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Interspecific hybridization and plant breeding: From historical retrospective through work of Mendel to current crops

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Abstract: There is a relatively long history of plant hybridization traced back to ancient time, both from theoretical as well as practical perspectives. At first considered as an evolutionary dead-end, it was soon recognized to have important role in plant speciation. Beside his work on pea, G.J. Mendel also conducted interspecific hybridization using several species including *Hieracium*. Current knowledge shows that the frequent occurrence of wide hybridization in nature is often connected with polyploidy. Interspecific hybridization has played a role in plant domestication and numerous crops are allopolyploids, sometimes of complex hybrid origin. This has been also used in practical breeding, extending even to intergeneric crosses which benefit from heterosis, transgressive segregation and introgression phenomenon. This review aims to provide a a historical retrospective and summarize both current knowledge and the usage of interspecific hybridization in crop breeding.

Keywords: allopolyploid; breeding; crop; domestication; heterosis; hybridization; interspecific hybrids

Historical retrospective on plant hybridization

The history of plant hybridization is related to the identification of male and female components of the flower. The earliest historical evidence regarding artificial pollination is found in Akkadian Code of Hammurabi (18 century B.C.) where specific terms for the inflorescences of the female and male date trees and for fertilization were used. The artistic depiction of artificial pollination appears first in the 9th century B.C. in Aramaic relief from Tell Halaf in northeastern Syria, depicting a man climbing a date palm, apparently to fertilize the female tree by applying the male inflorescences to the flowers.

The first written records on the structure and function of plant flowers and their relation to the fruits is given by THEOPHRASTUS (c. 371–287 B.C.) in *Historia plantarum* and *De causis plantarum*. He described the practice of artificial pollination of the female date tree by the inflorescence of the male, and compared it to the sexual process among fish. In his work, Theophrastus used the terms 'male' and 'female' in the modem sense (Negbi 1995).

During the Middle Ages, there was no novelty in view of plant hybridization until ALONSO DE HERRERA published the first modern treatise on agriculture in his *Obra de Agricultura* (1513; '*Treatise on Agriculture*'). This thesis showed that many current breeding methods had already been developed at that time. He refered to the Roman agronomists, Virgilius, Varro, Plinius and Columella in particular. Moreover, Herrera provided recommendations

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about the seeds to be used for sowing cereals. For example, he recommended taking the grains from the bottom of the spike, which is similar to current bulk selection methods. He assumed that they will perform better due to their heavier weight. He also recognized the influence of environment in stating that '*no good crops are to be expected from poor seed unless favoured by good growing conditions;*' and the importance of specific adaptation when he wrote that the seed has to be harvested from similar conditions to those where seed was to be grown '*from hot to hot, from cold to cold, from dry to dry, from mild to mild, from humid to humid, ...*'.

The advent of the modern history of plant hybridization can be dated back to the work of Rudolph Jacob Camerarius. He contributed particularly to the investigation of sexual differentiation in plants by identifying and defining the male (anther) and female (pistil) reproductive parts of the plant and also by describing their function in fertilization, showingthat pollen is required for this process (*De sexu plantarum*, 1694; 'On the sex of plants'), and in *Opuscula botanica* (1697; 'Botanical Works'). Although it is Camerarius, who is most commonly considered the first author to describe plant sexuality, it was actually Adam Zalužanský ze Zalužan who defined male, female and bisexual plant individuals (dioecious and monoecious plants) for the first time in the pioneering chapter '*De Sexu Plantarum*' of his book *Methodus Herbaria, Libri Tres* from 1592. He also stressed that the individuals of both sexes formed the same species and should not be classified as different taxa or varieties (Funk 2013).

The first written reference on spontaneous plant hybridization was by Cotton Mather in 1716, describing crosses between Indian and yellow corn, and between gourds and squash (Zirkle 1934). In the same year, Thomas Fairchild reported the first artificial hybrid from a cross between carnation (*Dianthus caryophyllus*) and sweet William (*Dianthus barbatus*) (reviewed in Roberts 1929). Contrary to common belief, Fairchild was distraught by his success because he regarded all plant species as created by God at the time of Creation. He thus feared the consequences of disturbing this natural order, as many others also thought in his time. Therefore, his work is largely unknown and many authors ascribe the first artificial hybrid to C. Linnaeus experiments on *Tragopogon* in 1759 (reviewed in Roberts 1929). It was in his *Plantae Hybridae* (1753), where he initiated the discussion about the role of hybridization in plant speciation and provided examples of 17 bigeneric (intergeneric) crosses and 17 congeneric (interspecific) crosses. Antoine Nicolas Duchesne (1766), while working with a strawberry collection, documented the separation of sexes in wild strawberry and identified the garden strawberry (*Fragaria* × *ananassa*) (Darrow 1966), demonstrating that species can change.

The 1849 work of Carl Friedrich Gärtner, *Versuche und Beobachtungen über die Bastarderzeugung im Pflanzenreich* (The Production of Hybrids in the Plant Kingdom), contained a summary and discussion on the knowledge about plant hybridization (Gärtner 1849). Gärtner himself noted both the uniformity of the first hybrid generation and the diversity of the forms in the second and successive generations. He stated that both parental types and entirely new ones reappeared in these later generations and that the variability was found in all of the characteristics of the progeny. A few years later in 1863, Charles Naudin contrasted the uniformity of the first hybrid generation with '*the extreme medley of forms*' in the second generation, '*with some approaching the specific type of the father, others that of the mother*' (Harvey 2003). The first scientific reports targeting exclusively plant hybridization were the publications of Joseph Gottlieb Kölreuter about hybridization experiments (*Vorlaufige Nachricht von einigen das Geschlecht der Pflanzen betreffenden Versuchen und Beobachtungen* (1761), *Fortsetzung* (1763), *Zweyte Fortsetzung* (1764), and *Dritte Fortsetzung* (1766). Kölreuter demonstrated that hybrids from interspecific crosses are often sterile. As a result, he concluded that hybrid plants are produced only with difficulty and are unlikely to occur in nature without human intervention or disturbance of the habitat. He also showed that F_1 hybrids are usually morphologically intermediate relative to their parents and that successive generations tend to revert back to the parental forms (Mayr 1986). This discovery refuted an earlier suggestion by Linnaeus that hybrids were constant or true-breeding and represented new species. The character of hybrids had been explained from the viewpoint of taxonomy and fertility, a practice common among the botanists of that time (in Roberts 1929). Kölreuter made over 500 crosses involving 138 species such as *Nicotiana, Dianthus*, *Matthiola*, *Hyoscyamus* and *Verbascum*. Although he often found sterility, there were cases of fertile hybrids displaying heterosis (hybrid vigour) not only in vegetative growth, but also in number and size of flowers. By making reciprocal crosses

Kölreuter disproved the ancient theory of the different contributions of male and female parents. Due to his interest in flower structure and pollination, he examined the shape, size and color of the pollen grains from over 1 000 species. Kölreuter's attention to detail was remarkable. For example, he counted 3 154 flowers in *Verbascum* hybrids, and 4 863 pollen grains in a single *Hibiscus* flower and subsequently tested how many are needed for fertilization. Possibly this inspired Mendel in his work. In contrast to his progressiveness in experimentation, Kölreuter was rather conservative in his conceptual framework. He complied to common beliefs in a created and well-designed world. As a consequence, he admired sterility of hybrids, which supported view on sharply separated species in the world. In his view, if the hybrids were fertile and frequent, then there would be confusion and disorder in nature. A second major concept which shaped Kölreuter's thinking was the assumption that laws in biology are the same as in chemistry and physics. He viewed fertilization, the mixing of male and female gametes, as chemical process resulting in traits blending. Together with essentialism this influenced his theory of inheritance. Kölreuter insisted that essences are uniform, and the material of the two parents is blended into intermediate state after hybridization. Hybrids should be therefore exactly intermediate between parents. Thus, the observed exceptions puzzled him. He explained them as a result of irregular or incomplete blending. However, he was fair in admitting that the results of his experiments conflicted his fundamental beliefs (Mayr 1986). The dominating opinion during his time was that an offspring was already pre-formed in the female or the male and that the embryo was developed after sex and the origin predetermines the offspring's characteristics or similarities to the parent (Bentley 1960).

Kölreuter found that in general, only closely related plants, and not always even these, can be crossed. He concluded that the continued self-pollination of hybrids finally results in the re-appearance of the original parental forms. Similarly to Mendel, Kölreuter's work has been neglected but not forgotten. One reason for the relative neglect of his work is the unfortunate manner in which he published his results, as his publications consist of preliminary progress reports and different aspects of the same cross (F_1, reciprocal F_1, F_2, backcrosses) were often reported in entirely different sections.

There were several scientists, who were Mendel's contemporaries, conducting hybridization experiments, often aiming for practical outcomes. For example, R. Geshwind applied hybridization to forest trees as well as to breeding roses. Actually, in his first experiments that date to 1845, prior to work of Mendel on pea, he obtained hybrids of *Pyrus* and *Sorbus* trees (in Roberts 1929). He noticed that not only new varieties, but also new species can occur among offspring upon self-pollination.

Mendel's interest on species evolution (speciation)

Gärtner's and Kölreuter's work very likely influenced Mendel's experimental set up as well as his scientific work. Fortunately, he decided not to recapitulate the experiments, but applied the knowledge to intraspecific crosses with pea, likely inspired by previous results of Thomas A. Knight (1799). We know that after *Pisum* (Mendel 1866), Mendel investigated many other species from the genera *Aquilegia*, *Antirrhinum*, *Calceolaria*, *Campanula*, *Cheiranthus*, *Cirsium*, *Dianthus*, *Geum*, *Hieracium*, *Ipomoea*, *Linaria*, *Lychnis*, *Matthiola*, *Mirabilis*, *Phaseolus*, *Tropaeoleum*, *Verbascum* and *Zea* (Cetl 1973). By far, the largest number of experiments was conducted in *Hieracium* (Mendel 1870), which have been often interpreted as failure. Recently, van Dijk and Ellis (2016) have shown that the assumption of Mendel's studies on *Hieracium* arised from a misunderstanding that could be explained by a missing page in Mendel's first letter to Carl Nägeli. Mendel's writings clearly indicated his interest in '*constant hybrids*', hybrids which do not segregate and which were '*essentially different*' from '*variable hybrids*' such as those in *Pisum*. Thus, it is argued that Mendel's main motivation for the *Hieracium* experiments was his interest in hybridization and speciation, rather than the inheritance of traits. Notably, even before the publication of Darwin's 'Origin of Species' in 1859, C. Nägeli accepted that species were not constant, but could evolve (cited in Junker 2011). Nägeli was an expert in the genus *Hieracium*, which seemed to be particularly suitable for studies on speciation. It is a highly polymorphic genus consisting of many distinct and easily recognizable species connected by a continuum of intermediate forms. In contrast to others, Nägeli did not deny evolutionary role of hybridization, especially in the early steps of speciation (van Dijk & Ellis 2016).

Therefore, Mendel used different titles for his work with pea (*hybriden*) and *Hieracium* (*bastarden*).

Similarly, Bronn's translation of *Darwin's Origin* (in Junker 1991), used the word '*Bastard*' for hybrids formed from different species ('*hybrid*' in Darwin) and the word '*Blendlinge*' for hybrids from different varieties of the same species ('*mongrel*' in Darwin), which is identical to '*Mischlinge*' by Focke (1881). On the other hand, word '*hybriden*' originates from Latin '*hybrida*', used for '*offspring of a tame sow and a wild boar*', or more generally for '*anything a product of two heterogeneous things*'.

Occurrence of interspecific hybrids in nature

Modern evolutionary studies of hybridization were laid down by three key discoveries. The first discovery by Winge (1917, 1932) showed that genetically stable and fertile hybrid species could be derived instantaneously by the duplication of a hybrid's chromosome complement (i.e. allopolyploidy). This hypothesis was soon confirmed experimentally (Dorsey 1936; Sax 1936), and allopolyploidy is now recognized as a prominent mechanism of speciation in flowering plants and ferns (Stebbins 1959; Soltis & Soltis 2009). A second important discovery resulted from the work of Müntzing (1930) on homoploid hybridization. He postulated that the sorting of chromosomal rearrangements in successive generations of hybrids could, by chance, lead to the formation of new population systems that are homozygous for a unique combination of chromosomal sterility factors. Thus, the new hybrid population would be fertile, stable, and at the same ploidy level as its parents, yet at least partially reproductively isolated from both parental species. Müntzing (1936) also showed that polyploids were generally more vigorous and hardier. The importance of hybridization in plant speciation and evolution received opposing views of being either a creative evolutionary force or an evolutionary dead-end.

Natural hybridization can be defined as an interbreeding of individuals from two distinct populations, and individuals in those populations must be distinguishable on the basis of one or more heritable characters. Both homoploid and allopolyploid hybrid speciation involve the formation of novel genetic combination, which may lead to the novel adaptations that allow persistence of the hybrid lineage, often in an environment distinct from that of either parent and is recognized as a common phenomenon in plants (Soltis & Soltis 2009; Abbott et al. 2013). For the first time, Linnaeus admitted that new species might arise by hybridization in *Disquisitio de sexu plantarum* (1760), and rejected the previous view of immutability. He stated that although hybridization is widespread, the generation of hybrid lineage and speciation via hybridization is rare. Nowadays, we know that new hybrid lineages must establish reproductive isolation in order to overcome genetic assimilation and competition with parental species (Winge 1917; Müntzing 1930). As mentioned above, hybrid lineage may be formed through allopolyploid or homoploid speciation. Allopolyploid hybrid speciation is more common (Soltis & Soltis 2009). A recent review found that 11% of species across 47 plant genera are of allopolyploid origin (Barker et al. 2016). It has long been observed that crossing two plant species or genotypes can create a hybrid with faster growth, more biomass or greater reproductive output than its parents (Jones 1917; East 1936). This phenomenon is called hybrid vigor or heterosis. Both Kölreuter (1766) and Darwin (1876) described the phenomenon of heterosis in their experimental crosses of plants. It was Shull's (1908, 1911) work on maize, that determined the genetic mechanism causing heterosis. Similar to heterosis, transgressive segregation occurs when phenotypic trait values in hybrid populations fall outside the range of parental variation. Transgressive segregation is distinct from heterosis because it is manifested predominantly in the F_2 and following generations and may persist indefinitely once established (Rieseberg & Carney 1998). Transgressive segregation demonstrates how hybridization can produce novel phenotypes, thus enable adaptation to new ecological niches and play a significant creative role in evolution. On the other hand, where there is no fertility barrier between hybrids and parents, there is potential for gene flow. Hybrids may backcross with either or both of the parents, resulting in alien introgression forms.

Interspecific hybridization and plant domestication

During the domestication process, several important crops have originated through interspecific hybridization accompanied by the whole genome duplication (Smýkal et al. 2018; Purruganan 2019). Molecular studies revealed the hybrid origin of a large number of domesticated crops, including wheat (Marcussen et al. 2014), tall fescue (Humphreys et al. 1995), cotton (Wendel & Crown 2003), banana (Heslop-Harrison & Schwarzacher 2007), oilseed rape (Lu et al. 2019), apple (Cornille et al. 2014), date palm (Flowers et al. 2019) and several citrus fruit species (Wu et al. 2014). There is increasing evidence on the key role of interspecific hybridization in crop diversification and range expansion after domestication, possibly aiding the spread of domesticated species to new agricultural environments or adapting to new cultural preferences (Warschefsky et al. 2014; Janzen et al. 2018).

Various examples of interspecific hybridization between domesticated species and their wild relatives can be found among perennial fruit crops. Recent genomic study in date palm, *Phoenix dactylifera*, an iconic fruit species likely domesticated in the Middle East, revealed that this species hybridized with wild *Phoenix theophrasti* in the Eastern Mediterranean (Flowers et al. 2019). Similarly, modern apple originated in Central Asia from *Malus sieversii*, and as apples moved westwards, it hybridized consequently with Caucassian *M. pumilio* and thereafter with the European crabapple (*Malus sylvestris*) (Cornille et al. 2014).

Arguably, one of the most important results of interspecific hybridization is the origin of hexaploid bread wheat (*Triticum aestivum*). At first, there was hybridization between *T. urartu* (AA) as the male parent (Dvorák & Zhang 1990; Luo et al. 2010) and species relative to *Aegilops speltoides* (BB) leading to the domesticated tetraploid durum wheat *T. dicoccum* (BBAA). Subsequently, this tetraploid hybridized with diploid *Aegilops tauschii* (DD) to result in the formation of allohexaploid *T. aestivum* (BBAADD). This happened about 12–15 000 years ago within the corridor from Armenia to the southwestern coast of the Caspian Sea (Dvorak et al. 1998). Also cotton (*G. hirsutum* AD_1 and *G. barbadense* AD_2), one of the most important economic crops providing fiber, originated through interspecific hybridization. There is an evidence that *G. herbaceum* (A_1 genome) and *G. arboreum* (A_2 genome), both from Africa, provided A genomes, while *G. raimondii* from America provided D genome to allotetraploid cottons (Wendel & Crown 2003). Interestingly, allopolyploid cottons appear to have arisen within the last million years, as a consequence of transoceanic dispersal of the A genome taxa to the New World followed by hybridization with an indigenous diploid species with D genome. Subsequently, allopolyploids radiated into three modern lineages, including those containing the commercially important species *G. hirsutum* and *G. barbadense* (Wendel & Crown 2003).

Cultivated octoploid strawberry (*Fragaria* × *ananassa*) originated as an accidental hybrid in the collection of A. Duchesne back in late 18th century (Duchesne 1766). Recent genome sequencing identified that wild progenitors of North American *F. virginiana* and South American *F. chiloensis*, are also products of allopolyploid evolution (Edger et al. 2019).

The textbook example of interspecific hybridization is a 'U Triangle' (named after theory first published in 1935 by Woo Jang-choon, a Korean-Japanese botanist) of Brassicas. There are three diploid species, namely *B. rapa* (AA, $n = 10$), *B. nigra* (BB, $n = 8$) and *B. oleracea* (CC, $n = 9$), whose hybridizations lead to the origination of three allotetraploids, *B. juncea* (AABB, $n = 18$), *B. napus* (AACC, $n = 19$), and *B. carinata* (BBCC, $n = 17$). *B. napus* is thought to originate 7 500 years ago via at least two different hybridization events between *B. oleracea* and *B. rapa* (Lu et al. 2019).

(In)stability of hybrid genomes

In the plant kingdom, homoploid hybrids are rare (Yakimowski & Rieseberg 2014). This is probably caused by the problems in meiosis when chromosomes from different parental species frequently fail to pair with each other and random segregation of univalents produces non-functional gametes. Therefore, polyploidization (whole-genome doubling) of sterile diploid F_1 hybrids or production of unreduced gametes by the progenitors during initial cross, or in the hybrids itself, are usually necessary for fertility restoration.

Allopolyploids possess three or more chromosome sets from two or more species. Those originating from the same parent are called homologues, whereas those from different parents are called homoeologues. For the stability of the hybrid genomes in successive generations and the proper transmission of the parental chromosomes into gametes through meiosis, it is necessary to avoid the intermingling of homoeologous chromosomes. In theory, each chromosome in an allotetraploid can pair either with its homologue or with one of the two homoeologues. The ratio of homologous vs. homoeologous chromosome pairings should be 1 : 2. However, very few hybrids exhibit this ratio. This is caused either by sequence divergence avoiding initiation of chromosome pairing or by the presence of a molecular mechanism hampering the pairing of homoeologues. An example of such a system is *Ph1* (*Pairing homoeologous 1*) presented

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in polyploid wheats (Sears & Okamoto 1958). This locus has been mapped to the long arm of chromosome 5B in tetraploid and hexaploid wheats. However, even after sixty years of extensive research, the mode of action of *Ph1* is still not completely understood. The most recent study indicated that *Ph1* locus contains a cluster of defective cyclin-dependent kinases (CDKs) and S-adenosyl methionine-dependent methyltransferase genes and inserted paralog of the ZIP4 (Knight et al. 2010; Greer et al. 2012; Martin et al. 2014, 2017). It seems that *Ph1* is of general mode-of-action and is efficient at least in the close relatives of wheat. Once introgressed from wheat to the relative species, it has an ability to modify chromosome pairing of the host genome, such as in the case of 5B introgression in autotetraploid rye (Lukaszewski & Kopecky 2010). Besides *Ph1*, chromosome pairing control systems have been found also in *Brassica* allopolyploids (*PrBn*), oats, fescues, and many other allopolyploids (Jenczewski & Alix 2004; Kopecký et al. 2009). However, several studies indicate that strict homologous chromosome pairing during meiosis might not be enough for stabilization of the hybrid genome. It was evidenced earlier, that octoploid ×*Triticale* (amphiploids of bread wheat with rye) possessing *Ph1* reverts back to bread wheat (loss of the entire rye genome) during seed multiplication (Tsunewaki 1964). This elimination of rye chromosomes is caused by the reduced chromosome pairing of rye chromosomes leading to the formation of univalents and thus, improper transmission to the developing gametes. Similarly, the less frequent pairing of rye chromosomes compare to the wheat chromosomes was observed in disomic additions and substitutions of individual rye chromosomes in bread wheat and in tetraploid ×*Triticale* (Orellana et al. 1984; Lukaszewski & Gustafson 1987). The pairing of homologous chromosomes initiates from the telomeric regions of the chromosome arms in leptotene. Several studies suggest that chromosomes (by their telomeric ends) have to be attached to the nuclear envelope via LINC protein complexes. This ensures sliding of the chromosome on the inner surface of nuclear envelope to find its counterpart leading to the formation of leptotene (telomere) bouquet. Naranjo (2014) indicated that reduced pairing of rye chromosomes in wheat appears to be a consequence of disturbed migration of rye telomeres into the bouquet. Similarly, Murphy and Bass (2012) observed that the desynaptic mutant of maize displays multiple defects in telomere-nuclear envelope interactions, homologous chromosome synapsis, recombination and chromosome segregation. In wheat-rye introgression lines, the frequency of out-of-bouquet rye telomere positioning at leptotene was similar to the frequency of synapsis of the normal and inverted chromosome arms in a heterozygote for an inversion of a rye chromosome arm in wheat (Perníčková et al. 2019).

The establishment of the molecular mechanism of diploid-like pairing behaviour is probably not instant following hybridization. Some allopolyploids with a meiotic regulator, when resynthesized from putative progenitors, display disrupted meiosis with homoeologous chromosomes pairing, such as resynthesized *Brassica napus* (Gaeta & Pires 2010). Xiong et al. (2011) found increasing aneuploidy rate for ten successive generations of resynthesized *B. napus*. The authors also observed frequent homoeologous chromosome pairing and replacement of chromosomes of one parental species by the other (prevalence of C-genome). However, they identified two lines retaining the expected original chromosome constitution. Interestingly, these two lines had the highest seed yield, and thus, there is likely selection against chromosome aberrations with reduced fertility.

Homoeologous chromosome pairing opens a way for genome dominance

Despite the general feature of strict pairing of homologues in allopolyploids, there are several fertile hybrids displaying homoeologous chromosome pairing and recombination. One of such peculiar cases is a hybrid of cultivated bulb onion (*Allium cepa* L.) with its wild relative *A. roylei* Stearn. The chromosome pairing ability was exploited to develop introgression lines of cultivated onion with a chromosome segment from *A. roylei* carrying resistance to downy mildew (Kofoet et al. 1990). Another example of extensive pairing of homoeologues is hybrids of *Lolium* with *Festuca* (×*Festulolium*). On the one hand, homoeologous pairing can facilitate introgression of any segment from one species to another (Kopecký et al. 2010); on the other, it introduces huge variability and genomic instability to the progeny. It enables a shift in the genome composition in hybrid progeny. In *Allium cepa* × *A. roylei* hybrids, the *A. roylei* genome appears to predominate: the percentage of *roylei* alleles in the F_2 population was on average 56% vs. 44% of *cepa* alleles and the parental chromosome constitution shifted from 8*cepa* + 8*roylei* in F_1 generation to 6.7*cepa* + 9.3*roylei* in F_2 generation (van Heusden et al. 2000; Kopecký et al. 2022). Earlier studies observed chromosomal dominance in all cultivars selected from *Lolium multiflorum* × *Festuca pratensis* hybrids. These hybrids exhibit the prevalence of the *Lolium* chromosomes (Kopecky et al. 2006). Zwierzykowski et al. (2006, 2011) conducted a study over eight successive generations of such hybrids and observed a slow but consistent gradual replacement of the *Festuca* chromosomes by *Lolium* chromosomes. Similar genome dominance at the chromosome level has been observed in hybrids of *Alstroemeria aurea* × *A. inodora*, *Gasteria lutzii* × *Aloe aristata* and in various lily hybrids (Takahashi et al. 1997; Kamstra et al. 1999; Karlov et al. 1999; Khan et al. 2009).

It is evident that Mendel's law of equal segregation is often, if not always, violated in interspecific hybrids with homoeologous chromosome pairing. It was previously observed that some genes or chromosomes in animals and plants display a biased (greater) transmission at the expense of its homoeologue, a phenomenon known as meiotic drive (Henikoff et al. 2001; Pardo-Manuel De Villena & Sapienza 2001). Meiotic drivers may operate in several modes including the most known female meiotic drive. Female meiosis offers an opportunity to change the proportion of parental chromosomes. The products of the first female meiotic division are egg cell, which participates on fertilization, and polar body, whose genetic material is not transmitted further. This creates an opportunity to direct certain chromosomes preferentially to the egg cell and hence, to the next generation, and eliminates their counterparts. Recent research indicates that the female meiotic drive is the most probable explanation of the *Lolium*- and *A. roylei*- genome dominance (Kopecký et al. 2022). Female meiotic drive underlying subsequent substitution of one parental genome by the other has been only rarely reported in plant hybrids (Fishman & Saunders 2008). This is probably due to the fact, that a large majority of plant hybrids display strict homologous, but not homoeologous, pairing. The drive acts via preferential orientation of one of the two parental chromosomes toward one pole in meiotic divisions. Hence, meiotic pairing of homoeologues is a prerequisite for the female meiotic drive. In contrast to plants, examples showing meiotic drive as the key force of genome dominance have been reported in animals (Akera et al. 2017).

Use of interspecific hybrids in crop breeding

Hybridization of the plants from two distinct species has been used in plant breeding (Mason & Batley 2015) with various aims: (1) merging of entire genomes of parental species to widen the gene pools of one or the other parental species, (2) merging of parental species' genomes to combine their desirable traits (amphiploid forms), and (3) introgression of desirable trait(s) from one (frequently wild) species into elite cultivars of another species (introgression forms) (reviewed in Prohens et al. 2017).

Among amphiploid forms combining both complete parental genomes, ×*Triticale*, a hybrid of wheat (*Triticum*) and rye (*Secale cereale*, $2n = 2x = 14$, RR) is a one of the most successful synthetically developed hybrids. ×*Triticale* combines high yield inherited from wheat with the ability to grow in harsher conditions due to abiotic stress tolerance inherited from rye (Arseniuk 2015). The second approach, introgression breeding, involves interspecific mating followed by one or more rounds of backcrossing to the recipient parent. This proved to be an efficient way to transfer agronomically beneficial alleles from wild relatives to crops including resistance to pests and diseases, tolerance to abiotic stresses, and root-related traits (Anamthawat-Jónsson 2001; Scholten et al. 2007; Placido et al. 2013; Molnár-Láng 2015). Successful introgression has been demonstrated in wheat, where short arm of rye chromosome 1 (1RS) was introgressed into bread wheat to form 1RS.1BL chromosome. This originally brought several genes for resistance to pathogens and pests of wheat (Zeller 1973) and many currently sown bread wheat cultivarscarry such introgression (Lukaszewski 1990).

Following success in rye and wheat, there were attempts to obtain the hybrid between barley (*Hordeum vulgare*) and wheat (Kruse 1973). Unfortunately, the incompatibility of barley genome with other genomes from Triticeae hampered the success of this approach (Molnár-Lang et al. 2014). Testing of various *Hordeum* species has ultimately led to the successful amphiploid cross of *Hordeum chilense* ($2n = 2x = 14$, $H^{ch}H^{ch}$) and *Triticum turgidum* ($2n = 4x = 28$, BBAA) which resulted in ×*Tritordeum martini* Pujadas (Martín et al. 1999). Two cultivars obtained by backcrossing the amphiploid to wheat in order to change the cytoplasm from barley to wheat were released and ×*Tritordeum* is today commercialized with rheological and baking performances similar to bread wheat (Visioli et al. 2020; Nitride et al. 2022). Moreover, compared to wheat, it shows better tolerance to drought, a key trait in current breeding. Other hybrids were obtained in combinations $H^{ch}H^{ch}DD$, $H^{ch}H^{ch}RR$ and DDRR between *H. chilense*, *Aegilops tauschii* ($2n = 2x = 14$, DD) and *Secale cerele* ($2n = 2x = 14$, RR). $H^{ch}H^{ch}DD$, and DDRR are fertile, but $H^{ch}H^{ch}RR$ is sterile, although the phylogenetic distance is bigger between H and D genomes than between H and R genomes. Similarly, interspecific hybridization of wheat with *Thinopyrum ponticum* was used to develop wheat cultivars with blue aleurone. The presence of blue-aleurone layer in seeds is associated with high level of anthocyanins. Anthocyanins are compounds with great importance for human health due to their antioxidant, anti-inflammatory, antimicrobial and anti-carcinogenic potential. The major anthocyanidin of the blue-aleurone wheat is delphinidin-3-glucoside (Trojan et al. 2014). It is the most potent angiogenic inhibitor among anthocyanins and may be helpful in cancer prevention and treatment (Lamy et al. 2006). Delphinidin is also said to be more effective in the inhibition of tumorogenesis, by blocking the activation of the mitogen-activated protein kinase than other anthocyanins (Hou et al. 2004). Cytogenetic analysis revealed six different types of introgressions ranging from a ditelosomic addition (cv. Blue Norco) to a disomic substitution (cv. Blue Baart), substitution of complete (homologous) chromosome arms (line UC66049) and various translocations of distal parts of a chromosome arm(s) (Burešová et al. 2015). Similarly, several other agronomically important traits have been transferred from wild relatives into cultivars of wheat and ×*Triticale* such as the soft grain endosperm structure from *Aegilops speltoides* into bread wheat (Pshenichnikova et al. 2010), and leaf rust resistance from *Aegilops tauschii* to ×*Triticale* (Majka et al. 2018).

Interspecific hybridization is also a popular tool in forage grass breeding. ×*Festulolium* hybrids obtained by crossing fescues (*Festuca* sp.) with ryegrasses (*Lolium* sp.), combine complementary agronomic attributes of both parental species. Ryegrasses are known for their high seed yield, digestibility and palatability and display extraordinary rapid and intensive spring growth. Fescues, on the other hand, are species with excellent abiotic stress tolerance (Jauhar 1993; Cernoch & Kopecky 2020). To date, almost 100 ×*Festulolium* cultivars have been released worldwide (Humphreys & Zwierzykowski 2020). Using introgression breeding, various genetic stocks has been released. One of the first mapped introgression was a segment carrying mutation of *sid* (senescence induced degradation) introgressed from *F. pratensis* into short arm of chromosome 6 of *L. multiflorum* (Thomas et al. 1994). Mutation of the *sid* gene (sid^{y}) hampers the enzymatic step which destroys the green color by opening the tetrapyrrole macrocycle, for what the genotypes are called *staygreen*.

Probably most severe abiotic stress with increasing significance in forage grasses is summer drought (Cernoch & Kopecky 2020). Tolerance to drought has been introgressed from fescues into ryegrasses in several breeding programs (Humphreys & Pašakinskiene 1996; Kosmala et al. 2006). Quantitative trait loci (QTLs) for drought tolerance have been introgressed in a form of a single segment of *F. arundinacea* chromosome located interstitially on the long arm of the *L. multiflorum* chromosome 3 (Humphreys & Pašakinskiene 1996). Other *L. multiflorum* plants with segments carrying genes for drought tolerance have been developed by crossing with *F. glaucescens* and *F. mairei* (Morgan et al. 2001; Cao et al. 2003). Winter freezing is another kind of abiotic stress, which hampers wider utilization of ryegrasses, especially in some geographic areas including Northern Europe and alpine and mountainous regions. Genes encoding tolerance to freezing were successfully introgressed into *Lolium* species from *F. pratensis* and *F. arundinacea*. Transfer of freezing tolerance genes was reported from *F. pratensis* chromosome 3 into *L. perenne* and chromosomes 2 and 4 into *L. multiflorum* (Grønnerød et al. 2004; Guo et al. 2005; Kosmala et al. 2006). Besides abiotic stresses, ryegrass cultivars are often susceptible to several pathogens (rusts, bacterial wilt, and helminthosporium). Fescue species, however, are known to carry biotic resistance genes. Introgression lines of *L. multiflorum* with *F. pratensis* segments occupying the terminal region of *L. multiflorum* chromosome 5 responsible for crown rust (*Puccinia coronata*) resistance have been developed by Roderick et al. (2003).

In addition to cereals and grasses, interspecific hybridization is frequently used in Brassicaceae family. The hybrids between *Raphanus raphanistrum* ($2n = 2x = 18$, RR) × *Brassica oleracea* ($2n = 2x = 18$, CC) were obtained by Karpechenko (1927). He realized that this process created a new species, and proposed the name *Raphanobrassica*, but the earlier name *Brassicoraphanus* has priority. Pollinating *Brassicoraphanus* by *B. nigra* ($2n = 2x = 16$, BB) results in amphiploid hybrid of three species (RRBBCC), which is fully fertile upon chromosome doubling. Besides these, there is a large number of hybrids

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with numerous *Brassica* species involved (reviewed in Kaneko & Bank 2014).

Introgression approach has been used also in bulb onion (*Allium cepa*) breeding to introgress genes responsible for resistance to diseases. Alleles for leaf blight, anthracnose and downy have been introgressed from a wild relative, *A. roylei* (Kofoet et al. 1990; van der Meer & de Vries 1990; Scholten et al. 2016; Khrustaleva et al. 2019). The putative downy mildew resistance locus *Pd1* has been allocated to the region spanning the most distal ~18% of the long arm of chromosome 3 (Van Heusden et al. 2000). It is not always possible to introgress chromosome segments from one to the other species directly, due to crossability problems. For that, a bridge species, whichis easily crossable with both of the species of interest (donor and recipient) has to be used instead. For example, *A. roylei* has been proposed as a bridge species for introgression of traits from Welsh onion (*A. fistulosum* L.) into cultivated bulb onion, because of a very low fertility of the hybrids between bulb onion and Welsh onion (Khrustaleva & Kik 1998). One outcome of interspecific hybridization is the development of cytoplasmic male sterility (CMS) for hybrid crops production (Whelan 1981; Bohra et al. 2016). CMS has long been used to economically produce hybrids that harness growth vigor through heterosis. Studies on heterosis in *Brassica* have stimulated research on CMS systems. The first CMS system described in an open-pollinated radish (*Raphanus sativus*) cultivar (Ogura 1968) has since been reported to be widespread in wild radish populations in Japan (Yamagishi & Terachi 1994) and in *Raphanus raphanistrum* in both Asia and Europe (Giancola et al. 2007). CMS systems have also been found in durum and bread wheat (Martín et al. 2009, 2018) and *B. carinata* (unpublished results) using the amphiploid ×Tritordeum ($\mathrm{H^{ch}H^{ch}AABBDD}$) and *R. raphanistrum* × *B. carinata* (RRBBCC) with cytoplasm of barley and *B. carinata*, respectively.

To conclude, there is an extensive list of interspecific crosses used in crop breeding that is not necessarily limited to crop wild relatives and to cases of trait introgressions. It can be hypothesized that future hybridization approaches extending to even crosses of not domesticated species might yield useful crop with novel traits (Mason & Batley 2015).

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