Review

The Pros and Cons of Rye Chromatin Introgression into Wheat Genome

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Abstract: Rye is one of the most commonly used sources of elite genes in wheat improvement programs. Due to the high collinearity of the genomes of both cereal species, it is possible to obtain interspecific chromosomal translocations and substitution lines. Rye chromatin is used to transfer numerous genes for resistance to biotic and abiotic stresses into the wheat genome. Introgression has also resulted in improved agronomic traits. However, despite the numerous advantages, the transfer of large fragments or whole chromosomes has been quite often accompanied by a decrease in end-use quality. This paper presents an overview of the benefits and drawbacks of using rye as a source of variability in wheat breeding.

Keywords: abiotic; agronomic; disease; end-use; introgression; pest; rye; translocation; wheat

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1. Introduction

Wheat is cultivated from the equator to the Arctic Circle, from sea level to a height of 4500 m above the sea level in Tibet [1]. However, the best conditions for its cultivation are found in the latitudes 30–60° N and 27–40° S [2]. The observed increase in wheat production and yield over the last 70 years is a direct result of the Green Revolution. However, just as it has contributed to a significant improvement in productivity, it has led to a significant genetic erosion and loss of diversity [3]. To expand the gene pool, multiple wild and cultivated related species from *Triticeae* have been used in breeding programs.

In this review, we will summarise information concerning the use of rye as a source of diversity and traits essential for further progress in wheat breeding. We will discuss how fragments of the rye genome contribute to improving the resistance of wheat to biotic and abiotic stresses and how they affect the agronomic traits and end-use value. We hope that this review will help both breeders and researchers around the world, and it will indirectly contribute to improving rye genetic resource characterisation as a source of new genes/alleles for wheat breeding programmes.

2. Wheat Genome Evolution and Gene Pools

Common wheat (*Triticum aestivum* L.) has a complex genome comprising three related genomes that are derived from three different diploid species. It is therefore an allohexaploid (*allo*, from Greek, means “different”) with $2n = 6x = 42$ (AABBDD) [4]. It is considered certain that common wheat was formed as a result of two hybridisation events between *Triticum urartu* Thumanjan ex Gandilyan ($2n = 2x = 14$, AuAu) and an *Aegilops speltoides*-related species ($2n = 2x = 14$, BB) that occurred 0.5 million years ago, forming *Triticum turgidum* ssp. *diccoides* Korn. ex Asch. & Graebn., and then 10,000 years ago between tetraploid *T. turgidum* ssp. *diccoides* ($2n = 4x = 28$, AABB) and diploid *Aegilops tauschii* ssp. *strangulata* (Eig) Tzvel. ($2n = 2x = 14$, DD) [5–7].

According to the genetic similarities, 21 pairs (seven pairs in each genome) of wheat chromosomes are divided into the seven homoeologous groups, each containing a pair of chromosomes from the A, B and D genomes [8]. Homoeologous chromosomes retain a high degree of DNA sequence homology and gene synteny but differ in numerous functional gene complexes in numerous noncoding and highly repetitive DNA sequences [7,9,10]. Nevertheless, wheat behaves like a diploid and homoeologous chromosomes do not pair with each other during meiosis [11–13]. The restriction of homoeologues pairing is related to the genetic control of pairing and physical divergence [4,14].

Following the concept of gene pools proposed by Harlan and de Wet and further developed by Jiang et al., the three gene pools, i.e., primary, secondary and tertiary, are related to common wheat [15,16]. Species belonging to each of them are used in breeding programs. Within the primary common wheat gene pool are wheat primitive domesticated forms, landraces and the closely related wild species, including tetraploid *Triticum dicoccoides* Körn. ex Asch. & Graebn. and the tetraploid A and D genome donors, which carry homologues and hybridise directly with cultivated wheat [1,17]. The secondary gene pool consists of the remaining species polyploid species of the genus *Triticum* and *Aegilops* that have at least one homologous genome in common with wheat [17]. More distant diploid and polyploid species from the tribe *Triticeae* with nonhomologous genomes are classified as the tertiary gene pool of wheat [1,17].

3. Rye General Description

Rye (*Secale cereale* L.) is a diploid species ($2n = 2x = 14$, RR) belonging to the family *Poaceae*, subfamily *Pooideae*, tribe *Triticeae*. It is a small grain cereal species with a high resistance to biotic and abiotic stresses. Therefore, it can be grown under challenging conditions for other cereal crops. Rye can be grown in infertile, sandy, acidic or saline soils, with the exception of highly saline ones, and, also, on poorly prepared fields. Compared to other small grain cereals, rye is attacked by fewer pathogens, and such infections cause substantially lower yield loss. Rye is also more tolerant to drought than other small-grain cereals, due to its well-developed root system [18].

4. Rye Chromosomes as a Source of Desirable Genes and Alleles for Wheat

The use of elite genes from distantly related species is possible through a distant hybridisation approach. Rye, included in the tertiary gene pool of wheat, is one of the most widely used alien sources of diversity and resistance in wheat breeding. The methods for transferring rye chromatin into the wheat genome are not new and have been extensively described in many previous works [14,16,19–22]. Generally, the first step is to obtain addition or substitution lines, which are then used to generate translocation lines that are used in breeding [19]. A sequence analysis of the wheat and rye genomes revealed highly conserved collinearity of their genomes, which should considerably facilitate introgression [23]. However, exchanges of chromosome fragments between heterologous chromosomes occurred during evolution in both wheat and rye, resulting in significant differences in the collinearity of most rye chromosomes compared to their wheat homoeologues. Only chromosome 1R is completely syntenic; chromosomes 2R, 3R, 5R and 6R show a relatively high degree of homoeology with chromosome groups 2, 3, 5 and 6 of wheat and contain large syntenic blocks. In contrast, chromosome 4R shows only partial homology to wheat group 4, while it shows a significant similarity to wheat chromosome group 7 and, partially, to group 6. Chromosome 7R shows low collinearity with wheat chromosomes [23]. Looking at individual chromosome arms, previous results have already indicated that the highest collinearity occurs within 1RS, 1RL, 2RL, 3RS, 4RS, 5RS and 6RS with their homoeologues in wheat [24,25]. Translocations occur in the other chromosome arms, which greatly hinders chromosome pairing and recombination. As a result, obtaining wheat–rye recombinant chromosomes is significantly impaired [26,27].

4.1. Chromosome 1R

Chromosome 1R and, in particular, its short arm 1RS have been extensively used in bread wheat improvement programs worldwide [28].

4.1.1. Introgression Types

In particular, the 1RS.1BL translocation of whole-chromosome arms is the most commonly utilised source of alien rye chromatin in wheat breeding programs [29]. The karyotype of wheat with the 1RS.1BL translocation contains a chromosome pair in which the short arm of wheat chromosome 1B was replaced by a centric break–fusion event with the short arm of chromosome 1R. [30]. It is assumed that there are several independent sources of translocation [31]. The most popular sources of 1RS in wheat cultivars were German 1R(1B) substitution lines of the “Salzmünder Bartweizen” and “Zorba” wheats derived from wheat–rye crosses in the 1920s–1930s by G. Riebesel and G. Kattermann. In both cases, the German cv. “Petkus” was used as the rye component. The Russian cultivars “Aurora” and “Kavkaz” are among the other most common sources of 1RS.1BL translocation, but both also trace their origins back to the cultivar “Petkus” [32,33]. Therefore, there is a significant problem with the lack of genetic differentiation of this genome fragment. The same translocation was introduced into tetraploid wheat lines by crossing common wheat 1RS.1BL and durum wheat [34]. Another source of this translocation is Japanese wheat cv. “Salmon”. It was obtained in the 1970s and was derived from octoploid triticale [35]. The use of this cultivar in breeding has been reported only once and resulted in the line KS 80-H-420022, developed by Kansas State University (Manhattan, KS, USA) [36]. Since 2000, new lines with the 1RS.1BL translocation have appeared, using other rye cultivars such as “Paldanghomil”, “Aigan”, “Baili”, “Weiling” and “Weining” as 1RS donors [28,37–39]. To date, more than a thousand lines and cultivars containing 1RS.1BL translocation have been developed worldwide [40].

1RS.1AL translocation has also been used in wheat breeding programs, although on a much smaller scale than that discussed above. To date, about 100 cultivars and lines containing this translocation have been identified [40]. It was first described in the cv. “Amigo”, developed in the late 1970s in the USA. The 1RS from the Argentinian “Insave” rye cultivar was introduced via the octoploid triticale cv. “Gaucho” [41,42]. The “Amigo” cultivar was mainly used in American breeding programs [40]. The second source of 1RS.1AL translocation was the line GRS1201 obtained in 1990s in the USA [43]. Its pedigree also traced back to the rye cv. “Insave” (short wheat selection/“Scout”(TX69A345-2)/“Insave F.A.”) [43]. There are also several sources of 1RS other than “Insave”, such as those derived from the original “Petkus” rye, transferred via triticale cv. “Rhino” and “Presto”. Early substitutions also included the wheat line E12165 1R from the International Maize and Wheat Improvement Center (CIMMYT) and wheat cv. “Veery” [44,45]. However, they did not attract much interest from breeders.

1RS.1DL translocation is the least used in breeding programs [40]. It was obtained in the 1970s in Australia and contains 1RS from the rye cv. “Imperial”.

The substitution lines 1R(1A), 1R(1B) and 1R(D), containing whole 1R chromosomes, were also created; however, they are mainly used as research material or in the creation of translocation lines, and only a few cultivars contain the substitution 1R(1B).

4.1.2. Resistance to Biotic Factors

The 1RS segment contains numerous race-specific disease-resistance genes. The translocation most commonly used in wheat breeding, 1RS.1BL with 1RS derived from the cv. “Petkus”, carries the *Pm8* gene for resistance to powdery mildew (*Blumeria graminis* (DC) E.O. Speer f. sp. *tritici* Em. Marchal) [33]. The phenotypic effect of this gene is sometimes suppressed by its wheat orthologue *Pm3*, which is present in some wheat genetic backgrounds [46]. In addition, this 1RS fragment also carries the *Lr26*, *Sr31* and *Yr9* genes for resistance to brown rust (*Puccinia recondita* Roberge ex Desm. f. sp. *tritici*), stem rust (*Puccinia graminis* f. sp. *tritici* Eriksson & Henning) and yellow rust (*Puccinia striiformis*

Westend. f. sp. *tritici* Eriks.), respectively. However, the resistance determined by these genes has already been overcome by new virulent biotypes of the respective pathogens [47]. Of particular concern is the breakthrough of *Sr31* gene resistance by the Ug99 stem rust race group [48]. This race, identified in East Africa, threatens a major part of the global wheat production [49]. Further works and the use of alternative 1RS sources have enabled the transfer of other resistance genes into wheat, such as *PmCn17* (powdery mildew), *YrCn17*, *YrR212* and *yrCH45-1b* (yellow rust) [50,51]. The 1RS.BL also carries the gene *Dn7*, providing broad-spectrum resistance to several biotypes of the Russian wheat aphid (*Diuraphis noxia* Kurdjumov), which is an economically important pest of wheat [52].

On the other hand, due to the use of different 1RS sources, the 1RS.1AL translocation enriched the wheat gene pool with the *Pm17* gene, which is allelic to *Pm8* and determines the resistance to powdery mildew, and *Sr1RS^{Amigo}*, which provides a resistance to stem rust [42,53]. In addition to carrying genes providing a resistance to fungal pathogens, this translocation is also beneficial for providing resistance to pests such as wheat aphid (*Schizaphis graminum* Rondani) determined by the *Gb2* and *Gb6* genes, wheat curl mite (*Aceria tosichella* Keifer) conditioned by the *Cmc3* gene, English grain aphid (*Sitobion avenae* Fabricius) and bird cherry-oat aphid (*Rhopalosiphum padi* Linnaeus), for which the genes have not yet been identified [54–56]. 1RS.1DL translocation introduced another rust resistance gene (*Sr50*) into wheat [57]. Wheat lines containing 1R (1D) substitutions showed an increased resistance to English grain aphid and bird cherry-oat aphid. However, the genetic basis of this resistance has not yet been established [56,58]. In turn, 1R (1B) substitution resulted in an increased allelopathic activity against weeds [59].

It is also interesting to note the use of the wild species *Secale africanum* Stapf as a 1R^{af} donor. This species is characterised by an extremely high resistance to yellow rust [60]. All lines containing the 1R^{af}S chromosome arm introgression either in the form of disomic 1R^{af}S addition, 1R^{af} (1D) substitution or disomic, as well as monosomic, 1R^{af}S.1BL translocation were immune or highly resistant to the highly virulent CYR32 race of yellow rust, which overcame the resistance provided by *Yr9* originating from the *cereale*-1R [61]. Moreover, a high resistance to this pathogen was also observed in amphiploids formed with common wheat (AABBDDR^{af}R^{af}) and durum wheat (AABBR^{af}R^{af}). Noticeably, the introgression of 1R^{af}L in the form of 1DS.1R^{af}L translocation and 1R^{af}L monotelocentric addition resulted in a high susceptibility to the above pathogen race. Therefore, it can be speculated that the 1R^{af}S contains a novel so-far unidentified yellow rust resistance gene (s) and may be applicable in wheat improvement programs [61].

4.1.3. Resistance to Abiotic Factors

The introgression of 1RS is helpful in improving wheat resistance to drought stress. The presence of 1RS.1BL translocation causes a significant increase in root length [62]. This trait improves the water and minerals uptake from deeper soil layers, resulting in increased drought tolerance [63]. Totally, 15 quantitative trait loci (QTL) regions (six additive and nine epistatic) were detected in the rye chromosome arm of the 1RS.1BL translocation line. Three of the four QTL regions for the root traits were located in the distal rye segment of the 1RL region; the presence of this fragment significantly increased the root biomass in the 1RL.1BL translocation line [64,65].

The 1RS.BL translocation lines performed better than the normal 1BL lines under water deficit conditions, especially in terms of the growth rate [66,67]. The proline content was also higher in the translocation line under both the control and drought stress conditions [68]. Proline plays a key role in plant stress tolerance. It removes reactive oxygen species and, as a molecular chaperone, enables enzymes activity [69]. A high frequency of 1RS.1BL translocation was observed among Iranian dryland wheat lines, which may indicate that their drought stress tolerance is determined by transferred rye genes [70].

In addition to a wide range of resistance to abiotic and biotic factors, the 1RS introgression into the wheat genome improved the responsiveness of genotypes in an in vitro culture by enhancing the callus growth, somatic embryogenesis and regeneration of the

microspore-derived haploid embryos [71–74]. The “Bobwhite” cultivar model in a wheat tissue culture and transformation study actually contained 1RS.1BL translocation [75].

4.1.4. Agronomic Traits

In general, the presence of 1RS.1BL translocation is associated with a significant yield increase. Higher aboveground biomass at maturity, higher grain number per spikelet and higher spikelet number per spike, as well as a higher test weight and 1000-grain weight, were observed [76,77]. The most recent studies also indicated that the presence of this translocation causes an increase in grain length [78]. It has also been suggested that a higher yield was associated with post-anthesis stress tolerance, which increased the grain weight [79]. However, some studies suggested a lack of yield increase in the lines containing 1RS.1BL translocation [80–83]. It appeared that there was a significant interaction between the grain yield and the rye and wheat genotypes that were used for production of the translocation lines [38,39]. It was also pointed out that the lines with 1RS.1BL translocation had the highest yields, while those with 1RS.1DL had the lowest among the homoeologous series of 1RS translocations [84]. However, further studies have shown that the influence of the rye chromatin source may be more crucial than its position in the wheat genome [44]. The presence of 1RS.1BL translocation was also linked to the “stay green” phenotype [85]. The delay of leaf aging after flowering and, therefore, the prolonged delivery of assimilated carbon to the grain play a key role in increasing the productivity [86].

4.1.5. End-Use Quality

Despite the fact that introgression brings a number of advantages discussed above related to the increase in resistance to biotic and abiotic factors, it significantly reduces the baking quality. This is due to the introduction the *Sec-1* locus encoding ω -secalins, i.e., rye storage proteins, into the wheat genome and the simultaneous loss of the *Glu-3* loci encoding glutenins and the *Gli-1* loci encoding gliadins [87]. An imbalance in the ratio of monomeric and polymeric proteins is reflected in the stickiness and weakness of the dough [88–90]. Glutenins have a positive effect on dough development time and loaf volume, while gliadins affect the loaf volume potential and dough viscosity [88,89,91–94]. Since the occurrence of *Sec-1* locus coincides with the loss of the *Gli-1* and *Glu-3* loci, it is difficult to ascertain whether the absence of wheat glutenins and gliadins, the presence of rye secalins or a combination of both significantly reduces the wheat dough quality, as manifested by a low bread volume, poor mixing tolerance and dough stickiness [88,93,95]. Several studies indicated that 1RS.1AL translocation negatively affected the baking quality to a lesser extent compared to 1RS.1BL and 1RS.1DL [84,96,97]. Furthermore, the reduction of glutenin was not as drastic in the presence of this translocation, and consequently, a lower dough strength reduction was observed [98,99]. The 1RS.1BL translocation had a significant negative effect on the kernel hardness and test weight, sedimentation volume and tractility [76]. Grains from the 1R(1B) substitution lines were even softer than those from lines containing the 1RS.1BL translocation [100]. In durum wheat, the 1RS.1BL translocation had no effect on the grain protein content but a decreased gluten content, swelling index of the glutenins and reduced micro-SDS sedimentation volume were observed [90].

The 1RS whole-chromosome arm substitutions into wheat proved to be surprisingly successful if compared with other similar-type substitutions in plants. No other case was reported for a similar wide spontaneous spread-out of such large alien chromosome fragment into cereal breeding materials, which are subjected to strong selection pressure for yields. Among the conducive conditions for such a transfer are a high level of retained chromosome homology, lack of undesirable “wild” effects from the cultivated donor species and a high buffering capacity of the wheat polyploid genome. The decrease of baking quality is the only serious problem, which was extensively studied using chromosome engineering methods [19,101]. The first attempts to replace the *Sec-1* rye gene with the *Gli-B1+GluB3* wheat ones revealed nonallelic positions of the wheat and rye genes and

a troublesome linkage with a set of desirable resistance genes (*Pm8*, *Lr26*, *Yr9* and *Sr31*) located between the storage protein loci that had to be exchanged. In the next round of crossing-over stimulation (at the absence of the *Ph1*-pairing homoeology control gene from the wheat 5B chromosome), the double-recombinant chromosome was selected that contained two small intercalary insertions and all the desired wheat and rye alleles [101]. However, another unexpected linkage emerged between the *Sec-1* allele and genetic factors controlling the root system efficiency, being the main advantage of the 1RS.1BL substitution after the disease resistances were broken [19]. The next round of cytogenetic work was necessary to overcome this linkage. Similar inputs of work were necessary in another series of genetic engineering experiments with 1RS.1DL translocation on breaking the linkage between the *Sec-1* locus and the locus for stem rust resistance [102]. The aim was to transfer to wheat a possibly small rye chromosome fragment containing the stem rust resistance gene and lacking the *Sec-1* gene while retaining the wheat gliadin *Gli-D1* gene. Success required 20 years and three rounds of chromosome engineering procedures (based also on the *Ph1/ph1* system) [103]. Generally, the induced homoeologous recombination approaches required a large input of time and labour but provided a higher guarantee of final success than the competitive methods based on chromosome fragmentation like irradiation [104] or the use of gametocidal chromosomes [21]. Such procedures are simpler, but the chances to get a genetically balanced introgression are small. As a rule, the transferred fragments are built in random positions and are of non-compensating types that seldom exert no negative effects on the yield [19]. The ongoing progress in genome mapping and recombinant DNA technology gives hope for a more quick and precise transfer of desirable genes.

4.2. Chromosome 2R

Several attempts have been made to use chromosome 2R for wheat improvement. Apart from *S. cereale*, *Secale africanum* Stapf. has also been used [105].

4.2.1. Resistance to Biotic Factors

The use of 2R resulted in an improved wheat resistance to brown rust. Its genetic background is diverse. The *Lr45* gene was introduced through the 2AS-2RS.2RL and *Lr25* through the 4BS.4BL-2RL translocation [42,106,107]. However, the genetic background of resistance to brown rust, which was introduced by the 2BS.2RL translocation, has not been identified [108]. The resistance to stem rust was obtained in lines containing the 2DS.2RL (*Sr59*) and 2BS.2RL (unknown gene) translocations [108,109]. Moreover, lines containing the 2R(2B) and 2R(2D) disomic substitutions were highly resistant to stem rust at both the seedling and adult plant stages, and this resilience is likely to be determined by the novel gene(s) [110]. An increased resistance to powdery mildew was observed in translocation lines containing 4BS.4BL-2RL (*Pm7*) and 2BS.2RL (unknown gene), as well as in lines containing the disomic substitution 1R(1D)+2R-addition (*Pm*/ZHM2RLb) and substitution 2R(2D) (unknown gene) [42,108,111,112]. The use of the 2R^{afr} introgression from *S. africanum* provided a resistance to yellow rust [105]. An increased resistance to this pathogen was observed in the 2R^{afr} addition, 2R^{afr}(2D) substitution and 2DS.2R^{afr}L translocation lines. Since the resistance determined by *Yr9* located on 1RS has already been overcome, lines containing 2R^{afr}L could be a valuable input for wheat resistance breeding [105]. The 2BS.2RL translocation also increased the resistance to the Hessian fly (*Mayetiola destructor* Say) that is determined by the *H21* gene [42,113]. Furthermore, 2R introgression also induced a high allelopathic activity and improved the ability of wheat to suppress weeds [59].

4.2.2. Resistance to Abiotic Factors

2R introgression is generally considered to improve drought tolerance in wheat. Wheat containing the 2R disomic addition had increased water efficiency and improved rooting characteristics [114]. The 2AS.2RL translocation also had improved water efficiency, especially under drought stress [114,115]. However, the improvement of drought tolerance

is dependent on the genetic background of the wheat cultivar used and its interaction with the genes located on the 2RL segment of a particular rye cultivar [116].

4.2.3. Agronomic Traits

Similar to drought stress resistance, the final result for agronomic traits depends on the wheat and rye genotypes used and their interactions [116]. The presence of 2AS.2RL translocation increased the grain yield and shoot biomass at maturity, which was particularly noticeable under drought stress [114]. 2BS.2RL translocation increased the yield, shoot biomass, number of grains per spike and number of grains per plant but simultaneously delayed maturity and reduced the grain weight and harvest index [117]. However, in another experiment using a different set of wheat and rye cultivars, this translocation reduced the number of spikes, delayed maturation and increased the number of grains/spike under optimal irrigation conditions and reduced the number of spikes and the grain-filling period under drought conditions [116]. Moreover, the 2R-addition also reduced the pollen fertility [118]. Notably, the lines containing the 2R^{af} introgression from *S. africanum* had a significantly reduced plant height as a result of the presence of strong dwarf genes; additionally, elongated spikes, as well as a higher number of spikelets per spike and 1000-grain weight, were observed [105]. The results encourage the further use of innovative lines containing 2R^{af} in wheat improvement.

4.2.4. End-Use Quality

Unlike 1R, the presence of 2R does not have such a destructive effect on the end-use quality of the wheat grain [108]. None of the known genes encoding storage proteins are located on 2RL [75]. Although a reduced flour yield and grain hardness were observed in the lines containing the 2BS.2RL translocation, these weaknesses could be eliminated by an appropriate selection. In addition, a slight reduction in mixograph-mixing and bake-mixing times were observed, but these did not significantly reduce the quality. However, an improvement in water absorption and flour colour was observed. On the other hand, there were no significant differences in the flour protein content, loaf volume or mixograph-mixing tolerance [119]. Due to the presence in both arms of the 2R of the factors responsible for the increase in soluble dietary fibre and arabinoxylans, their significant increase was observed in wheat lines containing 2R introgression [120].

4.3. Chromosome 3R

The use of chromosome 3R in wheat improvement programs is rather negligible. This could be due to the low 3R transmission in backcrossing [121]. The first obtained wheat translocation line containing 3R introgression turned out to be non-compensating and contained 3RS from rye and 3AS from wheat [122]. In later attempts, 3AL.3RS, 3BL.3RS, and 3DL.3RS translocations were successfully obtained [110,122].

4.3.1. Resistance to Biotic Factors

Segment 3RS contains the stem rust resistance gene *Sr27* [123]. There is also a second gene on the 3R chromosome that determines a broad spectrum of resistances to stem rust. The 3R(3D) substitution lines were characterised by a high resistance to stem rust at the seedling stage, as determined by the *SrSatu* gene [124]. In one of the lines, the presence of an additional, unknown gene for stem rust resistance was also postulated [124]. In the lines containing the 3RS.3DL transcript, an increase in resistance to *D. noxia* was observed [125]. However, the genetic basis of this resistance remains unknown. Introgressions of 3R and 3RS also provided resistance to the Hessian fly [110].

4.3.2. Resistance to Abiotic Factors

Increased aluminium tolerance was observed in the 3R addition line. Twenty-seven upregulated genes have been identified in this line, possibly reflecting the induction of tolerance mechanisms [126].

4.3.3. Agronomic Traits

Unfortunately, both 3RS.3AL. and 3RS.3BL translocations resulted in a reduced yield and hectolitre test weight [127].

4.3.4. End-Use Quality

Little is known about the effect of 3R on the end-use quality. However, this chromosome does not contain any known genes that affect the flour quality and its breadmaking quality [127]. The lines containing 3R(3B) substitutions had high iron and zinc contents and, simultaneously, low cadmium contents [110].

4.4. Chromosome 4R

Due to the low homology and poorly conserved collinearity between rye 4R and wheat 4A, 4B and 4D, there is a low recombination frequency and problems with compensation. Therefore, the use of 4R in wheat improvement is extremely difficult [27].

4.4.1. Resistance to Biotic Factors

The potential of this chromosome in wheat breeding is enormous and remains unexploited. This chromosome contains genes determining the resistance to diseases and pests such as brown rust (*Pr-j* and *Pr-l*) powdery mildew (*Pm6*), fusarium head blight and *Diuraphis. noxia* [125,128–131]. So far, it has been possible to exploit the powdery mildew resistance determined by a gene located on 4R. The introgression of rye chromatin in the form of complex translocations 5DS-4RS.4RL, 4RS-5DS.5DL and 4BL.4RL + 4RS.7AS provided immunity, and cytologically stable lines were developed [132,133]. A resistance to powdery mildew, yellow rust and sharp eyespot (*Rhizoctonia cerealis* van der Hoeven), which is most likely determined by novel genes, was obtained in the 4R disomic addition line [134]. The 4R addition lines also contained the resistance gene Karnal bunt (*Tilletia indica* Mitra) [135]. There were attempts to transfer the resistance to Russian wheat aphid (*D. noxia*) with the use of irradiation and induce homoeologous recombination. The success was dubious; two resistant recombinants, carrying smaller introgressed rye fragments, were less viable and fertile than the donor 7DS.4RL^{mon} substitution line, resulting from an earlier centric translocation in a hybrid between wheat and perennial rye, *Secale montanum*. A low level of chromosome homology and structural differences between the donor and recipient chromosomes make rye–wheat chromosome engineering in group 4 extremely difficult [27].

4.4.2. Resistance to Abiotic Factors

Genes that determine drought tolerance, such as the relative water content and general adaptability, have also been localised on chromosome 4R in the disomic addition line [30].

4.4.3. Agronomic Traits

The presence of 4R introgression in the genetic background of wheat increased the number of spikelets and grains per spike, thousand-grain weight, anther size and pollen grain number, but it also caused an increase in plant height and susceptibility to lodging [134].

4.4.4. End-Use Quality

A higher grain protein content was observed in wheat lines containing the 4R addition, and the 1R + 4R line had a high gluten strength [110]. Additionally, the addition of 4R originated from the perennial, hybrid rye *Secale cereanum* and increased the protein and arabinoxylan contents in wheat grain [136].

4.5. Chromosome 5R

The presence of a non-compensation and low recombination frequency problem has also been reported for chromosome 5R and its wheat homologues [19,27]. Similar to 4R, this is a major factor limiting the use of valuable genes located on 5R in wheat improve-

ment. The first report of spontaneous 5R(5A) substitution dates back to the late 1930s and early 1940s [137,138].

4.5.1. Resistance to Biotic Factors

An increased resistance to powdery mildew has been observed in lines containing the 5RS.5AL and 5RS.5AL+1RS.1BL translocations, as well as the 5R single disomic substitution [110,139]. An increased resistance to yellow rust was noted in lines containing the translocations 5RS.5AL, 5RS.5AL +4R+6R and 5R(5D). These lines may be the source of novel resistance gene(s) against the pathogen causing this disease [110,140]. Xi et al. identified the presence of probable new gene(s) for the resistance to yellow rust in wheat lines containing the 5RL chromosome arm [141]. The introgression of the 5R^{af} chromosome from *S. africanum* also incorporated the yellow rust resistance gene(s) [142]. Seedlings of lines containing the 5RS.5AL translocation were resistant to stem rust [124]. Furthermore, the presence of the 5R introgression correlated with reduced levels of septoria leaf blotch and fusarium head blight infection under field conditions [110,143]. Genes determining the resistance to *D. noxia* and *M. destructor* are also located on chromosome 5R and have been transferred with it to wheat [110,125].

4.5.2. Resistance to Abiotic Factors

An increased tolerance for copper has been observed in wheat lines containing the 5R(5A) substitution [144,145].

4.5.3. Agronomic Traits

In both lines containing the 5R^{af}(5D) substitution and the 5R^{af}S.5DL translocation from *S. africanum*, an increase in spike length was observed [142]. An increased spike size and multispiket formation were observed in the 5R(5A) and 5R(5D) substitution lines [139,141]. The substitution of 5R(5A) also resulted in a phenological period extension from germination to heading and a changed type from spring to winter compared to the wheat component due to the deletion of a single *Vrn-A1* gene [139].

4.5.4. End-Use Quality

In the grain of wheat cv. “Viking”, which contains 4BL.5RL translocation, high levels of iron, copper and zinc were detected [146]. Additionally, recent research indicates that grains of wheat lines containing 5R introgression from rye have increased iron and zinc contents [110]. Both 5R and 5R^{af} increased the grain protein content, whereas 5R decreased the wheat grain hardness [139,142].

4.5.5. Others

In the line containing the 5R(5A) substitution, a significant increase in the somatic embryogenesis parameters like callus formation and regeneration capacity was observed in the in vitro cultures of inflorescences [147].

4.6. Chromosome 6R

Several elite genes are located on chromosome 6R, but its exploitation in wheat breeding is hampered. The long arm of 6RL causes a genetic imbalance in the wheat genome [148]. Lines containing small-segment introgressions like 6D.6RL^{Ku} may provide a solution to this problem [51]. Chromosome 6R, like the discussed above 3R, shows a much lower transmission frequency compared to the other rye chromosomes [121].

4.6.1. Resistance to Biotic Factors

By introgressing 6R, it was possible to achieve an increased resistance of wheat to some fungal diseases, nematodes and pests. The disomic substitution of 6R(6D) enabled the identification of *Yr83*, a new gene determining the resistance to yellow rust [149]. The 6BS.6RL and 6RS.6AL translocations provided a powdery mildew resistance in wheat.

This was determined by the *Pm20* and *Pm56* genes, respectively [150,151]. An increased resistance to powdery mildew was also observed in wheat lines containing the 6D.6RL^{Ku} translocation with the rye minichromosome, 1R+6R substitution, 6R disomic addition and 6RL monotelosomic or ditelosomic addition [51,110,133,148,152]. The presence of the 1R+6R substitution was also associated with decreased infection levels by pathogens causing septoria leaf blotch and fusarium head blight, stem rust and yellow rust in wheat [110]. The same research team observed an increased resistance to *Diuraphis noxia* and *Mayetiola destructor* in wheat lines containing 1R+6R substitutions [110]. A Hessian fly resistance determined by the *H25* gene was found in the translocation line 4BS.4BL-6RL produced with the use of irradiation [42]. Progress in nematode resistance breeding against *Heterodera avenae* and *Heterodera filipjevi* may be achieved by using both the 6DS.6RL translocation and the 6R(6D) substitution lines containing the *CreR* gene for resistance to cereal cyst nematode [26,153]. The 6R introgression in wheat also improved its allelopathic activity and weed suppressive ability [59].

4.6.2. Agronomic Traits

The evaluation of agronomic traits was performed for a substitution line 6R(6A). It had a strong stem, high spike density, high yield and low satiation grain [154].

4.7. Chromosome 7R

Chromosome 7R has not been used in wheat breeding programs, although it contains genes for resistances to brown rust, stem rust and *D. noxia* [128,155,156]. This is due to the low degree of homology to group 7 chromosomes in wheat. However, the addition of the single rye chromosome 7R significantly increased the *D. noxia* resistance of the recipient wheat [156]. The 7R disomic addition line of wheat showed an improved drought resistance [157]. Moreover, the 7R addition wheat line had a reduced severity of zinc deficiency symptoms [158].

5. Rye Genetic Resources and Perspective for Their Use in Wheat Breeding

The global collection of the genus *Secale* genetic resources currently comprises 27,547 accessions and includes five species. The most numerous is the gene pool of the only cultivated species, *S. cereale*. This collection comprises 18,499 accessions, of which 68.8% are preserved in European gene banks. Thirty-six point eight percent of the collected accessions are traditional varieties and landraces [159]. Rye is an open-pollinated species with high genetic variation among individuals. This variation occurs not only within landraces but, also, in old commercial cultivars [160,161]. Studies evaluating the rye gene pool, including molecular studies, are becoming increasingly common [162–166]. Despite the availability of high-throughput genotyping and phenotyping methods, a considerable number of accessions have not been characterised even to a minimal extent. This significantly hinders their use in breeding programs. Considering the high resistance of rye to biotic and abiotic stresses and the possibility of its chromatin introgression into the wheat genome, the collected genetic resources seem to be an exceptional and relatively poorly exploited reservoir of genetic variability for wheat breeding programs. However, the intensification of multilevel studies characterising the accessions stored in gene banks is a prerequisite for researchers and, later, also breeders and farmers to be able to take advantage of this valuable reservoir.

6. Future in the Hands of Molecular Biologist

The introgressions of rye chromatin fragments into wheat described in this paper were achieved using chromosome engineering techniques. These results were obtained by cytological methods and a titanic amount of work over a microscope. The dynamic development of genetic engineering techniques allows to assume that the future of interspecies gene transfers will belong to them. Of particular note are techniques such as RNA interference (RNAi) gene silencing and genome editing using zinc-finger nucleases

(ZFNs), transcription activator-like effector nucleases (TALENs) and, especially, nuclease-deactivated Cas9 (CRISPR/Cas9) [167,168]. The first steps in this direction have already been taken and, at least in a few cases, have been successful [169,170]. The application of CRISPR/Cas9 targeting the *ZIP4* gene located at the *Ph1* locus in wheat resulted in a significant increase in the frequency of homoeologous crossing-over in hybridisations with rye [171]. Understanding the mechanisms regulating chromosome pairing in different species still needs some work. However, it should be recognised that the development of tools to increase the frequency of crossing-over between chromosomes of cultivated species and their wild relatives has the potential to become an essential instrument for accelerating breeding and increasing the introgression precision of desired alleles and genes.

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