Review Article

Genetic control of compatibility in crosses between wheat and its wild or cultivated relatives

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Summary

In the recent years, the agricultural world has been progressing towards integrated crop protection, in the context of sustainable and reasoned agriculture to improve food security and quality, and to preserve the environment through reduced uses of water, pesticides, fungicides or fertilisers. For this purpose, one possible issue is to cross-elite varieties widely used in fields for crop productions with exotic or wild genetic resources in order to introduce new diversity for genes or alleles of agronomical interest to accelerate the development of new improved cultivars. However, crossing ability (or crossability) often depends on genetic background of the recipient varieties or of the donor, which hampers a larger use of wild resources in breeding programmes of many crops. In this review, we tried to provide a comprehensive summary of genetic factors controlling crossing ability between Triticeae species with a special focus on the crossability between wheat (Triticum aestivum L.) and rye (Secale cereale), which lead to the creation of Triticale (x Triticosecale Wittm.). We also discussed potential applications of newly identified genes or markers associated with crossability for accelerating wheat and Triticale improvement by application of modern genomics technologies in breeding programmes.

Introduction

The Triticeae tribe belongs to the Poaceae family previously known as Gramineae (Soreng et al., 2015). This tribe is of great agronomical importance, as it contains several crops and their close relatives such as wheats (Triticum species), barley (Hordeum), rye (Secale), Triticace (Triticosecale) (Soreng et al., 2015), as well as numerous wild species from genders Aegilops, Agropyron, Amblyopyrum, Dasypyrum, Elymus, Leymus, Pascopyrum, Roegneria and Thinopyrum (Soreng et al., 2015). Triticeae are growing in a wide range of areas and climates allowing them to adapt to very diverse conditions, from cold-wet to hot-dry regions. This adaptability is a huge asset as cultivated, or wild species have developed a large reservoir of genes and alleles to improve their resistance to biotic (pathogens, insects, nematodes...) and abiotic (frost/heat and salinity tolerance, drought resistance...) stresses but also to improve agronomic traits such as yield, earliness or protein content, in the context of sustainable and reasoned agriculture to improve food security and quality, and to preserve the environment.

Among the Poaceae, bread wheat (Triticum aestivum L.) is one of the most important crop worldwide and the staple food for one-third of the world’s population with 220 million hectares and an annual production of ~770 million tons in 2020 (http://www.worldagriculturalproduction.com/crops/wheat.aspx). Today’s agriculture has to face an unprecedented challenge: to keep pace with the human demand in an environmentally and socially sustainable manner (Godfray et al., 2010). To meet this challenge, wheat yield should increase by ~2% per year over the next 30 years while the current yield increase worldwide is only 0.9% per year and even stagnating in the main producing countries [Figure 1 (Le Gouis et al., 2020; Ray et al., 2013)]. This goal would be achievable under the assumption of favourable growing conditions but is less likely under climate change that affects not only yield but also yield stability (Brisson et al., 2010; Porter and Semenov, 2005; Tester and Langridge, 2010). In this context, breeding for wheat varieties that have better resistance to biotic and abiotic stresses is of crucial importance and consequently a priority for agriculture.

Bread wheat is an allohexaploid species (AABBDD; 2n = 6x = 42) derived from two successive interspecific crosses that involved three related diploid species [for review and details, see The International Wheat Genome Sequence Consortium (Marcussen et al., 2014; IWGSC, 2014, 2018; https://www.wheatgenome.org/)]. The first one occurred about 3-0.8 million years ago (MYA) and took place between T. urartu (AA genome) and a yet-unknown species related to the Sisopsis section (Ae. speltoidees, Ae. longissima, Ae. sharonensis, Ae. searsii and Ae. bicornis; SS genome related to wheat BB genome). This natural cross gave rise to tetraploid species (T. dicoccoides) that further evolved to give T. turidum, the ancestor of current durum wheat. The second cross arose ~0.4 MYA and involved this newly created tetraploid species and Aegilops tauschii (DD genome) leading to hexaploid bread wheat. This second polyploidisation event occurred when tetraploid wheat started to spread with the migration of the first farmers, just at the time they reached the south of the Caspian Sea, a region that has a rich diversity for Ae. tauschii. Hexaploid wheat started to be widely cultivated 7–10 000 years ago.
For example, at the beginning of the 20th century in the world (in million tons). The data come from the site http://www.fao.org/worldfoodsituation/csdb/en/.

Figure 1 Evolution of wheat production (green line), utilisation (red dashed line) and stocks (black bars) between 2011 and 2021 in the world. The data come from the site http://www.fao.org/worldfoodsituation/csdb/en/.

(Balfourier et al., 2019; Preece et al., 2017; Zohary and Hofp, 2000; Zohary et al., 2012), especially because the D-genome brought adaptation to diverse climates as well as endosperm softness giving a better bread-making quality (Chantret et al., 2005). Subsequently, wheat evolved with human migration while it was grown by the first farmers in Western Europe and Eastern Asia. This species adapted over the years to the environment of these areas and spread around the world during the 16th century (Balfourier et al., 2019).

The key event for bread wheat domestication is the occurrence of natural mutations leading to favourable characteristics for grain and spike traits compared with wild species. Three loci are essential for that: the brittle rachis locus (Br) and two additional loci, Tg (Tenacious glumes) and Q, causing naked grains (Faris et al., 2003; Jantasuriyarat et al., 2004; Nalam et al., 2006). Moreover, the Q-locus simultaneously controls the shape of the spike ['spelt/square-head'] (Faris et al., 2003)]. These mutants were certainly more attractive to the farmers as their non-threshing spikes are easier to harvest and the naked-soft grains easier to grind. Domestication, cultivation and now breeding resulted in current elite cultivars that share only a small fraction of the natural diversity. During the processes of domestication, wheat has undergone important genetic bottlenecks, resulting in a very narrow genetic base, especially when considering the D-genome. More recently, modern breeding has also participated to reduce the genetic variability especially in winter elite germplasm (Feuillet et al., 2005). Subsequently, wheat evolved with human migration while it was grown by the first farmers in Western Europe and Eastern Asia. This species adapted over the years to the environment of these areas and spread around the world during the 16th century (Balfourier et al., 2019).

The success rate of gene transfer from wild relatives to cultivated wheat varieties largely depends on relatedness between the species involved. There are three gene pools that have been defined in crop improvement traces back to the early 1940s and gained in prominence during the 1970s and 1980s [for a review, see (Hajjar and Hodgkin, 2007)]. For example, the wild diploid species Aegilops umbellulata (UU) was used to introduce resistance to leaf rust in wheat through X-irradiation of a T. aestivum addition line (AAABBDD + one Ae. umbellulata chromosome; Sears, 1956). This gave 40 translocation lines among which one showed normal pollen transmission and was resistant to leaf rust. The resistant gene was named Lr9, and it remains an essential and efficient gene for resistance to leaf rust (Nocente et al., 2006).

Since the beginning of the 1970s, many other significant successes have been obtained in wheat by the introduction of dwarfing genes (Rht-B1 and Rht-D1) derived from Japanese varieties (Norin 10) (Borovevic and Borovevic, 2005) and disease and pest resistances coming from rye (Secale cereale), Agropyron, Aegilops or Thynopyrum species (Muñoz-Sanz et al., 2020). Numerous Poaceae species have already been successfully crossed with wheat to introgress traits of agronomical importance (for review, see Table 1). Thus, while the natural genetic diversity in wheat elite material is significantly lower than the one observed in landraces, breeding programmes have brought a new type of diversity to wheat cultivars, namely structural variations related to alien introgressions (Figure 2b). To date, novel alleles have been introgressed from more than 50 species from 13 genera, highlighting the importance of these so-called alien introgressions for wheat breeding (Wulff and Moscou, 2014). The best-known one is the rye (S. cereale), 1RS translocation that harbours genes involved in multiple disease resistance (Pm8/Sr31/Lr26/Yr9) and yield enhancement. Other examples of introgressions include Sr36/Pm6 from T. timopheevii, Lr28 from Ae. Speltoides, and Pch1 and Sr38/Lr37/Yr17 from Ae. ventricosa. Some of these introgressions have been widely used around the world in commercial lines, e.g. the 1RS.1BL translocation that can be found in 10% of the worldwide genetic wheat diversity (Balfourier et al., 2019; Rabinovich, 1998).

Genetic gene pools to improve wheat diversity

The success rate of gene transfer from wild relatives to cultivated wheat varieties largely depends on relatedness between the species involved. There are three gene pools that have been defined according to this latter point (Table 2; Feuillet et al., 2008). The
primary gene pool includes bread wheat itself and closely related species sharing completely homologous genomes with wheat and comprising landraces (including primitives T. spelta, T. macha, T. vavilovi, T. compactum and T. sphaerococcum), tetraploid cultivated (T. turgidum ssp durum AABB) or wild derivatives (T. dicoccoides and T. dicoccum) as well as diploid species such as T. monococcum (AA), T. boeoticum (AA), T. urartu (AA) and Ae. tauschi (DD). Genes from this group can easily be transferred to bread wheat through direct hybridization, recombination between homologous chromosomes and selection of the best progenies (Gill et al., 1991; Gill and Raupp, 1987). No cytogenetic manipulation is necessary except embryo rescue in some extreme cases. This gene pool has been widely used, especially the Ae. tauschi accessions, to improve diversity of the D-genome through the production of synthetic wheats derived from the cross between Ae. tauschi and tetraploid wheats (Fritz et al., 1995; Jiang et al., 1993; McFadden and Sears, 1946; Reader and Miller, 1991). However and despite the synteny of the genomes, chromosomal rearrangements and linkage drag can limit introgression due to the inhibition of recombination, e.g. chromosome 4A of bread wheat, which cannot pair with any of the A-diploid wheat chromosomes [for a review see (Qi et al., 2007)].

The secondary gene pool encompasses polyploid species that share at least one homologous genome with the cultivated types (e.g. T. timopheevii, AAGG; Ae. ventricosa, DDNN), as well as Aegilops species of the Sitopsis section (related to the B-genome donor, e.g. Ae. speltoides, SS). In all these cases, pairing between related chromosomes remains possible when the genome is homologous to one of those from wheat (A, B and D), but it is difficult in the other cases, therefore reducing the transfer of alien genes. This requires the use of cytogenetic approaches (ph1 mutation; see further) or irradiation techniques.

Species from the Triticeae tribe that contain genomes other than A, B and D constitute the tertiary gene pool [e.g. genera Secale, RR; Hordeum [including H. bogdanii and H. bulbosum (XX)], HH; Agropyron, PP; Thinopyrum, EE; (Friebe et al., 1996; Harlan and Wet, 1971; Jiang and Gill, 1994)]. Most of these species are perennial but are essential for wheat improvement. In this case, the gene transfer is not possible through classical homologous recombination. However, since they are related (thus called homoeologous), gene transfer is achieved through cytogenetic or irradiation approaches or after in vitro culture.

One of the most famous introgression from this tertiary group is the 1RS/1BL translocation where the short arm of wheat chromosome 1B (1BS) is replaced by the short arm of rye chromosome 1R (1RS). There are only four sources corresponding to this translocation (Zarco-Hernandez et al., 2005; Zhao et al.,...
Table 1 Species from the Poaceae family, which were successfully crossed with hexaploid wheat

| Species | 2n | References |
|---------|----|-------------|
| Elymus dahuricus | 42 | Mujeeb-Kazi et al. (1982), Yen (1987) |
| Elymus caudata | 14 | Knobloch (1968) |
| Elymus columnaris | 28 | Kimber and Abubakar (1979) |
| Elymus comosa | 14 | Kimber and Abubakar (1979) |
| Elymus crassa | 28 | Jovkova et al. (1977) |
| Elymus cylindrica | 28 | Kimber and Abubakar (1979) |
| Elymus dichasians – Triticum dichasians? | 14 | Kimber and Abubakar (1979) |
| Elymus juvenalis | 42 | Kimber and Abubakar (1979) |
| Elymus kotschyi | 28 | Knobloch (1968) |
| Elymus longissima | 14 | Kimber and Abubakar (1979) |
| Elymus mutica | 14 | Knobloch (1968) |
| Elymus ovata | 28 | Kimber and Abubakar (1979) |
| Elymus setuloides | 14 | Chueca et al. (1977) |
| Elymus squarrosa | 14 | Kimber and Abubakar (1979) |
| Elymus triaristata | 42 | Kimber and Abubakar (1979) |
| Elymus triuncialis | 28 | Kimber and Abubakar (1979) |
| Elymus umbellulata | 14 | Kimber and Abubakar (1979) |
| Elymus variabilis | 28 | Knobloch (1968) |
| Elymus venticosus | 28 | Kimber and Abubakar (1979) |
| Agropyron ciliare | 28 | Sharma and Gill (1981a) |
| Agropyron cristatum | 14 | Limin and Fowler (1990) |
| Agropyron desertorum | 28 | Limin and Fowler (1990) |
| Agropyron desertorum (Fisch. ex Link) Schult. | 28 | Chueca et al. (1989), Limin and Fowler (1990) |
| Agropyron distichum | 28 | Piinaa (1981) |
| Agropyron elongatum | 14 | Frankie et al. (1992) |
| Agropyron intermedium | 42 | Sharma and Gill (1983) |
| Agropyron michoelii Rothev. | 28 | Chueca et al. (1990), Li and Dong (1991) |
| Agropyron podpaeae | 28 | Dewey (1981) |
| Agropyron scirpeum | 28 | Sharma and Gill (1981b) |
| Agropyron trachycaulum | 28 | Sharma and Gill (1981b) |
| Elymus altissimus | 28 | Lu and von Bohrer (1991) |
| Elymus anthoschizoides | 28 | Lu and von Bohrer (1991) |
| Elymus canadensis | 28 | Mujeeb-Kazi and Bernard (1982, 1985), Yen and Liu (1987) |
| Elymus caninus | 28 | Claesson et al. (1990), Sharma and Baenziger (1986) |
| Elymus caucasicus | 28 | Lu and von Bohrer (1991) |
| Elymus dahuricus | 42 | Mujeeb-Kazi and Bernard (1982), Yen and Liu (1987) |
| Elymus dolichasteros | 28 | Lu and von Bohrer (1991) |
| Elymus fibrosus | 28 | Mujeeb-Kazi and Bernard (1982) |
| Elymus giganteus | 28 | Mujeeb-Kazi and Rodriguez (1981) |
| Elymus parviglumis | 28 | Lu and von Bohrer (1991) |
| Elymus pendulins | 28 | Lu and von Bohrer (1991) |
| Elymus pseudonutans | 28 | Lu and von Bohrer (1991) |
| Elymus rectus | 42 | Li et al. (1994) |
| Elymus scabius | 42 | Ahmad and Comeau (1991) |
| Elymus seminacutus | 28 | Lu and von Bohrer (1991) |
| Elymus shandongensis | 28 | Lu and von Bohrer (1991) |
| Elymus tibeticus | 28 | Lu and von Bohrer (1991) |
| Elymus tibeticus | 28 | Lu and von Bohrer (1991) |
| Elymus tibeticus | 28 | Lu and von Bohrer (1991) |

Table 1 Continued

| Species | 2n | References |
|---------|----|-------------|
| Elytrigia acutam | 42 | Mujeeb-Kazi et al. (1984, 1987) |
| Elytrigia campestrum | 56 | Mujeeb-Kazi et al. (1989) |
| Elytrigia pungens | 56 | Mujeeb-Kazi et al. (1984, 1989) |
| Elytrigia repens | 42 | Comeau et al. (1985); Mujeeb-Kazi et al. (1984, 1989) |
| Elytrigia varnese | 42 | Mujeeb-Kazi et al. (1984, 1987) |
| Elytrigia villosa | 14 | Knobloch (1968) |
| Hordeum bulbosum | 28 | Falk and Kashka (1981) |
| Hordeum bulbosum | 14 | Falk and Kashka (1981) |
| Hordeum californicum | 14 | Gupta and Fedak (1985) |
| Hordeum chilense | 14 | Martin and Chapman (1977) |
| Hordeum claffonicum | 14 | Gupta and Fedak (1985) |
| Hordeum depressus | 28 | Jiang and Liu (1987) |
| Hordeum geniculatum | 28 | Pershina et al. (1988) |
| Hordeum jubatum | 28 | Comeau et al. (1988) |
| Hordeum marium | 14 | Jiang and Liu (1987) |
| Hordeum pusillum | 14 | Finch and Bennett (1980) |
| Hordeum spontaneum | 14 | Bates et al. (1976) |
| Hordeum vulgar | 14 | Kruse (1976) |
| Leymus angustus | 56 | Plourde et al. (1992) |
| Leymus angustus | 84 | Comeau et al. (1985) |
| Leymus cinereus | 28 | Mujeeb-Kazi et al. (1984, 1989) |
| Leymus innovatus | 28 | Plourde et al. (1989a) |
| Leymus multicaulis | 28 | Plourde et al. (1989b) |
| Leymus tricoides | 28 | Mujeeb-Kazi et al. (1984, 1989) |
| Pseudoroegneria juncea subsp. scythica | 14 | Plourde et al. (1990) |
| Pseudoroegneria stipifolia | 28 | Mujeeb-Kazi et al. (1984, 1987) |
| Pseudoroegneria strigosa | 28 | Mujeeb-Kazi et al. (1987) |
| Secale africanum | 14 | Knobloch (1968) |
| Secale anealare | 14 | Knobloch (1968) |
| Secale cereale | 14 | Backhouse (1916); Knobloch (1968) |
| Secale montanum | 14 | Knobloch (1968) |
| Secale tivialovi | 14 | Knobloch (1968) |
| Thinopyron curvifolium | 28 | Mujeeb-Kazi et al. (1984, 1987) |
| Thinopyron genuyi | 42 | Mujeeb-Kazi et al. (1984, 1987) |
| Thinopyron junciforme | 28 | Mujeeb-Kazi et al. (1984, 1989) |
| Thinopyron junceum | 42 | Charpentier et al. (1986); Mujeeb-Kazi et al. (1984, 1989) |
| Thinopyron sartor | 28 | Mujeeb-Kazi et al. (1984, 1987) |
| Thinopyron bessarabicum | 14 | Sharma and Gill (1983) |
| Thinopyron ponticum | 70 | Smith (1942) |
| Thinopyron pulcherrimum | 42 | Mujeeb-Kazi et al. (1989) |
| Thinopyron rechingeri (Th. sartor) | 28 | Mujeeb-Kazi et al. (1987) |

2012): two developed in Germany by Salzmuender and Wiehen- stephan between 1920 and 1930, one developed in Japan in the 1960s and one developed in the United States in the 1970s. Translocation harbours genes involved in multiple disease resis- tance (powdery mildew, stem rust, leaf rust, yellow rust, respectively, Pm8/Sr31/Lr26/Yr9) and yield enhancement with a better adaptation and abiotic stress tolerance, a high leaf area and higher grain weight (Moreno-Sevilla et al., 1995; Zarco- Hernandez et al., 2005).
Barriers that limit exploitation of wild species in wheat breeding

Exploitation of these three groups relies on three main features: the ability to make the cross between the related species and wheat, the germination capacity and fertility of hybrids and the capability of the homologous/homoeologous chromosomes to recombine properly with those of wheat. Usually, hybrids derived from crosses between species with different ploidy levels are poorly fertile because of imbalanced chromosome number in the F1 individuals, which affects pollen development and subsequent fertilisation (Kihara, 2013). This is due to an increased complexity of the meiotic process where chromosomes search in vain for their partners and remain as univalents or on the contrary form irregular bivalents (or even multivalents) between similar (homo- or homoeological) chromosomes generating unbalanced gametes (Lilienfeld, 1951). Fertilisation with such abnormal gametes thus mainly results in frequent aneuploid descents or new homoeologous-recombinant chromosomes. For example, fully sterile pentaploid hybrids derived from the cross between *T. aestivum* and other tetraploid species have been reported (Bhagyalakshmi et al., 2008; Padmanaban et al., 2017). A cross between *T. timopheevii* (AAGG) and *T. aestivum* is possible, but the fertility rate is affected (Bhagyalakshmi et al., 2008). Fertility is best achieved when the species with the highest ploidy level is used as female. However, and most of the time, enough seeds are recovered from the backcross between the hybrids and wheat to introduce alien genome fragments and to start the selection process (Padmanaban et al., 2017). For example, crosses between hexaploid *Triticum aestivum* and tetraploid *Triticum turgidum* allowed improved resistance of disease resistance, abiotic tolerance, grain quality and resistance to metal toxicity in the pentaploid hybrids (Han et al., 2016; Lopes and Reynolds, 2010; Padmanaban et al., 2017).

The most problematic process is the capacity of homoeologous chromosomes to recombine with each other. As an allopolyploid species, bread wheat possesses two genetic systems that control recombination: (1) one promoting the strict distribution of crossovers (COs) between homologous chromosomes; (2) the second preventing recombination between the homoeologous chromosomes. In allopolyploids, the latter hampers the incorporation of beneficial alleles into crop plants from their wild relatives (Able and Langridge, 2006). It has been known for ~60 years that homoeologous recombination in bread wheat is under the control of a major locus named Ph1 (for pairing homoeologous 1) located on the long arm of chromosome 5B (Riley and Chapman, 1958; Riley et al., 1959). This locus was cloned (Griffiths et al., 2006) and deciphered, and the authors demonstrated that the chromosome 5B copy of ZIP4 (TaZIP4-B2) suppresses homoeologous COs in wheat-wild relative hybrids (Rey et al., 2017). Ph1 mutation has been largely used to introduce new diversity in wheat (Figure 3; for review see (King et al., 2017)). In addition to Ph1, the other well-known locus is Ph2, a gene located on the short arm of chromosome 3D (3DS; Mello-Sampayo and Canas, 1971; Mello-Sampayo and Lorente, 1968)). This gene was recently cloned and shown as being TaMSH7-3D, a protein involved in mismatch repair (Serra et al., 2021). Current evidence suggests that Ph2 does not work in the same way as Ph1. For example, absence of Ph2 leads to a reduction or a delay in synopsis (i.e. intimate connection of chromosome axes along their lengths via the synaptonemal complex), whereas most nuclei complete synopsis in ph1 mutants of wheat (Martinez et al., 2001).

Most importantly, despite their usefulness to bring new favourable alleles or genes, introgressions suffer from linkage drag, i.e. the reduction in fitness in a cultivar due to deleterious genes introduced along with the beneficial gene (Klindworth et al., 2013). Additionally, the amount of alien chromatin present in the wheat genome is often unacceptable to breeders. Linkage drag arises as an effect of recombination suppression at the introgressed locus (Wulff and Moscou, 2014; Figure 4). Such reduction in recombination was described for tomato (Brouwer and St Clair, 2004; Paterson et al., 1990), barley (Johnston et al., 2013) and lettuce (Den Boer et al., 2013) especially when the introgressed parent species is distantly related to the recurrent parent. Moreover, suppression of recombination becomes stronger as the size of the introgressed segments becomes smaller (Brouwer and St Clair, 2004; Canady et al., 2006; Johnston et al., 2013). Similar results were observed in wheat. One of the best examples is the strong reduction of recombination between the *Ae. ventricosa* chromosome-7Dv segment carrying the Pch1 gene conferring eyespot resistance and wheat chromosome 7D (Wolland et al., 1988). Reducing the size of the Pch1 introgression through recombination would be of utmost interest since a significant reduction of yield and thousand-kernel weight is sometimes observed in the absence of the disease (Koen et al., 2002). To overcome this problem, chromosome engineering approaches have been applied to increase chromosomal fragmentation (Endo, 2007; Fedak, 2011; Feuillet et al., 2008; Qi et al., 2007), but they have not been successful for this fragment to date.

### Table 2  *Triticum aestivum* genetics gene pools groups

| Gene pools   | Species                  | Ploidy | Genome |
|-------------|--------------------------|--------|--------|
| Primary gene pool | *Triticum aestivum*       | hexaploid | AABBDD |
|             | *Aegilops tauschii*      | diploid | DD     |
|             | *Hordeum spontaneum*     | diploid | HH     |
|             | *Secale vavilovi*        | diploid | RR     |
|             | *Secale montanum*        | diploid | RR     |
|             | *Triticum turgitum*      | tetraploid | AABB |
|             | *Triticum dicocoides*    | tetraploid | AABB |
|             | *Triticum dicoccum*      | tetraploid | AABB |
|             | *Triticum monococcum*    | diploid | AA     |
|             | *Triticum boeoticum*     | diploid | AA     |
|             | *Triticum urartu*        | diploid | AA     |
|             | *Triticum spelta*        | diploid | AABBDD |
| Secondary gene pool | *Aegilops ventricosa*     | tetraploid | DDNN |
|             | *Aegilops speltoides*    | diploid | SS     |
|             | *Secale sylvestre*       | diploid | RR     |
|             | *Triticum timopheevii*   | tetraploid | AAGG |
| Tertiary gene pool | *Agropyron*              | diploid | PP     |
|             | *Hordeum bulbosum*       | diploid | HH     |
|             | *Hordeum bogdani*        | diploid | HH     |
|             | *Thinopyrum*             | diploid | EE     |
|             | *Secale*                 | diploid | RR     |
Interestingly, genes suppressing the repressor effect of \textit{Ph1} and, on the contrary, promoting homoeologous chromosome pairing have been reported in several wheat relatives (Li et al., 2017). This suggests that when these species are used as donor, homoeologous recombination is no longer a problem. In 1974, Kimber described a range of variation in \textit{Aegilops}, which he divided into groups of low, intermediate, high and super-high pairing (Fernández-Calvín and Orellana, 1994; Kimber, 1974). When the level of pairing of the \textit{Aegilops} accession is low, the \textit{Ph1} locus is only slightly inactivated and only a few rod bivalents were found in the hybrids between \textit{Aegilops} and wheat (Fernandez-Calvin and Orellana, 1992). On the contrary, if the level of pairing of the \textit{Aegilops} accession is super-high, the \textit{Ph1} locus is strongly inactivated and even some hexavalents were observed in hybrid plants (Fernandez-Calvin and Orellana, 1992). The most studied loci are \textit{Su-Ph1}, derived from \textit{Ae. speltoides} (Dvorak et al., 2006; Li et al., 2017), and chromosome 5Mg of \textit{Ae. geniculata} Roth (Koo et al., 2017, 2020); neither of these have been cloned. There are two different loci for \textit{Su-Ph1}, which map to \textit{Ae. speltoides} chromosome arms 3SL (\textit{Su1-Ph1}) and 7SL (\textit{Su2-Ph1}) (Dvorak et al., 2006). \textit{Su1-Ph1} was successfully introduced into the hexaploid cultivar Chinese Spring and from there into the tetraploid durum wheat cv. Langdon. The \textit{Ae. speltoides} fragment from chromosome 3S replaced the distal end of the long arm of chromosome 3A in both species (Li et al., 2017). Despite the homoeologous location of \textit{TaZip4-1}, the paralogue of \textit{Figure 3} Overview of the approach using \textit{ph1} mutant to introgress relevant DNA fragments from wild species in the wheat genome of elite lines. A primary cross is made between the \textit{ph1} mutant and the wild species to generate a hybrid. This plant is grown until flowering and homoeologous recombination can occur during meiosis leading to introgressions. This plant is then crossed with elite lines to introduce the alien fragment in their genome. Elite background is recovered either through successive backcrosses (BC; black arrow) or self-fertilisation (BC F; green arrow). Adapted from Baker et al. (2020).

\textit{Figure 4} Distribution of recombination events along chromosome 2D in the Chinese Spring x Renan RIL population. The lack of recombination in the distal part of the long arm (red arrow) is due to a ~40-Mb introgression in the Renan genome likely originating from \textit{Aegilops ventricosa}.

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TaZip4-B2 corresponding to Ph1 on chromosome 5B (Rey et al., 2017), the authors suggest that TaZip4-1 does not correspond to Su1-Ph1 (Li et al., 2017). Regarding Ae. geniculata, a potent homeologous pairing promoter locus (Hpp) was identified on chromosome 5Mg, and this chromosome recombined with chromosomes from homeologous group 5 (5A, 5B or 5D) in the presence of the Ph1 gene, even in proximal chromosome regions where recombination is usually suppressed (Koo et al., 2017). They developed a line that was homozygous for ph1B and heterozygous for 5Mg and an introgression from Thinopyrum intermedium (RobT T785.7S#3L; (Danilova et al., 2017)) carrying the wheat streak mosaic virus resistance gene, Wsm3. Homeologous recombination frequency was increased about 100-fold compared with the ph1B-mutant alone suggesting that such a material could help the generation of pre-breeding materials thereby accelerating wheat crop improvement.

Only about 10% of the wheat diversity has been used for wheat improvement yet. Introgessions from wild relatives have a huge impact all over the world, both in terms of performance and economics, especially with regards to occurrence of diseases and tolerance to climate changes (Rather et al., 2017; Redden et al., 2015; Tadesse et al., 2019).

The last impediment to exploit wild diversity in breeding is the ability to achieve crosses between the species. The barriers preventing interspecific hybridizations play a critical role in the development of new allopolyploids since F1 hybrids can be produced and are occasionally at least partially fertile through hybrid genome doubling. Chromosome doubling in wheat breeding is commonly used as it allows to reach 100% homozygosity at all loci in a single generation. This is commonly done using colchicine treatment after either androgenesis (anther culture and microspore culture) or embryo culture using wheat- maize wide hybridization (Devaux, 2021). There are two ways to prevent interspecific hybridizations: pre-zygotic (before fertilisation) and post-zygotic barriers (after fertilisation). Pre-zygotic barriers include gamete isolation, a process that occurs after pollen grains fall on stigmas but before fecundation of the ovule. In plants, gamete isolation may result in either self-incompatibility or competition between con- and hetero-specific pollen for fertilisation, which prevents interspecific hybridization (Heslop-Harrison and Heslop-Harrison, 1982). In this review, we present an overview on gamete isolation, especially crossing ability (or crossability, a term that will be used throughout this manuscript) in plants with a special focus on cereals and on the wheat/rye crossability.

Intraspecific self-incompatibility in plants

Crossability can be defined as the capacity to cross two individuals from the same species or from different species, subspecies, genders etc. to generate embryos or grains that are able to produce F1 plants. These hybrids will be fertile or not according to the genetic pools they are derived from. On the contrary, when a genetic barrier occurs at the fecundation level, the resulting absence of formation of endosperm and/or lethality of the embryo corresponds to crossing inability or non-crossability.

To achieve fertilisation, a pollen grain must adhere and hydrate on a suitable pistil, germinate and form a pollen tube, which can penetrate the pistil’s transmitting tract. The transmitting tract provides the physiological environment to support pollen tube growth and contains chemotropic substances for tube guidance towards the ovary [for a detailed review on pollen-pistil interaction see (Hiscock and Allen, 2008)]. Upon arrival at the ovary, the two haploid sperm cells are released from the pollen tube to fuse with the egg and central cell for double fertilisation. Thus, in pollen-pistil interactions numerous proteins are required for successful seed formation in cell-cell communication and signalling, as well as for nutritional support of pollen tube growth [reviewed by (Higashiyama and Yang, 2017; Johnson et al., 2019)].

Despite the fact that intraspecific crossability does not directly relates with interspecific crossability, there are some elements suggesting that both could be governed by the same mechanisms (Heslop-Harrison, 1982). There can be unilateral incompatibility between taxonomically closely related species. For example, wheat is self-compatible while rye is self-incompatible. When rye is pollinated with wheat, the wheat pollen is rejected while, on the contrary, when wheat is pollinated with rye, the pollen is accepted by the wheat pistil and fecundation may sometimes occur (see below). Several mechanisms controlling self-incompatibility have been described in dicots that may serve as bases to understand crossability in Triticeae.

Control of intraspecific self-incompatibility

Self-incompatibility (SI) is a genetically controlled mechanism in angiosperms that prevents self-fertilisation and promotes outcrossing. SI mechanisms act through inhibition of pollen germination directly on the stigma or pollen tube growth in the style. In many angiosperms, SI is controlled by a single multiallelic locus, the S-locus. However, system with multiple loci controlling SI have also been identified. Interestingly, SI systems arose several times independently during the evolution of the angiosperms [for a review see (Charlesworth et al., 2005)].

SI is either gametophytically controlled, i.e. the genotype of the pollen grain determines the recognition specificity, or sporophytically, where the paternal genotype of the pollen determines the compatibility phenotype. This is described more in detail below: Gametophytic self-incompatibility (GSI)

GSI is widespread throughout the plant kingdom and has been described in diverse families, e.g. Campanulaceae, Fabaceae, Leguminosae, Onagraceae, Papaveraceae, Plantaginaceae, Poaceae, Ranunculaceae, Rosaceae, Scrophulariaceae and Solanaceae (Brewbaker, 1957; Franklin et al., 1985; Igic and Kohn, 2001) for an exhaustive review, see (McClure and Franklin-Tong, 2006)]. In a diploid plant with GSI, half of the haploid pollen grains will carry one allele and the other half the other allele of its parent. For example, an S1S2 plant will give rise to 50% S1 and 50% S2 pollen (Figure 5). A self-incompatible reaction occurs when the S allele of the pollen grain matches one of the alleles of the diploid pistil; hence, this pollen cannot fertilise the corresponding ovule.

In single locus GSI systems, three levels of compatibility are observed in a cross: fully-incompatibility (100% of the pollen is inhibited), half-compatibility (50% of pollen grains grow normally and fertilise the ovules) or full-compatibility (100% of pollen grains develop normally) (McClure and Franklin-Tong, 2006) (Figure 5). Two molecular mechanisms for GSI have been described at the molecular level: S-RNase and the SI system of Papaver rhoeas.

S-RNase—S-locus F-box gene system. In the S-RNase system, which is present in the Plantaginaceae, Rosaceae, Rubiaceae, Rutaceae and Solanaceae, pollen tube growth of incompatible...
grains is arrested in the transmitting tissue of the style. Molecular investigation over many years resulted in the identification of linked genes at the S-locus, a polymorphic pistil-expressed ribonuclease (S-RNase) that controls the female specificity (Lee et al., 1994; Murfett et al., 1994) and an S-locus F-box gene (SLF or SFB) that controls the pollen specificity [see (Tao and Lezzoni, 2010) for review]. While these genes constitute the sufficient set for a self-incompatibility reaction in Prunus (Entani et al., 2003; Ushijima et al., 2004) and Antirrhinum (Lai et al., 2002; Qiao et al., 2004), further studies in the Solanaceae and the Malpighiales subtribe of the Rosaceae showed that rather than having just one SLF/SFB gene, a whole suite of these F-box genes [S-locus F-Box Brothers, SFBB, reviewed by (Sassa, 2016)] are linked to the S-locus and contribute to the SI interaction. The pistil-secreted S-RNase is taken up by the growing pollen tube where they exert a cytotoxic effect in case of an incompatible reaction. Kubo and collaborators (Kubo et al., 2010) proposed that the SI reaction is based on a collaborative non-self-recognition system in which each SFB/B protein acts as a component of the SCF (Skp1-Cullin1-F-box)-type E3 ubiquitin ligase complex to mediate the ubiquitination and degradation of a subset of non-self-S-RNases. Self-RNase fails to be recognised and is hence not degraded (Kubo et al., 2015). This model is supported by gain-of-function experiments, and the investigation of CRISPR/Cas9 generated frameshift mutants in Petunia inflata (Hua et al., 2007; Sun et al., 2018). On the other hand, studies of SI in Prunus including results from SFB-knockout mutants indicate a different mode of action. The proposed model surmises that the non-self-S-RNases that are taken up by the pollen tube are detoxified by a general inhibitor while the SFB protects self-S-RNase e from degradation. Thereby, the self-RNase stays active and causes pollen tube arrest (Matsumoto and Tao, 2016a). Possible candidates for the general inhibitor are the S-locus F-box-like genes, since it has been shown that these proteins recognise S-RNAses and co-immunoprecipitate (Chen et al., 2018; Matsumoto and Tao, 2016b). We expect that, in the future, these models will be extended to accommodate the various other proteins required in the SI reaction either on the pollen or pistil side, such as the HT-B protein (McClure et al., 1999) and the 120-kDa glycoprotein in Solanaceae pistil (Hancock et al., 2005) and the M-locus glutathione S-transferase (MGST) (Ono et al., 2018) in Prunus avium pollen.

**SI system of Papaver rhoes.** In poppy, the site of pollen tube inhibition in an incompatible reaction occurs at the surface of the stigma and is very rapid upon contact or just after germination of the pollen (Matsumoto and Tao, 2016a). SI in poppy is a ‘one-to-one’ self-recognition system. Pollen tube growth arrest is the consequence of the pistil S-determinant (PrS), a ~14 kDa secreted protein, interacting with the pollen S-determinant (PrpS), a ~20 kDa transmembrane protein, inducing a Ca2+-dependent signalling cascade (Wheeler et al., 2009). Upon the change of intracellular Ca2+ concentration, several activities take place (Figure 6): (1) Ca2+-dependent phosphorylation of a 26-kDa cytosolic protein (Pr-p26) thus reducing its pyrophosphatase activity, (2) depolymerisation of actin filaments and reorganisation of the microtubule cytoskeleton. Furthermore, the p56 mitogen-activated protein kinase (p56-MAPK) is activated, which induces programmed cell death (PCD) of the pollen cell as evidenced by cytochrome c (Cyt c) leakage, activation of caspase-like activities and, eventually, DNA fragmentation (Eaves et al., 2014; McClure and Franklin-Tong, 2006).

**Sporophytic self-incompatibility (SSI)**

Sporophytic self-incompatibility (SSI) was characterised in Brassicaceae (the family in which the molecular components have been identified; for review, see Doucet et al., 2016; Leducq et al., 2013) but was also identified in Asteraceae, Betulaceae, Caryophyllaceae, Convolvulaceae, Polemoniaceae and Sterculiaceae. In SSI, both male and female cells produce two components, and the SI phenotype of both stigma and pollen is determined by the diploid genotype of the parent plant. As a consequence, sporophytic systems are characterised by the occurrence of dominant-recessive and co-dominance effects within pollen and stigma. In some cases, dominance may exist...
between pairs of alleles, which complicates compatibility/incompatibility relationships. However, this dominance effect results sometimes in the production of double recessive alleles. Contrary to a population for which all S-alleles would be co-dominant, dominance increases the probability of having compatible individuals (Dickinson et al., 2003). Frequency between recessive and dominant S-alleles reflects the dynamic balance between reproduction (favoured by recessive alleles) and self-pollination prevention (favoured by dominant alleles; Ockendon, 1974).

A pollen grain is incompatible when the dominant allele(s) of the pollen parent matches the dominant allele(s) in the recipient pistil. In the well-studied SI system of the Brassicaceae, pollen rejection occurs shortly after contact with the stigma, either by blocking hydration of the pollen, or by pollen tube arrest preventing penetration into the stigma. Three tightly linked genes are located at the S-locus (Figure 7): (1) the S-locus cysteine-rich protein/S-locus protein 11 (SCR/SP11), a small cysteine-rich protein, which is the male determinant and expressed in the anther tapetum from which it is deposited into the pollen exine (Schopfer and Nasrallah, 2000; Takayama et al., 2000); (2) the S-receptor kinase (SRK) (Takasaki et al., 2000), a transmembrane protein kinase, which constitutes the female determinant; (3) the S-locus glycoprotein (SLG), an abundant protein in the stigmatic papillae, which is highly similar to the extracellular domain of the SRK. SLG appears not to be essential for the SI response but may have an accessory role (reviewed in Kemp and Doughty, 2003). In the current model (Figure 7), the pollen SCR/SP11 protein binds to the extracellular domain of the SRK, SLG appears not to be essential for the SI response but may have an accessory role (reviewed in Kemp and Doughty, 2003). In the current model (Figure 7), the pollen SCR/SP11 protein binds to the extracellular domain of the SRK, SRK was shown to interact with the M-locus protein kinase (MLPK), a plasma membrane-localised serine/threonine kinase (Murase et al., 2004) and the Armadillo repeat-containing protein 1 (ARC1) with E3 ubiquitin ligase activity, which is specifically expressed in stigmas.

The phosphorylated ARC1 in turn ubiquitinates EXO70A1 and glyoxylase 1 (GLO1) thereby leading to their proteasomal degradation. EXO70A1 is part of the exocyst complex, which facilitates transport of vesicles to the plasma membrane. It has been
Figure 7  Molecular model of the self-incompatibility (SI) response in the *Brassicaceae*. The S-locus consists of three genes, SRK, SP11 and SLG. The SRK receptor kinase (in blue) is the female factor and covers the plasma membrane of the stigma papilla cell. SP11 (in red) is the male component that is mainly expressed in the anther tapetum where it accumulates in the outer layer of the pollen cell wall during maturation. The pollen SP11/SCR ligand binds to stigma SRK, leading to auto-phosphorylations of SRK as well as phosphorylation and activation of ARC1. ARC1 ubiquitinates EXO70A1 and GLO1. The ubiquitination of EXO70A1 blocks further hydration of the incompatible pollen, whereas the proteasomal degradation of GLO1 is thought to lead to an increased level of the cytotoxic methylglyoxal (MG). Adapted from (Jany et al., 2019; Takayama and Isogai, 2005).

Self-incompatibility in Poaceae

SI is widespread among the grasses with self-incompatible and self-fertile species often present in the same tribe [Table 3; (Baumann et al., 2000; Connor, 1979; Do Canto et al., 2016)]. Perennial grasses tend to show a higher frequency of SI than that of annuals (Beddows, 1931). Studies in rye (*Secale cereale*; (Lundqvist, 1954) and in Phalaris coerulescens (Hayman, 1956) have shown that in the Poaceae, SI is gametophytically mediated by two unlinked and multiallelic loci, S and Z. A pollen grain will be incompatible when both its S and Z alleles are present in the pistil (Figure 8). The degree of compatibility ranges from 0%, 50%, 75% or 100%, depending on the genotypes of pollen and stigma, and reciprocal crosses can show different degrees of compatibility. For example, a cross between genotypes *S1S2Z1Z2* (as the female recipient) and *S1S2Z1Z2* (as the male donor) is incompatible (pollen genotypes: either *S1Z* or *S2Z*), whereas the reciprocal cross pollen is 50% compatible (Yang et al., 2008). Pollen tube growth is typically arrested shortly after pollen tube emergence (Shivanna et al., 1982) with *Cynodon dactylon* being a notable exception where tube growth is inhibited within the style (Thomas and Murray, 1975).

In contrast to single locus GSI and SSI in diploids, neither does the two locus system of grasses break down in autotetraploid plants nor is there any dominance or competitive interactions between the alleles of diploid pollen or tetraploid styles (Fearon et al., 1984a, 1984b; Lundqvist, 1957, 2009).

Genes linked to either S or Z will show disturbed segregation in partially compatible crosses (Leach, 1988); hence, distorted segregation analysis provides a means to locate the SI loci in the genome. Initial studies with isozymes demonstrated linkage of the S-locus to phosphoglycoisomerase (*PGI-2*) and a leaf peroxidase (*Prx-7*) located on chromosome 1R in *Secale cereale* (Wricke and Wehling, 1985), and chromosome 6 in *Lolium perenne* (Cornish et al., 1989). The Z-locus co-segregated with the beta-glucosidase and esterase 4/11 isozymes located on chromosome 2R in rye (*Poa annua*; Fuong et al., 1993; Gertz and Wricke, 1989). These and further early studies (Leach and Hayman, 1987) suggested that the SI system is conserved across the Poaceae. Detailed molecular mapping experiments carried out in *Secale cereale* (Hackauf and Wricke, 2005), *Phalaris coerulescens* (Bian et al., 2004), *Hordeum bulbosum* (Kakeda et al., 2008) and *Lolium perenne* (Shinozuka et al., 2010; Yang et al., 2009) confirmed the syntenic chromosomal locations of S and Z [for details see (Klaas et al., 2011)] and thus support a monophyletic origin.

In spite of various attempts to clone the genes over the last decades, the molecular nature of S and Z still remains elusive. However, several promising candidates have been identified. For example, the TC116908 gene, which shows similarity to ubiquitin-specific proteases, has been put forward as a possible candidate for Z in rye (Hackauf and Wehling, 2005). Based on their map-based cloning experiment in *Lolium perenne*, Shinozuka et al. (2010) suggested LpTC116908, the ortholog of the rye gene, and *LpDUF247*, the male and female determinants. Candidate genes for S were proposed by (Kakeda, 2009) from linkage analyses in *Hordeum bulbosum*, and more recently by (Manzanares et al., 2016) from their fine-mapping study in *Lolium perenne*. Their study provides strong evidence for the LpDUF247 gene being the pollen S-determinant, including allelic...
Table 3  Poaceae subfamilies and tribes with example of self-compatibility (SC) and self-incompatibility (SI) species. Clade BOP represent Bambusoideae, Oryzioideae, Pooideae families and clade PACMAD represent Panicoidae, Aristidoideae, Chloridoideae, Micrairoideae and Danthonioideae families. No information for the following subfamilies Aristidoideae, Micrairoideae and tribes Olyreae, Aristidoae, Micraireae, Eriachneae and Hubbardiae (extracted from [Baumann et al., 2000; Chen et al., 2017; Connor, 1979; Crain et al., 2020, Do Canto et al., 2016; Lian et al., 2021])

| Clade | Subfamily | Tribe | Species | SI |
|-------|-----------|-------|---------|----|
| BOP   | Bambusoideae | Arundinariae | Arundinaria simonii | Yes |
|       | Bambusoideae | Bambuseae | Dendrocalamus sinicus | No |
| Dryzioideae | Oryzeae | Oryza barthii | Yes |
|        | Oryzaeae | Oryza longistaminata | Yes |
| Pooideae | Poeae | Alopecurus myosuroides | Yes |
|        |       | Alopecurus pratensis | Yes |
|        |       | Anthoxanthum odoratum | Yes |
|        |       | Arrhenatherum elatius | Yes |
|        |       | Avena barbata | No |
|        |       | Briza australis | Yes |
|        |       | Briza elatior | Yes |
|        |       | Briza media | Yes |
|        |       | Briza minor | No |
|        |       | Bromus inermis | Yes |
|        |       | Bromus tectorum | No |
|        |       | Cynosurus cristatus | Yes |
|        |       | Dactylis aschersoniana | Yes |
|        |       | Deschampsia flexuosa | Yes |
|        |       | Festuca pratensis | Yes |
|        |       | Festuca rubra | Yes |
|        |       | Holcus lanatus | Yes |
|        |       | Lolium multiflorum | Yes |
|        |       | Lolium perenne | Yes |
|        |       | Lolium rigidum | No |
|        |       | Lolium temulentum | No |
|        |       | Phalaris arundinacea | Yes |
|        |       | Phalaris coerulescens | Yes |
| Triticeae | Hordeum bulbosum | Yes |
|        | Hordeum vulgare | No |
|        | Secale cereale | Yes |
|        | Thinopyrum | Yes |
|        | intermediate | No |
|        | Triticum aestivum | No |
| PACMAD | Panicoidae | Andropogoneae | Miscanthus sinensis | Yes |
|        |       | Sorghastrum nutans | Yes |
|        |       | Themeda australis | No |
|        |       | Zea mays | No |
|        |       | Panicum virgatum | Yes |
| Chloridoideae | Cyndontaeae | Chloris gayana | Yes |
|        |       | Chloris striate | No |
|        |       | Cyonodon dactylon | Yes |
|        |       | Oryza sativa | No |
|        |       | Molinia caerulea | Yes |
| Danthonioideae | Danthonieae | Danthonia linkii | No |

polymorphism, and mutation or deletion of the gene in self-compatible species. The fact that both the S and Z candidates contain the same protein domain (DUF247) of unknown function warrants further investigation into the molecular role and evolutionary origin of this domain. Recently, this same team fine mapped a QTL for self-compatibility (SC) on chromosome 5 of L. perenne (Cropano et al., 2021). They reduced the region to a 3-Mb segment containing 57 genes among which, seven were relevant candidates.

Interspecific crossability in wheat

Obtaining F1 hybrids after crossing wheat with a related species is a prerequisite to the transfer of alien genes. One of the first study regarding crossability between wheat and wheat relatives was published about a century ago (Backhouse, 1916) and showed that crossability between wheat and rye was a recessive trait. These results were further confirmed (Leighty and Sando, 1928; Meister and Tjumjakoff, 1928; Riley and Chapman, 1967; Taylor and Quisenberry, 1935).

Crossability has mainly been studied with rye. Crosses are achieved when wheat is used as female while the reciprocal cross is almost impossible (Jalani and Moss, 1980). The success rate of hybridization depends on the wheat genotype’s ability used to perform the crosses. Wheats were therefore classified into three classes depending on their crossability (Tozu, 1966): high (>47%), medium (17-20%) or low (<10%) crossability. (Lange and Wojciechowska, 1976) compared with the crossability rate of 177 wheat varieties originating from diverse countries in the world. They showed that crossable varieties (>25% crossability) came from Argentina, Brazil, China, Iran, Japan, and Yugoslavia and that those with crossability ranging from 20% to 25% came from Mexico and India. Another study evaluating 1400 wheat cultivars exhibited similar results with most of the crossable lines coming from China, Japan, Iran and Siberia and suggesting that crossable lines mainly originate from Asia (Zeven, 1987).

To study whether environmental conditions (light and temperature) could affect crossability, Bertin et al. (2009) used progeny derived from the cross between cv. Hobbit-sib, a semi-dwarf winter wheat that is not crossable with rye and has a translocated karyotype with 5BL-7BL and 5BS-7BS chromosomes and its nearly-isogenic line, Hobbit-sib (CS-5BL, 7BL), that has a normal karyotype with the 5B and 7B chromosomes that have a short arm from Hobbit-sib and a long arm from Chinese Spring (Miura et al., 1992). Among the progeny, they selected three crossable and seven non-crossable lines to produce additional recombinant lines that they assessed during four growing seasons (two winters and two summers). They saw that crossability was higher for some lines in warmer field environments (range temperature: 9–19 °C; mean 14 °C) with large amount of light (150 h and 215 h of sunshine in summer 2007 and 2008 respectively) while their crossability dropped dramatically to a few per cent in winter conditions (range temperature 2–10 °C; mean 6–7 °C; 55–56 h of sunshine), with seed set possibly as low as 3% even for the normally crossable variety Chinese Spring becoming not crossable. However, some lines remained consistently crossable whatever the conditions suggesting that they could be useful for breeders willing to enlarge wheat diversity using related species usually poorly crossable with wheat such as rye (Bertin et al., 2009).
Similarly, the effect of temperature on seed production in hybrids derived from crosses between wheat and diploid cultivated barley *Hordeum vulgare* or tetraploid wild-barley *Hordeum bulbosum* was also studied. Such crosses were initially performed to produce haploid wheat plants (Barclay, 1975). For example, four different temperatures (12, 15, 18 and 21 °C) were evaluated in reciprocal crosses involving the wheat variety Chinese Spring and two spring barley varieties (Betzes, Martonvasari 50; Molnár-Láng and Sutka, 1994). Like for rye, best results (3.26% of seeds) were observed at high temperature (21 °C) when wheat was used as the female parent, but this was only true for the Chinese Spring x Betzes combination while only 1–2 seeds (~0.1%) were obtained when Chinese Spring was crossed with Martonvasari 50 independent of the temperature. Interestingly, results were opposite in the reciprocal crosses, and the highest amount of seeds (2.36%–4.88%) was observed at 12–15 °C for both barley varieties. This therefore confirmed that temperature plays a major role for interspecific hybrid production and also that the wheat genotype is important.

### Physiology of non-crossability in wheat

Several studies have been conducted to tentatively identify the mode of action of the dominant inhibitor genes of wheat/rye or wheat/H. bulbosum crossability. Results show that the rye (or wild barley) pollen grains germinate on the wheat stigma and that differences between crossable and non-crossable lines appear later, during pollen growth and just before fecundation (Figure 9). Significant differences are neither observed in pollen grain germination speed (Jalani and Moss, 1980; Lange and Wojciechowska, 1976, 1977; Tozu, 1966, Zeven and van Heemert, 1970), nor in the mean number of germinated pollen grains (Jalani and Moss, 1980; Lange and Wojciechowska, 1976) between the wheat × wheat controls and wheat × rye crosses.

Jalani and Moss (1980) also observed that the poorly crossable Chinese Spring/Hope 5B substitution line (a line where the pair of chromosomes 5B of the variety Chinese Spring is substituted by the homologous chromosomes from the variety Hope) showed more germinated rye-pollen grains compared with Chinese Spring itself, which is highly crossable. This confirms that inhibition of crossability does not occur at the pollen grain germination stage. No difference in pollen tube growth speeds between wheat and rye-pollen grains was observed, development of rye-pollen tubes appeared even a bit faster.

Jalani and Moss (1980) also compared the number of pollen tubes growing from the stigma to the microstyle, 30 min., 45 min., 1, 2, 5, 6 and 12 h after pollination. Results showed no significant differences in the style and at the base of the style in wheat × wheat controls and in the wheat × rye crosses. However, significant differences depending on the genotypes were observed concerning the time necessary for the pollen tubes to reach the maximum number at the top or in the middle of the embryo sac as well as at the microstyle. The maximum was achieved 1 h after pollination in the control but needed between 2 and 6 h in the wheat × rye crosses. Jalani and Moss (1980) showed a high correlation (r = 0.97, P > 0.01) between the number of microstyles with pollen tubes and the number of grains formed indicating that the difference of crossability between genotypes (i.e. mode of action of inhibitor genes) is probably located at this level. Therefore, when pollen tubes are growing and start to penetrate the style, the development rate of pollen tubes differs between crossable and non-crossable lines, and the slower pollen tubes never reach the base of the style (Jalani and Moss, 1980; Lange and Wojciechowska, 1976). We can thus conclude that the lack of fertilisation is probably the major reason explaining the low number of grains obtained in non-crossable varieties.

### Genetics of wheat/rye crossability

Genetics of gamete isolation in wheat is a well-documented mechanism especially with regards to the wheat/rye pollination (Matsuoka et al., 2014). In the beginning of the 20th century, Backhouse (1916) noticed that most wheat varieties did not produce seeds when crossed with rye, except Chinese landraces that gave exceptionally high level of viable F1 seeds. During the last five decades, several genes and QTLs involved in wheat/rye crossability have been identified. These genes are distinguished by their effect on inhibition of fecundation, which is usually studied after pollination with regards to endosperm development and number of grains obtained (Krolow, 1970). None of the genes involved in wheat/rye crossability have been isolated so far, which prevents a finer molecular analysis of their mode of action, mechanisms, expression, regulation and partners.

### Kr genes (Kr1, Kr2 and Kr3)

First crossability genes (named ‘Kr’ for ‘Kreuzbarkeit’, the German word for ‘crossability’) were evidenced by Lein (1943) who identified two genes, *Kr1* and *Kr2*, involved in crossability between wheat and rye. Lein suggested that the variety ‘Chinese 466’ carried the recessive alleles at these two genes and was therefore *Kr1Kr1kr2kr2* and highly crossable. On the contrary, other lines that were either *Kr1Kr1kr2kr2* or *Kr1Kr1Kr2Kr2* were only poorly or not crossable respectively. Lein finally suggested that *Kr1* had a stronger effect compared with *Kr2* regarding wheat/rye hybrid grain production. Mapping of these two genes was achieved more than 20 years later (Riley and Chapman, 1967) using a set of substitution lines developed in the highly
crossable variety Chinese Spring in which each pair of homoeologous chromosomes was replaced with the homologous one from the variety Hope, a non-crossable variety. They showed that the lines where chromosomes 5A and 5B from Chinese Spring were substituted by those of Hope presented crossability rates of 26.2% and 6.4% respectively, while Chinese Spring and the other substitution lines exhibited crossability rates rising to 74.3%. It was concluded that $Kr1$ locates on chromosome 5B and $Kr2$ on chromosome 5A. Hope has a dominant allele for $Kr1$ which acts as inhibitor of wheat/rye crossability while Chinese Spring carries recessive alleles ($kr1kr2$) that favor wheat/rye crossability (Riley and Chapman, 1967). A more resolute analysis using ditelosomic lines (lines missing one chromosome arm at a homozygous state) located $Kr1$ and $Kr2$ on the long arms of chromosomes 5B and 5A respectively (Lange and Riley, 1973). This study as well as others also confirmed that the effect of $Kr1$ was stronger than the one of $Kr2$ (Deng-Cai et al., 1999; Krolow, 1970; Tixier et al., 1998; Zheng, 1992). A third gene, $Kr3$, was located in a homoeologous position on chromosome 5D, but this gene had a much lower effect on wheat/rye crossability compared to that of $Kr1$ and $Kr2$ (Bertin et al., 2009; Krolow, 1970; Mishina et al., 2009; Tixier et al., 1998). It was hypothesized that the reproduction barrier caused by $Kr$ genes prevents interspecific crossing by inhibiting pollen tube growth therefore blocking pollen from fertilising ovary (Bertin et al., 2009; Romero and Cuadrado, 1992).

The dominant alleles of $Kr1$ (5.5% of heritability) and $Kr2$ genes are the sources of the limited crossability between wheat and rye and wheat and wild barley (Mishina et al., 2009; Riley and Chapman, 1967; Tixier et al., 1998). Different levels of crossability were displayed (Lein, 1943; Tixier et al., 1998). These levels were established in wheat-rye cross: crossability $\leq 5\%$ means the two $Kr$ genes have dominant alleles ($Kr1Kr1/Kr2Kr2$; Tixier et al., 1998), crossability reached 10%–30% and 30%–50% the genotypes corresponds to $Kr1Kr1/kr2kr2$ and $kr1kr1/Kr2Kr2$ (Riley and Chapman, 1967; Tixier et al., 1998) and to the crossability $\geq 50\%$, the two genes must have recessive alleles ($kr1kr1/kr2kr2$; Lein, 1943; Romero and Cuadrado, 1992; Tixier et al., 1998). The suppression of wheat-rye crossability by $Kr$ genes is not completely dominant, and some seeds (or no seeds

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Figure 9 Schematic representation of pollen tube development and fertilisation in wheat, after selfing and after manual cross-pollination with pollen from an incompatible species. Prior to cross-pollination, the recipient plant needs to be emasculated.
for the crossable lines) may always be obtained (or not) independent of the variety used and the environmental conditions.

Genetic complexity of the crossability trait was confirmed by Bertin et al. (2009) who elaborated an approach to fine-map \( Kr_1 \) gene on chromosome arm 5B L. They used three crossable and eight non-crossable lines, selected from the 71 recombinant substitution lines derived from a cross between Hobbit-sib and its nearly-isogenic line, Hobbit-sib (CS-5B,7BL) (Lamoureux et al., 1992). The aim of this cross is to develop additional F1 heterozygotes with segmental recombination on 5B L that were further evaluated for their crossability together with the parental lines. They used a set of 31 markers to molecularly characterise these lines as well as some descendants originating from their crosses and they combined these data with crossability phenotypes. They revealed that two different regions located on the long arm of chromosome 5B and including \( Kr_1 \), could be involved in crossability in this cross (Bertin et al., 2009). Moreover, they obtained lines combining these two favourable regions, which exhibited up to 50% of crossability suggesting that they could be useful for breeders to introduce new diversity from alien wheat relatives.

Several additional studies have revealed that the mechanisms governing crossability between wheat and wild barley was probably the same as the one controlling crossability between wheat and rye (Snape et al., 1979). Evaluation of crosses between wheat and \( Hordeum bulbosum \) wild barley, using the same set of Chinese Spring/Hope substitution lines (Riley and Chapman, 1967) showed that chromosomes 5B \(( Kr_1 )\), 5A \(( Kr_2 )\) and 5D \(( Kr_3 )\) had the strongest effect with regards to wheat/\( H. bulbosum \) crossability, but the crossability rates were lower in this latter case compared to what was achieved with crosses between wheat and rye. The strongest effect observed with substitution of chromosome 5B suggests that both mechanisms are controlled by the same genes. This result was confirmed later with a finer mapping of \( Kr_1 \) and \( Kr_2 \) on the long arms of chromosomes 5B and 5A respectively (Falk and Kashaa, 1983; Fedak and Jui, 2011; Sitch et al., 1985). Finally, the tiny effect of \( Kr_3 \) on chromosome 5D (Krolow, 1970) was confirmed, but this gene weakly affects either wheat/rye or wheat/\( H. bulbosum \) crossability (Falk and Kashaa, 1983; Snape et al., 1979; Zheng, 1992).

### Other genes that may affect wheat/rye crossability

Several studies have identified additional loci affecting wheat/rye crossability. It was found that homoeologous chromosomes from group 3 could carry factors affecting crossability between wheat cv. Chinese Spring and \( H. bulbosum \) (Miller et al., 1983). It was further confirmed that chromosomes 3D and 3B had the major effect (Romero and Cuadrado, 1992). Similarly, Zheng (1992) identified \( Kr_4 \) on chromosome 1A. This gene had a stronger effect than \( Kr_2 \) but a lower effect compared to \( Kr_1 \) (Deng-Cai et al., 1999; Luo et al., 1993; Zheng, 1992). Finally, a QTL was located on the long arm of chromosome 7A using a doubled-haploid (DH) population derived from the cross between the highly crossable variety Chinese Spring and the non-crossable French variety Courtot (Lamoureux et al., 2002; Tixier et al., 1998). Interestingly, this QTL was found to have a stronger effect than \( Kr_1 \) in this population.

### \( SKr \) gene

Initial studies working on mapping of crossability genes used either substitution lines (Riley and Chapman, 1967) or aneuploid stocks missing chromosome arms or even entire chromosomes (Lange and Riley, 1973; Snape et al., 1979). The advent of molecular markers in the early 1990s has allowed the development of high-density genetic maps that permitted the application of QTL approaches to decipher more precisely the genetic control of wheat/rye crossability. However, to solve the problem of the low polymorphism rate found in wheat, genetic maps were developed using crosses involving synthetic wheats that were not suitable for mapping crossability genes.

The first intervarietal wheat genetic map was obtained from the cross between Chinese Spring and Courtot (CsCS; Cadalen et al., 1997). Fortunately, this cross-involved two lines that showed opposite behaviour regarding wheat/rye crossability, Chinese Spring being highly crossable with rye (95% of success) while Courtot rarely gives seeds (0-10%) when crossed with this species. The DH progeny (187 individuals) (Felix et al., 1996; Cadalen et al., 1997) derived from this cross was thus suitable for QTL detection for this trait. A QTL analysis was conducted using this segregating population (Tixier et al., 1998). Unexpectedly, the major QTL was detected on the short arm of chromosome 5B, close to the RFLP marker Xfba367-5B. This locus represented ~17% of the variability of the trait and was named ‘\( SKr \)’ (for Suppressor of \( Kr \)). This relatively low value was explained either by a large phenotypic variance, mostly due to environmental effects, or by the fact that Xfba367-5B, although the most distal marker on chromosome 5B, might not be very close to the \( SKr \) gene. As expected, the crossable allele was brought by Chinese Spring. Two additional loci were located on chromosome 7A, close to Xtam51-7A, and on chromosome 5B long arm, close to marker Xwgs583-5B. These two loci explained respectively 5.9% and 3.3% of the additive value. The locus on the long arm of chromosome 5B probably corresponds to \( Kr_1 \), but interestingly, it had a lower effect than the locus on chromosome 7A. Altogether, these three loci explained 65% of the difference in crossability between the two parents (Tixier et al., 1998). These results were confirmed using a different population derived from the cross between Chinese Spring and a chromosome substitution line of Chinese Spring, which has its chromosome 5B replaced by that of Cheyenne [low crossability; (Mishina et al., 2009)].

Fine mapping of the \( SKr \) locus was conducted on the same CsCS population, and marker density was improved using microsatellites as well as AFLP markers (Lamoureux et al., 2002; Sourdille et al., 2003). The closest marker to \( SKr \) was found to be an AFLP fragment, E36M49-287, which was further cloned, sequenced and named DL103. To use the syntenic relationships between wheat and rice to develop additional markers, this clone was mapped on the rice genetic map and locates on short arm of chromosome 11 of rice. However, this approach was unsuccessful, probably because of complexity of the synteny within this region in wheat that is syntenic with segments from chromosomes 5, 6, 11 and 12 of rice separated by undetermined regions (Lamoureux et al., 2002).

To go towards the positional cloning of \( SKr \), a new segregating population was developed (Alfares et al., 2009). The highly crossable CsCS DH line MP98 that carried Chinese Spring allele at the \( SKr \) locus was backcrossed with Ct followed by six generations of selfing to generate a SSD population of 618 individuals referred as MP98-Ct. Collinearity with rice and barley was exploited to develop additional markers. Among the 12 barley ESTs that exhibited a 5B-specific band, only two were polymorphic between the two parents and were mapped and derived into
PCR markers for high-throughput genotyping assays. Despite the low success rate, this allowed to improve the genetic map as well as to better see the relationships between wheat and barley. Interestingly, the SKr locus co-segregates with the GSP locus involved in grain softness protein (Chantret et al., 2005), and 14 SB-specific new markers were developed from this sequence among which, SSR Cfb306 co-segregated with SKr. A physical map was then generated by anchoring the linked markers to BAC clones from Chinese Spring (Allouis et al., 2003). Positive clones were sequenced representing two contigs of ~300 kb and ~120 kb. This allowed the development of only one additional SSR (Cfb341) that also co-segregated with SKr confirming the complete linkage of this sequence with the crossability locus. The Cfb306 and cfb341 SSR markers are efficient tools for introducing crossability alleles of SKr into breeding programmes (Alfares et al., 2009). These markers can improve the genetic diversity of different species when crossing or producing Triticales (Alfares et al., 2009).

Only five genes were annotated on the collinear rice region (Figure 10), but the sequencing was not complete in wheat, with no certainty that the two contigs actually flank the SKr locus and without any obvious candidate (Alfares et al., 2009). These five genes are determined thanks to markers, one of them located in a gene showing homology to the pentatricopeptide gene Os12g44170 in rice (Alfares et al., 2009). Other markers brought to light the presence of other genes, plasma membrane ATPase1 and N-acetylglucosaminyltransferase (Alfares et al., 2009). Markers can be useful for further improvement of the physical map as well as for marker-assisted breeding for wheat/rye crossability.

**Improving crossability of cultivated wheat varieties**

One of the most remarkable realisations derived from wheat/rye hybridization is Triticale (× Triticosecale Wittmack), which is the first man-made interspecific hybrid species. The initial aim was to combine quality of wheat (especially productivity and bread-making quality) with the robustness of rye that can grow on less favourable lands. The first haploid wheat/rye hybrid was generated in Scotland at the end of the 19th century [Wilson, 1873, cited by (Leighty, 1916)]. However, the first fertile hybrid was generated 60 years later only, and the production has increased since then with the discovery of colchicine that allows chromosome doubling of haploid hybrids [for a review, see (Oettler, 2005)]. Breeding and production of Triticale started in the 1960s in Poland, and in the 1980s in the rest of Europe. In 2016, world Triticale production has risen to over 20 million tons, half of that coming from Germany and Poland combined showing that Triticale is an important cereal in the European Union and worldwide (Skowrońska et al., 2020). Indeed, Triticale is of agronomic interest for livestock feed production, industrial energy crop and pathogen resistance (Ellis et al., 2014; Sisodia and McGinnis, 1970; Skowrońska et al., 2020). It may be a promising alternative to wheat especially in poor-land regions (Sisodia and McGinnis, 1970; Skowrońska et al., 2020).

Interestingly, wheat/rye amphiploid hybrids never appeared naturally while hybrid seeds resulting from crosses between hexaploid wheat and rye usually germinate freely and form vigorous and aggressive F1s (Riley and Chapman, 1967). This is because chromosomal stocks remained haploid leading to sterile gametes after meiosis. However, diploid gametes may rarely

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**Figure 10** Extended genetic and physical maps at the SKr locus and syntenic relationships with rice. (a) Genetic map of the SKr locus on wheat chromosome arm 5BS. (b) Physical map at the SKr locus on wheat chromosome 5BS. (c) Detailed representation of the BAC clones identified at the 5B homeologous GSP [1793L02 in blue, (Chantret et al., 2005), Chantret et al. (2008)] and SKr loci. The gene order on partially sequenced BAC 317L24 (in orange) corresponds to the order established on the genetic map for cfb341 and GBR0233. GSP-1 (grain softness protein). (d) Collinearity with genes located on rice chromosomes 1, 2, and 12L. (e) Rice BAC clones associated with the different wheat orthologous genes on chromosome 5BS. The 11 rice genes on chromosomes 1, 2or 12 are annotated as follows: (1) Os01g14180: Expressed protein; (2 a, b, c) Os02g13990: U2 small nuclear ribonucleoprotein A (U2A); (3) Os12g44250: vesicle-associated membrane protein; (4) Os12g44240: N-acetylglucosaminyltransferase; (5 a, b) Os12g44220: ATPase; (6) Os12g44210: ATPase, AAA family domain-containing protein; (7) Os12g44190: ATPase 3; (8) Os12g44180: nodulin; (9) Os12g44170: pentatricopeptide; (10 a, b, c) Os12g44160: oxidoreductase; and (11 a, b) Os12g44150: plasma membrane ATPase. Grey: other genes present on rice chromosome 12. Adapted from Alfares et al. (2009).
occur leading to natural polyloid species. This was the case for the creation of tetraploid and hexaploid wheat, but in this case, the diploid and tetraploid species lived in sympatry in the same environment. This was not the same for wheat and rye. Contrary to wheat, rye was a southwest Asian Neolithic crop that became later than wheat, a cultivated plant, and not necessarily in the Fertile Crescent. Rye is an integral part of the ‘secondary crops’, which first evolved as weeds in cultivated habitats (since the origins of agricultural) and was only later established as crops (Prece et al., 2017; Weiss et al., 2012). There are thus no genomic resources for Triticale, and genetic diversity can only be increased by doing new crosses involving different varieties of wheat and rye (Friebe et al., 1996; Jiang and Gill, 1994; Schneider et al., 2008).

Since only a few Asian varieties can easily be crossed with rye (Zeven, 1987), one way to face this challenge is to introduce crossability genes in wheat elite varieties. This can be achieved using marker-assisted selection (MAS) with the SSRs developed for SKr (Alfares et al., 2009). This approach was evaluated and shown to be successful for six varieties (Alfares et al., 2009). It was further applied at a larger scale for 12 additional lines (Bouguennec et al., 2018) opening the way to enhance Triticale genetic diversity more easily and to improve traits of agronomic interest in Triticale or wheat as well as to study further barriers to intergeneric crosses.

Conclusions

In summary, crossability between wheat and alien species is controlled by plenty of factors among which, Kr1, Kr2, Kr3 and Kr4 play an important role in this crossability as stated above. Concerning other suggested genes, they participate in a minor part of crossing-compatibility compared with the Kr group. Only the Skr locus seems to be a major player, but it remains poorly understood, and research is necessary to elucidate the function of the different genes present at this locus. Furthermore, the role of Skr gene in crossability remains to be investigated, but this will require the isolation of the best candidate gene. To this day, wheat crossing compatibility with alien species remains unclear, and crosses between wheat and rye are still complex. Several studies are necessary to enrich the cultivated gene pools by incorporating favourable alleles, genes or gene complexes derived from the diverse gene pools of wheat relatives leading to new powerful wheat and Triticale varieties.

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Conflict of interest

The authors declare no conflict of interest.

Author contributions

J.L, UB and PS followed the literature and shared writing of the manuscript. All authors approved the manuscript.

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