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Review

Loving the Alien: The Contribution of the Wild in Securing the Breeding of Cultivated Hexaploid Wheat and Oats

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Abstract: Cereal production is of strategic importance to the world economy. Although the primary aim of breeding programs is to develop cultivars with improved agronomic performance, including high grain yield and grain quality, as well as disease and lodging resistance, nowadays the adaptability to changing environmental conditions seems to be an extremely important feature. The achievement of these breeding objectives in diploid cereal species such as rice, barley, or maize is straightforward. The genetic improvement of polyploid crops such as hexaploid wheat and oats for increased crop production is highly demanding. Progenitor species and wild relatives, including taxa at lower ploidy levels, have preserved a high degree of useful genetic variation. The world's genebank collections of wheat and oat germplasm provide extremely rich resources for future breeding and utilization. This review highlights the immense potential of cultivated wild relatives as donors of genes for a wide range of biotic and abiotic traits and their impact on wheat and oat breeding. This review covers methods allowing access to these genetic resources, and it highlights the most (and most recently)-exploited related species for gene introgression in wheat and oats. Further, it will also deal with the impact of genomics and cloned genes on the advanced discovery, characterization, and utilization of genetic resources in these two cereals.

Keywords: crop wild relatives; wheat; oat; introgression breeding; pre-breeding; discovery breeding; wide crosses

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1. Introduction

As major cereal crops cover a significant proportion of arable land [1], their continuous genetic improvement, particularly in terms of disease resistance and nitrogen-use efficiency, substantially supports, by the renunciation of pesticides and the saving on fertilizers, the movement to sustainable agriculture. Elite germplasm becomes short of useful genetic variation over time. This decrease periodically encourages breeders to remember the great allele diversity of crop wild relatives (CWR) and landraces that are stored globally in seed banks and intensify pre-breeding activities for elite germplasm enhancement. Although more challenging to explore, crop ancestors and widely related species meet great expectations as they reveal new alleles not only for traits such as resistance to diseases and tolerance to abiotic growth constraints, e.g., water deficits and heat, but also for yield and quality improvement.

The early work with alien germplasm was driven by common wheat (*Triticum aestivum*, 2n = 6x = 42, AABBDD genomes) and rapeseed (*Brassica napus*, 2n = 4x = 38, AACC) through attempts to unravel the wild relatives involved in polyploid formation [2,3]. A major success of introgression breeding was already reported in 1930, when the recessive and durable, race-non-specific adult plant stem rust-resistance gene *Sr2* was transferred from cultivated emmer (*T. dicoccum* syn. *T. dicoccon*, 2n = 4x = 28, AABB) into common

wheat [4]. The *Sr2* locus was later recognized also to confer partial resistance to leaf rust, stripe rust and powdery mildew [5], and a role for it was suggested in controlling cell death in response to stress [6]. The expansion of the gene pool concept by Harlan and de Wet [7], who proposed groupings of a crop and related species based on successful introgressions among them, paved the way for breeders to choose appropriate plant materials from CWR for successful introgression breeding. Along with the establishment of advanced molecular marker technologies, methods and resources, particularly noteworthy advanced backcross QTL analysis [8] and introgression libraries [9], were developed in the 1990s for coping with alien genes that determine quantitative traits. Finally, pan-genomics (reviewed, e.g., in [10]) guided in genotyping arrays the assembly of signatures for the variable gene fraction recognized through the comparison of the genome sequences from multiple, both closely and distantly related, individuals. These molecular tools use thousands of single nucleotide variants (SNV syn. SNP, single nucleotide polymorphism) markers and provide useful data for convoying introgression breeding. Genotyping-by-sequencing [11], another high-volume marker approach combining SNV discovery and scoring, was added to the molecular marker toolbox and shown to be highly useful for plant species for which whole genome sequence information is scarce. It appears that the potential of molecular marker technologies, 15 years ago identified as a shortcoming for assisting introgression breeding and gene deployment in breeding programs [12], can now be fully realized to produce new cultivars carrying genes from CWR. The shortening of the generation time through speed breeding [13], a technique employing easy protocols, can be seen as another milestone on the way to the exploration of CWR in a reasonable time. Complementing conventional breeding approaches, de novo domestication through genome editing was recently developed for several crops [14–17]. The conversion of wild into cultivated variants of cloned domestication and improvement genes makes CWR directly amenable for breeding, while retaining all other trait variation.

In this review, we present the contributions of wild relatives to the genetic enhancement of the two most important hexaploid temperate cereals, wheat and oats.

2. Wheat

2.1. Wheat, An Outstanding Grass Species

Wheat is one of the most consumed cereal species. This crop shows high adaptability to diverse environments as a result of genome plasticity, and thus has become the most widely cultivated species: it is grown on 221 million hectares with a production quantity of 771 million tons [18]. Sixty-six percent of global wheat production is used for food [19], and nutritional end-uses include different types of bread, noodles, cakes, pastries, cookies, crackers, bulgur, and even patties (from green spelt). Wheat trading, with 25% of the production in 2021 being exported [20], plays a major role in food security. As only several countries are central for the international wheat trade [21], supply shortages, such as experienced in the COVID-19 pandemic and now in the Ukraine war, have a severe impact on food availability. Wheat belongs to the Triticeae tribe within the *Poaceae* family. This genus group consists of nearly 500 species, most of which are perennials [22]. The embedding of common wheat, the most important representative of the *Triticum* species, into such a vast community of relatives has provided the basis for its successful continuous genetic improvement over the last century. Several of the many successful studies on the use of Triticeae members for the enhancement of cultivated wheat are reported in the following subsections.

2.2. Synthetic Hexaploid Wheat and Examples of Re-Synthesized Polyploids from Other Crops

Allopolyploids such as common wheat that have not recurrently formed suffer from a narrow genetic base [23]. However, this evolutionary constraint can be easily countered by using artificial polyploids for gene transfer. These important genetic resources are produced as chromosomally doubled hybrids (induced by treatment with colchicine or other antimitotic agents) from their progenitors, with interploid crosses requiring additional

embryo rescue and in vitro culture due to endosperm-development failure and embryo abortion [24,25]. Natural and artificial polyploids can be readily hybridized as they fully share the same genomes. Indeed, recurrent backcrossing (usually two rounds) to cultivated genetic backgrounds is needed to counter the low vigor of these primary polyploids, but, concurrently, homologous recombination-based introgressions are obtained.

Species re-synthesis was applied early in common wheat [26] and rapeseed [27], in the latter of which hybridization can be performed both sexually and somatically [28]. Since then, many primary synthetics and derivatives thereof, which provide new allele diversity from accessions of the lower ploidy level species *T. durum* (pasta wheat; 2n = 4x = 28, AABB), *T. dicoccum*, *T. dicoccoides* (wild emmer; 2n = 4x = 28, AABB) and *Aegilops tauschii* (2n = 2x = 14, DD), were developed and characterized in wheat [29]. A data survey on pre-breeding activities by the International Maize and Wheat Improvement Center revealed that at least 86 varieties have been selected from synthetic hexaploid wheat derivatives and released in 21 countries [30]. Of the released varieties, cultivar Largo and its derivatives were found to carry new major genes conferring resistance to insects [31–34] and stem rust [35]. Recently, Molero et al. [36] identified a locus of possibly dominant inheritance on chromosome 6D within an *Ae. tauschii* introgression that contributes to heat tolerance with no yield penalty in high-yield potential environments. An overview of documented genes captured in synthetic wheat from *Ae. tauschii* is presented in [37].

Recent work in the cultivated allotetraploid peanut (*Arachis hypogaea*, 2n = 4x = 40, AABB) reported neotetraploids that were obtained from crosses with accessions of *A. ipaënsis* (2n = 2x = 20, BB) and *A. duranensis* (2n = 2x = 20, AA), the two genome donors of the cultivated peanut, and other related wild diploid species, including *A. batizocoi* (BB), *A. magna* (BB), *A. valida* (BB), *A. correntina* (AA), and *A. stenosperma* (AA) [38,39]. The authors state that these synthetics are being used in breeding programs and carry alleles for traits including resistance to major diseases and adaptation to environmental stresses that frequently do not show genetic variation in cultivated peanut. These recent studies from the peanut clearly show that the creation of artificial polyploids through interspecific crosses is still a valid approach for accessing the genetic diversity of wild species.

2.3. Direct and Bridge Crosses

Gene introgression from wheat relatives can be achieved by direct hybridization with common wheat, which is used as female parent in the initial cross (Figure 1). Other methods that have been established for the exploitation of wheat species of lower ploidy level use bridge crosses with durum wheat.

2.3.1. Waiting for Rare Gametes: The Challenge Associated with the Exploitation of Lower Ploidy Level Species That Share Genomes with Common Wheat

The F1 hybrids between common wheat and diploid and tetraploid species that carry the haploid genomes of the species involved in the crosses are tetraploids and pentaploids, respectively. As fertile hybrids possessing gametes that are equipped with a full triploid chromosome complement are rare, many initial crosses must be made to obtain sufficient working material. Alternatively, embryo rescue of the hybrids can be employed [40]. Forty-two-chromosome wheat lines are recognized through chromosome counts in self-pollinated or backcross-derived progenies, while specific introgression lines are identified by phenotypic and/or genotypic assessments. Many designated genes conferring resistance to major diseases, such as powdery mildew and rusts, were directly transferred from compatible lower ploidy level species into common wheat (Table 1), and there was also a gene for increased protein and micronutrient (iron and zinc) content from wild emmer [41,42].

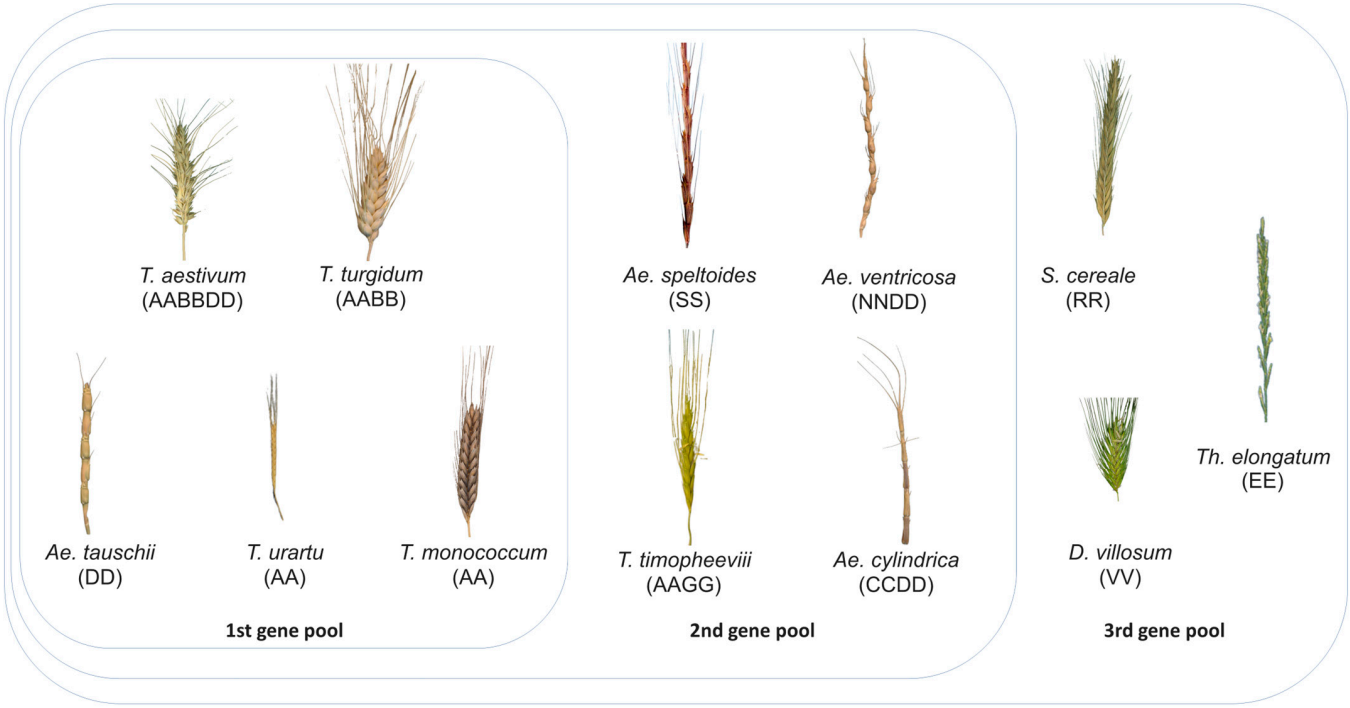

Figure 1. The gene pools of common wheat (*Triticum aestivum* L.) grouped based on the feasibility of gene transfer among species. Not all species are shown.

For gene transfer from wild emmer, three-way crosses using durum wheat as a bridge and hexaploid wheat as a pollinator (*T. dicoccoides*/*T. durum*//*T. aestivum*) were established, as the fertility of the F_1 pentaploid hybrids of these three-way crosses was increased compared to that of the direct crosses [43]. Recently, *PmG16* and the map-based cloned gene *Pm69* were transferred by this method (Table 1). Furthermore, tetraploid durum wheat can also be used to bridge the transfer of useful alleles from diploid species to common wheat. The triploid F_1 hybrids, similar as mentioned above, can then be either directly used for backcrossing with common wheat or, after establishment of an artificial hexaploid, through chemically induced genome doubling. This approach was followed for resistance genes *Sr22b* and *Sr60* from *T. monococcum*, and *Pm60* and *Pm60b* from *T. urartu* (2n = 2x = 14, A^uA^u) (Table 1). Notably, these genes were cloned in the diploid species before being transferred into common wheat. Besides using direct crosses with common wheat, *Sr21* and *Sr22* were also made available using the triploid hybrid bridge, whereas *Yr15* was additionally introgressed by durum wheat-assisted three-way crosses (Table 1).

Table 1. Gene transfers from fully compatible diploid and tetraploid wheat species (progenitors) into common wheat.

Gene	Origin	Introgression Method	Reference
Pm1b	*T. monococcum*	Direct cross	[44,45]
Pm4a	*T. dicoccum*	Direct cross	[46,47]
Pm4d	*T. monococcum*	Direct cross	[48]
Pm16 = Pm30	*T. dicoccoides*	Direct cross	[49,50]
Pm26	*T. dicoccoides*	Direct cross	[51]
Pm31	*T. dicoccoides*	Direct cross	[52]
Pm34	*Ae. tauschii*	Direct cross	[53,54]

Table 1. *Cont.*

Gene	Origin	Introgression Method	Reference
Pm35	*Ae. tauschii*	Direct cross	[55,56]
Pm50	*T. dicoccum*	Direct cross	[57]
Pm60	*T. urartu*	Triploid hybrid bridge	[58]
Pm60b	*T. urartu*	Triploid hybrid bridge	[58]
Pm64	*T. dicoccoides*	Direct cross	[59]
Pm69	*T. dicoccoides*	Three-way cross	[60]
MlZec1	*T. dicoccoides*	Direct cross	[61]
PmG16	*T. dicoccoides*	Three-way cross	[62]
Yr15	*T. dicoccoides*	Direct cross Three-way cross	[43,63,64]
Yr35	*T. dicoccoides*	Direct cross	[65]
YrAS2388R	*Ae. tauschii*	Direct cross	[66,67]
Lr14a	*T. dicoccum*	Direct cross	[4,68,69]
Lr21 [1]	*Ae. tauschii*	Direct cross	[70]
Lr39	*Ae. tauschii*	Direct cross	[71]
Lr42	*Ae. tauschii*	Direct cross	[72,73]
Lr53	*T. dicoccoides*	Direct cross	[65]
Sr21	*T. monococcum*	Direct cross Triploid hybrid bridge	[74,75]
Sr22	*T. boeoticum*	Direct cross Triploid hybrid bridge	[74,75]
Sr22b	*T. monococcum*	Triploid hybrid bridge	[76]
Sr35	*T. monococcum*	Direct cross	[77,78]
Sr60	*T. monococcum*	Triploid hybrid bridge	[79]
SrTA1662	*Ae. tauschii*	Direct cross	[80]
GPC-B1 [2]	*T. dicoccoides*	Direct cross	[81]

[1] *Lr21* introgressions were also made through synthetic hexaploid wheat line RL5406 [82]. [2] Also called *NAM-B1* as the gene encodes a NAC domain transcription factor [83].

2.3.2. The Induction of Homoeologous Pairing

Before methods for the targeted induction of homoeologous pairing were known, introgressions from the secondary and the tertiary gene pool of wheat were achieved via both compensating (substituting corresponding chromosome segments) and non-homoeologous (causing genetic imbalance through the loss and addition of chromosome segments) translocations that occurred spontaneously or were induced by facilitating the meiotic appearance of two homoeologous univalents (double monosomics), radiation treatment, or high-pairing lines (reviewed in [84]). The discovery of the genetic control of the strict pairing and recombination of homologous chromosomes in wheat [85,86] was essential for the conscious induction of homoeologous recombination. The disruption of meiotic pairing regulation in alien species-wheat F_1 hybrids was achieved with either deletion mutants [87] or suppressors (available from different wheat wild relatives) [88–90] for the *Ph1* locus on chromosome 5B and promoters for homoeologous recombination such as found in *Ae. geniculata* [91]. A recent study in common wheat combined *ph1b* and homoeologous recombination promoter factor(s) to further increase recombination, even in the proximal regions of the chromosomes where recombination is known to be rare [92].

Introgressions can finally also be achieved through the generation of addition and substitution lines. Single monosomic addition lines are obtained by crossing an amphidiploid such as historical triticale (2n = 8x = 56, AABBDDRR) with common wheat. To generate single monosomic substitution lines, single disomic addition lines, recovered after selfing, are then used to pollinate wheat lines that are monosomic for the homoeologous chromosome pair carried by the additions. For example, to produce hybrids of the genome constitution 20″ + 1B′ + 1R′, the gametes to combine must either have the constitution 20′ − 1B′ + 1R′ of the disomic addition line and 20′ + 1B′ of the monosomic line or 20′ + 1B′ + 1R′ of the disomic addition line and 20′ − 1B′ of the monosomic line. In subsequent segregating selfing progeny, lines without the single common wheat chromosome can be identified. Single disomic substitution lines are then used in *ph1*-based introgression programs.

In the secondary gene pool of wheat, consisting of Triticeae members with at least one genome common to bread wheat, useful variation is mostly obtained through translocations. Although several species belong to the secondary and tertiary gene pools, *Aegilops* is the largest genus in the secondary gene pool and most closely related to common wheat: *Ae. tauschii* is the direct progenitor of the wheat D genome (thus, per definition, a member of the primary gene pool) and *Ae. speltoides* (2n = 2x = 14, SS) of the section Sitopsis shares ancestry with an unknown, most likely extinct, diploid species that donated the wheat B genome [93]. The study also found that the four remaining Sitopsis species are phylogenetically clustered with the D genome lineage and may have contributed to the genome constitution of the unknown B genome progenitor. Members of the genus *Aegilops* have provided nearly 50 designated resistance genes against fungal diseases and pests [37,94–96]. Among them, *Ae. speltoides* is the most exploited species.

Dasypyrum villosum (2n = 2x = 14, VV) is an open-pollinating annual Mediterranean grass in the tertiary gene pool of wheat. Although known for its apparently high allele diversity, *D. villosum* was just recently explored in more detail, especially in China. Five documented *D. villosum* accessions, with genomes designated V#1 to V#5, have been used to develop wheat-*D. villosum* disomic addition, substitution, and translocation lines [97]. Of these accessions, at least three were donors of resistance genes to diverse pathogens (Table 2).

Table 2. Gene transfers from diploid *Dasypyrum villosum* into common wheat.

Disease	Gene	Line(s)	Chromosome Constitution	Reference
Powdery mildew	*Pm21*	Several NAU427 DvRes-1	T6AL.6V#2S Cryptic 6V#2S introgression not published	[98] [99] [100]
	Pm55	NAU421	T5AL.5V#4S	[101]
	Pm62	NAU1823	T2BS.2V#5L	[102]
	Pm67	NAU1817	T1DL.1V#5S	[103]
	PmV	Pm97033 RIL 12401 Dv6T25 Dv6T31	T6DL.6V#4S T6AL.6V#4S-6V#2S short distal 6VS segment short proximal 6VS segment	[104] [105] [106] [106]
	Pm5V	NAU1908	T5DL.5V#5S	[107]
Stripe rust	*YrCD-3*	22-12	T3DL.3V#3S	[108]
	Yr5V	NAU1908	T5DL.5V#5S	[107]
Stem rust	*Sr52*	Several	T6AS.6V#3L	[109]
Sharp eyespot	-	NAU2V–8	T2DS.2V#4L	[110]
Cereal cyst nematode	*CreV*	NAU423	T6AS.6V#4L	[111]
Wheat spindle streak mosaic virus	*Wss1*	NAU413	T4VS.4DL	[112]

As a major disease in the wheat-growing regions of China, resistance to powdery mildew was widely investigated and six genes have been characterized so far. Since its description in 1995, the all-stage resistance gene *Pm21* has been widely used in Chinese wheat-breeding and many cultivars were released [113]. To allow future use of this important resistance gene, new powdery mildew resistance genes from *D. villosum* including *PmV*, a *Pm21*-homolog carried by a wheat-*D. villosum* T6DL.6V#4S translocation for which small segmental translocation lines were identified in a large *ph1b*-based population, adult plant resistance genes *Pm55* and *Pm62*, and more recently, all-stage resistance gene *Pm67* are available for gene stacking with *Pm21*. In addition, the mining of 38 *Pm21* gene variants can also contribute to a longer use of the *Pm21* locus once their reaction to powdery mildew were characterized and the useful genes were transferred into common wheat [114].

Further overviews of wheat-alien translocations are presented in [84,115,116].

2.4. Impact of Genomics and Cloned Genes on the Advanced Utilization of Genetic Resources in Wheat

Developments in marker technologies over the last ten years have contributed, and still do contribute, to the systematic and large-scale exploration of species from the third gene pool of wheat. Molecular markers basically have the potential to identify chromatin of any wild relative in the common wheat background and are rapid when compared to cytological methods. Kompetitive allele-specific PCR (KASP) assays for single-copy SNPs that differentiate common wheat from wild relatives, and thus relatively easy heterozygous from homozygous hybrid lines in backcross populations, were recently developed for 10 wheat wild relatives ranging between 114 for *T. urartu* and 322 for *Thinopyrum intermedium* (2n = 6x = 42; $StStJ^rJ^rJ^{vs}J^{vs}$) [117]. This flexible molecular marker format was used at the Nottingham BBSRC Wheat Research Centre to study hundreds of homoeologous introgressions from *Ae. caudata* (2n = 2x = 14, CC) [118] and *Amblyopyrum muticum* (2n = 2x = 14, TT) [119] into wheat. Whole-genome sequencing of *Am. muticum* introgression lines has shown that KASP markers, despite an even genome coverage, have limited power for determining the precise size of incorporated segments and will likely overlook small segments [120]. Still, these and other resources [121,122] will make the species from the third gene pool of wheat among the most extensively exploited in future wheat breeding.

Linkage drag of detrimental alleles has regularly thwarted alien gene use in agriculture. For example, the introgression in common wheat of *Sr22* from *T. boeoticum* (2n = 2x = 14, A^bA^b) was burdened by a yield penalty [123]. After it was recognized that the gene was effective against Ug99 stem rust, efforts were undertaken to develop lines with reduced introgression fragments. Here, the availability of dense genetic maps was enough for the controlled targeting of the closely related chromosome fragment and the identification of recombinant lines in segregating populations [124]. The cloning of *Sr22* from a hexaploid introgression line [75] has allowed further allele-mining from diploid species, and the validation of predicted functional and nonfunctional alleles using transgenic assays in hexaploid wheat [125] enables the future transfer of effective alleles only. The *Th. ponticum* (2n = 10x = 70, $JJJJJJJ^sJ^sJ^sJ^s$)-derived genes *Lr19* and *Fhb7*, conferring a broad resistance without yield penalty to leaf rust [126,127] and Fusarium species [128,129], respectively, are closely linked to the yellow flour gene *Psy-E1* [130], which limits their use in wheat breeding. Three studies developed new small segment translocation lines based on *ph1b*-induced homoeologous recombination along with molecular marker enrichment for these segments to resolve this linkage drag effect: Li et al. 2023 [131] shortened the alien segment on wheat chromosome 7DL using wheat line SDAU 2028, whereas Zhang et al. 2022 [132] transferred a new *Fhb7* allele derived from diploid *Th. elongatum* (2n = 2x = 14, EE) and available in a Chinese Spring-*Th. elongatum* disomic substitution line 7E(7B) into chromosome 7B. Similarly, Xu et al. 2023 [133] obtained a smaller *Th. ponticum* chromosome segment on chromosome 7DL that retained *Lr19* but not *Psy-E1*, using translocation line K11695 [134].

Regarding the transfer of disease-resistance genes, the loss or reduced effectiveness of resistance (especially to the three wheat rust pathogens) from the progenitors was regularly observed in synthetic wheat. Thus, suppression was mediated by genes located either on the A and/or B genome chromosomes of some tetraploid genetic backgrounds such as Langdon durum [135] or on the D genome chromosomes of *Ae. tauschii* [136]. The stem rust suppressor *SuSr-D1* identified in Canthatch common wheat was cloned [137], allowing now for the targeted removal of the suppression allele by molecular markers or its inactivation by genome editing.

When cloned genes are available, the relationship of genes located in the target regions can be clearly answered as shown for the powdery mildew resistance loci *Pm3* [138], *Pm4* [47], *Pm5* [139], and *Pm24* [140]. Therefore, true allelism must also be questioned for *T. monococcum*-derived *Pm1b* [141], despite the fact that a genetic allelism test was carried out and a specific host response to powdery mildew isolates compared to other *Pm1* alleles was found [45]. The knowledge of whether genes are allelic or tightly linked is mandatory for creating virtually permanent gene stacks.

Among the genes that have been successfully cloned, the broad-spectrum all-stage resistance gene *Yr15* [64] and its allelic variants *YrG303* and *YrH52* [142] possibly have a high potential for longer use in agriculture, as they encode a tandem kinase-pseudokinase protein, like the barley stem rust-resistance gene *Rpg1* [143], a gene that has remained effective against most isolates in North America since its deployment in cultivar Kindred in 1942 [144]. *Yr15* has been now distributed in European commercial cultivars such as in the German spring wheat cultivar Kapitol and advanced breeding lines [145].

3. Oat

3.1. Oat—Common and Unique

Oat is a versatile crop with a wide range of applications, including human food, animal feed, and industrial materials. The primary aim of breeding programs is to develop cultivars with improved agronomic performance, including high grain yield and grain quality, disease and lodging resistance, as well as adaptability to changing environmental conditions.

It is significantly easier to achieve breeding objectives in diploid cereal species such as rice, barley or maize. It is much more difficult to conduct targeted breeding in polyploid crops such as wheat and oats. Despite the similarities in genome size between these hexaploids, wheat has immense significance in human nutrition, and substantial resources are allocated to research for this species. As a result, CWR utilization is more common in wheat than oats. *Hordeum*, *Secale*, and *Triticum* belong to the tribe Triticeae, *Avena* to the tribe Aveneae, and because of this the polyploid structure oat and wheat are not fully comparable [146]. Moreover, *Avena* has proven to be more recalcitrant to interspecies gene transfer compared to species from the tribe *Triticeae* due to postzygotic sterility barriers [147].

The main source of diversity for improving the cultivated oat has been the wild relatives of oats. Many genes providing desirable traits, especially disease-resistance genes, have been found in wild and weedy oat species as well as in landraces, breeding lines, or cultivars. However, it is mainly hexaploid taxa that have been utilized in oat breeding [148]. The main obstacle that is hindering oat improvement using wild or cultivated diploid and tetraploid species is the lack of chromosome pairing in hybrids [149]. Nonetheless, many oat cultivars now possess genes derived from wild relatives, and their contribution to global oat production is significant. This review highlights the immense potential of cultivated wild relatives as donors of genes for a wide range of biotic and abiotic traits and their impact on oat breeding.

3.2. Introduction to the Genus Avena

Understanding the relationships between species within the genus *Avena* is essential for genetics and breeding efforts, as well as for the efficient transfer of genes to the cultivated

oat. The genus *Avena* L. belongs to the tribe *Aveneae*, family *Gramineae*. It is divided into three karyological groups with 14, 28, and 42 chromosomes, and includes both wild and cultivated species [150]. Attempts to classify species within the genus *Avena* have been made many times [148,150–154]. Currently, most authors use the taxonomy based on Baum's numerical system [151] updated by Leggett [152], Zeller [154], and Loscutov and Rines [155]. According to this taxonomy, the genus *Avena* comprises 30 species, including 16 diploids (2n = 2x = 14), 8 tetraploids (2n = 4x = 28), and 6 hexaploids (2n = 6x = 42) (Table 3). Individual species were assigned to seven sections: *Ventricosa*, *Agraria*, *Ethiopica*, *Pachycarpa*, *Avenotrichon*, *Tenuicarpa*, and *Avena*. All species of the genus *Avena* are annual and self-pollinating, with the exception of *A. macrostachya*, which is a perennial and cross-pollinating species [156].

Table 3. Current classification of the genus *Avena* L.

Section/Species	Chromosome Number	Genomic Constitution
Section: *Avenotrichon*		
A. macrostachya Bal. ex Coss. et Dur.	2n = 4x = 28	CmCmCmCm
Section: *Ventricosa*		
A. clauda Dur.	2n = 2x = 14	CpCp
A. eriantha Dur.	2n = 2x = 14	CpCp
A. ventricosa Bal. ex Coss.	2n = 2x = 14	CvCv
Section: *Agraria*		
A. brevis Roth.	2n = 2x = 14	AsAs
A. hispanica Lag.	2n = 2x = 14	AsAs
A. nuda L.	2n = 2x = 14	AsAs
A. strigosa Schreb.	2n = 2x = 14	AsAs
Section: *Tenuicarpa*		
A. atlantica Baum et Fedak	2n = 2x = 14	AsAs
A. canariensis Baum Rajhathy et Sampson	2n = 2x = 14	AcAc
A. damascena Rajhathy et Baum	2n = 2x = 14	AdAd
A. hirtula Lag.	2n = 2x = 14	AsAs
A. longiglumis Dur.	2n = 2x = 14	AlAl
A. lusitanica (Table Mar.) Baum Comb et Stat.	2n = 2x = 14	AsAs
A. matritensis Baum Sp. Nov	2n = 2x = 14	AA?
A. prostrata Ladiz.	2n = 2x = 14	ApAp
A. wiestii Steud	2n = 2x = 14	AsAs
A. agadiriana Baum et Fedak	2n = 4x = 28	AABB (DDDD)
A. barbata Pott. ex Link.	2n = 4x = 28	AABB
Section: *Ethiopica*		
A. abyssinica Hochst	2n = 4x = 28	AABB
A. vaviloviana (Malz.) Mordv.	2n = 4x = 28	AABB
Section: *Pachycarpa*		
A. magna Murphy et Terrell	2n = 4x = 28	CCDD
A. murphyi Ladiz.	2n = 4x = 28	CCDD
A. insularis Ladiz.	2n = 4x = 28	CCDD
Section: *Avena*		
A. byzantina Koch.	2n = 6x = 42	AACCDD
A. fatua L.	2n = 6x = 42	AACCDD
A. ludoviciana Dur.	2n = 6x = 42	AACCDD
A. occidentalis Dur.	2n = 6x = 42	AACCDD
A. sativa L.	2n = 6x = 42	AACCDD
A. sterilis L.	2n = 6x = 42	AACCDD

Most species in the genus *Avena* are wild forms. Among cultivated forms, the following hexaploid species are of the greatest economic importance: *A. sativa* L. (common oat) and *A. byzantina* C. Koch. (red oat), and to a lesser extent diploid species *A. strigosa* Schreb. (grey oat). Diploid species *A. nuda* L., *A. brevis* Rotch., and *A. hispanica* Lag. [151] are of marginal economic importance among cultivated forms, similarly to tetraploid *A. barbata* Pott. ex Link and *A. abyssinica* Hochst (Ethiopian oat) [152].

Four primary genomes (A, B, C, and D) have been identified in the genus *Avena* based on the combined data from karyotype analysis, FISH, GISH, C-banding, and interspecific hybrid chromosome pairing experiments [154,157]. In diploid species, only the A or C genomes are present; in tetraploid species, the A, B, C, or D genomes can be found; and in hexaploid species, the A, C, and D genomes have been described. The A and C genomes are present in all karyological groups; the D genome is found in tetraploids and hexaploids, while the B genome is only present in certain tetraploids [158–160]. The B or D genomes have not been identified in any of the currently known diploid species [161]. Taking into account the structural differences in chromosomes, five subgenomes have been distinguished within the A genome of diploids: Ac, Ad, Al, Ap, and As. Similarly, two subgenomes have been identified within the C genome, i.e., Cp and Cv [149,150]. Diploid species belong to three sections, including *Ventricosa*, which comprises three species with the C genome, and sections *Agraria* and *Tenuicarpa*, which include four and nine diploids with the A genome, respectively.

Baum [151] has divided tetraploid species into three groups. The first group includes *A. macrostachya*, an autotetraploid, whose genome is a specific form of the C genome designated as Cm [162,163]. The second group, known as the "barbata group", includes species with an AABB genomic composition: *A. barbata, A. vaviloviana,* and *A. abyssinica.* The third group is composed of species with a CCDD genomic composition. The species belonging to the third group are *A. magna, A. murphyi* [160], and the relatively recently discovered (by Ladizinsky [164]) *A. insularis*. The genome composition of the tetraploid species *A. agadiriana* has not been definitively determined. However, research conducted by Tomaszewska et al. [165] has suggested that the genomic composition of this species may be DDDD, and not AABB as previously reported [166].

Based on the structural similarity of chromosomes and chromosomal pairing in hybrids, the genome composition of all hexaploids has been described by Rajhathy and Thomas [150] as AACCDD, which has been confirmed by whole-genome sequencing analyses [167]. There is much controversy regarding the distinctiveness of species among hexaploids, especially as intertaxa hybrids are fertile. Ladizinsky and Zohary [168], based on the identical genomic composition and fertility of hybrids, have suggested that all hexaploids belong to one species, *A. sativa*. Rajhathy [169] distinguishes four hexaploid species: *A. sativa*, *A. byzantina*, *A. fatua* and *A. sterilis*. Baum [151] and Zeller [154] in turn distinguish seven hexaploid species: *A. atheranta*, *A. fatua*, *A. hybrida*, *A. occidentalis*, *A. sativa*, *A. sterilis*, and *A. trichophylla*, while Jellen et al. [147] argue that there are eight hexaploid taxa and add *A. byzantina* to the seven mentioned above. On the other hand, Loscutov and Rines [155] identify six hexaploid taxa: *A. sativa*, *A. byzantina*, *A. fatua*, *A. sterilis*, *A. occidentalis*, and *A. ludoviciana.* Therefore, the taxonomic status of *Avena* hexaploids is ambiguous; however, Loscutow and Rines' [155] taxonomy seems to fit best in the context of contemporary research [159].

3.3. Use of Wild Relatives in Oat Improvement

Numerous studies have highlighted the common oat as a classic example of a cultivated species with a relatively narrow gene pool [170–172]. Historically, improvements since the end of the 19th century have focused on small but consistent increases in grain yield. A significant breakthrough occurred in the mid-twentieth century when researchers uncovered the potential of related wild oat species as valuable sources of genetic variability for cultivars [173–175]. As a result, breeders and researchers began exploring genebank resources to identify accessions carrying desirable genes.

Various genes have been identified in the oat species collected in global genebanks, including disease- and pest-resistance genes, genes enabling adaptation to specific or changing environmental conditions, genes conditioning high content and quality of protein, fat, or β-glucans in grains, tolerance to low and high temperatures, drought resistance, lodging resistance, early maturation, rapid vegetative growth, high yielding potential or insensitivity to day length [156,173,176–189]. A detailed characterization of gene resources and traits identified in various common oat relatives is discussed in reviews by Loscutow and Rines [155] and Boczkowska et al. [190].

3.4. Limitations in the Use of Wild Relatives of the Oat

Wild species variability is not always equally accessible to breeders and depends on the degree of genetic barriers separating some of these species [149]. The larger the phylogenetic distance between the crossed taxa, the greater the difficulty in obtaining fertile hybrid offspring. Interspecific crossing barriers result from the different levels of ploidy or lack of genome homology. They cause sterility in the obtained hybrids and constitute a significant limitation in the direct utilization of genes determining beneficial traits [150]. Understanding the genetic relationship between individual species at different ploidy levels is a prerequisite for effective selection of parental components for crossbreeding in order to obtain interspecific hybrids that carry desirable traits and could be the initial material for new cultivars [173,191–193].

An obstacle in expanding the oat gene pool is the presence of numerous translocations in the genome. The most common are translocations from the C to D genome; less common are those from A to C or from D to C [159,194]. However, rare translocations from A to D and from D to A genomes have also been identified [165]. Reconstruction of the ancestral state of oat chromosomes revealed the loss of at least 226 Mb of gene-rich regions from the C genome in favor of the A and D genomes [167]. The presence of large and fairly common intergenomic translocations 7C-17A (1C/1A) [163,195] and 3C-14D (6C/5D) [196] was detected within the cultivated hexaploid gene pool itself [197,198]. Kianian et al. [199] proposed describing the genomic organization of hexaploids as segmental homoeology, rather than whole-chromosome homoeology, due to the significant involvement of chromosomal rearrangements, such as translocations, inversions or duplications, in their evolution. Very frequent rearrangements of oat chromosomes result in pseudo-linkage and suppression of recombination and limit the improvement of cultivated oat forms [200]. The segmental chromosomes' homoeology affects segregation, localization, and deployment of QTLs in breeding programs [199].

Harlan and de Wet [7] presented a classification of wild species based on their crossing potential with cultivated forms. They distinguished three gene pools (Figure 2). A similar classification of wild species in the genus *Avena* was presented by Leggett and Thomas [148]. The first gene pool includes all wild hexaploid species. The free transfer of genes to cultivated forms occurs through conventional crossing, backcrossing, and recurrent selection [156]. The second gene pool includes tetraploids with a CCDD genomic composition, i.e., *A. magna*, *A. murphyi*, and *A. insularis*. The transfer of genes from this gene pool to hexaploid cultivated forms is partially limited. F_1 hybrids can be relatively easily obtained; they are self-sterile but partially female-fertile and their fertility can be restored through backcrossing [154,156]. The third gene pool comprises tetraploids with an AABB genomic composition, i.e., *A. barbata*, *A. abyssinica*, *A. vavilovonia*, and *A. agadiriana* as well as all diploids. The transfer of genes from these species to cultivated forms is limited and requires overcoming the crossing barriers through the use of in vitro cultures and polyploidization.

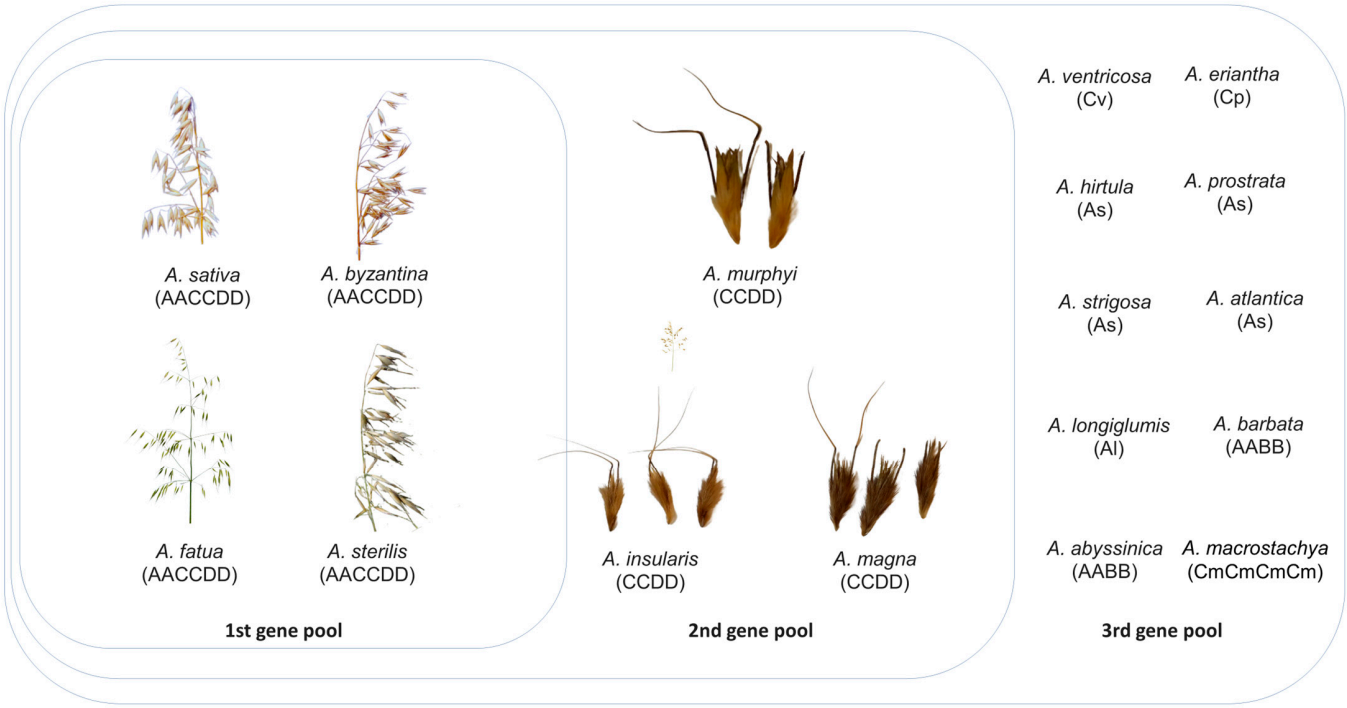

Figure 2. The gene pools of the common oat (*Avena sativa* L.) grouped based on the feasibility of gene transfer among species. Not all species are shown.

3.5. Cultivar Enhancement through Direct Crosses with Hexaploid Species

In the common oat breeding programs involving interspecific crosses, hexaploid species, which belong to the first gene pool, are most often used as the source of desirable genes [155,194]. Oat breeders have a broad spectrum of hexaploid species represented not only by wild or weedy species but also *A. sativa* and *A. byzantina* landraces. As a result, there are many examples of introgressions from these easily available resources. Nevertheless, Frey [173] considered the wild species *A. sterilis* as the most promising source of new genes available to breeders. Among the genotypes of this species, genes for BYDV tolerance and resistance to powdery mildew, crown rust, or nematodes have been identified. Additionally, this species is a source of genes that determine high protein and oil content in grains, as well as traits related to early maturity, rapid vegetative growth, and high yield [154,177,183,184,188,201–204]. Therefore, *A. sterilis* can be found in the pedigrees of many American cultivars, e.g., Starter, where this wild species contributed to increased grain protein content, Ozark (with improved winter hardiness [205]), or Sheldon (with high yielding potential [206]). However, most commonly, *A. sterilis* accessions have been used as a source of qualitatively inherited major disease-resistance genes, particularly against crown rust. The latter disease, caused by the fungus *Puccinia coronata* f. sp. *avenae* Eriks. (*Pc*), is one of the most widespread diseases of oats [207–209]. Crown rust infection causes a reduction in yield, decreases grain quality, and reduces plant resistance to lodging [208]. Genes determining resistance to specific races of this pathogen were initially identified in the cultivars of *A. sativa* and *A. byzantina*, and the first research in this field was conducted by Parker [210]. In subsequent years of breeding for resistance, alternative sources of *Pc* genes were sought, which turned out to be genotypes of *A. sterilis, A. strigosa*, and *A. abyssinica* [211]. Among over 100 identified genes conferring resistance to crown rust, approximately 50 originated from *A. sterilis*, 22 from *A. strigosa*, 1 from *A. abyssinica*, 1 from *A. magna*, and the remaining genes from cultivated forms [211–214]. The development of cultivars resistant to crown rust mainly utilized *A. sterilis* genes (*Pc38*, *Pc39*, *Pc48*, *Pc58*, *Pc59*, *Pc60*, *Pc61* and *Pc68*) [215,216]. An exception is the *A. magna*-derived *Pc91* gene, currently providing the most effective resistance to crown rust found in HiFi, Stainless or CDC Morrison cultivars. Genes conferring resistance to powdery mildew (*Pm1*, *Pm3*,

Pm11, *Pm12*, and *QPm.18*) [217–220], as well as stem rust (*Pg13*, *Pg15*, and *Pg17*) [221], also originated from *A. sterilis*. Among the aforementioned genes, *Pm1*, *Pm3*, *QPm.18*, and *Pg13* have been introduced into cultivars.

Grain protein content is one of the agronomically important traits improved with the use of *A. sterilis* genetic variation. Cox and Frey [178] identified transgressive segregants with high protein content in the progeny of *A. sativa* × *A. sterilis* hybrids. Lyrene and Shands [203] found that a higher protein proportion can be accompanied by an increase in husk content. Additionally, these authors pointed out that selecting progeny of *A. sativa* × *A. sterilis* hybrids based solely on grain protein content would also be associated with an increase in husk content in the grain, as well as a reduction in grain filling, decreased yield, and, in some cases, spikelets-shattering and awn formation. Hence, the authors suggested that breeding programs should prioritize maintaining a high level of agronomic traits, even if this approach may slow down progress in increasing grain protein content. Takeda and Frey [222], analyzing interspecific hybrids of *A. sativa* × *A. sterilis*, found that it is necessary to conduct three to five backcrosses to obtain lines with high grain protein content, while maintaining satisfactory levels of agronomic traits. The same authors [223] obtained lines with a very high level of grain protein content already in early backcross generations, but these traits were accompanied by unfavorable agronomic properties. Rossnagel and Bahtty [224] utilized American breeding lines containing *A. sterilis* in their pedigree as a source of genes for high grain protein content and obtained hybrids characterized by increased protein quantity, with retained high-yielding potential and grain quality. The recurrent selection method was also applied to increase oil content in groat up to 16% [206,225,226]. One of the important directions in oat breeding was to reduce straw height and improve lodging resistance by using dwarfing genes. The *Dw8* gene, which reduces plant height, was obtained from *A. fatua* [227,228]. However, the resulting dwarfism was too extreme to be used in *A. sativa* cultivars [229]. *A. fatua* germplasm was also used to improve adaptation to arid regions of the cultivars Sierra, Mesa, or Montezuma and introduce extreme earlines into the cultivar Rapida [230,231].

3.6. Non-Hexaploid Species as a Source of Desirable Genes

Attempts to transfer genes from di- and tetraploids to *A. sativa* have been carried out using, among others, addition and substitution lines [149]. Monosomic and disomic *A. sativa* addition lines were obtained by adding *A. strigosa* [232,233], *A. hirtula* [234], *A. barbata* [235], and *A. abyssinica* [233]. chromosomes. Similarly to wheat, the addition lines were utilized in oats for gene mapping on chromosomes and obtaining substitution lines, which are more stable and fertile than addition lines [149]. Substitution lines of *A. sativa* were obtained by replacing its chromosomes with their counterparts derived from *A. barbata*, *A. prostrata* [235], *A. strigosa* [236], and *A. abyssinica* [233].

The transfer of extraneous genetic variation can also occur through translocation induced by ionizing radiation. For the first time, translocation lines with resistance genes for stem rust [237] and powdery mildew [238] from *A. barbata* and crown rust from *A. strigosa* [239] were obtained by this means in *A. sativa*. The addition and substitution lines were the starting material for inducing translocations [233,238].

Another possibility for the transfer of extraneous genetic variation is the weakening or removal of the control mechanism for homologous pairing. The common oat (*A. sativa*) is a hexaploid, but cytologically it behaves like a diploid, forming 21 bivalents during meiosis [240]. Bivalent pairing and disomic inheritance indicate that homoeologous chromosomes do not normally conjugate [150]. In wheat, the gene controlling bivalent pairing (*Ph*) is located on the long arm of chromosome 5B [241]. The absence of chromosome 5B results in the formation of multivalents through homoeolog pairing. Jauhar [242] has argued that the process of homologous pairing control is more complex in *A. sativa* than in wheat, and it is likely that more genes are involved in regulating this mechanism. Gauthier and McGinnis [243] observed a lower degree of homologous chromosome pairing in nulli haploids of hexaploid oat compared to wheat, suggesting stronger control of bivalent

pairing in *A. sativa*. To date, no chromosomes of cultivated oats have been identified that could potentially harbor a specific gene or genes regulating bivalent pairing that would correspond to the wheat *Ph* gene [148,194].

The effect of weakening the control mechanism was observed in interspecific hybrids, when one of the crossing components was the CW57 genotype of the diploid species *A. longiglumis* [240]. This genotype is a suppressor of genes controlling bivalent pairing in interspecific hybrids, causing the induction of homoeologous conjugation and the formation of a large number of trivalents and quadrivalents. Utilization of the *A. longiglumis* CW57 homoeologous pairing system is constrained by the presence of a suppressor gene in this accession and is due to the sterility of *A. longiglumis* × *A. sativa* hybrids. Nevertheless, genes for powdery mildew resistance from *A. prostrata* and *A. barbata* [238] were transferred to *A. sativa* using this mechanism. In addition, a synthetic hexaploid, Amagalon, carrying a major crown rust resistance gene, *Pc91*, was developed from *A. magna* × *A. longiglumis* CW57 hybrids [244]. Understanding the pairing control system of *Avena* would make gene transfer from the secondary and tertiary gene pools less complicated.

In summary, only *Pc23* (*A. strigosa*), *Pc91* (*A. magna*), and *Pc94* (*A. strigosa*) genes were incorporated from non-hexaploid *Avena* species into *A. sativa* [245–247] (Table 4). Resistance to *Blumeria graminis* was introduced into hexaploid oat from *A. hirtula* (*Pm2*), *A. barbata* (*Pm4*), *A. macrostachya* Bal. (*Pm5*), and *A. eriantha* (*Pm7*) [248]. The *Pg16* gene, which confers resistance to *Puccinia graminis*, is also derived from *A. barbata*, while the *Pg6* and *Pg7* genes originate from *A. strigosa* [221]. Of the genes listed, only *Pc91* (HiFi, Stainless, CDC Morrison), *Pc94* (Leggett), and *Pm7* (Canyon, Yukon, Klaus, Harmony, Benny) were introduced into *A. sativa* cultivars.

Table 4. Gene transfers from diploid and tetraploid oat species into the common oat.

Disease	Gene	Origin	Introgression Method	Reference
Crown rust	*Pc15*	*A. strigosa*	Triploid hybrid bridge, monosomic substitution line irradiation	[239]
	Pc23	*A. strigosa*	Synthetic octoploid backcrosses	[246]
	Pc91	*A. magna*	Triploid hybrid bridge	[244]
	Pc92	*A. strigosa*	Autoteraploid, Triploid hybrid bridge	[247]
	Pc94	*A. strigosa*	Autoteraploid, Triploid hybrid bridge	[245]
Stem rust	*Pg6*	*A. strigosa*	Direct crosses Synthetic octoploid backcrosses	[244]
	Pg16	*A. barbata*	Direct crosses irradiation	[237,249]
Powdery mildew	*Pm2*	*A. hirtula*	-	[248]
	Pm4	*A. barbata*	Direct crosses, Disomic addition line irradiation	[238]
	Pm5	*A. macrostachya*	Direct crosses with *A. magna*, backcrosses with *A. sativa*	[250,251]
	Pm7	*A. eriantha*	Direct crosses with *A. sativa*, embryo rescue, backcrosses with *A. sativa*	[252]

The emergence of new pathogen races necessitates continuous efforts to search for new sources of resistance, leading to the discovery of new resistance genes [253–261]. Even though many highly effective resistance mechanisms can still be identified in hexaploid stocks stored especially in small national genebanks, diploid and tetraploid species have proven to be a better source, especially of adult plant resistance [190,213]. It is worth noting

that no effort to introduce resistance from diploid or tetraploid *Avena* species into hexaploid oats has been made in the last 15 years, with the most recent described by Rines et al. [262]. Furthermore, unlike in wheat, none of the *Avena* genes have been cloned [213].

3.7. Synthetic Polyploids

An alternative approach to breeding, based on introducing genes that determine desirable traits from non-cultivated species, is the domestication of selected wild species, or the synthesis of new artificial tetraploid, hexaploid, or octoploid forms [263,264]. Ladizinsky [265] presented an attempt to domesticate two wild tetraploid oat species, *A. magna* and *A. murphyi*, and selected domesticated *A. magna* lines are undergoing productivity evaluations in their native region of Morocco [266,267]. Domesticated tetraploids might be more successful than the common oat in the warm climate of North Africa or the Iberian Peninsula. In addition, domesticated tetraploids have been used to produce synthetic hexaploids. Although they may not be directly utilized as new cultivars, they can serve as bridging forms enabling gene transfer between di- and tetraploids and the cultivated hexaploid oat [264]. Amagalon, mentioned earlier, serves as an example of a synthetic hexaploid [244], and it was used as the parental form to develop a number of cultivars, with HiFi [268] being one of the most important among them. Another synthetic hexaploid is Strimagdo, obtained from a cross between *A. strigosa* Saia and domesticated *A. magna* [264]. The process of developing synthetic octoploids and hexaploids involved crossing *A. macrostachya* with *A. sativa*. As a result, F_1 hybrids were obtained through embryo rescue, vegetative cloning, and colchicine treatment. Afterwards, these hybrids were backcrossed with *A. sativa* cultivars to achieve the desired ploidy level. They gave rise to three groups of broad hybrid material, decaploids (2n = 10x = 70), octoploids (2n = 8x = 56), and plants with chromosome numbers between 40 and 49, which allowed selection of stable hexaploids (2n = 6x = 42). *A. macrostachya* derivatives were used as components to obtain breeding lines with improved winter hardiness and resistance to various diseases and pests, as well as larger seeds and higher protein content [269].

3.8. The Oat in the Genomic Era

For many years, research in oat genetics and breeding was severely hindered by the lack of highly saturated genetic maps, consistent chromosome nomenclature, and complete genome sequences. The breakthrough came initially with the publication of Chaffin et al. [270], where a consensus map of the cultivated hexaploid oat was developed based on 12 recombinant inbred line (RIL) populations. This facilitated the full utilization of molecular markers to confirm the transfer of external chromatin and select appropriate segregants in oat breeding. The next breakthrough occurred between 2020 and 2022, when the complete genome sequence of the oat *Avena sativa* line OT3098 was published [271], followed by the cultivars Sang [167] and Sanfesan [272]. The fully annotated cv. Sang reference genome plays a special role here, as it can assist breeders and researchers in better comprehending the segregation anomalies observed in various mapping studies and overcoming breeding barriers.

4. Conclusions

With the advent of molecular markers in the 1980s, to their high-throughput use over the last decade, introgression breeding in wheat has been constantly refined. Translocation lines can now be easily converted to true introgressions by employing the long-known *ph1b*-system for precisely following homoeologous recombination in segregating populations. Concurrently, approaches for obtaining small segmental introgressions at a large scale for individual species can be realized now to systematically assess their effects on the phenotype prior to implementation in costly breeding programs.

The progenitor species and wild relatives, including taxa at a lower ploidy level, are a valuable source of genes for the improvement of the cultivated oat; however, their use is limited by crossbreeding barriers and the lack of a wheat *ph1* system counterpart.

Recent advances in oat genetics and genomics have made molecular breeding possible and will enable the application of modern breeding strategies in future These advancements are instrumental in developing oat cultivars that are better adapted to changes in global climate conditions.

In recent years, the genomic selection of complex traits was successfully added to the molecular breeding toolbox of both wheat and oats, whereas genome editing has yet to come. It is expected that genomic selection can be more efficient than genome editing for improving complex traits, as more genetic components are considered simultaneously. However, genome-editing methods that involve targeted mutagenesis will become important for breeding both simple and complex traits because of the ease, speed, and cost-effectiveness with which beneficial gene signatures from species of the secondary and tertiary gene pools may be "utilized" for the fine-tuning of advanced breeding materials. Despite the unquestionable advantages of genome editing, in comparison with other major crops (e.g., rice or maize), the adoption of the CRISPR-Cas system for the improvement of wheat and oats has lagged behind. Among the factors that have contributed to this delay in the application of genome editing in these crops are the slow advances in wheat and oat transformation methods or, until recently, the lack of high-quality reference genomes. Nevertheless, continued progress in improving modern technologies and the allied application of available modern breeding techniques can contribute to the transition to true precision breeding.

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