

HYBRIDIZATION BETWEEN DIPLOID *AEGILOPS* SPECIES AND BREAD WHEAT

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Abstract. The purpose of the current study was to estimate the crossing ability and chromosome pairing behavior of intergeneric F₁ hybrids between 7 diploid *Aegilops* species without the D genome (*Ae. speltoides*, *Ae. longissima*, *Ae. searsii*, *Ae. markgrafii*, *Ae. heldreichii*, *Ae. uniaristata*, *Ae. umbellulata*) and *Triticum aestivum*. The highest crossability was recorded when the spikes of *Ae. heldreichii* were pollinated with the pollen of bread wheat line -172ACS (15.38%). The phenotypes of the hybrid plants were intermediate between *Aegilops* and common wheat. Observations of mitosis in root tip cells and meiosis in pollen mother cells revealed that the F₁ hybrids possessed 28 chromosomes. Chromosome pairing at metaphase I of the pollen mother cells in the F₁ hybrid plants was low.

Keywords: Intergeneric hybridization, wheat, *aegilops*, seed setting, fertility.

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1. Introduction

Common wheat (*Triticum aestivum* L.) is one of the most important cereal crops in the world. Wild relatives and related species represent a large reservoir of valuable traits, including resistance to diseases and pests and tolerance to drought and salt that can be exploited to improve wheat (Feldman & Sears, 1981; Zhou *et al.*, 1999; Wang & Shang, 2000).

The *Aegilops* genus consists of 11 diploid, 10 tetraploid and 2 hexaploid species (Van Slageren, 1994), with extremely diverse genomic formula, including the D, S, U, C, N and M genomes. Some *Aegilops* species belong to the secondary gene pool of wheat, i.e. at least one of their genomes is homologous with a cultivated wheat genome, allowing favourable traits to be transferred to wheat using conventional crossing and normal recombination methods. *Aegilops* species played an important role in the evolution of cultivated wheat. The ancestor of the D genome of wheat is the species *Aegilops tauschii* (Coss.) (syn. *Ae. squarrosa*) (McFadden & Sears, 1946), whereas the S genome of *Ae. Speltoides* (Tausch) bears the greatest resemblance to the B genome of cultivated wheat (Feldman *et al.*, 1995; Balint *et al.*, 2000; Feldman, 2001).

Many of the species in the *Aegilops* genus have good resistance to disease and insect pests (Gill *et al.*, 1983; 1985, 1987; Raupp *et al.*, 1993, 1995, 1997; Zaharieva *et al.*, 2001). Among other things, some *Aegilops* species are excellent sources of resistance

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to the various rusts and powdery mildew (Damania & Pecetti, 1990; Dimov *et al.*, 1993). Numerous wheat - *Aegilops* interspecific hybrids and addition and translocation lines have been developed (Friebe *et al.*, 1992, 1995a, b, 1996a, b, 1999, 2000) and many agronomically useful traits (disease and insect resistance, stress and salt tolerance) have been incorporated into the wheat gene pool from these species (Cox & Hatchett, 1994; Cox *et al.*, 1994; Gill *et al.*, 1987; Raupp *et al.*, 1993; Friebe *et al.*, 1996a).

The diploid species are distributed in Southwest and Central Asia. The center of the distribution is in southeast Turkey, i.e., the northern part of the fertile-crescent belt. Six species (*A. muticum*, *T. monococcum* subsp. *aegilopoides*, *T. urartu*, *Ae. speltoides*, *Ae. caudata* and *Ae. umbellulata*) are distributed in the central part of the group distribution. Several species of the S genome group (*Ae. bicornis*, *Ae. longissima*, *Ae. sharonensis* and *Ae. searsii*) are found south of the center, the species of the M/N-genome group (*Ae. comosa* and *Ae. uniaristata*) west of the center and *Ae. tauschii* is in the eastern part of the distribution area. The geographical distribution of the various diploid species indicates that the group has undergone an extensive differentiation in its early stages of development (M. Lang, e-book).

Considering that *Ae. speltoides* carries resistance genes against a number of diseases, including stem and leaf rust, triticologists have begun to use this quality effectively. For example, by R. Mago and colleagues (Mago *et al.*, 2009), including Ug99 (TTKSK), gene *Sr39* - wheat stem rust [*Puccinia graminis* f. sp. *tritici* (Pgt)] conferring resistance to all known pathotypes was introgressed into wheat from *Aegilops speltoides* together with *Lr35* gene conferring resistance to leaf rust [(*P. tritricina* (Pt)] in the mature plant.

Ae. longissima possesses numerous genes of agronomic interest and can be a valuable source of resistance to leaf rust, stem rust, powdery mildew, pests and extreme environmental conditions (Aminov & Aliyeva, 2012).

A new source of resistance to the highly virulent Ug99 race of stem rust (*Puccinia graminis tritici*) was discovered in the short arm of chromosome 3S^s of *Aegilops searsii*. To transfer that resistance gene to bread wheat, V. Liu and colleagues (Liu *et al.*, 2011) created three double-monosomic chromosome populations (3A/3Ss, 3B/3Ss, and 3D/3Ss) and introduced stem rust (Ug99) resistant wheat – *Ae. searsii* used molecular marker and cytogenetic analysis methods to identify the Robertson translocation. As a result, three Robertsonian translocations resistant to stem rust (T3AL•3SsS, T3BL•3SsS, T3DL•3SsS) and one recombinant (T3DS-3SsS•3SsL) translocation were identified.

Aegilops markgrafii has been found to be resistant to wheat stripe rust (*Puccinia striiformis* Westend) (Valkoun *et al.*, 1985), leaf rust (*P. recondita* Roberge ex Desmaz. f. sp. *tritici*) (Gill *et al.*, 1985; Valkoun *et al.*, 1985; Iqbal *et al.*, 2007), stem rust (*Puccinia graminis* f. sp. *tritici*) (Valkoun *et al.*, 1985; Dyck *et al.*, 1990), powdery mildew (*Blumeria graminis* f. sp. *tritici*) (Gill *et al.*, 1985; Valkoun *et al.*, 1985; Baldauf *et al.*, 1992), greenbug [*Schizaphis graminum* (Rondani)] (Baldauf *et al.*, 1992) and hessian fly [*Mayetiola destructor* (Say)] (Gill *et al.*, 1985). Therefore, *Ae. caudata* is an excellent gene source for wheat improvement. The genes and alleles of interests can be introduced into wheat by interspecific hybridization (Friebe *et al.*, 1996).

The purpose of this study was to conduct intergeneric hybridizations to transfer the useful genes controlling the important agronomic traits of *Aegilops* L. to bread wheat lines through hybridization and to study the crossing ability of alien chromosomes during the meiosis process in the obtained hybrids.

2. Materials and methods

Plant Material

For the material of the study were used common wheat lines 171ACS ({*Aegilotriticale* [(*T. durum* Desf. × *Ae. tauschii* Coss.) × *Secale cereale* L. ssp. *segetale* Zhuk.] × *T. aestivum* L. ‘Chinese Spring’}, 172 ACS (they differ from each other only colour of spike), *T. Abscheronicum* Aliyeva et Aminov and *Triticum* and diploid *Aegilops* species (table 1).

The emasculation and pollination in the *field* were *carried out* during the months of April-May in 2017 at the Absheron Research Base of Genetic Resources Institute. No embryo rescue or hormone treatment was applied for the production of F₀ seeds. The seeds were collected from mature spikes in the month of June-July and the crossability of the used genotypes in each hybrid cross was calculated as the percentage of F₀ seeds obtained relative to the number of florets pollinated for each crosses.

Table 1. Species and varieties of wheat and *Aegilops* that used in this study

Plants	Genome	2n	Accessions
Sectio <i>Truncata</i>			
<i>Ae. speltooides</i> Tausch	SS	14	Iran, Israel
Sectio <i>Emarginata</i>			
<i>Ae. longissima</i> Schweinf. et Muschl.	S ¹ S ¹	14	Unknown
<i>Ae. searsii</i> Feldman et Kislev ex Hammer	S ^s S ^s	14	(Israel) k-2305, Syria k-570409
Sectio <i>Cylindropyrum</i>			
<i>Ae. markgrafii</i> (syn <i>Ae. caudata</i>) (Greuter) Hammer	CC	14	Turkey
Sectio <i>Comopyrum</i>			
<i>Ae. heldreichii</i> (Boiss.) Holzm.	M ^h M ^h	14	Unknown
<i>Ae. uniaristata</i> Vis.	NN	14	Unknown
Sectio <i>Aegilops</i>			
<i>Ae. umbellulata</i>	UU	14	Lerik, Ismaili (Girdmancay)
Sectio <i>Urtu</i>			
<i>T. urartu</i> Thum. Ex Gandil	A ^u	14	Turkey
Sectio <i>Monococcum</i>			
<i>T. boeoticum</i> Boiss.	A ^b	14	Azerbaijan (Shamakhi), Darband, Turkey(k-61042)
<i>T. monococcum</i> L.	A ^b	14	Nakchevan
Sectio <i>Timopheevii</i>			
<i>T. araraticum</i> Jakubz.	A ^b G	28	(Shorbulag)
Sectio <i>Triticum</i>			
<i>T. aestivum</i> L. em Thell. Line 171ACS	A ^u BD	42	
172ACS	A ^u BD	42	
cv. Siete cerros var. <i>erythroleucon</i>	A ^u BD	42	
<i>T. abscheronicum</i> Aliyeva et Aminov	A ^u B	28	

Meiotic Preparations

When the plants reached the flag leaf stage, spikes were sampled, stages of meiosis were determined in acetocarmine squashes of 1 of 3 anthers per flower. If appropriate stages were present, the remaining 2 anthers were fixed in ethanol-acetic acid (3:1) for 24 h and stored at 4°C in 70% alcohol until use. Preparations were made from pollen mother cells (PMCs) by squashing pieces of anthers in 45% acetic acid. Slide preparations were examined using phase-contrast microscopy and then placed on dry ice to remove the cover glass. The images were captured with a Motic (China).

3. Results and discussion

By involvement of *Aegilops species* into interspecific crosses, it is possible to enrich bread wheat with new gene blocks that determines adaptability, resistance to stress factors, productivity and grain quality. Thomson (1930) hypothesised that the use of a female parent with a high chromosome number is more successful than the reciprocal cross. Cross plant of *Aegilops*/common, wheat grows vigorous and looks like female parents and male parents. Cross fertility is different for *Aegilops* L., but overall performance is bad.

Table 2 shows the results of intergeneric hybridizations of different bread wheat lines with diploid species of the genus *Aegilops* L.. As can be seen from the table, in the hybrid combinations between bread wheat lines and *aegilops* species, the highest seed setting was 15.38% (*Ae. heldreichii* × 172ACS) and the lowest 1.25% (171ACS × *Ae. searsii*). The obtained hybrid seeds were usually small and weak. In order to determine the nature of pairing between alien chromosomes in F1 plants obtained from the germination of these seeds, the meiosis was studied.

Ae. speltoides.

Results of crossing between 2 accessions of *Ae. speltoides* with diploid wheat species (*T. urartu* Thum. ex Gandil. and *T. boeoticum* Boiss.), also bread wheat lines (171 and 172ACS) was failed. The hybrids between *T. urartu*, *T. boeoticum*, bread wheat line 171ACS with *Ae. speltoides* was sterile. In terms of hybridization between 172ACS and *Ae. speltoides*, we obtained 2 week hybrid seeds. These seeds were germinated in Petri dish and the obtained seedling was transplanted into the experimental field, but these plants were destroyed before completing the vegetation period.

Samples (k-2, k-389, k-452, k-1015, k-1316, k-1595) of *Ae. speltoides* species from VIR by I.F. Lapochkina and colleagues (Lapochkina, 1996; Lapochkina *et al.*, 2000) in wheat, were evaluated in terms of being able to conjugate with chromosomes. Rodina variety of common wheat was used as the mother form in crossing. The seed setting was 0.5-2.0%. F1 hybrids are sterile. It should be noted that the wide range of mechanisms of action of *Ae. speltoides* creates wide opportunities for its use in selection. Thus, during *T. aestivum* × *Ae. speltoides* type hybridizations, *Ae. speltoides* allows successful introgression of agriculturally important traits into the wheat genome by weakening the Ph system of wheat (i.e., enabling homeologous conjugation). Some scientists have shown that it is more appropriate to use bread wheat as a mother in reciprocal combinations such as *T. aestivum* × *Ae. speltoides* and *Ae. speltoides* × *T. aestivum* (Spetsov, 2000). So, in hybrids with *Ae. speltoides* cytoplasm, the seed setting was very low and made up 2.6%.

Ae. longissima

In the two combinations between 171ACS and *Ae. longissima*, the seed setting was almost the same and was 5.71 and 8.33%, respectively. 6 hybrid seeds belonging to the second combination did not germinate and 2 out of 4 seeds from the first combination germinated, but those plants were destroyed after being transferred to the field. Aminov notes that in practice, the number of bivalents in reciprocal hybrids of *Ae. longissima* with hexaploid wheat *T. macha* varies between 0.8-1.2, and in reciprocal hybrids with common wheat Opal variety varies between 3.1-3.3. Based on the results of the chromosom pairing test, all this gives us the reason to say that *Ae. longissima* cannot be considered the donor of the B genome (Aminov, 2000b).

Ae. searsii

Ae. Searsii - sample of Israel origin was involved in hybridization with 171ACS, and sample of Syrian origin with 172ACS line. 171ACS \times *Ae. searsii* (Israel) k-2305 combination, a single seed (1.25%) was obtained, and this single seed gave sterile F₁ plant with 97cm hight. 172ACS \times *Ae. searsii* (Syria) k-570409 combinations also were completely sterile. Previous articles demonstrated that its hybrids with *T. aestivum*, chromosome conjugation was also very low, averaging only 1.85 chiasms per cell (Feldman, 1979; Pietro *et al.*, 1987).

Ae. markgrafii

Hybridization between *Ae. markgrafii* k-2257 of Turkish origin and cultivated wheat *T. monococcum* L. was failed.

Fertility of two hybrid combinations between 172 ACS with *Ae. markgrafii* (Turkey *accessions* k-2257) was 1,52 and 25,00%. Obtained one weak seed from first combination did not germinate. As for the next combination, one seed from 6 germinated and gave normal F₁ plant. This hybrid seed was germinated in Petri dishes and the obtained seedling was transplanted into an experimental field for further investigations. However, this intergeneric hybrid plant was completely sterile due to the difference of ploidy level of parent forms, so that we could not get any seed from 1330 spike florets.

Backcross hybridization between this hybrid with various types of common wheat lines (172ACS, cv. Siete cerros var. *Erythroleucon*) was ineffective.

Morphologically, F₁ hybrids appear to be intermediate between the parental species tend to one parent. Although the hybrids was intermediate position on the height of the plant, the length of the spike and the amount of spikes in the spike, they prefer parent forms according to the number of productive tillers.

Regarding the traits of hybrid plant, the height was 92cm (P₁♀ 141cm, P₂♂ 47 cm), the length of the spike was 17cm (P₁♀ 15cm, P₂♂ 16,5 cm), the length of flag leaf was 17 (P₁♀ 31cm, P₂♂ 5cm), the length of peduncle was 15cm (P₁♀ 22cm, P₂♂ 5 cm). The tillering of hybrid plant was greater than parent forms.

Cytogenetic study of meiosis in F₁ was carried out according to the standard methods. Pollen mother cells (PMCs) for studies of meiotic chromosome behavior were prepared by means of the standard Carnoy fixative and acetocarmine squash method. During the meiosis process in F₁ plants observed 28 chromosomes as expected. There were approximately 3 ring, 6 rod bivalents and 10 univalents. In crosses *Ae. Markgrafii* with *T. aestivum*, a mean of two bivalents were found by Muramutsu (1959), Riley and Law (1965) and Upadhyya (1966), while Kihara and Lilienfeld (1935) detected about 4 bivalents with trivalents varying from 0 to 2.

Upathya (1966) reported that particular genotypes of *Ae. 318Audate* may increase chromosome pairing in hybrids with *T. aestivum*. The low value of bivalents in the hybrid indicates that the three genomes of the hybrid are not related to each other as was expected, since *Ae. caudata* brings the C genome and *T.aestivum* the A, B and D genomes.

Ae. heldreichii

Only 3 weak seeds (7.14%) were obtained from the hybrid combination between tetraploid wild wheat *T. araraticum* (Armenia/Shorbulaq) and *Ae. heldreichii*. Although we did not get in obtaining seeds from either the straight or reciprocal combination between the 171ACS line and *Ae. heldreichii*, the reciprocal crossing of the 172ACS line with *Ae. heldreichii* was successful in both cases and in those combinations, the seed set was lower than the straight combination in which *Aegilops* was taken as the male parent by 1.61% (1 seed) and in the reciprocal combination taken as female, it was relatively high and made 15.38% (4 seeds). The only seed belonging to the straight combination did not germinate and 2 out of 4 seeds belonging to the reciprocal combination (50%) germinated and gave F₁ plants. The height of these sterile plants was 87 cm. The F₁ hybrids from the *Ae. heldreichii* × 172 ACS cross exhibited a low setting percentage and were morphologically different from the 2 parents, except for a similar perennial of *aegilops* parent. All plants had 28 somatic chromosomes with 7 chromosomes from *Ae. heldreichii*. During the study of the meiosis process, 1-2 ring bivalents, 7-8 rod bivalents were observed in most metaphase stage. Chromosome pairing configurations in the hybrid PMCs were very complex and a high frequency of univalent and a variety of trivalent configurations were observed.

Ae. uniaristata

The hybrid combination of *Ae. uniaristata* with the wild diploid eincorn *T. boeoticum* Boiss (collected from Gobustan), was unsuccessful, while the combination with the synthetic tetraploid *T. abscheronicum* Aliyeva et Aminov was successful (2.08%). The only seed obtained had 100% germination and although it gave an F₁ plant, the height of plant was 50cm and was sterile.

Ae. umbellulata

In the hybrid combination between 171ACS and *Ae. umbellulata* (UU) collected from Girdmanchay, the seed setting was 14.52%, only 1 out of 9 seeds germinated and gave a normal tetraploid F₁ plant (ABDU, 2n=4x=28). The average height of the plant was 121 cm and its fertility was 0.06%. Thus, one grain was obtained from 1554 spike flowers. Chromosome pairing was observed to be very low during the study of meiosis, on average 0.31 ring, 0.62 rod bivalents, 21.15 univalents, 0.33 trivalents and 3.90 chiasm were recorded for each PMCs. In the F₁ hybrid from the combination 171ACS × *Ae. umbellulata*, the formation of ring and rod bivalents, as well as trivalents, at least slightly, was undoubtedly possible due to the pairing between wheat and *aegilops* homeologous chromosomes.

Dvorjak et al. (1989) also reported that homeologous conjugation occurred between the 1U chromosome of *Ae. umbellulata* and the common wheat chromosomes 1A, 1B and 1D and the 1U chromosome, which itself controls the 7 subunits of gliadin, was compared to 1A and 1B and 1D was determined to be closer.

Table 2. Results of crossing between wheat and *Aegilops* species

Hybrid combinations	flower	seed	Seed setting, %	Fertility, %	Number of hybrid plants	Height, (cm)
171ACS × <i>Ae. speltoides</i> (Iran)	46	-	-	-	-	-
<i>T. urartu</i> (Turkiye) × <i>Ae. speltoides</i> (Iran)	22	-	-	-	-	-
<i>T. boeoticum</i> (Darband) × <i>Ae. speltoides</i> (Iran)	136	-	-	-	-	-
172ACS × <i>Ae. speltoides</i> (Iran)	46	2	4.35	100	2	-
171ACS × <i>Ae. longissima</i>	70	4	5.71	50	2	118
171ACS × <i>Ae. longissima</i>	72	6	8.33	-	-	-
171ACS × <i>Ae. searsii</i> (Israil) k-2305	80	1	1.25	100	1	97
172ACS × <i>Ae. searsii</i> (Suriya) k-570409	50	-	-	-	-	-
172ACS × <i>Ae. markgrafii</i> (Turkiye) k-2257	24	6	25	16.67	1	92
172 ACS × <i>Ae. markgrafii</i> (Turkiye) k-2257	66	1	1.52	sterile	-	-
<i>T. monococcum</i> (Nakhchivan) <i>Ae. markgrafii</i> (Turkiye) k-2257	118	-	-	-	-	-
<i>T. araraticum</i> (Shorbulaq) × <i>Ae. heldreichii</i>	42	3	7.14			
172ACS × <i>Ae. heldreichii</i>	62	1	1.61	sterile	-	-
<i>Ae. heldreichii</i> × 172ACS	26	4	15.38	50	2	87
<i>T. abscheronicum</i> × <i>Ae. uniaristata</i> k-643	48	1	2.08	100	1	50
171ACS × <i>Ae. umbellulata</i> (Girdmanchay)	50	9	14.52	0.06	1	121

Aegilops L. genus has 5 fundamental genomes, which are C, D, M, S and U. The genomes play an important role in the origin and evolution course of common wheat (Davoyan *et al.*, 2012; Li *et al.*, 2011; Timonova *et al.*, 2013). In our research, the material involves 7 species of *Aegilops* L genus, containing 5 chromosome groups. *Aegilops* L. genus belongs to self-pollination and often cross-pollinated plants have ability of nature outcross. Cross of common wheat and *A. speltoides*, *Ae. Tauschii*, *Ae. cylindrica*, *Ae. ovata* genus all have been reported (Kozub *et al.*, 2008; Loureiro *et al.*, 2006a; Sharma & Gill, 1986), but most of the research focuses on distant related cross applying at genetic breeding. In the research, we used the 4 species of *Aegilops* L to cross with common wheat. In condition of embryo rescue, the easiest cross is *Ae. tauschii*/common, getting 46.49% genus cross superlatively, the second is *Ae. ovata*/common, getting 14.76% genus cross superlatively, the third is *Ae. cylindrica*/common, getting 12.11% genus cross superlatively and *A. speltoides* gets the lowest cross seed-set rate in our research. The cross of common wheat and different

Aegilops L. species or different gene of the same *Aegilops* L species all perform different cross ability, it means that they have different potential cross ability with common wheat. Guadagnuolo et al. (2001) used common wheat and *Ae. cylindrica* to carry out pollination experiment in field, and got 1% and 7% genus cross seed, (Loureiro *et al.*, 2006a; Loureiro *et al.*, 2006b) got 0.39% *Ae. ovata*-common wheat genus crossbred in experiment of field condition. The experiment result shows that the seed-set rate of *Ae. cylindrica*/common wheat exceeds 10%. In the experiment, implementing embryo rescue enhances seed-set rate, overcomes the uncertainty conducted by nature factor in field and reveals cross seed-set ability of *Aegilops* L. and common wheat (Sharma & Gill, 1986).

Sterility in F₁ hybrids of distant forms is due to disturbances in the meiosis process, which results in a lack of functional gametes (Stefanowska, 1998).

Unlike species (*Ae. cylindrica*, *Ae. tauschii* etc.) that shares the D genome with wheat these diploid species have no common genomes with wheat. Nevertheless, differences with respect to meiotic pairing have been reported for some combinations between *T. aestivum* cultivars and *Aegilops* spp. accessions. Gene transfer may also occur through translocations or transmission of an extra chromosome (Wang *et al.*, 2000). The presence of gametocidal genes (Gc) in some *Aegilops* spp., genes that induce breakage-fusion in wheat or *Aegilops* chromosomes, may result in the generation of deletions and translocations (Zaharieva & Monneveux, 2006). These gametocidal genes were identified on chromosome 4 M of *A. geniculata* (Kynast *et al.*, 2000). Hybridization is possible and the hybrids show some female fertility, so all these facts point to potential routes for gene transfer from wheat to *Aegilops* species. Determination of the frequency of crop-wild transgene flow under field conditions is necessary in order for the development of regulatory strategies to manage the possible transgenic hybrids. To reduce the potential for introgression of resistance genes in the *Aegilops* genus, it is therefore important to control *Aegilops* spp. along the borders of wheat fields to prevent hybrid formation. If they are produced, it is important to prevent the pollination of the hybrids and the formation of backcross seed.

Since the intergeneric hybridizations between *Triticum* L. and *Aegilops* L., which is considered as the secondary gene pool of wheat, belong to incongruent crosses, it is natural that the level of chromosome pairing between their chromosomes is low, and the differences between the ploidy levels of the parental forms are accompanied by a number of violations of the meiosis process, therefore also causes the emergence of weak and sterile and in the best case, semi-sterile hybrids from the fertilization of unbalanced gametes.

4. Conclusion

Most of the wheat - *Aegilops* hybrids obtained from hybrid combinations without homologous chromosomes were sterile or showed low fertility, which indicated a low level of chromosomal conjugation during meiosis.

We can't overlook the possibility of diploid species that become gene introgression object.

Almost all wheat-aegilops hybrids involved backcross hybridization but it was ineffective.

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