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Review Article

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

Julie Laugerotte[1], Ute Baumann[2] and Pierre Sourdille[1]*

[1]Genetics, Diversity and Ecophysiology of Cereals, INRAE, Université Clermont-Auvergne, Clermont-Ferrand, France
[2]School of Agriculture, Food and Wine, University of Adelaide, Glen Osmond, South Australia, Australia

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**Correspondence* (Tel +33 (0)4 43 76 15 17; fax +33 (0)4 43 76 15 10; email pierre.sourdille@inrae.fr)

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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*), Triticale (*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 *Sitopsis* section (*Ae. speltoides, 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. diccocoides*) that further evolved to give *T. turgidum*, 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

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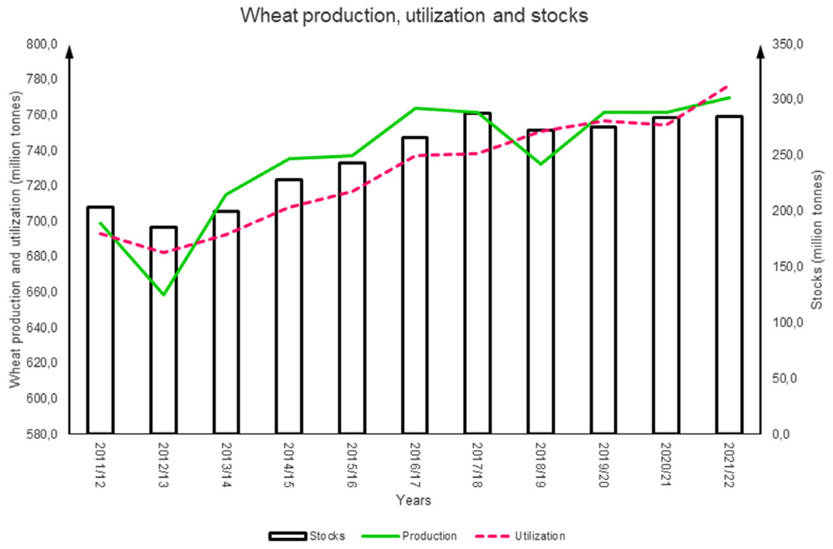

Figure 1 Evolution of wheat production (green line), utilisation (red dashed line) and stocks (black bars) between 2011 and 2021 in the world (in million tons). The data come from the site http://www.fao.org/worldfoodsituation/csdb/en/.

Sea, a region that has a rich diversity for *Ae. tauschii*. Hexaploid wheat started to be widely cultivated 7–10 000 years ago (Balfourier *et al*., 2019; Preece *et al*., 2017; Zohary and Hopf, 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*., 2008; Figure 2a). For example, at the beginning of the 20th century in the United States, only five varieties were grown and one (Turkey) covered almost the total acreage (Cox *et al*., 1986). Therefore, a high strategic priority for wheat improvement worldwide is to enrich the cultivated varieties by incorporating favourable alleles, genes or gene complexes. This can be achieved by introgressing new diversity from the diverse gene pools related to wheat.

Introgression is defined as the transfer of more or less large portions of alien genomes into a cultivated species (Rieseberg and Wendel, 1993). Introgressions played a major role in the growth of genetic diversity (Wendel *et al*., 1989), adaptation to novel environmental conditions (Rieseberg *et al*., 2003), formation of new ecotypes or species (Rieseberg, 1997) or evolution of invasive species (Ellstrand and Schierenbeck, 2000). The use of wild relatives 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 (AABBDD + 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) (Borojevic and Borojevic, 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

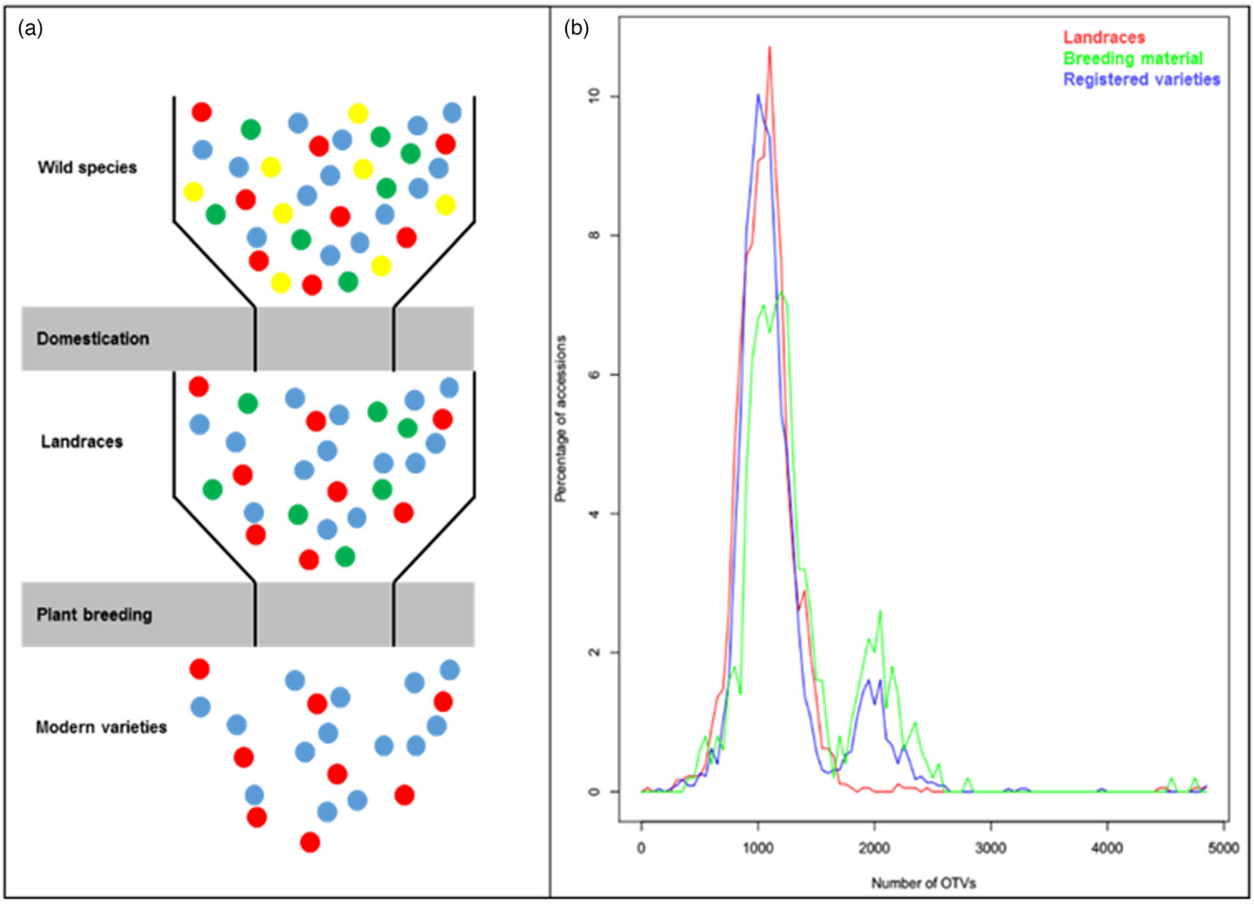

Figure 2 The wheat genetic diversity. (a) Schematic representation of the loss of natural genetic diversity through domestication and breeding in wheat. (b) Introduction of new genetic diversity through alien introgressions during wheat breeding. Percentage of wheat landraces (red), breeding material (green) and registered varieties (blue) as a function of the number of structural variations (OTVs: off-target variants) observed with a 420K SNP array. The peaks centred on 2000 OTVs illustrate the creation of a new type of diversity based on alien introgressions.

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. diccocoides* and *T. dicoccum*) as well as diploid species such as *T. monococcum* (AA), *T. boeoticum* (AA), *T. urartu* (AA) and *Ae. tauschii* (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. tauschii* accessions, to improve diversity of the D-genome through the production of synthetic wheats derived from the cross between *Ae. tauschii* 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

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Table 1 Species from the *Poaceae* family, which were successfully crossed with hexaploid wheat

Species	2*n*	References
Aegilops biuncialis	48	Knobloch (1968)
Aegilops caudata	14	Knobloch (1968)
Aegilops columnaris	28	Kimber and Abubakar (1979)
Aegilops comosa	14	Kimber and Abubakar (1979)
Aegilops crassa	28	Jovkova *et al*. (1977)
Aegilops cylindrica	28	Kimber and Abubakar (1979)
Aegilops dichasians = *Triticum dichasians?*	14	Kimber and Abubakar (1979)
Aegilops juvenalis	42	Kimber and Abubakar (1979)
Aegilops kotschyi	28	Knobloch (1968)
Aegilops longissima	14	Kimber and Abubakar (1979)
Aegilops mutica	14	Knobloch (1968)
Aegilops ovata	28	Kimber and Abubakar (1979)
Aegilops speltoides	14	Chueca *et al*. (1977)
Aegilops squarrosa	14	Kimber and Abubakar (1979)
Aegilops triaristata	42	Kimber and Abubakar (1979)
Aegilops tripsaccoides	–	Kimber and Abubakar (1979)
Aegilops triuncialis	28	Kimber and Abubakar (1979)
Aegilops umbellulata	14	Kimber and Abubakar (1979)
Aegilops variabilis	28	Knobloch (1968)
Aegilops ventricosa	28	Kimber and Abubakar (1979)
Agropyron ciliare	28	Sharma and Gill (1981a)
Agropyron cristatum	28	Chen *et al*. (1989)
Agropyron cristatum (L.)	14	Limin and Fowler (1990)
Agropyron desertorum	28	Limin and Fowler (1990)
Agropyron desertorum (Fisch. ex Link) Schult.	28	Chen *et al*. (1990); Limin and Fowler (1990)
Agropyron distichum	28	Pienaar (1981)
Agropyron elongatum	14	Franke *et al*. (1992)
Agropyron intermedium	42	Sharma and Gill (1983)
Agropyron michnoi Roshev.	28	Chen *et al*. (1990); Li and Dong (1991)
Agropyron podperae	–	Dewey (1981)
Agropyron scirpeum	–	Sharma and Gill (1981b)
Agropyron trachycaulum	28	Sharma and Gill (1981b)
Elymus altissimus	28	Lu and von Bothmer (1991)
Elymus anthosachnoides	28	Lu and von Bothmer (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 Bothmer (1991)
Elymus dahuricus	42	Mujeeb-Kazi and Bernard (1982); Yen and Liu (1987)
Elymus dolichaterus	28	Lu and von Bothmer (1991)
Elymus fibrosus	28	Mujeeb-Kazi and Bernard (1982)
Elymus giganteus	28	Mujeeb-Kazi and Rodriguez (1981)
Elymus parviglumis	28	Lu and von Bothmer (1991)
Elymus pendulinus	28	Lu and von Bothmer (1991)
Elymus pseudonutans	28	Lu and von Bothmer (1991)
Elymus rectisetus	42	Liu *et al*. (1994)
Elymus scabrus	42	Ahmad and Comeau (1991)
Elymus semicostatus	28	Lu and von Bothmer (1991)
Elymus shandongensis	28	Lu and von Bothmer (1991)
Elymus tibeticus	28	Lu and von Bothmer (1991)
Elymus tibeticus	28	Lu and von Bothmer (1991)
Elymus tshimganicus	42	Lu and von Bothmer (1991)
Elytrigia acatum	42	Mujeeb-Kazi *et al*. (1984, 1987)
Elytrigia campestre	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)
Haynaldia villosa	14	Knobloch (1968)
Hordeum bulbosum	28	Falk and Kasha (1981)
Hordeum bulbosum	14	Falk and Kasha (1981)
Hordeum californicum	14	Gupta and Fedak (1985)
Hordeum chilense	14	Martin and Chapman (1977)
Hordeum claifornicum	14	Gupta and Fedak (1985)
Hordeum depressum	28	Jiang and Liu (1987)
Hordeum geniculatum	28	Pershina *et al*. (1988)
Hordeum jubatum	28	Comeau *et al*. (1988)
Hordeum marinum	14	Jiang and Liu (1987)
Hordeum pusillum	14	Finch and Bennett (1980)
Hordeum spontaneum	14	Bates *et al*. (1976)
Hordeum vulgare	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 triticoides	28	Mujeeb-Kazi *et al*. (1984, 1989)
Psathyrostachys juncea	14	Plourde *et al*. (1990)
Pseudoroegneria geniculata subsp. scythica	28	Mujeeb-Kazi *et al*. (1984, 1987)
Pseudoroegneria stipifolia	28	Mujeeb-Kazi *et al*. (1984, 1987)
Pseudoroegneria strigosa	28	Mujeeb-Kazi *et al*. (1987)
Secale africanum	14	Knobloch (1968)
Secale ancestrale	14	Knobloch (1968)
Secale cereale	14	Backhouse (1916); Knobloch (1968)
Secale montanum	14	Knobloch (1968)
Secale vavilovii	14	Knobloch (1968)
Thinopyron curvifolium	28	Mujeeb-Kazi *et al*. (1984, 1987)
Thinopyron gentryi	42	Mujeeb-Kazi *et al*. (1984, 1987)
Thinopyron junceiforme	28	Mujeeb-Kazi *et al*. (1984, 1989)
Thinopyron junceum	42	Charpentier *et al*. (1986); Mujeeb-Kazi *et al*. (1984, 1989)
Thinopyron sartorii	28	Mujeeb-Kazi *et al*. (1984, 1987)
Thinopyrum bessarabicum	14	Sharma and Gill (1983)
Thinopyrum ponticum	70	Smith (1942)
Thinopyrum pulcherrimum	42	Mujeeb-Kazi *et al*. (1989)
Thinopyrum rechingeri(Th. sartori)	28	Mujeeb-Kazi *et al*. (1987)

chromosome 1R (1RS). There are only four sources corresponding to this translocation (Zarco-Hernandez *et al*., 2005; Zhao *et al*., 2012): two developed in Germany by Salzmunder and Wiehenstephan 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 resistance (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

Table 2 *Triticum aestivum* genetics gene pools groups

	Species	Ploidy	Genome
Gene pools	*Triticum aestivum*	hexaploid	AABBDD
Primary gene pool	*Aegilops tauschii*	diploid	DD
	Hordeum spontaneum	diploid	HH
	Secale vavilovii	diploid	RR
	Secale montanum	diploid	RR
	Triticum turgidum	tetraploid	AABB
	Triticum diccocoides	tetraploid	AABB
	Triticum dicoccum	tetraploid	AABB
	Triticum monococcum	diploid	AA
	Triticum boeoticum	diploid	AA
	Triticum urartu	diploid	AA
	Triticum spelta	hexaploid	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 bogdanii	diploid	HH
	Thinopyrum	diploid	EE
	Secale	diploid	RR

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 F_1 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 (homoeologous) 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 improvement 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, 1971; Mello-Sampayo and Canas, 1973; 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 synapsis (*i.e.* intimate connection of chromosome axes along their lengths via the synaptonemal complex), whereas most nuclei complete synapsis 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 (Worland *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.

Interestingly, genes suppressing the repressor effect of *Ph1* and, on the contrary, promoting homoeologous chromosome

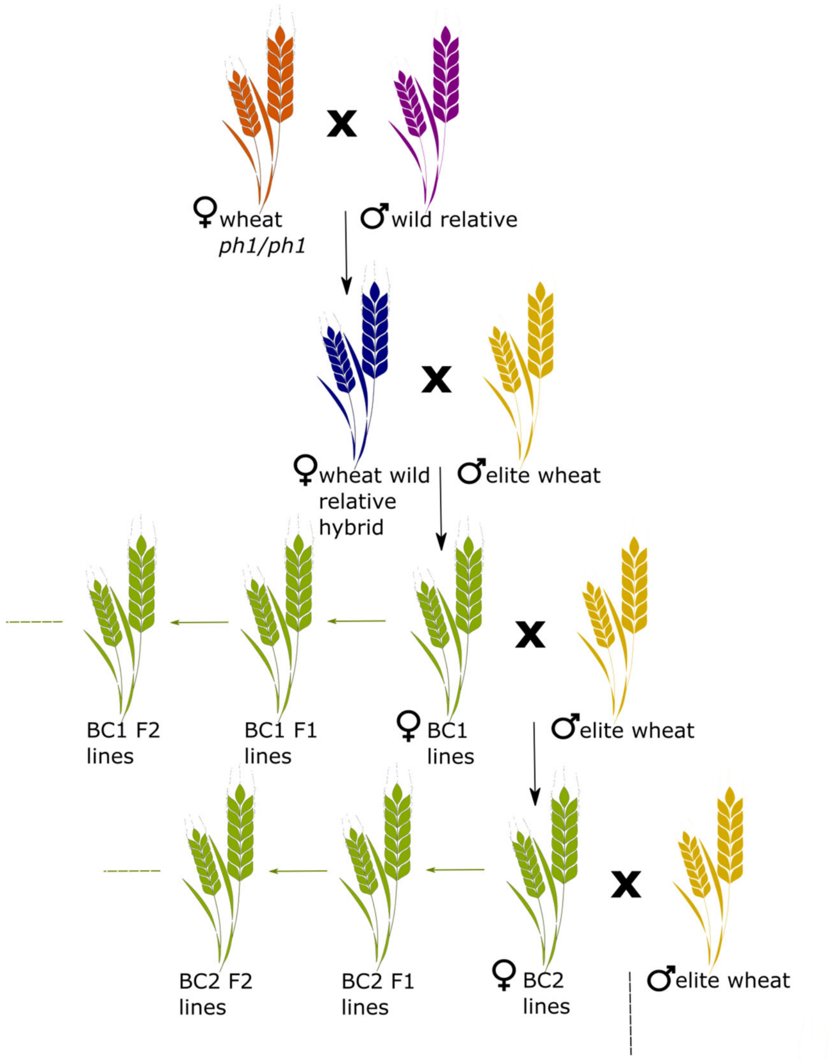

Figure 3 Overview of the approach using *ph1* mutant to introgress relevant DNA fragments from wild species in the wheat genome of elite lines. A primary cross is made between the *ph1* mutant and the wild species to generate a hybrid. This plant is grown until flowering and homoeologous recombination 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).

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 *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 *Aegilops* accession is low, the *Ph1* locus is only slightly inactivated and only a few rod bivalents were found in the hybrids between *Aegilops* and wheat (Fernandez-Calvin and Orellana, 1992). On the contrary, if the level of pairing of the *Aegilops* accession is super-high, the *Ph1* locus is strongly inactivated and even some hexavalents were observed in hybrid plants (Fernandez-Calvin and Orellana, 1992). The most studied loci are *Su-Ph1,* derived from *Ae. speltoides* (Dvorak *et al*., 2006; Li *et al*., 2017), and chromosome 5Mg of *Ae. geniculata* Roth (Koo *et al*., 2017, 2020); neither of these have been cloned. There are two different loci for *Su-Ph1,* which map to *Ae. speltoides* chromosome arms 3SL (*Su1-Ph1*) and 7SL (*Su2-Ph1*) (Dvorak *et al*., 2006). *Su1-Ph1* was successfully introduced into the hexaploid cultivar Chinese Spring and from there into the tetraploid durum wheat cv. Langdon. The *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 *TaZip4-1*, the paralogue of *TaZip4-B2* corresponding to *Ph1* on chromosome 5B (Rey *et al*., 2017), the authors suggest that *TaZip4-1* does not correspond to

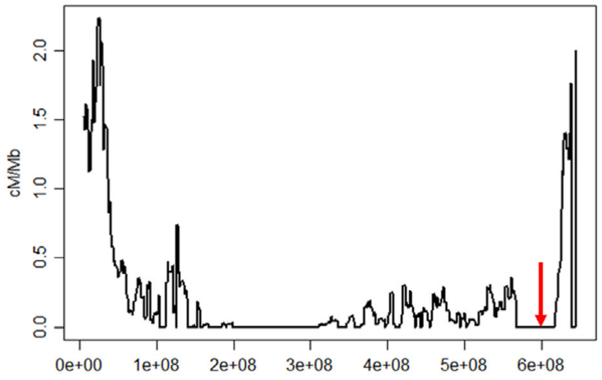

Figure 4 Distribution of recombination events along chromosome 2D in the Chinese Spring x Renan RIL population. The lack of recombination in the distal part of the long arm (red arrow) is due to a ~40-Mb introgression in the Renan genome likely originating from *Aegilops ventricosa*.

Su1-Ph1 (Li *et al*., 2017). Regarding *Ae. geniculata*, a potent homoeologous pairing promotor locus (Hpp) was identified on chromosome 5Mg, and this chromosome recombined with chromosomes from homoeologous 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 T7BS.7S#3L; (Danilova *et al*., 2017)) carrying the wheat streak mosaic virus resistance gene, *Wsm3*. Homoeologous 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. Introgressions 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 S_1S_2 plant will give rise to 50% S_1 and 50% S_2 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 rhoes*.

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

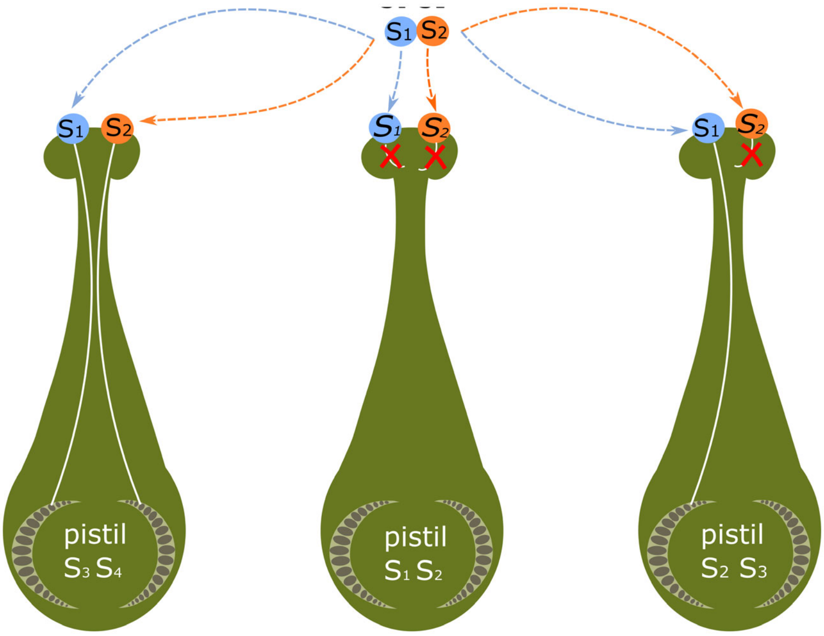

Figure 5 Genetic control of gametophytic SI (GSI). In GSI, the pollen SI phenotype is gametophytically controlled. Thus, half the pollen from an S1S2 plant is phenotypically S1 and the other half is S2. Pollen inhibition occurs on a 'like-matches-like' basis. When there is a match between the pollen S-haplotype and either of two haplotypes present in the pistil, an incompatible reaction results and inhibition of that 'self' pollen occurs. This results in three classes of reaction: incompatible (all pollen is inhibited), half-compatible (50% inhibited) or compatible (pollens not inhibited). Adapted from McClure and Franklin-Tong (2006).

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 Iezzoni, 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 *Maleae* 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 es are 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 (PrsS), a ~ 14 kDa secreted protein, interacting with the pollen S-determinant (PrpS), a ~ 20 kDa transmembrane protein, inducing a Ca2+-dependant 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-incompatiblity (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

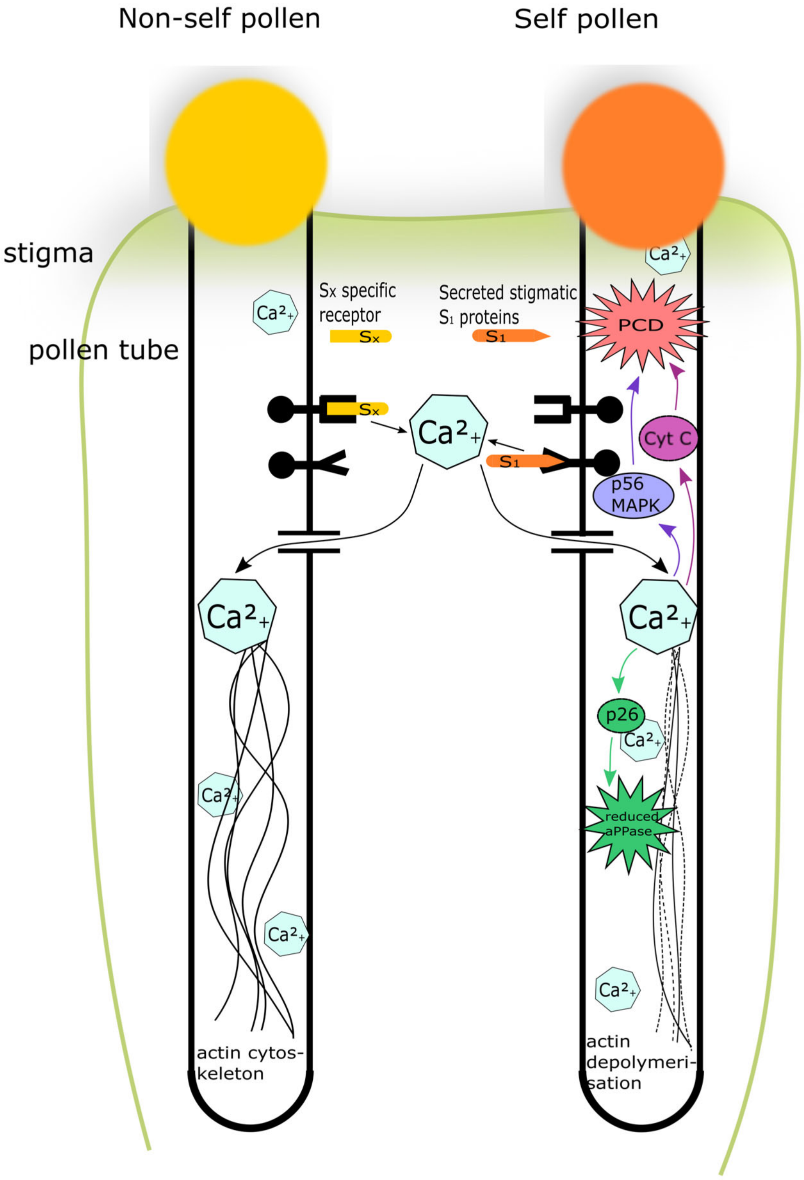

Figure 6 Model of the cellular mechanisms involved in gametophytic self-incompatibility (GSI) in poppy (*Papaver rhoeas*). In an incompatible reaction, the pistil S1 protein binds to the pollen S1 receptor triggering an intracellular change in calcium concentration. This causes the rapid modification of two targets: Pr-p26 shows an increase in phosphorylation leading to inhibition of its sPPase activity, and the actin cytoskeleton is reorganised and depolymerized. Both are predicted to cause rapid arrest of tip growth. Following this growth arrest, p56-MAPK is activated and emits a signal to the PCD. PCD is linked to cytochrome C caspase activity and DNA fragmentation. This ensure that incompatible pollen do no start growing again. Adapted from McClure and Franklin-Tong (2006).

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 *SRK* leading to autophosphorylation of its intracellular kinase domain (Kachroo *et al*., 2001; Takayama *et al*., 2001)). 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 proposed that degradation of this subunit may lead to disruption of vesicular secretion, which is necessary for compatible pollen

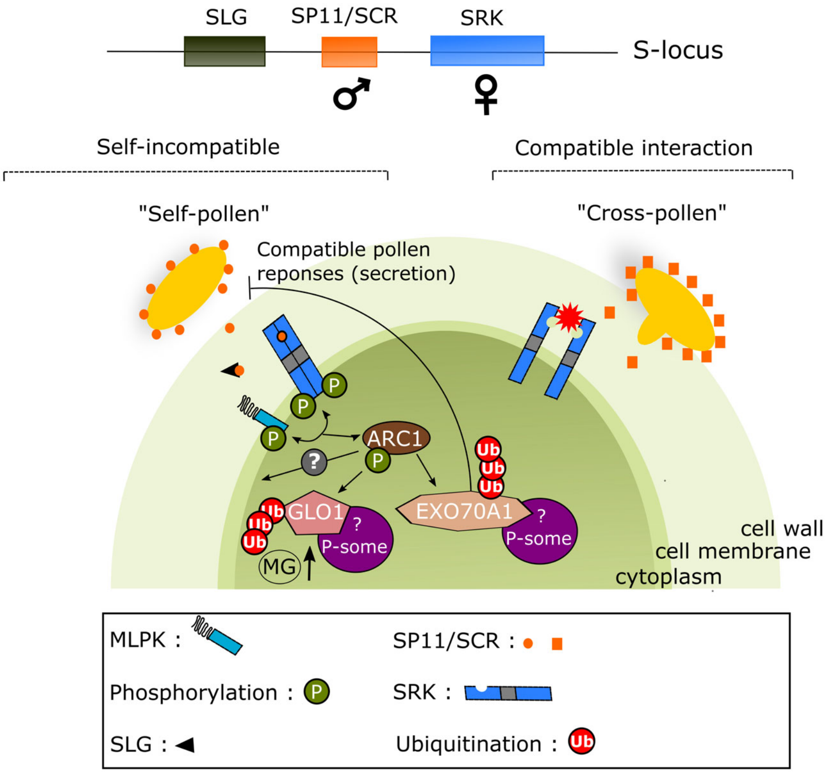

Figure 7 Molecular model of the self-incompatibility (SI) response in the *Brassicaceae*. The S-locus consists of three genes, *SRK*, *SP11* and *SLG*. The SRK receptor kinase (in blue) is the female factor and covers the plasma membrane of the stigma papilla cell. SP11 (in red) is the male component 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 GL01. 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)).

hydration and tube penetration [reviewed in (Goring, 2018)]. *GLO1* degradation could result in an increase in methylglyoxal levels in the stigma, which would have a cytotoxic effect (Jany *et al*., 2019).

Self-incompatibility in Poaceae

SI is widespread among the grasses with self-incompatibile 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 $S_1S_2Z_1Z_2$ as the female recipient and $S_1S_1Z_1Z_2$ as the pollen donor is incompatible (pollen genotypes: either S_1Z_1 or S_1Z_2), 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*., 1980). The Z-locus co-segregated with the beta-glucosidase and esterase 4/11 isozymes located on chromosome 2R in rye (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 Wehling, 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 *LpSDUF247* gene being the pollen S-determinant, including allelic 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.

Table 3 *Poaceae* subfamilies and tribes with example of self-compatibility (SC) and self-incompatibility (SI) species. Clade BOP represent *Bambusoideae*, *Oryzoideae*, *Pooideae* families and clade PACMAD represent *Panicoideae*, *Aristidoideae*, *Chloridoideae*, *Micrairoideae* and *Danthonioideae* families. No information for the following subfamilies *Aristidoideae*, *Micrairoideae* and tribes *Olyreae*, *Aristideae*, *Micraireae*, *Eriachneae* and *Hubbardieae* [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	Arundinarieae	*Arundinaria simonii*	Yes
		Bambuseae	*Dendrocalamus sinicus*	No
	Oryzoideae	Oryzeae	*Oryza barthii*	Yes
			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 intermedium	Yes
			Triticum aestivum	No
PACMAD	Panicoideae	Andropogoneae	*Miscanthus sinensis*	Yes
			Sorghastrum nutans	Yes
			Themeda australis	No
			Zea mays	No
		Paniceae	*Panicum virgatum*	Yes
	Chloridoideae	Cynodonteae	*Chloris gayana*	Yes
			Chloris striate	No
			Cynodon dactylon	Yes
			Oryza sativa	No
	Arundinoideae	Molinieae	*Molinia caerulea*	Yes
	Danthonioideae	Danthonieae	*Danthonia linkii*	No

Interspecific crossability in wheat

Obtaining F_1 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

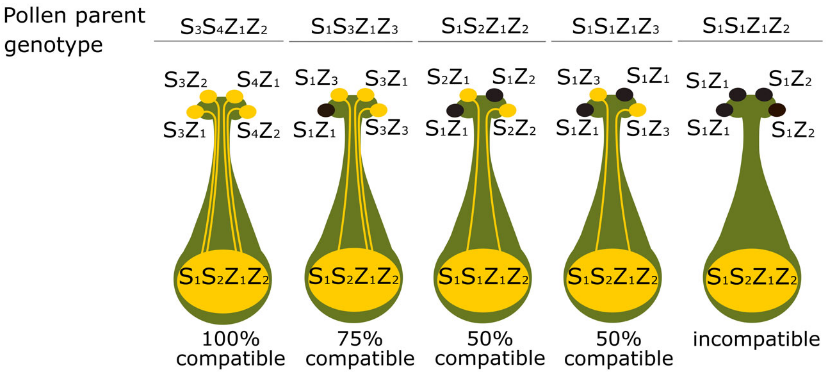

Figure 8 Genetic control of gametophytic self-incompatibility (GSI) by two multiple-allelic loci S and Z. When both pollen S and Z alleles are matched in the pistil, incompatibility occurs and pollen growth is inhibited. Adapted from Yang *et al*. (2008).

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; 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 geminated 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 micropyle, 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 x 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 micropyle. 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 micropyles 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 fecundation 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

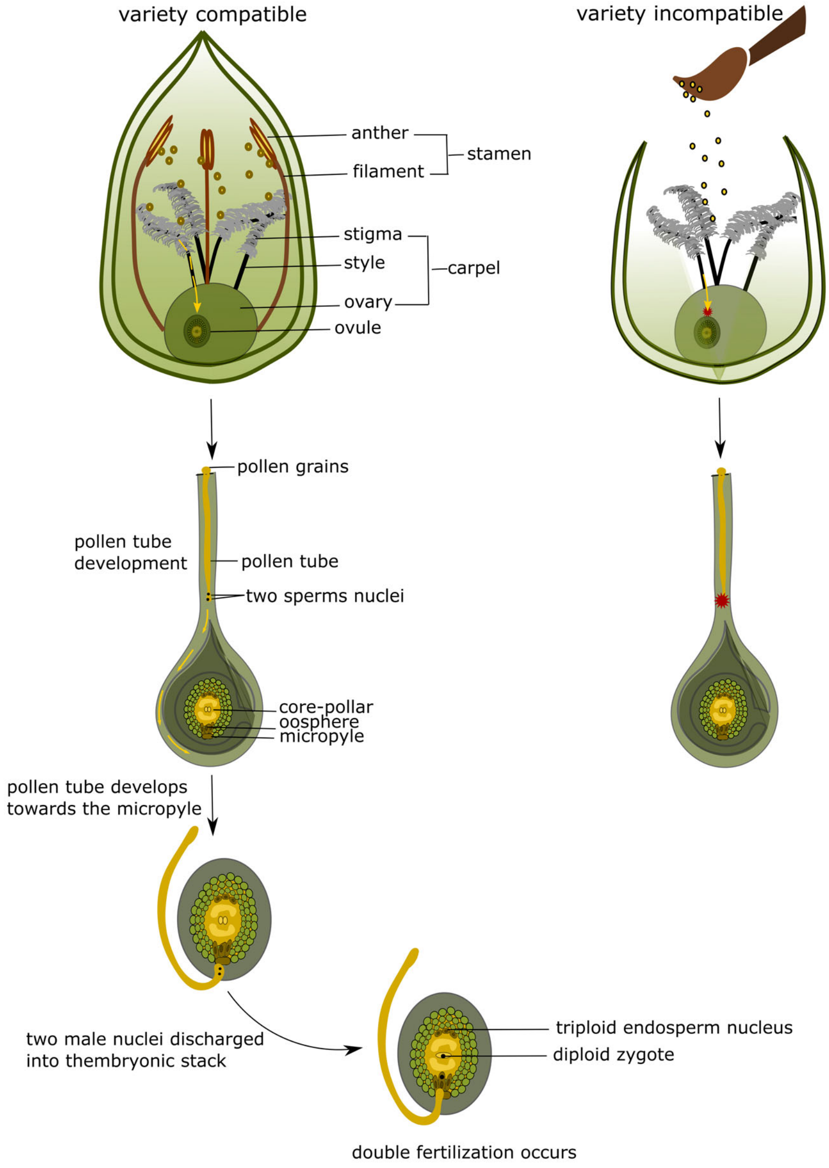

Figure 9 Schematic representation of pollen tube development and fertilisation in wheat, after selfing and after manual cross-pollination with pollen from an incompatible species. Prior to cross-pollination, the recipient plant needs to be emasculated.

crossable variety Chinese Spring in which each pair of homoeologous chromosomes was replace 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 rather favour 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 hypothesised 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 ≤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 ≥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 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 *Kr1* gene on chromosome arm 5BL. 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-5BL,7BL) (Miura *et al*., 1992). The aim of this cross is to develop additional F1 heterozygotes with segmental recombination on 5BL 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 locating on the long arm of chromosome 5B and including *Kr1*, 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 (*Kr1*), 5A (*Kr2*) and 5D (*Kr3*) 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 *Kr1* and *Kr2* on the long arms of chromosomes 5B and 5A respectively (Falk and Kasha, 1983; Fedak and Jui, 2011; Sitch *et al*., 1985). Finally, the tiny effect of *Kr3* on chromosome 5D (Krolow, 1970) was confirmed, but this gene weakly affects either wheat/rye or wheat/*H. bulbosum* crossability (Falk and Kasha, 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 *Kr4* on chromosome 1A. This gene had a stronger effect than *Kr2* but a lower effect compared to *Kr1* (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 *Kr1* 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 (CsCt; 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 *Xwg583-5B*. 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 *Kr1,* 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 CsCt 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 CsCt 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

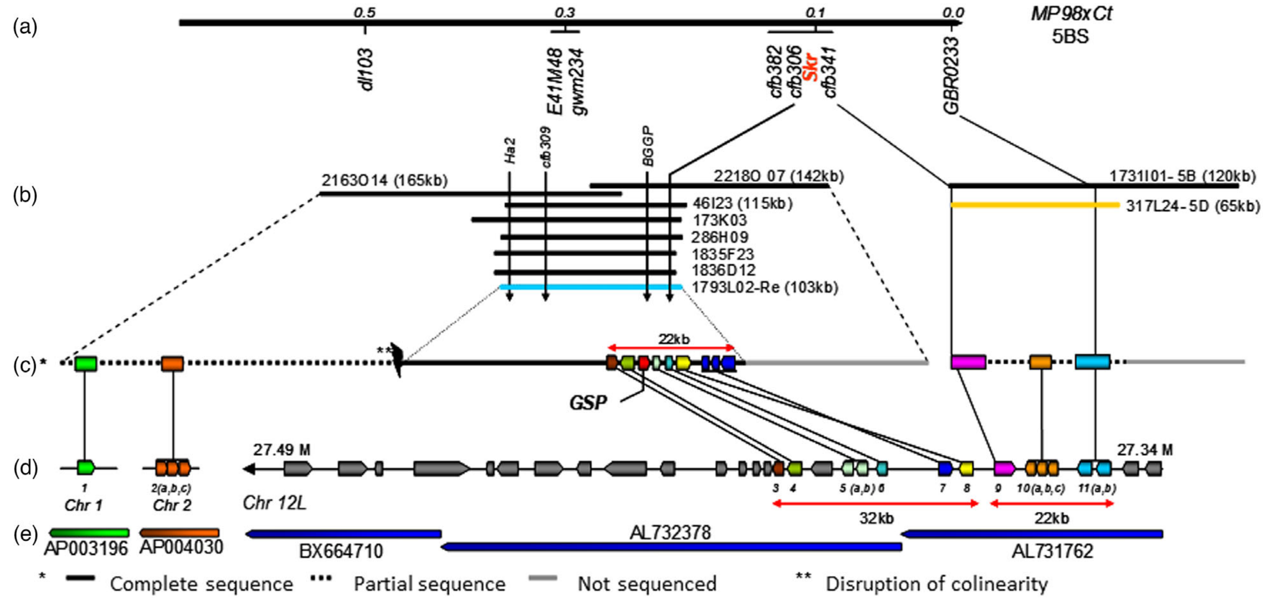

Figure 10 Extended genetic and physical maps at the *SKr* locus and syntenic relationships with rice. (a) Genetic map of the *SKr* locus on wheat chromosome arm 5BS. (b) Physical map at the *SKr* locus on wheat chromosome 5BS. (c) Detailed representation of the BAC clones identified at the 5B homoeologous 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).

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 5B-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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occur leading to natural polyploid 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 (Preece *et al*., 2017; Weiss *et al*., 2012). There are thus no genetic 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 maker-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

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

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