome selection experiments are related to quality improvement involving the use of different prediction models divided between parametric and non-parametric. Michel et al. (2018) proved the benefit of GS over marker assisted selection investigating the prediction of dough rheological traits in early generations and adopting the parametric RRBLUP, W-BLUP function. Genomic prediction models are routinely used in the CIMMYT spring bread wheat program since 2013 (Guzman et al., 2016). These models have also been successfully applied in genomic predictions for Fusarium head blight resistance in a DW panel (Moreno-Amores et al., 2020).

Landscape genomics

The selective pressure of abiotic stresses often varies in space, causing the evolution of advantageous mutations under their local environment, leading that genotype to have better fitness than the same genotype originating elsewhere. This differentiation process is called local adaptation and is driven by spatially divergent natural selection (Kawecki and Ebert, 2004). To trigger local adaptation, spatially divergent selection needs to overwhelm the homogenizing effect of gene flow. The study of the genetic bases of plant adaptation is crucial for the conservation and management of wild and cultivated species. Climatic stresses require a rapid evolution of populations to

quickly adapt to new conditions and avoid extinction. Furthermore, to identify the genetic basis of adaptation, it is necessary to distinguish the under-selection (adaptive) genes from the pool of neutral genes. One possible approach is landscape genomics which aims to identify the gene-environment association, in particular loci associated with certain environmental variables. The landscape genomics analyses are providing unprecedented insight into the evolutionary processes and molecular basis that govern environmental adaptation. In the context of climate change, this type of analysis investigates how the species are adapting to the various types of stress they are subjected to but also could help to identify the wild relative introgression and its contribution to local adaptation (He et al., 2019). Landscape genomics integrates molecular analyses with climatic and geographic data in which samples have been collected to identify adaptive genes (Sork et al., 2013). This association analysis can be considered a valid alternative to GWAS when working with wild accessions or landraces, as they are naturally adapted to the place of origin. Moreover, the relationship between phenotypic variation and climatic factors, in DW, has been widely studied and confirmed (Annicchiarico et al., 1995; Royo et al., 2014). Recently, landscape genomics has been applied in many species such as *Populus trichocarpa*, *Beta vulgaris* spp. *maritima*, and *Arabidopsis thaliana*. He et al. (2019) used the landscape genomics approach to find genomic windows associated with environmental adaptation in hexaploid wheat underlining the contribution to local adaptation given by wild emmer. In addition, 93 rice landraces from sub-Saharan regions were used to study adaptation to the local environment (Meyer et al., 2016). In landscape genomics, environmental information is screened for association with genetic variations through univariate or multivariate gene-environment association (GEA) analysis (Rellstab et al., 2015; Forester et al., 2018). Many statistical models have been developed for association analysis. For example, some methods involve a logistic association model such as the Spatial Analysis Method (SAM or SAM β ADA), multiple logistic regression, and Generalized Estimating Equations (GEEs). Other methods involve a linear association model such as General linear models, redundancy analysis (RDA), bayenv, Spatial Generalized Linear Mixed Model (SGLMM), Latent Factor Mixed Models (LFMMs), and GWAS mixed models (Rellstab et al., 2015). However, to make the results more reliable, it would be a good practice to compare results coming from different association models.

There are 19 bioclimatic variables that can be screened, which can be downloaded from the WorldClim database, concerning the period 1970-2000; moreover, data reporting global soil salinity layers for the years 1986, 1992, 2000, 2002, 2005, 2009, and 2016 are also available. Using this association model, it is possible to detect candidate genes associated with salinity, thanks to the historical data available on the Global Salinity Soil Map website, as it was done in *Medicago truncatula* (Guerrero et al., 2018).

The relationship between genotype and environment could be also used to predict the spatial distribution of adaptive genetic variants in future climates and the future maladaptation or genomic offset that provide a direct estimate of the expected genomic vulnerability of the species toward ongoing climate change (Capblancq et al., 2020; Cavanagh et al., 2020; Capblancq and Forester, 2021).

Speed breeding

Recent advances in high-throughput phenotyping techniques have greatly increased the accuracy of breeding programs, having the advantage of being non-destructive and large-scale methods. However, the classic breeding programs, that have allowed the improvement of varieties, have the disadvantage of being extremely long and articulated and they take 10–15 years to release a variety. A technique that allows a rapid advancement of breeding generations is known as ‘speed breeding’. This technique allows up to 6 generations of wheat per year and involves the use of fully enclosed, controlled-environment growth chambers with the addition of supplementary lighting (Watson et al., 2018). Several protocols for rapid and high-throughput phenotyping have been developed for the characterization of several important traits related to biotic and abiotic stresses in bread wheat. In durum wheat, a protocol has been developed providing multi-trait phenotyping and trying to accelerate even more the breeding cycles by using early filial generations (Alahmad et al., 2018). These ‘speed breeding’ techniques integrate perfectly with the new technologies of high-throughput genotyping and genomic selection.

Genetic diversity and signature of divergence in landrace germplasm

Until a few years ago, DW was well adapted to the Mediterranean environment. More recently, due to the climate crisis, drought, salinity, and low nutrient inputs occurring during flowering, pollination, and grain-filling represent the major stresses which adversely affect crop yield and quality, thus hampering agricultural productivity. Landraces coming from the Mediterranean basin are considered a particularly important group of genetic resources thanks to their high variability and tolerance to drought, pests, and adaptability to low farming systems (Lopes et al., 2015). Nowadays, the recovery, conservation, and enhancement of landraces are becoming central to increase the resilience of agricultural systems. However, how to exploit the genetic diversity of landraces to deal with environmental stress resilience is unclear and scattered (Lopes et al., 2015).

With the advance in genomic sequencing technologies and the release of the DW genome (Maccaferri et al., 2019), there has been a growing interest in comparing the patterns of genetic variation observed in landraces and modern varieties. These analyses were often focused on panels of landraces with a specific geographical origin. Population structure analysis was conducted for example in Iranian, Ethiopian, Tunisian, Turkish, and Italian germplasm revealing that, in most cases, landraces clustered separately from modern cultivars (Fayaz et al., 2019; Alemu et al., 2020; Alsaleh et al., 2022; Miazzi et al., 2022). Interestingly, a high level of genetic variation within landrace populations was detected, according to their geographical and climate of origin, revealing the importance of these factors in shaping wheat genome (Alipour et al., 2017; Taranto et al., 2022). On the other hand, cases of synonyms or homonyms as well as the presence of higher admixture of accessions between different populations of landraces were discovered, probably

due to the exchange of seeds associated with human migration over time.

Examining wider collections, including landraces from different geographic origins, opens the possibility of investigating relationships on a wider global level and provides also a more precise estimation of the genetic diversity within each group. Genotyping the already mentioned core GPD by means of the iSelect 90K SNPChip followed by structure analysis showed comparatively limited genetic diversity in modern cultivar and a closer relationship to specific landrace population (North Africa and Transcaucasia). Landraces from Ethiopia appeared instead as the more isolated and distant to modern cultivars, while a high admixture level within landrace populations was confirmed (Maccaferri et al., 2019).

In addition, genome-wide population structure uncovers divergent selection during modern wheat breeding, suggesting the existence of untapped gene pools which will provide a basis for DW improvement in the next future. Many hotspots of selection were detected in the genomic regions where there are located the genes for adaptation, quality, grain yield, and stress response (Taranto et al., 2020; Soriano et al., 2021). These hotspots included important loci such as the photoperiod (*Ppd*), the vernalization (*Vrn*), and the dwarfing (*Rht*) genes, as well as loci associated with nitrogen use efficiency, plant architecture and grain yield (*TaASN3*, *asparagine synthetase 3*; *NR1*, *nitrate reductase 1*; *Fd-GOGAT*, *ferredoxin-dependent glutamate synthase*; *GS*, *glutamine synthetase*; *Sus2*, *sucrose synthase 2* and *TEF*, *transcript elongation factor*). In addition, genes related to quality such as pasta-making quality and color of semolina and other durum wheat-end products were also divergent between landraces and modern cultivars. In detail, loci for gluten composition (HMW/LMW, high/low molecular weight, and α , β , γ , and ω gliadins), as well as loci involved in the carotenoid pathway (*Psy*) and polyphenol oxidase reaction (*Ppo*) were identified in hotspot regions (Requena-Ramírez et al., 2022; Taranto et al., 2022). Other divergent loci with implications in disease resistance, plant-microbe interactions, abiotic stresses, and plant development corresponded to gene models involved in important biological functions (Soriano et al., 2021). However, the identification of these genes and their allelic variants in the germplasm of indigenous DW varieties has been mainly carried out by *in-silico* analysis, at least for now. Future studies will be needed to validate the potential of the new allelic variants discovered in landraces.

Environmental adaptation traits from durum wheat landraces

In DW, domestication and, more lately, selection and fixation of favorable alleles had led to genetic erosion, lowering the buffering capacity of modern elite cultivars towards varied climatic conditions and strongly reducing potential for improvement (Tanksley and McCouch, 1997; Lopes et al., 2015). The systematic search and discovery of genetic resources from landraces by means of genotypic and innovative phenotypic profiling of genetic resource collections and the introduction in elite crops through pre-breeding efforts are being currently implemented in bread wheat and could be a promising strategy also for DW (Reynolds et al., 2021; Sharma et al.,

2021; Schulthess et al., 2022). Improvement of yield potential of landraces, by considering them as recipients, can be undertaken as an alternative strategy for developing better cultivars adapted to climate change. Inherent agronomic inferiority and disease susceptibility would hinder the direct utilization of landraces for breeding programs. However, the genomic tools and approaches we have described (i.e. genomic prediction and selection) could also strengthen pre-breeding efforts aiming at the improvement of genetic backgrounds of landraces, thereby attempting to achieve agronomic superiority starting directly from landraces as recipients and making this second alternative approach a possible and viable option (Adhikari et al., 2022). Finally, more complex breeding approaches, to develop new “synthetic” wheat crops exploiting genetic resources from wild species instead of landraces, also exist and have been already undertaken in the past (Reynolds et al., 2007; Balla et al., 2022).

Desirable genes were already identified in landraces and exploited for DW cultivars improvement by classical breeding. The most renowned DW cultivar is Cappelli, which is assumed to have been selected from the North-African landraces (De Cillis, 1942). However, the cv. Cappelli has a height of about 1.80 meters; therefore, several breeding activities were focused to create new variability by crossing the cv. Cappelli with Syriacum landraces (Aziziah, Eiti, Sinai, Tripolino). The result was the introduction of cultivars such as Capeiti 8 and Patrizio 6 which had slightly lower height, higher yield, earliness, and lodging resistance compared to Capelli, while preserving grain quality. Other similar examples of superior DW varieties, obtained by introgressing traits from landraces, were released in the frame of other breeding programs conducted in different countries (Kabbaj et al., 2017; Martínez-Moreno et al., 2020).

Molecular mapping technologies such as bulk segregant analysis (BSA), gene/QTL mapping, and genome-wide association studies (GWAS), supported by the high-throughput genotyping tools and strategies previously described, importantly increased the rate of discovery of genes/QTLs regulating biotic, abiotic stress resistance, agronomic and quality traits from landraces. Several studies have been already undertaken so far to identify new genes/traits in landraces useful for breeding (see Table 3 for a comprehensive but not exhaustive list). As can be clearly appreciated, in most recent studies traits and genes have been often also mapped by taking advantage of the newly released genomic tools for DW here described, to further support their prompt exploitation in breeding.

Besides introducing new abiotic stresses, climate changes are shaping the dynamics of plants and pathogens resulting in more complex biological interactions difficult to predict and characterized by new outbreaks. Therefore, landraces are being widely explored as a potential source of new resistance traits, in regions where plant and pathogens co-evolved. Resistance sources to *Fusarium* head blight, rust, common bunt, stem sawfly, tan spot, and *Septoria tritici* blotch disease have been discovered within different DW landrace collections and majority of these have also been successfully mapped in the latest years. As pivotal examples leaf and stem rust resistance sources were mapped in the Portuguese DW landraces PI 192051 and Aus26582, by developing RIL mapping populations, beside alternative contribution from other sources (Qureshi et al., 2017; Qureshi et al., 2018; Aoun et al., 2019). Similarly, a resistance gene to

Zymoseptoria tritici was mapped in the Tunisian DW landrace ‘Agili 39’ (Ferjaoui et al., 2022).

Concerning abiotic stress resistance, it is well recognized that Mediterranean DW landraces represent a particularly important group because of their documented better adaptation to drought (Moragues et al., 2006; Royo et al., 2014). Therefore, landraces from this region potentially include adaptive traits that could be exploited to boost the breeding for heat/drought tolerance and promote cultivars adaptation to stress-prone environments. Up to now, drought, heat, and salinity resistance traits have been studied in landraces coming from the Mediterranean basin, such as in Jordanian, Israeli-Palestinian, Tunisian, Italian, and Spanish, but also Afghan landraces (Al Khateeb et al., 2017; Shamaya et al., 2017; Hamdi et al., 2020; Frankin et al., 2021; Naranjo et al., 2022; Taranto et al., 2022). However, works concerning the mapping analysis of resistance traits to abiotic stresses are less in number than the biotic stresses ones. Just in two cases, abiotic stress resistance sources have been genetically mapped. A salinity resistance trait has been identified in an Afghan DW landrace and mapped. Moreover, using a GWAS approach on a worldwide collection of DW landraces, drought stress tolerance was associated to a locus of DW genome found to be collinear with a previously identified QTL in bread wheat (Shamaya et al., 2017; Wang et al., 2019). In order to improve the genetic characterization of abiotic resistance traits from landraces, an important contribution is expected from the development of adequate protocols for the abiotic stress evaluation, following similar strategies to those applied in bread wheat for high-throughput and accurate stress response phenotyping in large collections (Rasheed and Xia, 2019; Langridge et al., 2021; Shan et al., 2022).

Landraces are typically low yielding and can show lower agronomic attributes. Therefore, several studies enquired agronomic traits variability in landraces, focusing mainly on yield, phenology and morphological traits (Table 3). GWAS studies, based on high-throughput genotyping tools, helped in defining genomic regions affecting such agronomic traits in landraces highlighting available superior alleles. Among others, the contribution to the yield of root system architecture traits and phenology were highlighted (Mengistu et al., 2016; Kidane et al., 2017a; Desiderio et al., 2019; Gupta et al., 2020; Alemu et al., 2021; Ávila et al., 2021; Royo et al., 2021).

Quality traits of durum wheat landraces

DW semolina is considered the ideal raw material for the production of pasta or macaroni products, especially in Italy, which is the first producer and consumer of DW in Europe (<http://www.internationalpasta.org>, accessed on 12 November 2022). The aptitude of the raw material to be transformed into a high quality end-product mainly depends on grain protein content (GPC) and composition that directly affect wheat’s market price and end-use value (Shewry, 2019).

Grain protein content, mainly above 12-13%, is highly related to the amount and composition of glutenins and gliadins proteins, that are the principal components of gluten and are responsible for the viscoelastic properties and extensibility of semolina, respectively. Past breeding activities aimed at improving grain yield resulted in a loss of

TABLE 3 Publication list regarding resistance/tolerance traits to biotic and abiotic stresses, morpho-agronomic and quality traits identified in durum wheat landraces.

Category	Gene/QTL Trait	Landrace (Origin)	Analysis Type	References
Biotic stress	Fusarium head blight resistance	Tunisia	GWAS	Ghavami et al., 2011
	Fusarium head blight resistance	Syria	Trait phenotyping	Talas et al., 2011
	Leaf and stem rust resistance	diverse	Gene/QTL mapping	Aoun et al., 2017
	Leaf and stem rust resistance	Portugal	Gene/QTL mapping	Aoun et al., 2019
	Leaf and stem rust resistance	Kazakhstan	GWAS	Genievskaya et al., 2022
	Leaf rust resistance	diverse	GWAS	Aoun et al., 2016
	Leaf rust resistance	Portugal	Gene/QTL mapping	Qureshi et al., 2017
	Leaf rust resistance	Portugal	Gene/QTL mapping	Qureshi et al., 2018
	Leaf rust resistance	Middle Est	Gene/QTL mapping	Kthiri et al., 2019
	Resistance to common bunt	Syria	Trait phenotyping	Mamluk and Nachit, 1994
	Septoria tritici blotch disease resistance	Tunisia	Gene/QTL mapping	Medini et al., 2014
	Septoria tritici blotch disease resistance	Tunisia	Trait phenotyping	Ferjaoui et al., 2015
	Septoria tritici blotch disease resistance	Ethiopia	GWAS	Kidane et al., 2017b
	Septoria tritici blotch disease resistance	Tunisia	Gene/QTL mapping	Aouini, 2018
	Septoria tritici blotch disease resistance	Tunisia	Trait phenotyping	Ouja et al., 2020
	Septoria tritici blotch disease resistance	diverse	Trait phenotyping	Ben M'Barek et al., 2022
	Septoria tritici blotch disease resistance	Tunisia	Gene/QTL mapping	Ferjaoui et al., 2022
	Stem rust resistance	Italy	GWAS	Laidò et al., 2015
	Stem rust resistance	diverse	GWAS	Chao et al., 2017
	Stem rust resistance	Ethiopia	GWAS	Liu et al., 2017
	Stem rust resistance	Italy	GWAS	Saccomanno et al., 2018
	Stem rust resistance	diverse	Trait phenotyping	Olivera et al., 2021
	Stem rust resistance	Ethiopia	Trait phenotyping	Chiko et al., 2022
Stem rust resistance	Iran	GWAS	Mehrabi et al., 2022	
Stem sawfy resistance	diverse	Gene/QTL mapping	Varella et al., 2019	
Tan spot resistance	diverse	Trait phenotyping	Laribi et al., 2021	
Yellow/stripe leaf and stem rust resistance	diverse	Association analysis/single marker scan	Bansal et al., 2013	
Yellow/stripe rust and common bunt resistance	diverse	Trait phenotyping	Annicchiarico et al., 1995	
Yellow/stripe rust resistance	Ethiopia	GWAS	Alemu et al., 2021	
Abiotic stress	Allelopathy	Italy	Trait phenotyping	Scavo et al., 2022
	Cold	Iran	Trait phenotyping	Mohammadi et al., 2014
	Drought	diverse	Trait phenotyping	Pecetti et al., 1994
	Drought	diverse	Trait phenotyping	Annicchiarico et al., 1995
	Drought	Jordania	Trait phenotyping	Al Khateeb et al., 2017

(Continued)

TABLE 3 Continued

Category	Gene/QTL Trait	Landrace (Origin)	Analysis Type	References
	Drought	Israeli Palestina	Trait phenotyping	Frankin et al., 2021
	Drought	diverse	GWAS	Wang et al., 2019
	Heat	diverse	Trait phenotyping	Sareen et al., 2020
	Heat	Spain	Trait phenotyping	Naranjo et al., 2022
	Heat	Italy	Trait phenotyping	Taranto et al., 2022
	Salinity	Afganistan	Trait phenotyping	Shavrukov et al., 2011
	Salinity	Afganistan	QTL Mapping	Shamaya et al., 2017
	Salinity	Italy	Trait phenotyping	Maucieri et al., 2018
	Salinity	Tunisia	Gene functional characterization	Hamdi et al., 2020
	Salinity	Jordania	Trait phenotyping	Al Khateeb et al., 2020
Agronomic traits	Agromorphological traits	Marocco	Trait phenotyping	Taghouti et al., 2013
	Agromorphological traits, phenology	Italy	Trait phenotyping	Fiore et al., 2019
	Agromorphological traits (phenology, yield and morphology)	Spain	Trait phenotyping	Ruiz et al., 2012
	Agronomic (plant height, yield traits and phenology) and physiology trait	diverse	GWAS	Royo et al., 2021
	Agronomic trait (phenology, biomass and yield plant height)	Ethiopia	GWAS	Mengistu et al., 2016
	Agronomic trait (phenology, biomass and yield plant height)	diverse	Trait phenotyping	Royo et al., 2014
	Flowering time	diverse	GWAS	Gupta et al., 2020
	Flowering time, yield	diverse	GWAS	Royo et al., 2020
	Heading date, seed weight, and morphology	Iran	Gene/QTL mapping	Desiderio et al., 2019
	Morphology, phenology, yield component, GXE interaction	Ethiopia	Trait phenotyping	Mulugeta et al., 2022
	Morphology and yield	diverse	GWAS	Wang et al., 2019
	Morphology and yield, descriptors pigmentation, phenology	Oman	Trait phenotyping	Al Lawati et al., 2021
	Phenology, plant height, yield, and yield components	Ethiopia	GWAS	Kidane et al., 2017a
	Root system architecture traits	Ethiopia	GWAS	Alemu et al., 2021
	Spike height and shape	Marocco	Trait phenotyping	Sahri et al., 2014
	Stem cross section height and heading date	Spain	GWAS	Ávila et al., 2021
	Yield component	India	GWAS	Sukumaran et al., 2018
	Yield component	diverse	Trait phenotyping	Pecetti et al., 1994
	Yield component (kernel and spikes) and heading date	Italy	Trait phenotyping	Marzario et al., 2018
	Yield component, plant height, phenology and biomass	diverse	GWAS	Soriano et al., 2018
	Yield phenology lodging resistance	Israeli Palestina	Trait phenotyping	Frankin et al., 2021
	Yield vigour, plant height, phenology	diverse	Trait phenotyping	Annicchiarico et al., 1995
	Yield vigour, plant height, phenology	Algeria	Trait phenotyping	Annicchiarico et al., 2009
Quality	Arabinoxylan iron zinc phytate and phenolic acids content	Iran Mexico	Trait phenotyping	Hernandez-Espinosa et al., 2020
	Carotenoid content	Spain	Trait phenotyping	Requena-Ramírez et al., 2021

(Continued)

TABLE 3 Continued

Category	Gene/QTL Trait	Landrace (Origin)	Analysis Type	References
	Carotenoid content	Spain	GWAS	Requena-Ramirez et al., 2022
	Carotenoid content, color characteristics, chemical composition and starch digestibility	Italy	Trait phenotyping	Melini et al., 2021
	Gliadins content	Bulgaria	Trait phenotyping	Melnikova et al., 2010
	Gluten strength	Spain, CIMMYT, Italy, France and US	Trait phenotyping	Nazco et al., 2014b
	Glutenin protein composition	diverse	Trait phenotyping	Moragues et al., 2006
	Low molecular weight glutenin	Spain	Allelic variation	Ruiz et al., 2018
	High molecular weight glutenin	Italy	Mass spectrometry	Visioli et al., 2021
	Grain morphology and color	diverse	GWAS	Chou et al., 2022
	Grain quality	Marocco	Trait phenotyping	Taghouti et al., 2013
	Grain quality	Mexico	Trait phenotyping	Hernández-Espinosa et al., 2018
	Grain quality, yield, protein content, gluten strength and yellow color index	diverse	Trait phenotyping	Nazco et al., 2012
	Malting brewing related traits	Italy	Trait phenotyping	Alfeo et al., 2018
	Morpho-physiological characters	diverse	Trait phenotyping	Annicchiarico et al., 1995
	Phenolic and flavonoid content	Italy	Trait phenotyping	Dinelli et al., 2009
	Phenolic content	Italy	Trait phenotyping	Lo Bianco et al., 2017
	Physico-chemical traits, malt related traits, sugars	Italy	Trait phenotyping	Alfeo et al., 2021
	Phytochemical, antioxidant capacity and phenolic acids	Italy	Trait phenotyping	Di Loreto et al., 2018
	Polyphenolic content and antioxidants	Tunisia	Trait phenotyping	Boukid et al., 2019
	Prolamins	Spain	Trait phenotyping	Chacón et al., 2020
	Protein content, dry gluten index, yellow index, ash P/L W G baking aptitude	Italy	Trait phenotyping	Ruisi et al., 2021
	Proteomic profiling (Metabolic and CM-protein fraction)	Italy	Trait phenotyping	Di Francesco et al., 2020
	Quality and rheological traits	diverse	Trait phenotyping	Ladhari et al., 2022
	Quality traits	Ethiopia	Trait phenotyping	Dagnaw et al., 2022
	Quality traits	Spain	Meta-QTL analysis	Roselló et al., 2018
	Quality traits and nitrogen use efficiency	Tunisia	Trait phenotyping	Ayadi et al., 2022
	Quality traits	Italy	Trait phenotyping	Fiore et al., 2019
	Rheological parameters	Italy	Trait phenotyping	Spina et al., 2021
	Volatile organic compounds proteins	Italy	Trait phenotyping	Vita et al., 2016

genetic variability for quality-related traits, probably because of the negative relationship between yield and GPC (Nazco et al., 2014a; Subira et al., 2014). As proof of this, Roncallo et al. (2021) observed a decreasing trend in GPC over the last 85 years using a DW collection including accessions representative of the Argentina, Italy, Chile, France, CIMMYT and other countries breeding programs.

Previous studies suggested the potential quality-enhancing landraces as reservoir of new allelic variants for gluten quality improvement (Table 3) (Moragues et al., 2006; Nazco et al.,

2014b; Roselló et al., 2018; Ruiz et al., 2018; Hernández-Espinosa et al., 2018). Roselló et al. (2018) performed a pasta-making quality QTLome using a Mediterranean collection of DW landraces and observed how landraces had higher GPC than modern cultivars but lower gluten strength. This result is due to very few allelic combinations of glutenin subunit loci in modern cultivars (Nazco et al., 2014b), while landraces showed a higher genetic variability useful to recovering and broadening allelic variation of gluten composition.

Other parameters can affect pasta production such as color (Table 3). Semolina and pasta color are constituted by yellow (desirable) and brown (undesirable) pigments (Colasuonno et al., 2019). Usually, DW landraces showed lower total carotenoid contents and higher values of browning compounds compared to commercial cultivars (Digesù et al., 2009; Subira et al., 2014; Taranto et al., 2015). However, the first DW landraces with carotenoid esterification ability were identified by Requena-Ramírez et al. (2021) and could represent donor sources in DW biofortification programs.

Although DW is mostly used for pasta production, it is an ingredient in typical breads in some areas of Southern Italy. It is the case of “Pane nero di Castelvetrano” and “Pane di Monreale” which are two traditional breads constituted by two Sicilian landraces, Timilia and Russello (Palumbo et al., 2008; Melini et al., 2021; Visioli et al., 2021). The most notable characteristic of Timilia is the dark color of semolina, due to the high content of antioxidant phenolic compounds (Giancaspro et al., 2016; Bianco et al., 2017; Taranto et al., 2022). To preserve these landraces and derived-products, a traceability approach was developed using the high molecular weight glutenins, suggesting a method to verify the varietal identity from the seed to the final product (Visioli et al., 2021).

Conclusions

In conclusion, recent findings unveiled the strategic role of landraces in the genetic improvement of durum wheat. Studies on genomic divergence among *T. turgidum* sub-species indicated that the allelic variations of domesticated accessions and their wild relatives, lost during the domestication and breeding processes, were and will be recovered by exploring and exploiting landraces genetic diversity. In particular, in a context of climate changes, understanding the environmental and genetic factors behind the adaptation of landraces can help to introduce beneficial alleles in elite varieties to overcome stress and increase yield. The availability of durum wheat reference genome and the increasingly precise molecular techniques at affordable costs are giving a big boost to accurately identify the genetic determinants underpinning resistance/tolerance against biotic and abiotic stresses.

The recent application of genomic technologies (i.e. genome-wide association and genomic prediction analysis) on durum wheat landrace resources paves the way to accelerate the next-generation breeding programs to overcome the gap of knowledge of these underexplored resources and identify advantageous alleles that have been lost in modern varieties.

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CB: writing original draft. DB and FT: conceptualization and writing. FT, GD, AF: writing, review, and editing. All authors contributed to the article and approved the submitted version.

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The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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