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Review

Potential of Wild Relatives of Wheat: Ideal Genetic Resources for Future Breeding Programs

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Abstract: Among cereal crops, wheat has been identified as a major source for human food consumption. Wheat breeders require access to new genetic diversity resources to satisfy the demands of a growing human population for more food with a high quality that can be produced in variable environmental conditions. The close relatives of domesticated wheats represent an ideal gene pool for the use of breeders. The genera *Aegilops* and *Triticum* are known as the main gene pool of domesticated wheat, including numerous species with different and interesting genomic constitutions. According to the literature, each wild relative harbors useful alleles which can induce resistance to various environmental stresses. Furthermore, progress in genetic and biotechnology sciences has provided accurate information regarding the phylogenetic relationships among species, which consequently opened avenues to reconsider the potential of each wild relative and to provide a context for how we can employ them in future breeding programs. In the present review, we have sought to represent the level of genetic diversity among the wild relatives of wheat, as well as the breeding potential of each wild species that can be used in wheat-breeding programs.

Keywords: wheat germplasm; *Aegilops-Triticum*; next generation sequencing; genetic diversity; breeding program; environmental stresses

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1. Introduction

Climate change and subsequent increasing abiotic and biotic stresses threaten food security globally, as they can hinder the potential yield performance, increase the number of pests and diseases generations, alter synchrony between plants and pests, increase risk of invasion by migratory pests, increase incidence of insect-transmitted plant diseases, and reduce the effectiveness of biological control, especially for natural enemies [1,2]. One worthwhile strategy for increasing crop productivity and stability that may be applied in a wide range of environments is 'crop genetic improvement' through the introgression of novel genes, QTLs, and even novel alleles from wild relatives to local or modern varieties [3]. As such, breeders must simultaneously both improve the genetic background and reduce the impact of environmental stresses on the grain production. Among cereal crops, wheat has a significant role in supplying the 20% of all calories consumed by people worldwide. Due to climate change, mainly caused by biotic and abiotic stresses, the demand for wheat bread wheat is predicted to increase dramatically in the future as the global human population increases. Hence, wheat production will have a vital bearing on food security in the coming decades [4].

After the green revolution, numerous bread wheat varieties were released by agronomists and breeders in different parts of the world. Although this task helped to

increase the breeding population of wheat, the genetic basis of the wheat was narrowed through the shearing of the breeding lines and various breeding cycles, which in turn decreased species variability. Wild relatives of wheat offer great possibilities for breeders to develop new varieties with a more appropriate genetic background for various agricultural systems [5]. Hence, the use of an ancestors' gene pool is an appropriate strategy for developing new superior bread wheat cultivars. Wheat wild relatives are closely related species that have a long history in wheat breeding, mostly for abiotic stress tolerance. These species are identified as the critical resources required to sustain global food supply [4]. The tribe *Triticeae*, which is part of the *Pooideae* subfamily of the grass family *Poaceae*, includes the genera *Triticum* and *Aegilops* L. These relatives provide important gene pools for wheat-breeding programs, since they are connected to the most important agricultural crop, *Triticum aestivum* L. [6]. In this review, we have summarized the phylogenetic relationships among wild wheats and their potential applications in wheat breeding.

2. The Trend of Bread-Wheat Evolution

Wheat was domesticated from its wild relatives during the pre-pottery Neolithic (PPN) period nearly 12,000 years ago, in the Middle East's Fertile Crescent, which included several wide ranges of geographical zones from Lebanon, Israel, Jordan, and Syria via southeast Turkey, as well as into Iraq and western Iran via the Tigris and Euphrates rivers [7] (Figure 1). Research conducted by Weide et al. [8] reported that the first hybridization between wild wheats occurred in the west of Iran.

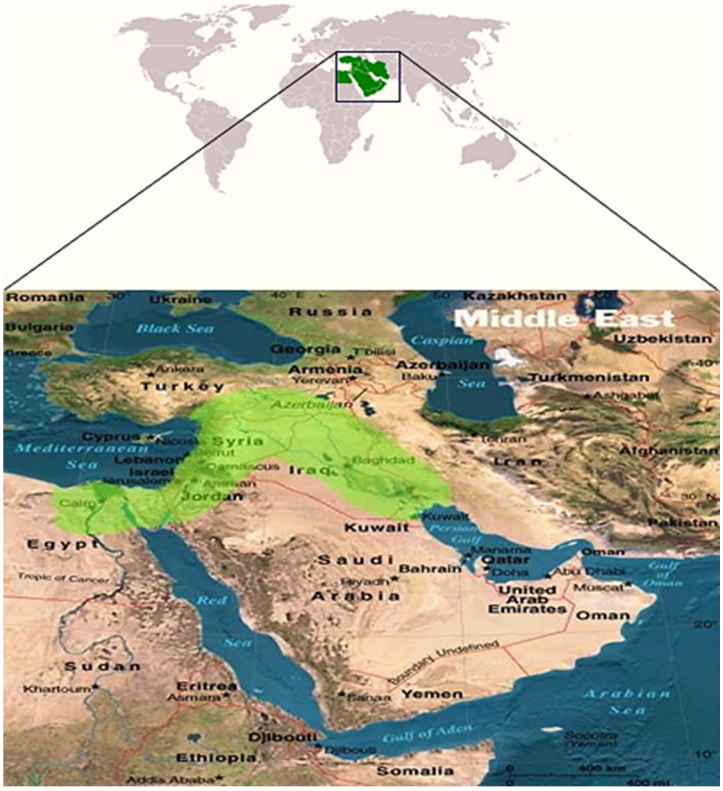

Figure 1. The position of the Fertile Crescent (FC) in the Middle East and world. This region embraces a wide geographical range between the Persian Gulf and the eastern coast of the Mediterranean Sea (highlighted in green).

Triticum and *Aegilops* are two key genera which include various wild wheat with different genomic constitutions and which have played direct or indirect roles in wheat domestication. Table 1 shows some of the key articles that have denoted how wheat evolution occurred.

Table 1. Some key articles regarding the trend of wheat evolution.

Article	Reference
Evolution in the genus *Triticum* and the origin of cultivated wheat	[9]
Genome symbols and plasma types in the wheat group	[10]
Cytogenetics of wheat and its close wild relatives-*Triticum* and *Aegilops*	[11]
Genome symbols in the Triticeae (Poaceae)	[12]
Phylogenetic relationships of *Triticum* and *Aegilops* and evidence for the origin of the A, B, and D genomes of common wheat (*Triticum aestivum*)	[13]
Evolution of domesticated bread wheat	[14]
Wheat domestication: Lessons for the future	[15]
Distinguishing wild and domestic wheat and barley spikelets from early Holocene sites in the Near East	[16]
Emergence of agriculture in the foothills of the Zagros mountains of Iran	[17]
On the Identification of domesticated Emmer wheat, *Triticum turgidum* subsp. *dicoccum* (Poaceae), in the Aceramic Neolithic of the Fertile Crescent	[18]
DArTseq-based analysis of genomic relationships among species of tribe Triticeae	[19]
Domestication and crop evolution of wheat and barley: Genes, genomics, and future directions	[20]
Bread wheat: a role model for plant domestication and breeding	[21]
Roadmap for accelerated domestication of an emerging perennial grain crop	[22]
Current progress in understanding and recovering the wheat genes lost in evolution and domestication	[23]

Although phylogenetic relationships among wild relatives of wheat have been extensively reviewed by many researchers e.g., [24], we report here an information flow diagram for the trend of wheat domestication (Figure 2). This diagram shows wheat's evolution process and a general viewpoint of relationships among the close relatives of common wheat, which descended from a 3 million-year-old common ancestor and gave rise to the *Aegilops* and *Triticum* taxa [25]. Briefly, the *T. urartu* Tumanian ex Gandilyan (with A-genome) and *A. speltoides* Taush. (with B genome) have created a tetraploid form of wheat known as emmer wheat (*T. turgidum* ssp. *dicoccoides* (Körn) Aschers and Graebner Thell.), due to the natural hybridization processes occurring several hundred thousand years ago [13]. *T. turgidum* L. ssp. *dicoccum* Thell. and free-threshing *T. turgidum* L. spp. *durum* Desf. are the result of the domestication of wild emmer. A second hybridization event occurred between *A. tauschii* Coss. and *T. turgidum*, which resulted in the hexaploid bread wheat *T. aestivum* L. [13]. Consequently, the polyploidy genome of *T. aestivum* with an AABBDD genome contains three sub-genomes AA, BB, and DD from *T. urartu*, *A. speltoides*, and *A. tauschii*, respectively. Furthermore, Table 2 shows all wild wheat species with various alien genomic constitutions.

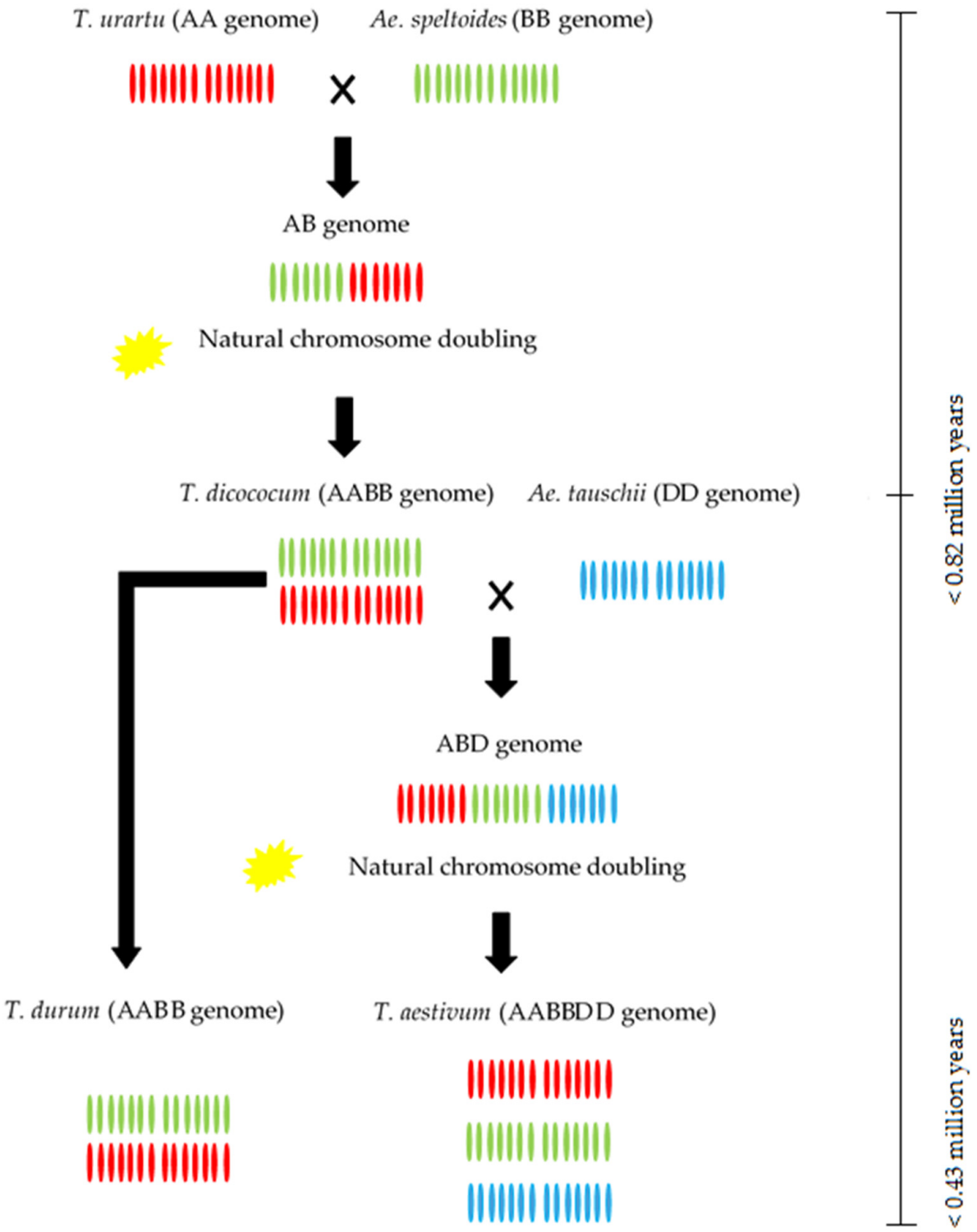

Figure 2. Information flow diagram for the domestication trend of wheat.

Table 2. List of different *Aegilops* and *Triticum* species along with their genomic constitutions.

Species	Genome		
	References		
	[26]	[27]	[10]
T. monococcum L.	A		
T. urartu Tumanian ex Gandilyan			A
Ae. speltoides Tausch	S		
Ae. bicorne (Forsk.) Jaub. & Sp.	S^b		
Ae. longissimum Schweinf. & Muschli in Muschli	S^l		
Ae. sharonensis Eig			S^l
Ae. searsii Feldman & Kislev		S^s	
Ae. mutica Bioss.	Mt		T
Ae. tauschii Coss.	D		
Ae. comosa Sibth. & Sm.	M		
Ae. uniaristata Vis.	M^t	Un	N
Ae. caudata L.	C		
Ae. umbellulata Zhuk.	C^u	U	
T. dicoccoides Korn	AB		
T. dicoccum Schrank	AB		
T. durum Desf.	AB		
T. turgidum L.	AB		
T. persicum (Percival) Vavilov ex Zhukovsky	AB		
T. aestivum L. em. Thell.	ABD		
T. spelta L.	ABD		
T. compactum Host	ABD		
T. sphaerococcum Perc.	ABD		
T. macha Dek. et Men.	ABD		
T. timopheevi Zhuk.	AG		M
T. zhukovskyi Men. et Er.		AAG	AA^UG
Ae. ovate L.	C^UM^O	UM	UM
Ae. biuncialis Vis.	C^UM^b	UM	
Ae. columnaris Zhuk.	C^UM^c	UM	
Ae. triaristata Wild.	C^UM^t	UM	UM
Ae. recta (Zhuk.) Chen.	C^UM^tX	UMUn	UMX
Ae. variabilis L.	C^US^V	US	US^l
Ae. triuncialis L.	C^UC	UC	
Ae. cylindrica Host	CD		
Ae. crassa (4x) Boiss.	DJ	DM	D^CX
Ae. crassa (6x) Boiss.	DJX	DDM	D^CXS^S
Ae. vavilovi (Zhuk.) Chen.		DMS	C^CXS^S
Ae. ventricosa Tausch	DM^V	DUn	DN
Ae. juvenile (Thell.) Eig		DMU	

3. Levels of Genetic Diversity in Wheat Germplasm

3.1. Phenotypic Diversity

Wild wheat species are highly diverse and variable in terms of agronomic and morphological traits. The distribution of these species in different ecological zones has resulted in several species with unique traits. The first studies on phenotypic diversity in wild wheat species and landraces referred to a study conducted by Percival [28], which described diversity through plant height, spike length, number of spikelets, and straw quality among landraces of bread wheat from Iran. Jaradat [29] indicated significant genotypic variation for developmental and yield traits among Jordanian wheat landraces. Anker et al. [30] investigated 76 accessions of wild wheat species including *T. boeoticum* ssp. *boeoticum*, *T. boeoticum* ssp. *thaoudar*., *T. urartu* and *T. monococcum* in terms of 17 agronomic and morphological characteristics. The germplasm accessions showed significant variation for flowering data, length of spike, length of awns, and length of anthers. Arzani et al. [31] investigated a collection of wild relatives including 24 *Aegilops* and *Triticum* accessions

belonging to *Ae. crassa*, *Ae. umbellulata*, *Ae. caudata*, *Ae. cylindrica*, *Ae. glabra*, *Ae. squarrosa*, *Ae. triuncialis*, *T. monococcum*, *T. dicoccides*, and *T. compactum* from different regions of Iran. These authors estimated genetic diversity using 25 agronomical and morphological characters, and finally reported that for qualitative qualities, there is a lot of variance across species, as well as inter- and intraspecific variation for quantitative traits. Later, a study involving 254 accessions of *Ae. tauschii* from several regions of Iran indicated a high diversity for spike-related characteristics such as rachis node length, spike width, number of seed per spike, rachis node width, spikelet glum length, seed length, and width [32]. The evaluation of 68 accessions of *Ae. tauschii* ssp. *strangulata* and *Ae. tauschii* ssp. *tauschii* sampled from different regions of Iran indicated significant variation within populations for most phenotypic traits, such as peduncle length, plant height, awn length, number of fertile tillers, spike length, and biological yield. Likewise, an experiment using 180 accessions of *Aegilops* and *Triticum* genera was performed by Pour-Aboughadareh et al. [33] to evaluate genetic diversity using different agronomic characters. In this study, the Shannon–Weaver (HSW) and Nei's (HN) genetic diversity parameters revealed intermediate to high phenotypic diversity for most traits in *Triticum* and *Aegilops* species. These researchers recommended that the genetic diversity among studied Iranian *Aegilops* and *Triticum* species such as *Ae. crassa*, *Ae. cylindrica* and *Ae. umbellulata* can provide new insights for the rediscovery of valuable agronomic traits, which can be exploited for the improvement and adaptation of common wheat. In view of this fact, several studies have been performed to measure the extent and pattern of phenotypic diversity in the wheat germplasm collections using different traits. Table 3 shows that attempts have been made to characterize the estimate of genetic diversity levels in wild relatives of wheat using phenotypic data.

Table 3. List of several studies that reveal high levels of phenotypic diversity in wild relatives of wheat.

Target Species	Traits	References
A. tauschii	Plant height, peduncle length, number of tillers per plant, number of spikes per plant, number of spikelets per spike, spike length, leaf length, number of grains per spike, length and width of rachis node and spike, seed color, glume color, glume hairiness	[32–37]
T. boeoticum	Plant height, peduncle length, spike length, number of spikes, number of spikelet per spike, number of grains per spike, leaves number, glume shape, glume color, branched spike, anther color, grain color, awn color, plant height, glume length, flag leaf length, leaf length	[31,33,35,38,39]
T. aestivum	Plant height, peduncle length, number of tillers per plant, number of spikes per plant, number of spikelets per spike, spike length, leaf length, number of grains per spike, glume shape, glume color, branched spike, anther color, grain color, awn color, plant height, glume length	[31,33,36,39–45]
T. durum	Leaf length, number of seeds per spike, spike dry matter, spike length, number of spikes, number of spikelets per spike, thousand seeds weight, harvest index, grain yield, various physiological traits	[31,33,46–49]
T. dicoccoides	Plant height, peduncle length, number of tillers per plant, number of spikes per plant, number of spikelets per spike, spike length, heading date, flag leaf length, flag leaf width, harvest index, glume shape, glume color, branched spike, anther color, grain color, awn color, glume length	[31,33,37,46–48,50]
T. urartu	Plant height, peduncle length, leaf length, number of spikes, spike length, number of spikelets per spike, seed yield	[33,34,51]

Table 3. *Cont.*

Target Species	Traits	References
Ae. caudate, Ae. cylindrical, Ae. crassa, Ae. speltoide, Ae. umbellulata, Ae. neglecta, Ae. triuncialis, Ae. strangulata, Ae. ligustica, Ae. biuncialis, Ae. columnaris, Ae. vavilovii	Glume shape, glume color, branched spike, anther color, grain color, awn color, plant height, glume length, flag leaf length, spike length, number of stems, plant height, peduncle length, number of spikes, number of spikelets per spike, length and width of rachis node and spike, number seeds per spike, seed color, glume hairiness	[31–33]
T. monoccocum	Plant height, grain per spike, heading time, maturity time, hairiness, waxiness, growth habitus and grain hull	[34,52]
T. dicoccum	Plant height, grain per spike, heading time, maturity time, hairiness, waxiness, growth habitus and grain hull	[52]
T. aegilopoides	Plant height, spike length, number of stems	[34]

3.2. Plant Genetic Resources and Molecular Diversity

Over the last three decades, many studies have been performed to characterize the genetic diversity in ancestral and wild relatives of wheat based on different molecular-marker systems. A general pattern change in plant genetic resources (PGR) was triggered by the political system, as well as the advancement of molecular biology and electronic data processing, as seen here for wheat [53]:

I. PGR maintenance in situ versus ex situ. Ex situ servicing has lost its hegemony [54]. Wild wheats are successfully preserved in the wild, while landraces thrive in the field. The predicted improvement was not achieved using new approaches [53].
II. Inclusion of underutilized and neglected crop varieties [55]. Some plants are likely extinct in conventional farming zones, although landraces for others have only recently been discovered. Wild relatives have become increasingly important in wheat breeding, with *Secale*, *Aegilops*, *Hordeum*, and other genera being used in addition to wild *Triticum* varieties [53].
III. Techniques for determining taxonomic diversity both inside and between taxonomic groups. Insights into population dynamics and evolution are being gained thanks to modern technology.
IV. Genetic loss is an issue in genebanks as well [56].
V. Landraces have a wide range of morphological variation. Breeders are less familiar with infraspecific classification schemes, which are helpful for characterization and handling.
VI. Measurement techniques: Molecular markers are used to classify genetic variations on a basic basis, without taking into account ecological adaptation.
VII. Traditional assessment programs can be expanded by genebanks. Pre-breeding will become more important.
VIII. Under long-term storage and reproduction conditions, genebanks are accurate and cost-effective, but strategic reproduction principles are needed [57].

Genetic resources are critical for the current and future sustainability of world wheat production. They include a wide variety of genetic variation, which is essential for increasing and sustaining wheat production potential by providing novel sources of resistance and tolerance to biotic and abiotic stressors [58]. The germplasm preserved is particularly rich in wild crop relatives, traditional farmer cultivars, and ancient cultivars, all of which form a significant genetic diversity reserve. Ex situ or in situ conservation of material protects against genetic degradation and provides a source of resilience to biotic and abiotic stressors, and enhances quality and yield characteristics for future crop improvement. Breeders use well-adapted cultivars from particular regions to build modern high-yielding wheat cultivars, which are an assembly of genes or gene combinations. International agricultural research has greatly increased the availability of broadly adaptable, genetically varied germplasm [58]. Traditional approaches are often overlooked, whereas new possibilities

are exaggerated. Landrace preservation in genebanks and on farms is difficult. The role of PGR is traditional. Orthodox approaches can be used to study landraces, but molecular methods can answer complex questions [53]. According to numerous studies, a high level of genetic diversity among wild relatives of wheat has been reported, which may refer to their natural distributions in a wide range of ecosystems and even in natural hybridization among various species. Hence, herein, we have only listed some studies that use at least one molecular marker system to investigate the level of genetic diversity, the genetic makeup of the population, as well as complementary genetic tests, such as association mapping or gene cloning. In accordance with previous reports, we found that, among wild wheats, *Ae. tauschii* Coss. has been the most subjected to genetic studies (Table 4). Indeed, this confirms the potential of this species for future wheat breeding programs.

Table 4. List of several studies that reveal a high level of molecular diversity in wild relatives of wheat.

Marker	Species	References
RAPD	*Ae. kotschyi*, *Ae. variabilis*, *Ae. tauschii*, *Ae. cylinddrica*, *Ae. crassa*, *Ae. biuncialis*, *Ae. triuncialis*, *Ae. geniculata*, *T. boeoticum*	[59–64]
RFLP	*Ae. geniculata*	[65]
AFLP	*Ae. kotschyi*, *Ae. variabilis*, *T. turgidum*, *T. dicoccon*, *T. dicoccoides*, *T. araraticum*, *T. monococcum*, *Ae. geniculata*, *Ae. ventricosa*	[66–70]
IRAP	*T. monococcum*, *T. boeoticum* subsp. *boeoticum*, *T. boeoticum* subsp. Thaoudar., *T. urartu*	[71]
REMAP	*T. boeoticum*	[72]
TRAP	*Ae. tauschii*, *Ae. cylindrica*, and *Ae. crassa*	[73]
ISSR	*Ae. ventricosa*, *Ae. taucshii*, *Ae. cylindrica*, *Ae. umbellulata*, *Ae. triuncialis*, *Ae. biuncialis*, *Ae. crassa*, *Ae. kotschyi*, *Ae. speltoides*	[59,74–76]
SSR	*T. turgidum*, *T. dicoccon*, *T. dicoccoides*, *T. araraticum*, *T. monococcum*, *Ae. geniculata*, *Ae. ventricosa*, *Ae. crassa*, *Ae. cylindrica*, *Ae. biuncialis*, *Ae. triuncialis*, *Ae. tauschii*	[63,66,70,77–86]
cpSSR	*Ae. cylinddrica*, *Ae. kotschyi*, *Ae. peregrina*, *Ae. triuncialis*, *Ae. uniaristata*, *Ae. speltoides*, *Ae. longissima*, *Ae. sharonensis*, *Ae. searsii*, *Ae. bicornis*, *Ae. tauschii*, *Ae. crassa*, *Ae. vavilovii*, *Ae. ventricosa*, *Ae. juvenalis*, *T. urartu*, *T. boeoticum*, *T. araraticum*, *T. dicoccoides*	[87,88]
EST	*Ae. caudata*	[89]
EST-SSR	*Ae. cylindrica*, *Ae. tauschii*, *Ae. triuncialis*, *Ae. crassa*	[90]
SINE	*Ae. umbellulata*	[91]
ITE	*T. boeoticum*	[64]
SCoT	*T. turgidum*, *T. boeoticum*, *T. urartu*, *Ae. tauschii*, *Ae. caudata*, *Ae. crassa*, *Ae. neglecta*, *Ae. triuncialis*, *Ae. speltoides*	[73,92,93]
CBDP	*T. turgidum*, *T. boeoticum*, *T. urartu*, *Ae. tauschii*, *Ae. caudata*, *Ae. crassa*, *Ae. neglecta*, *Ae. triuncialis*, *Ae. speltoides*	[94,95]
DArT	*T. turgidum*, *Ae. Kotschyi*, *Ae. cylindrica*, *Ae. neglecta*, *Ae. columnaris*, *Ae. biuncialis*, *Ae. triuncialis*, *Ae. juvenalis*, *Ae. tauschii*	[96–98]
SNP	*T. turgidum*, *Ae. Kotschyi*, *Ae. cylindrica*, *Ae. neglecta*, *Ae. columnaris*, *Ae. biuncialis*, *Ae. triuncialis*, *Ae. juvenalis*, *Ae. tauschii*	[97,99–103]

4. Potential of Wild Relatives for Use in Wheat Breeding Programs

Farmers' desired qualities (yield potential, large seed, high seed weight) and breeders' preferred characteristics (high seed weight, large seed, yield potential) both benefit from genetic variety in wheat germplasm (e.g., biotic and abiotic resistance) [103]. It is clear that an increasing number of genetic diversity studies on wheat and their wild relatives are revealing the ideal potential of these natural resources and also suggesting ways of devis-

ing targeted methods to exploit the diverse existence of ex-situ germplasm collections [5]. To date, various attempts have been made to improve common wheat by using genetic diversity in wild relatives. Arguments for the greater use of wheat relatives' include: the taxonomic relationship between wheat and its relatives, cross-compatibilities, F1 fertility, and subsequent progeny, exploration and utilization of this natural resource, and availability and regional financial support based on their geographic distribution [104]. In this section, we highlight some representative examples in which wild wheats showed specific ability versus different environmental stresses.

4.1. Drought

The extensive use of advanced lines has resulted in the loss of genetic basis of bred varieties of wheat that has, in some cases, led to increased susceptibility to various abiotic stresses [103]. Drought or a lack of water is one of the most significant environmental factors affecting global wheat production. Drought tolerance is a multi-dimensional quantitative characteristic that has a dramatic impact on plant development stages [105]. The impacts of drought stress have been intensely studied in wheat and its relatives. Among wild wheats, *Aegilops* species have been considered as an ideal source for improving the genetic background of bread wheat to tolerate drought stress.

Several *Aegilops* species, such as *Ae. speltoides*, *Ae. tauschii*, and *Ae. geniculata*, have indicated the ability to overcome drought stress [106,107]. Introgression of drought tolerance to bread wheat was achieved by hybridization between durum wheat and *Ae. tauschii* species. DNA fingerprinting of synthetic hexaploid (SHs), materials showed that they can respond well to water deficit due to their excellent features, such as a longer root system and higher soluble carbohydrates [108]. The use of carbon isotope discrimination (Δ) has been proposed to estimate transpiration efficiency, water use efficiency, and drought tolerance in different wild wheat species [109]. This method was performed by Waines et al. [110] on several *Aegilops* species. Their results revealed a high intraspecific variation in most species, and, among the tested species, Δ values were highest in *Ae. speltoides*. Wild emmer wheat (*T. dicoccoides*) can donate excellent drought tolerance compared to other wheat species. It is clear that this ancestral species can better overcome drought conditions compared to durum wheat [111]. Therefore, *T. dicoccoides* is one of the most important sources for drought tolerance and is highly proper as a donor for developing agronomical and physiological features related to tolerance in cultivated wheat species. In a comprehensive study conducted by Pour-Aboughadareh et al. [112], a set of 180 accessions belonging to 12 wild and domesticated species along with two commercial tolerant and sensitive control varieties were examined in terms of shoot dry mass and chlorophyll fluorescence parameters under two water regimes: optimum irrigation (FC = 100%) and drought stress (FC = 30%). A considerable number of wild wheats with alien genomes, such as *Ae. crassa* (DM genome), *T. urartu* (A^u genome), *Ae. cylindrica* (DC genome), and *Ae. caudata* (C genome), indicated a higher tolerance to drought stress as compared with the domesticated genotypes and tolerant control, reflecting greater drought adaptations in these species.

Upon exposure to drought stress, plants undergo many physiological and molecular changes. One of these changes is the production of reactive oxygen species (ROS) in different plant tissues. The ROS family—-including singlet oxygen ($^1O_2$), superoxide (O^{2-}), hydroxyl radical (OH), and hydrogen peroxide (H_2O_2)—-act as signal molecules in the response to drought stress. On the other hand, increasing the production of ROS may result in cellular damage and finally cell death [113]. Therefore, antioxidant gene overexpression could induce tolerance to this stress. Plants have antioxidant systems in place to scavenge excess ROS and protect themselves from the harmful consequences of oxidative stress by generating various antioxidants. A detailed description of antioxidant mechanisms can be found in the review by Bose et al. [114].

Some research has focused on the state of antioxidant activities and the ROS pathway in bread wheat germplasm. Recently, Ahmadi et al. [115] examined the antioxidant activities in several wild relatives of wheat in response to drought stress. The wild ac-

cessions used in their study revealed more activities in the expression of antioxidative enzymes—including catalase (CAT), guaiacol peroxidase (GPX), superoxide dismutase (SOD), and ascorbate peroxidase (APX)—than the cultivated wheats. Remarkably, four wild wheats—*T. boeoticum*, *Ae. crassa*, *Ae. cylindrica*, and *Ae. Umbellulata*—responded well to severe drought stress (FC = 25%) by elevating enzymatic antioxidants as the primary defense system, which contributes to the cell's ability to maintain oxidative equilibrium. In another study, Pour-Aboughadareh et al. [116] showed a high rate of variability among *Ae. cylindrical, Ae. tauschii*, and *Ae. crassa* species, along with *T. aestivum* landraces in terms of several photosynthetic and physiological traits under severe water deficit stress. These authors stated that, among 200 samples related to these species, 19 accessions from *Ae. crassa* and 1 accession from *Ae. tauschii* indicated considerable tolerance to drought conditions through the maintenance of their biomass and other physiological capacities. When the top-ranked accessions were evaluated in terms of biochemical traits, *Ae. crassa* showed better potential for scavenging the ROS through higher activity of CAT, APX, GPX, and peroxidase (POD) antioxidant enzymes [117].

The root system, as an important organ for the uptake of water and nutrients, is the first part of a plant that senses water shortage [118]. Recently, many efforts have been made to indicate the relationships among root system features and drought tolerance adaptability in the wild relatives of wheat under drought conditions. Ahmadi et al. [119] focused on seedling root architectural traits in the whole collection of wheat germplasm containing 180 accessions along with two control bread wheat genotypes under two water regimes. They reported a high level of root variability in some wild wheat responding to drought stress. When the root system of the different species was compared under drought stress conditions, it was found that four species of wild wheat—*Ae. speltoides* (As a putative B genome), *Ae. cylindrica* (DC genome), *Ae. neglecta* (UM genome), and *Ae. tauschii* (D genome)—had a great ability to extend their root system. In another study, Djanaguiraman et al. [120] showed that *Ae. speltoides* was an ideal candidate for improving the root system architecture in wheat. These authors examined 48 Chinese spring wheat-alien chromosome lines belonging to *Ae. longissima*, *Ae. geniculate*, *Ae. searsii*, *Ae. peregrine*, *Ae. speltoides*, *Th. intermedium*, *L. racemosus*, and *D. villosum* in terms of several physiological and root features under drought stress. The results showed that the wheat-alien chromosome lines with chromosome segments from *Ae. speltoides* were identified as drought tolerant, so that their acceptable tolerance was associated with a deep and profuse root-system structure.

4.2. Salinity

Salinity stress is another environmental challenge that dramatically limits wheat production worldwide [121]. It has been reported that more than 800 million hectares of the world's total land are affected by salinity [122]. As a result, attempts to improve wheat salt tolerance are critical for long-term agriculture and might considerably increase wheat output. The screening of wheat germplasm has a significant role in breeding programs aimed at improving salinity tolerance [123]. Although a number of salt-tolerance traits have been characterized by Colmer et al. [124], we mention several key studies that have introduced wild wheats with superior salt-tolerance. The effects of salinity on plant growth include osmotic pressure, oxidative stress, ionic toxicity, and nutritional imbalance, which in turn severely limits the development and function of all plants.

Plants often have a variety of tolerance mechanisms that enable them to reproduce in marine environments, including reducing root Na^+ uptake and limiting salt concentration in the cytosol [125]. Effective removal of Na^+ from roots and shoots and the isolation of specific organelles, intracellular compartments, or cells of Na^+ are other important processes for surviving salinity stress [126]. Thus, the ability to maintain high K^+ and low Na^+ concentrations in leaves is associated with salt tolerance. Research on different wild wheats under salinity stress has indicated that some *Aegilops* species can withstand heavy salt stress and have a greater tolerance than other wheat species [127]. For example,

Gorham et al. [128] revealed that *Ae. tauschii* has a higher Na^+:K^+ ratio in their leaves than other species. In fact, this result suggested that there is a close relationship between Na^+ exclusion and D genome that enhanced the Na^+:K^+ ratio. In a study conducted by Ahmadi et al. [129], *Ae. tauschii* along with *Ae. neglecta* species responded well to severe salinity treatment at the seedling stage. Kiani et al. [130] found that *Ae. cylindrica* accessions differed significantly in terms of physiological characteristics, including their susceptibility to salt stress throughout the vegetative stage. The results from the last two reports have postulated the key impact of C genome on salt exclusion in this wild wheat. Furthermore, the observation of Ahmadi et al. [131] in the screening of wheat germplasm to explore the source of salinity tolerance revealed a high potential for some *Aegilops* and *Triticum* in coping with salinity stress. These researchers looked at root and shoot biomass, physiological parameters, and ROS scavenging enzymes in a core collection of 181 accessions that included landrace genotypes and various wild relatives of wheat. Based on their results, several wild species with alien genomes, such as *Ae. cylindrica* (DC), *Ae. caudata* (C), and *T. boeoticum* (A^b), revealed an appropriate response to salinity stress by increasing enzymatic antioxidants. These results support the fact that there is a good potential for salinity tolerance in wild relatives of wheat, which in turn reveals new insights for reconsidering the associations between wheat progenitors and salinity tolerance.

4.3. High Temperature

Crop growth rates are influenced by temperature conditions. The high temperature, as another environmental stress, has limited wheat production in the world. As a result of global warming, all crops may undergo many changes in their growth and development. Hence, an exploration of ideal sources of variability to high temperature tolerance for wheat and other field crops is required. High temperature fluctuations have a significant impact on plant development in a variety of ways. Chlorophyll concentration and the photosynthetic ability of leaves are reduced due to this stress [132]. Because thylakoid membranes are one of the most vulnerable cellular structures to this stress, there is a clear link between chlorophyll concentration and thylakoid membrane damage caused by high temperatures [133]. Thus, damaged thylakoid membranes leads to loss of chlorophyll content and reduced photosynthesis capacity [134]. In recent years, analyzing chlorophyll fluorescence has been one of the most popular approaches in plant physiology to measure photosynthetic activity. It plays a critical role in understanding key photosynthetic systems, plant responses to environmental change, and ecological diversity [135]. The analysis of chlorophyll fluorescence components, such as initial fluorescence (*Fo*), maximal quantum efficiency (*Fv/Fm*), and primary yield of photochemistry (*Fv/Fo*), is a critical approach for determining the integrity of the internal mechanisms within a leaf during photosynthetic activities. It also provides a precise method for assessing damage to photosystem II centers (PSII) and, as a result, identifying plants that are resistant to certain stressors, particularly high temperatures [112,136,137]. *Fo* is a measure of the stability of the light-harvesting complex among chlorophyll fluorescence components, and it is enhanced in the leaves of plants under high temperatures compared to optimal conditions [138]. In theory, an increase in this parameter might be read as a decrease in the rate constant of energy trapping by PSII, which could be the result of the light-harvesting complex becoming physically disconnected from the PSII core [139]. In genotypes of *Ae. tauschii* and *Ae. speltoides*, an increase in the *Fo* parameter has been recorded under high temperature stress [140]. Using this parameter, researchers have illustrated that *Ae. tauschii* had greater thermostability of the photosynthetic mechanism. High-temperature stress was also applied to wheat species at anthesis and maintained for 16 days, resulting in reductions in chlorophyll content, the number of grains per spike, grain weight, and grain yield per plant of 38, 40, 56, and 70%, respectively [141]. Pradhan et al. [141] indicated that among *Aegilops* species, *Ae. geniculate* and *Ae. speltoides* displayed a greater tolerance to high temperatures for grain yield (58–61% decline than optimum temperature), while *Ae. longissima* yields showed an 84% decline.

4.4. Low Temperature

Low temperature, as the fourth important abiotic stress, affects wheat growth and production in many regions of the world. Extreme cold stress causes a change in cell architecture by preventing exterior water mobility and converting internal water to a crystalline state. Low temperature stress-sensitive plants, as a rule, are unable to continue growing over extended periods of time and respond to cold by altering metabolite concentrations [142]. Generally, efforts to improve cold tolerance through existing plant genetic materials appear to have been unsuccessful because of limited genetic diversity for this characteristic. Wild relatives of wheat offer a potential source of additional genetic variability which could be utilized to improve the cold tolerance of wheat, and, up to now, numerous studies have focused on these species under different environmental conditions. Nonetheless, no work has been undertaken to investigate the whole set of wild relatives in response to cold stress. Only a few examples could be found. For instance, Limin and Fowler [143] found that *Ae. tauschii* responded well to freezing stress, while all species related to Sitopsis section were sensitive. However, it has been reported that *Ae. speltoides* and *T. turdidum* have a higher tolerance than other wild species [144,145]. In a study conducted by Stankova et al. [146], among different *Aegilops* species, *Ae. cylindrica* revealed the highest cold tolerance, whereas *Ae. genioulata* and *Ae. biuncialis* were identified as sensitive relatives. They also demonstrated that *Ae. triuncialis* and *Ae. neglecta* have intermediate tolerance. Moreover, Masoomi-Aladizgeh et al. [147] evaluated several *Ae. tauschii* accessions under controlled cold conditions, demonstrating the capability of this species in response to freezing stress.

4.5. Biotic Stresses

Unexpected biotic stressors similar to other environmental stresses continuously pose a danger to wheat production. Pathogen resurgences have occurred from the monoculture of contemporary wheat cultivars with limited genetic diversity, posing a danger to wheat supply [148]. Several living creatures, such as fungi, viruses, insects, nematodes, arachnids, and weeds, induce biotic stress in plants. Pathogenic fungi, among, other biotic stressors, pose a serious threat to wheat production across the world. Stripe rust, stem rust, leaf rust, powdery mildew, head blight, and other diseases negatively affect wheat production and grain quality worldwide. Yellow rust has historically caused and continues to cause substantial and severe losses in vulnerable wheat cultivars all throughout the world [149]. Aphid, hessian fly, green bug, and borers are among the most common insect pests that damage wheat.

Only a few of these biotic stress resistance genes in wheat have been identified and cloned thus far. Species from the primary gene pool (*Triticum* spp.), secondary gene pool (e.g., *T. timopheevii*), and tertiary gene pool (e.g., *Aegilops*), are among the R gene donors [150]. The wild relatives of wheat may be divided into main, secondary, and tertiary gene pools based on their genomic makeup [151,152]. These gene pools provide a plentiful supply of disease and pest resistance genes in wheat. Species with homologous genomes to farmed wheat make up the main gene pool. *T. aestivum, T. turgidum*, and species with the A and D genomes—*T. monococcum, T. urartu, T. boeoticum,* and *Ae. tauschii*—-make up this group [152]. Many genes providing disease and insect pest resistance have been transmitted by hybridization and backcrossing procedures, and some of them are still used in cultivar improvement [153,154]. An active collection of 280 *Ae. tauschii* accessions is kept at the Punjab Agricultural University (PAU) in Ludhiana, India. Various biotic stressors, including as leaf rust, stripe rust, powdery mildew, and Karnal bunt (KB), have been shown to carry resistance genes in these accessions. The KB resistance of *Ae. tauschii* is quite strong. The polyploid *Triticum* and *Aegilops* species, which share at least one genome with wheat, make up the secondary gene pool of bread wheat. Many resistance genes have been given by these species, which have been utilized in cultivar development [151].

It has been reported that, in wheat or its wild relatives, more than 240 rust resistance genes have been identified and formally recognized, the majority of which are race-specific

resistance genes [153]. The QTL regulating stripe rust resistance in *T. monococcum* was found on chromosome 2A (*QYrtm.pau-2A*), whereas the QTL controlling stripe rust resistance in *T. boeoticum* was found on chromosome 5A (*QYrtm. pau-5A*). Co-introgression of *T. boeoticum* sequences related to stripe rust-resistant QTL, *QYrtb.pau-5A* [155] revealed that one stripe rust-resistant gene from *T. boeoticum* acc. pau5088 was verified to be introgressed in cultivated wheat. *T. durum* was used as a bridge species to introduce leaf and stripe rust resistance genes from diploid species *Ae. umbellulata* and *Ae. caudata* [155,156]. In general, through the use of different approaches, a number of resistance genes have been transferred from wild relatives to bread wheat. Among the identified resistance genes, most numbers are related to leaf rust, followed by powdery mildew, and green bug [157]. In general, Table 5 indicates some identified or transferred resistance genes in various *Aegilops* species.

Table 5. Identified or transferred resistance genes from various Aegilops species into bread wheat.

Pest	Species	Gene	References	Disease	Species	Gene	References
Eyespot	*Ae. ventricosa*	*Pch1*	[158]	Stem rust	*Ae. speltoides*	*Sr32*	[159]
Powdery mildew	*Ae. speltoides*	*Pm1d*	[160]			*Sr47*	[161]
		Pm32	[162]		*Ae. comosa*	*Sr34*	[163]
		Pm53	[164]		*Ae. ventricosa*	*Sr38*	[165]
	Ae. longissima	*Pm13*	[166]		*Ae. searsii*	*Sr51*	[167]
	Ae. geniculate	*Pm29*	[168]		*Ae. geniculate*	*Sr53*	[169]
	Ae. umbellulata	*Pm57*	[170]	Leaf rust	*Ae. umbellulata*	*Lr9*	[171]
	Ae. tauschii	*Pm19*	[172]			*Lr76*	[173]
		Pm34	[174]		*Ae. speltoides*	*Lr28*	[163]
Cyst nematode	*Ae. ventricosa*	*Cre2*	[175]			*Lr37*	[165]
		Cre5	[176]			*Lr47*	[177]
		Cre6	[178]			*Lr51*	[179]
	Ae. triuncialis	*Cre7*	[180]			*Lr66*	[181]
	Ae. peregrine	*CreX*	[182]		*Ae. kotschyi*	*Lr54*	[183]
		CreY	[182]		*Ae. sharonensis*	*Lr56*	[181]
Root knot nematode	*Ae. peregrine*	*Rkn2*	[184]		*Ae. geniculate*	*Lr57*	[185]
	Ae. ventricosa	*Rkn3*	[186]		*Ae. triuncialis*	*Lr58*	[187]
Hessian fly	*Ae. ventricosa*	*H27*	[188]		*Ae. peregrine*	*Lr59*	[189]
	Ae. triuncialis	*H30*	[190]		*Ae. neglecta*	*Lr62*	[191]
	Ae. tauschii	*H22*	[192]	Strip rust	*Ae. comosa*	*Yr8*	[193]
		H23	[192]		*Ae. ventricosa*	*Yr17*	[165]
Green bug	*Ae. speltoides*	*Gb5*	[194]		*Ae. sharonensis*	*Yr38*	[181]
	Ae. tauschii	*Gb3*	[195]		*Ae. geniculate*	*Yr40*	[185]
Russian wheat aphid	*Ae. tauschii*	*Dn3*	[196]		*Ae. neglecta*	*Yr42*	[189]
Wheat curl mite	*Ae. tauschii*	*Cmc4*	[197]		*Ae. umbellulata*	*Yr70*	[173]

5. Transcriptome Analysis Uncovers Hidden Information about the Benefits of Wild Relative Potentials

Progress in biotechnological tools, such as the GeneChip® Wheat Genome array and RNA sequencing, have indicated that the transcripts associated with starch biosynthesis and defense proteins in hexaploid bread wheat are expressed 2–3 weeks after anthesis. The transcripts that are most numerous in growing plants, on the other hand, were associated with storage proteins that are expressed during the developmental phase [198–201]. While transcriptome analysis was done in hexaploid wheat during grain production [202,203], bread wheat and its wild progenitors have yet to be subjected to a thorough transcriptional characterization. Studying the expression of these key genomes at specific stages during grain development in bread wheat and its wild relatives can be very beneficial. This will be useful to understand the changes in wheat grain consistency that occurred during the transition from ancient bread wheat to modern bread wheat. Kaushik et al. [201] used RNAseq to study the development of bread wheat grains and their diploid progenitor cells to evaluate gene expression patterns and monitor differentially expressed genes. To

analyze gene expression profiles and screen differentially expressed genes, they used transcriptomics methods to compare the expression of key genes in hexaploid bread wheat and its three diploid parents during the entire grain production process. It can help to better understand the molecular mechanisms of metabolic pathways involved in the production and regulation of key components of grain growth. In addition, transcriptome sequencing of bread wheat and its ancestors is used to study the genetics of wheat endosperm growth.

5.1. Grain Development Related Proteins

Global wheat security is under threat due to the need for wheat to feed the world's growing population [203]. Wheat grain production is thought to be a significant determinant of yield and flour content. Understanding the process of wheat grain growth, as well as identifying key candidate genes that perform important functions during grain development, is crucial. Reduced expression of *TabZIP60* has been reported to improve grain yield and nitrogen uptake through RNAi interference by upregulating *TaNADH-GOGAT* expression. Compared to the wild type, the grain yield of the overexpression line increased by 16.6–26.8% [204]. Previous studies have used genome-wide association analysis study (GWAS) to classify new genomic regions related to grain yield and characteristics related to grain yield in 123 synthetic hexaploid wheat (SHW) grown under drought stress. Among them, 35648 derived single nucleotide polymorphism (SNP) genotypes were sequenced [205]. They found that SHW has a significant genetic diversity in grain yield and yield-related traits. Under drought stress, GWAS in 123 synthetic hexaploid wheat established multiple new genomic regions or haplotype blocks related to grain yield and yield-related traits. Most marker-trait associations (MTAs) are found in the genome, and some are annotated with drought stress functions. This further demonstrates that the given MTA is reliable. MTAs are also linked to a variety of characteristics on other chromosomes, but only inside the genes that have the same annotation. This led to the identification of candidate genes from the same gene family that are considered important in grain yield and yield-related characteristics in drought-stressed SHWs [205]. Wild relatives of wheat may be useful for studying different facets of evolution and growth involved in the production of bread wheat. Grain production involves several biochemical and physiological processes that occur in a variety of tissues [206]. There are major stages including fertilization, multinucleate endosperm, cellularization, and early grain filling, full grain filling, and desiccation [207]. Grain production is critical for completing a crop's life cycle because it accumulates various nutrient stocks as well as embryo development and maturation. The nutritional and economic value of wheat grain is determined by the accumulation of these nutrient stocks [201].

5.2. Nutrient Reservoir

Nutrient reserves (NRs), carbohydrate metabolism (CM), and defense proteins (DPs) are the most common genes involved in wheat grain production [206]. Carbohydrates are the most common, followed by storage proteins in NR. However, carbohydrates are metabolized by complex mechanisms affecting a variety of genes. The genes involved in anabolism and catabolism have been studied in CM, which has been designated as a separate class. Wheat genotypes contain different kinds of storage proteins in terms of consistency and quantity because the coding region of wheat storage protein is highly polymorphic [208]. Starch is the most prevalent nutrient in *T. aestivum*, followed by storage proteins and lipids [199]. Thus, the synthesis and aggregation of starch and storage proteins are crucial for the growth of wheat grain. Albumins, globulins, and gluten are the most common storage proteins. Glutenins and gliadins are two types of gluten. Glutenins are often made up of proteins with high and low molecular weights [201,208]. Prior research has revealed that the glutenin and gliadin subunits of wild wheat relatives varied greatly. Ahmadi et al. [209] used unique molecular markers to characterize the allelic variation of glutenin and gliadin in 180 *Aegilops* and *Triticum* accessions obtained from different parts of Iran. They revealed that the allelic status of *Glu-3A* and *Gli-As.2* was related to genomic

constitutions, resulting in a large variance in the gliadin and glutenin subunits in di- and tetraploid wild relatives of *Ae. umbellulata*, *Ae. caudata*, *Ae. tauschii*, and *T. urartu* genomes. As a result, previous studies may yield new avenues for improving dough consistency by reconsidering the connections between other progenitors and wild cousins. Researchers have been encouraged to hunt for unique and beneficial alleles to create new kinds that are better suited to new uses, given the discovery of this very varied gene pool.

5.3. Carbohydrate Metabolism

The most significant metabolic process in the formation of wheat grains is carbohydrate metabolism. According to research on the wheat grain proteome, 21% of differentially expressed proteins are involved in carbohydrate metabolism [210]. β-glucosidase is one of the most common enzymes studied in wheat. It is responsible for the hydrolysis of carbohydrates. Adenosine diphosphate ADP pyrophosphorylase, starch synthase [211], starch branching enzyme, and starch debranching enzyme [206] are the four major enzymes involved in the production of starch, the main ingredient of endosperm.

5.4. Defense Proteins during Grain Development

The preservation of developing grains is the next critical phase during grain production after the deposition of storage materials. To resist or postpone several biotic and abiotic pressures, plants can trigger a range of molecular and biochemical defense mechanisms through irreconcilable interactions between the host and biotic/abiotic stimuli, resulting in a variety of signaling pathways [212]. Several investigations have proven that amylase/trypsin inhibitors regulate wheat defense responses by inhibiting the enzyme activities of amylase and trypsin in pests [210,213,214]. Insect defensive responses are considered to be aided by the Bowman–Birk family of cysteine-rich proteases [215]. Considering the change in genome size, 55.62, 55.92, 68.13, and 103.33 million reads were generated for the genome species of *T. urartu*, *Ae. speltoides*, *Ae. tauschii*, and *T. aestivum*, respectively. There are significant differences in the genome size [216] and the number of genes [216–219] between wheat hexaploid and its diploid ancestors. The number of genes expressed in hexaploid wheat is not proportional to the size of its genome, although it is slightly higher than that in diploid wheat. It has also been suggested that the size of the genome in the polyploid genome is not proportional to gene expression [220–222]. In hexaploid wheat, however, a review of half the number of reads showed significantly fewer transcripts. Researchers discovered that *Ae. speltoides* (BB) shared the most transcripts of the three progenitors. When sub-genomic research was performed, it was discovered that the number of transcripts in hexaploid bread wheat's B genome was somewhat greater [201].

5.5. Carbohydrate and Protein Related Transcripts

Kaushik et al. [201] also analyzed the gene expression of three main protein classes: nutrient reserves, defense protein, and carbohydrate metabolism. Albumin, globulin, prolamin, and glutenin are storage proteins formed primarily during grain growth. The gene ontology study of transcriptome data of hexaploid bread wheat and its diploid ancestors shows that nutrient pool behavior is remarkably rich. When ancient diploid wheat and modern bread wheat were compared, albumin was found to be highly upregulated in bread wheat. As a result, *Ae. speltoides* had a higher expression of this gene in diploid progenitors (BB) [201]. Prolamins are proline and glutamine-rich proteins that make up roughly half of the nitrogen in wheat grains [216,223,224]. Gliadins, which belong to the prolamin family, are the oldest wheat nutrient reservoirs [225]. When compared to *T. monococcum*, these proteins were upregulated in bread wheat. Bread wheat transcriptome comparisons demonstrated an upregulation of α/β gliadin and γ-gliadin B in *Ae. tauschii* (DD and) *Ae. speltoides* (BB). The diploid progenitor AA genome (*T. urartu*) genotype exhibited a lower gliadin gene expression in this example. In comparison to its diploid progenitors, high molecular weight glutenins expressed more transition in bread wheat. Gluten is formed when gliadin and glutenin combine, and it is much higher in bread

wheat than in its diploid progenitors. α-β Gliadins were found to be actively expressed in wheat endosperm from 11 days to 4 weeks after anthesis [226]. High molecular weight glutenins were also found to be most abundant during early grain filling, a finding that had previously been recorded in *Norin* 61 bread wheat [227].

5.5.1. Carbohydrate Biosynthesis Genes

In bread wheat and its diploid progenitors, many glucose metabolism-related genes are differently expressed. Starch biosynthesis is carried out by two types of enzymes: granule associated starch synthase and starch synthases [228,229]. When hexaploid wheat was related to its diploid progenitors, granule bound starch synthase (GBSS-I) was down-regulated, and starch synthase genes were upregulated. This finding shows that hexaploid bread wheat produces less amylose and more amylopectin during grain production than its progenitors [201]. In bread wheat, major starch aggregation occurs during the early stages of grain production [230]. In *T. aestivum* and *Ae. tauschii*, stage-specific GBSS expression data is also related to this discovery. The starch in the endosperm is broken down to produce glucose, which is then used by the scutellum for the growth of the embryo [231]. Compared with hexaploid bread wheat, the gene expression of some important and abundant enzymes in starch metabolism such as AMY3 amylase and α-glucosidase is reduced in *Ae. speltoides* and *T. monococcum* [201,232]. In the late stage of grain filling, the gene expression of carbohydrate catabolism enzymes such as amylase and glucosidase was higher, but the gene expression of carbohydrate anabolism enzymes (such as starch synthase bound to carbohydrate granules) was larger at first. Therefore, although carbohydrate biosynthesis occurs early in the filling process, the consumption of carbohydrates for energy production (ATP) occurs later. This is due to the reduced amount of carbohydrates available from sources [233].

5.5.2. Defense Proteins

Wheat grains are mainly composed of carbohydrates and protein, which account for about 80% of grain weight. It is essential to safeguard these nutrient reservoirs in wheat grains against biotic and abiotic influences and to keep them alive before germination by defense proteins. Many differentially expressed genes linked to defense proteins are identified when different phases of bread wheat grain production are compared [206,234]. When opposed to *T. monococcum*, *Ae. tauschii*, and *Ae. speltoides*, a trypsin inhibitor, which is implicated in herbivorous pest resistance [235], was upregulated in hexaploid wheat. This suggested that both *Aegilops* species have an almost identical voice, which is better than *T. monococcum*. In diploid progenitors, a stage-specific study of this gene revealed a related pattern. In bread wheat, the defense protein thionin was found to be upregulated [236,237]. However, stage-specific expression showed that expression was higher in the early stages in hexaploids, while in diploids it was higher in the later stages. Some defense proteins, such as Bowman Birk type trypsin inhibitors (pathogen inactivator) [238,239], subtilisin chymotrypsin inhibitors (known to suppress insect larvae) [240], and wheat monomeric amylase inhibitors [241], were also downregulated in hexaploid wheat. The expression of both defense-related genes was shown to be higher in hexaploids at the early stages of grain filling and lower in diploids during the later stages.

6. Dynamic Wheat Transcriptome and Small RNA in Wild Relatives of Wheat under Abiotic Stresses

The genome's substructure aids in mapping dynamically transcribed sections to biotic and abiotic stressors during plant growth and adaptation. Transcriptome profiling was carried out on the wheat genome to provide a better understanding of both gene expression levels and harvests [242]. In 2004, 35 individual cDNA libraries representing extremely detailed developmental stages of different grains and seedling tissues were used to create microarrays with high-density from the publicly accessible wheat EST resource, which included 26,382 sequences [242]. However, due to the immobile existence of probes and the reliance on genome annotation quality, the microarrays provided insufficient expression

proof. Indirect measurement of gene expression levels was found to be illustrative of cDNA arrays through hybridization signs, and expression levels were detected to be illustrative of the tenacity of genuine transcript estimates in individual tissues or cell lines [243]. A systematic analysis of the entire transcriptional environment was carried out using next-generation RNA sequencing. Even though it demonstrated alternate splicing, it failed to display genome-wide gene function in terms of quantity [244,245].

Allohexaploid wheat is one example of the analysis of genetic associations between the three homologous genomes (A, B, and D) because it has recently suffered two allopolyploidization events. Several experiments have used microarrays and other methods to equate resynthesized or normal wheat allopolyploids to their progenitors [246–248]. In this survey, the non-additive gene expression in allohexaploid offspring was evaluated using the average parental gene expression level or number (i.e., the father's average (MPV)) [249]. Nonetheless, it has been found that additivity is more extensive than non-additivity [248]. MicroRNA (miRNA) and small interference RNA (siRNA) are small RNAs that control gene expression through post-transcriptional processes and epigenetic modifications [250,251]. In interspecific hybrids and allopolyploidies of *Arabidopsis*, changes in miRNA expression induce the non-additive expression of target genes, hindering developmental adaptability and vitality [252]. Subsequent studies have shown that the cis- and trans-regulation of miRNA and other genes can affect the normal changes in the biochemical and metabolic pathways that drive growth vigor and stress response [253,254]. In addition, by directing DNA methylation, siRNA, especially those related to transposable factors (TE), can act as a genomic shock absorber and control gene expression.

After polyploidization of wheat, the number of siRNAs corresponding to ET is significantly reduced, and it is rich in repeating sequences originating from TE (>80%), indicating that they play important roles during allohexaploidization [255]. Small RNA-mediated genome alteration and gene regulation are possibly involved in allohexaploidization, according to new evidence [256]. However, analysis of the homologous expression and limited abundance of RNA from individuals throughout the genome requires information from the genome sequence [257–259]. When these tools are combined with next-generation sequencing technologies, they can answer questions regarding how allohexaploidization affects homeolog expression and changes molecular pathways that lead to the nascent allohexaploid of wheat's growth vigor and adaptation, as well as whether small RNAs play a role in this process [242]. *T. aestivum* originated as a hybrid between *Ae. tauschii* and *T. turgidum* and outcompeted its parents in growth adaptability and vigor following chromosomal doubling. To further understand the molecular foundation for this achievement, Li et al. [244] used recently available A and D genome sequences to undertake mRNA and small RNA transcriptome studies in nascent allohexaploid wheat and subsequent generations, their progenitors, and the natural allohexaploid cultivar Chinese Spring [244]. Expressed protein-coding genes were found to be uncommon but essential for growth vigor. In addition, a considerable number of protein-coding genes showed an advantage in the expression level of the parent, and genes whose total homologue expression level in the offspring were the same as that of *T. turgidum* showed an advantage in the expression level of the parent, which is presumably involved in growth and those whose expression was similar to that in *Ae. Tauschii* possibly involved in adaptation. Furthermore, upon polyploidization, a large proportion of microRNAs exhibited nonadditive expression, theoretically resulting in differential expression of essential target genes. In addition, in heterozygous progeny, an increased density of small interfering RNAs was observed for transposable D homozygotes binding elements, which may explain the biased repression of D homoeologs. These findings shed light on small RNA-mediated dynamic homoeolog control pathways that can play a role in nascent hexaploid wheat heterosis [244]. In conclusion, Table 6 summarizes the important microRNAs which have been identified in various wild species of wheat under different growing conditions.

Table 6. The brief of identified microRNAs in wheat and some of its relatives.

Species	Tissue	Conditions	References
T. aestivum	seedlings, flag leaves, seeds, root, leaf, spike, immature and mature embryos, grain, shoot, spikelet, dry grain, embryo of germinating seed, shoot, spike, grains, flag leaves	N-stress, cold stress, heat stress, drought stress, dehydration stress, UV-stress, high temperature stress, salinity stress, water-deficit stress	[260–276] [277–283]
T. durum	roots, leaves, flag leaf, spikes, heads, seedling, young seedlings	N-stress, water deficit, stress, early water stress, heat stress	[277,283]
T. dicoccoides	leaves, plant	drought and stresses	[274,284,285]
Ae. sharonensis, *Ae. speltoides*, *Ae. tauschii*, *T. monococcum*, and *T. urartu*	leaf, root	drought stress	[286]

7. Next-Generation Sequencing in Bread Wheat

Encoded genomic sequence information is needed to fully leverage wheat's ability to feed the world's rising population. Since the bread wheat genome is so large, about 17 gigabases, conventional sequencing methods are challenging to use. Next-generation sequencing (NGS) can sequence a large genome in a limited amount of time. Refseq V1, as an important standard quality in hexaploid wheat reference genomes, was created by the International Wheat Genome Sequencing Consortium (IWGSC). It offered details on the locus and order of 107,891 genes from 21 sequenced chromosomes and has allowed for the discovery of more than 4 million molecular markers [242,287]. NGS could also help researchers obtain various reference-related genomes from bread wheat and review genome-wide relationships, epigenetic functionalities, and population genetics, among other things. This review compiles and discusses the existing knowledge about the use of NGS in wheat science, taking into account the relevance of wheat genomics and NGS. Exome capture combined with NGS technology is an important method for analyzing the wheat genome in depth. This approach may be used to sequence whole exon complements in the genome [288].

NGS technology is now commonly used to analyze transcripts. The sequence tags generated by these technologies represent genes that are expressed without prior knowledge of the gene sequence. Next-generation transcriptome sequencing can be used to analyze gene expression, the structure of genomic loci, and the sequence variations present in expressed loci [289]. This can be achieved by de novo assembly of the transcriptome sequence data or by aligning the reads with the genomic sequence. NGS technology revolutionized genome biology and has begun to provide important resources for the improvement of wheat crops. Compared to all of the previous sequencing technologies, these technologies provide a faster and cheaper method of generating wheat sequence data. Although the large size and complexity of the wheat genome make the use of NGS difficult, advances in sequencing technology and bioinformatics tools have made the application of NGS in wheat increasingly feasible. This type of application will eventually allow for a comprehensive package of wheat genome sequencing and annotations of the genome sequence to express genes and genomic variation across sub-genomes [290]. The application of NGS technology provides the opportunity to study and understand the structure and evolution of polyploid crop genomes. Discovery of numerous genome-wide molecular SNP markers has begun in wheat, which may have the largest and fastest impact on crop improvement. In the next few years, the challenge may shift from NGS analysis of the wheat genome to the association of sequence variation with heritable agronomic traits. As in rice, corn, and sorghum, the wheat genome sequence will advance our understanding of the genetic basis of agronomic traits, as well as aid the development of new technologies for improving wheat crops [290].

Genome-Wide Association Studies and SNP Microarrays

It is challenging to investigate wheat genetic variants. The most effective approach used to search for genetic mutations and their effects on phenotypes is to perform GWAS. Previously, genome-wide observations for various wheat genomes were obtained using single nucleotide polymorphism (SNP) microarrays. When compared to NGS, SNP microarray is less expensive and allows for a fast sequencing of the related genes. It aids in the comprehension of the marker traits connected in the creation of maps, as well as the ancestral relationships between populations. However, due to the sensitivity of recognition and the ability to recognize genetic variation, NGS outperforms SNP microarrays [291]. In addition, NGS-based genotyping will reveal new genetic variations and allow detailed analysis of population genetics.

Arora et al. [292] revealed that the variation of grain size in the germplasm of *Ae. Tauschii* and the genetic basis was analyzed using a GWAS. The grain length, width, and weight of 177 *Ae.tauschii* germplasm evaluations in 3 years showed an almost normal distribution, and the variation was 1.74, 1.75, and 2.82 times, respectively. These lines were genetically characterized using the Genotype Sequencing Protocol (GBS), which produced 11,489 SNP markers. Genetic diversity analysis revealed the existence of two distinct subgroups in *Ae. tauschi*. Based on GBS markers, the genetic similarity between germplasms was calculated, and GWAS was performed using 114 non-redundant germplasms and 5249 SNP markers. A total of 17 SNPs related to grain size traits distributed on seven chromosomes were revealed, of which 4444 had the most significant marker-trait associations with 6D, 5D, and 2D. For some related SNP markers, candidate genes related to cell division and differentiation were identified. Further efforts to validate these loci will help to understand their role in determining the grain size and allelic diversity in the current germplasm, as well as the effect on grain size when transferred to the bread wheat background [292].

In hexaploid wheat, GBS has recently become an important method for GWAS. GBS examines millions of SNP markers, which are used to discover genetic variation through the multiple analyses of samples from different genomes. Where the interested gene or locus genes necessitates map-based gene cloning, it is a popular method in forward genetics [293]. Outbreeding the mutant organism to create a population of mapping is part of map-based cloning in plants [294]. GWAS helps to promote crop improvement by raising awareness of Market Portrait Associations (MTAs). Lozada et al. [295] reported that, by using different panels of 239 soft red winter wheat (*T. aestivum* L.) genotypes, GWAS was performed on grain yield (GY), grain yield components, and agronomic characteristics over two growing seasons and eight site years. Analysis of variance showed the significant effects of the environment andgenotypes in the GY, and its components. Compared to other traits, including plant height and kernel weight, the narrow heritability of the GY is moderate. Using compressed linear mixed models and 5715 single nucleotide polymorphism markers to measure eight traits, 112 significant MTAs were detected. The MTA of GY and agronomic traits are consistent with the previously reported QTLs of winter and spring wheat. The highly significant MTA of the GY shows an overall negative allele effect on the minor alleles, indicating that the breeder has been selected for these alleles. The markers associated with multiple traits observed on chromosomes 1A, 2D, 3B, and 4B have slight positive effects and serve as potential targets for marker-assisted reproduction to select and enhance the GY and its related traits. After labeling verification, these multi-portrait sites have potential that can be used by MAS to enhance the GY and adaptability of soft red winter wheat [295].

GWAS was performed on 208 series durum wheat panels using 6211 DArTseq SNP. This panel has been phenotyped for 2 years under the conditions of yield potential (YP), drought stress (DT), and heat stress (HT). GWAS has identified the most important trait-marker linkages on chromosomes 2A and 2B, and the markers in the study explain variation in traits. Common markers were identified for stress tolerance indices: stress susceptibility index, stress tolerance, and stress tolerance index estimated for sub-DT and HT traits. The GWAS from the three environments of irrigation and stress and its comparison with

the trait itself and the stress index determined the QTL hotspots on chromosomes 2A and 2B [296]. Thirteen traits were evaluated in 373 *Ae. tauschii* germplasm grown under normal drought stress conditions and simulated with polyethylene glycol, and performed a genome-wide association study using 7185 SNP markers [297]. They used a general linear model and a mixed linear model to determine 208 and 28 SNPs related to all traits, and both models detected 25 important SNPs distributed throughout the genome. Public database searches revealed several candidate/flanking genes related to drought resistance, which were divided into three categories based on the type of protein encoded. In another study, Mehrabi et al. [298] evaluated a set of *T. durum* landraces using SNP markers and root system features, as well as some agronomic characteristics, over three stages of plant growth and development. They reported that most significant MTAs were identified on chromosome B. Furthermore, 167 QTLs were detected for root system and agronomic traits, among which 16 QTLs for root-related traits overlapped with different measured agronomic traits.

8. Concluding Remarks

Plant genetic resources are valuable assets for humankind. Among crop wild relatives, wild wheat species have an important role in durum and bread wheat evolution. Hence, thousands of *Aegilops* and *Triticum* accessions have been collected and are conserved in various genebanks worldwide. These resources have donated an assortment of alleles needed for resistance/tolerance to various environmental stresses, however, they have yet to be used sufficiently in breeding programs. Our review has highlighted the potential of wild kinds of wheat to use in future breeding programs. We believe that this paper provides useful information and improves the understanding of natural diversity among plant genetic resources and biotechnological tools for graduate students and also for the practical applicability of the researchers.

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