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EFFECT OF HOMOELOGOUS PAIRING *PH 1* – LOCUS OF *TRITICUM AESTIVUM* L. ON ITS F₁ – BRIDGE HYBRIDS WITH THE SPECIES (2X, 4X, 6X) *TRITICUM* L., (2X, 4X) *AEGILOPS* L., AND (2X, 4X) *LOLIUM* L. GENERA

ABSTRACT

Mono-5B Chinese Spring, mono-5B Jara, mono -5B Favorit exhibiting the deficiency of 5B-chromosome, the mutant –*Ph* Chinese Spring (*ph1b*, *ph1b*), mono-5A Chinese Spring, mopno-5D Chinese Spring with the genotype *Ph1*, *Ph1* and the varieties Chinese Spring, Jara, Favorit with the genotype *Ph1Ph1* were used in the crosses with 7 species of *Triticum*, 5 species of *Aegilops* and one species of *Lolium* genera to investigate the effect of the *Ph1*-locus on F₁-bridge hybrids. Altogether, 117 cross-combinations were made and 98 259 florets were pollinated. The effectiveness of the locus *Ph 1* was judged by the percentage of seed set of F₁- bridge hybrids. Wide variation of seed set was observed in F₁-bridge hybrids for all cross-combinations made. The deficiency of 5B chromosome exhibited higher effectiveness (10.7% - 4. 2%) than the recessive gene *ph1b* (3.2%). Out of the monosomics of 5B-chromosome, mono-5B Chinese Spring exhibited the stronger effectiveness on seed set of F₁- bridge hybrids (10.7%) probably due to the presence of the recessive crossability genes. Among the sources of the genotype *Ph1 Ph1*, mono-5A, -5D of the variety Chinese Spring showed higher percentage of seed set (2.4% and 1.9%), respectively than the disomic varieties Chinese Spring, Jara and Favorit (0.8%, 0.4% and 0.4%, respectively). Of the related species, three genotypes were identified as highly effective: *T. monococcum* L., *T. dicoccoides* Korn., and *Ae. speltoides* Taush. for obtaining the high fertile F₁-bridge hybrids and complementary to the deficiency of 5B-chromosome and the recessive gene *ph1b*.

Key words: gene *ph1b*, homoeologous pairing system, locus *Ph1*, 5B-, 5A-, 5D-chromosome monosomics, related species, *Triticum aestivum* L.

INTRODUCTION

In hexaploid wheat *Triticum aestivum* L., the meiotic pairing of homoeologous chromosomes is under the suppression control of the dominant genes *Ph* (pairing homoeologous) belonging to “ the genetic homoeologous pairing system “ (GHPS). The activity of this system in interspecific and intergeneric hybridization of wheat *T. aestivum* L. was presented in previous paper (Pilch 2005 a, b). The system GHPS ensures the diploid-like homologous behaviour of the chromosomes in wheat making impossible introgressions from wild species chromosomes into wheat.

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The principle suppression role in this system belongs to the locus *Ph 1* which is located on the long arm of chromosome 5BL (Okamoto 1957, Riley and Chapman 1958). In the absence of the gene *Ph 1* (mono-5B chromosome, nulli-5B chromosomes) or the presence its recessive mutation *ph1b* (Sears 1977) or the dominant gene *Ph 1* (Riley *et al.* 1961, Dover and Riley 1972) in the F₁- bridge hybrids of *T. aestivum* L. with the related species, the homoeologous-multivalent pairing of wheat chromosomes with the chromosomes of those species take place with the improved possibility of obtaining hybrid-kernels, thus allowing for translocations which involve fragments from alien chromosomes and the homoeologous chromosomes of wheat (Driscoll and Jensen 1963, Sears 1977, 1981, 1982). Thereby, the *Ph1* locus induces homoeologous recombinations between wheat and alien chromosomes and can be used in breeding improvements of hexaploid wheat.

This paper presents the effectiveness of the *Ph 1* locus in obtaining the hybrid kernels in the F₁- bridge hybrids of wheat with the species of genera (2x, 4x, 6x) *Triticum* L., (2x, 4x) *Aegilops* L., and (2x, 4x) *Lolium* L. frequently used in the generative introgressive hybridization. On the basis of these results, many winter and spring introgressions were developed with the improvements of the spike characters and the high technological parameters of kernels (Pilch 2004, 2005 b).

MATERIALS AND METHODS

The experimental material consisted of:

- A. the monosomic lines (2n=41) representing the deficiency of 5B-chromosome: mono-5B Chinese Spring, mono-5B Jara, mono-5B Favorit,
- B. the disomic (2n=42) mutant *Ph* Chinese Spring with the recessive genotype (*ph1b*, *ph1b*)
- C. the monosomic lines (2n=41) with the dominant genotypes (*Ph1 Ph1*): mono-5A Chinese Spring, mono-5D Chinese Spring,
- D. the maternal varieties of *T. aestivum* L. with the dominant genotypes (*Ph1 Ph1*): Chinese Spring, Jara, Favorit
- E. the related species: *T. monococcum* L., *T. beoticum* Boiss., *T. durum* Desf. cs Mirable, Fuensemuro, Khapli, *T. dicoccoides* Korn., *T. timopheevii* Zhukov., *T. karamyshevii* Zhukov., *T. sphaerococcum* Perc., *Ae. speltoides* Taush., *Ae. squarrosa* L., *Ae. ovata* L., *Ae. variabilis* Eig., *Ae. triuncialis* L., *L. perenne* L. cs Anna, Solen.

All monosomic lines, the disomic mutant *Ph* Chinese Spring and the varieties Chinese Spring, Jara, Favorit (entries A - D) were crossed as female to 13 related species listed in entry E, in the field. The emasculated spikes were bagged to avoid outcrossing. After 3-5 days, the stigmas of emasculated florets were pollinated twice with fresh pollen from the related species, then bagged again. Altogether, 117 cross-combinations were made and 98 259 florets were pollinated. The effectiveness of the locus *Ph1* was judged by the percentage of F₁ - bridge hybrid seed set (number of seeds per florets pollinated) at the development.

The percentages were transformed to arcsine 1/2x (arcsine-1/2x) according to Bartlett (1947) and these values were subjected to analysis of variance (Little and Hills 1975).

RESULTS

Wide variation was observed in the effectiveness of percentage seed set among 5B-monosomics of the varieties Chinese Spring, Jara, Favorit and the mutant-*Ph* Chinese Spring (*ph1b*, *ph1b*) in the hybridization with the related species (Table 1).

Table 1
Effects of the genotypes (*Ph1 ph1*) mono -5B and (*ph1b ph1b*) mutant *Ph* Chinese Spring in obtaining hybrid-F₁ kernels in the hybridization *T. aestivum* L. with the related species

Species related	Mono-5B Chinese Spring		Mono-5B Jara		Mono-5B Favorit		Mutant- <i>Ph</i> Chinese Spring		Total	
	a	b	a	b	a	b	a	b	a	b
<i>Triticum</i> L.										
<i>T. monococcum</i> L.	141	12.8	132	7.6	136	10.3	480	10.6	889	10.5
<i>T. beoticum</i> Boiss.	320	8.7	196	11.7	324	3.4	576	9.4	1416	8.2
<i>T. durum</i> Desf.	264	11.9	192	7.3	2916	8.8	320	2.5	3692	8.5
<i>T. dicoccoides</i> Korn.	332	17.8	288	5.9	114	34.2	224	26.8	958	18.3
<i>T. timopheevii</i> Zhukov.	96	51.1	224	12.9	2160	8.8	1984	2.3	4464	7.1
<i>T. karamyshevii</i> Zhukov.	198	9.6	224	3.1	250	4.8	4576	1.5	5248	5.4
<i>T. sphaerococcum</i> Perc.	111	18.9	192	5.2	309	4.9	320	6.6	932	7.2
<i>Aegilops</i> L.										
<i>Ae. speltoides</i> Taush.	192	9.9	128	1.6	168	2.4	7680	1.4	8168	1.6
<i>Ae. squarrosa</i> L.	642	4.2	528	2.6	503	2.2	480	6.1	2153	3.8
<i>Ae. ovata</i> L.	608	8.9	320	7.5	340	6.2	4896	3.4	6164	4.3
<i>Ae. variabilis</i> Eig.	416	14.9	384	10.7	72	6.9	2976	5.3	3848	6.9
<i>Ae. triuncialis</i> L.	736	18.2	864	15.3	114	14.9	7584	9.9	9298	11.2
<i>Lolium</i> L.										
<i>L. perenne</i> L.	960	1.1	1312	1.1	7528	0.4	15360	0.6	25160	0.6
Sum	5016		4984		14934		47456		72390	
Mean [%]	10.7		6.8		4.2		3.2		4.2	
S. error	0.8		1.5		2.2		1.9		1.5	
S. deviation	2.9		5.4		7.9		7.1		5.4	
Variance	8.8		28.7		62.7		50.6		28.8	
CV	28.3		36.8		51.9		52.6		36.4	

a — number of florets pollinated ; b — % of seed set F₁

Among them the highest effectiveness was exhibited in mono-5B Chinese Spring, followed by mono-5B Jara, mono-5B Favorit, and the mutant-*Ph* Chinese Spring (*ph1b*, *ph1b*). The mean percentage for mono-5B Chinese Spring was much higher (10,7%) as compared to the total cross-combinations made (4.2%). The variation ranged from 1.1% to 51.1%. The highest value showed the cross-combination with *T. timopheevii* Zhukov (51.1%). The second cross-combination was the group which contained three cross-combinations (*T. sphaerococcum* Perc., *Ae. triuncialis* L., *T. dicoccoides* Korn.) with a range 17.8% - 18.9%. The next cross-combination group involved *T. durum* Desf. and *Ae. variabilis* Eig. had 11.9% and 14.9% seed

set, respectively. The remaining seven cross-combinations presented a cross-combination below 10% seed set.

In the cross-combinations involving mono-5B Jara with related species, the effectiveness was in the range from 15.3% to 1.1% and the mean percentage was higher (6.8%) than that of all cross-combinations. Three distinct groups could be identified, among which the first one was represented by four cross-combinations with *Ae. speltoides* Taush., *T. timopheevii* Zhukov., *T. boeoticum* Boiss. and *Ae. variabilis* Eig. The second group with lower effectiveness comprised the cross-combinations with 6 species: *T. monococcum* L., *Ae. ovata* L., *T. durum* Desf., *T. dicoccoides* Korn., *T. sphaerococcum* Perc. and *T. karamyshevii* Zhukov. The third group having the lowest effectiveness included three cross-combinations with *Ae. squarrosa* L., *Ae. speltoides* Taush. and *L. perenne* L.

The effectiveness in seed set of mono-5B Favorit with other species was in the range of all 52 cross-combinations and averaged 4.2%. The values spreaded from 34.2% to 0.4% and the highest value in only one cross-combination with *T. dicoccoides* Korn. The second distinct group presenting lower effectiveness was composed of five cross-combinations involving *Ae. speltoides* Taush., *T. monococcum* L., *T. durum* Desf., *T. timopheevii* Zhukov., and *Ae. variabilis* Eig.. The final group having the lowest seed set was represented by seven cross-combinations containing *Ae. ovata* L., *T. sphaerococcum* Perc., *T. karamyshevii* Zhukov., *T. boeoticum* Boiss., *Ae. triuncialis* L., *Ae. squarrosa* L. and *L. perenne* L.

The mutant-*Ph* Chinese Spring (*ph1b*, *ph1b*) which possessed a different genotype as distinct from the 5B-chromosome monosomics showed the lowest effectiveness of seed set in the cross-combinations with the related species. The average was much lower in comparison to all 52 cross-combinations and achieved an average of only 3.2% (the range was from 26.8% - 0.6%). The highest percentage of seed set involved one cross-combination with *T. dicoccoides* Korn. The second distinct group presented lower effectiveness and included seven cross-combinations involving *T. monococcum* L., *Ae. triuncialis* L., *T. boeoticum* Boiss., *T. sphaerococcum* Perc., *Ae. squarrosa* L., *Ae. variabilis* Eig. and *Ae. ovata* L. The remaining five species (*T. durum* Desf., *T. timopheevii* Zhukov., *T. karamyshevii* Zhukov., *Ae. speltoides* Taush. and *L. perenne* L.) were in the cross-combinations with the lowest seed set, below 2.5%.

The results of the 5A and 5D-chromosome monosomics, and three hexaploid wheat varieties being the dominant homozygotes *Ph1*, *Ph1* which were used in the cross-combinations with the related species are presented in Table 2. Their effectiveness of seed set was much lower in comparison to the genotypes listed in Table 1, with an average of 1.3%. In this group, the cross-combination with the highest value was mono-5A Chinese Spring (2.4%). Next were the mono-5D Chinese Spring (1.9%), the variety Chinese Spring (0.8%), whereas the varieties Jara, Favorit had the lowest mean percentage (0.4%). In the cross-combinations involving mono-5A Chinese Spring with the related species the seed set variation ranged from 5.7% to 0.5%. All cross-combinations were separated into four different groups among which the highest effectiveness presented five combinations containing *T. karamyshevii* Zhukov., *T. durum* Desf., *T. dicoccoides* Korn., *Ae. speltoides* Taush., and *Ae. variabilis* Eig. The second group was represented by

three cross-combinations with *T. timopheevii* Zhukov., *T. sphaerococcum* Perc., and *Ae. squarrosa* L. The third group having much lower effectiveness was composed of four cross-combinations including *Ae. triuncialis* L., *T. monococcum* L., *Ae. ovata* L., and *T. boeoticum* Boiss. The fourth group with the lowest effectiveness occurred in the hybridization with *L. perenne* L.

Table 2
Effects of the genotypes (*Ph1 Ph1*) mono -5A, mono -5D and varieties in obtaining the hybrid-F₁ kernels in the hybridization *T. aestivum* L. with the related species

Species related	Mono-5A Chinese Spring		Mono-5D Chinese Spring		Chinese Spring		Jara		Favorit		Total	
	a	b	a	b	a	b	a	b	a	b	a	b
<i>Triticum</i> L.												
<i>T. monococcum</i> L.	821	2.2	809	1.1	758	0.3	811	0	856	0	4055	0.7
<i>T. boeoticum</i> Boiss.	832	1.7	832	2.0	739	0.5	720	0	780	0	3903	0.9
<i>T. durum</i> Desf.	212	5.7	196	6.6	320	1.9	450	0.4	498	0.4	1676	2.1
<i>T. dicoccoides</i> Korn.	201	5.5	196	3.6	260	0.8	320	0	300	0	1277	1.6
<i>T. timopheevii</i> Zhukov.	211	4.3	200	5.0	213	1.4	296	0	248	0	1168	1.9
<i>T. karamyshevii</i> Zhukov.	217	5.9	224	5.3	250	1.2	250	0	301	0	1242	2.2
<i>T. sphaerococcum</i> Perc.	198	3.0	110	4.5	152	2.6	191	1.0	178	1.7	829	2.4
<i>Aegilops</i> L.												
<i>Ae. speltoides</i> Taush.	256	5.1	1828	1.8	320	0.6	178	0	201	0	2783	1.8
<i>Ae. squarrosa</i> L.	164	3.0	174	2.3	267	1.1	192	0	251	0	1048	1.1
<i>Ae. ovata</i> L.	180	2.2	152	2.6	161	1.2	173	0	190	0	856	1.2
<i>Ae. variabilis</i> Eig.	132	4.5	132	6.1	180	0.5	121	0	149	0	714	2.1
<i>Ae. triuncialis</i> L.	196	2.5	175	1.7	188	1.1	170	0	178	0	907	1.1
<i>Lolium</i> L.												
<i>L. perenne</i> L.	1440	0.5	2176	0.6	621	0.5	550	0	624	0	5411	0.4
Sum	5060		7204		4429		4422		4754		25869	
Mean %	2.4		1.9		0.8		0.1		0.1		1.2	
S. error	0.8		0.9		0.5		0.5		0.6		0.6	
S. deviation	2.9		3.3		1.9		1.8		2.2		2.1	
Variance	8.8		10.9		3.6		3.3		4.9		4.5	
CV	28.3		33.0		36.9		251.6		260.9		33.2	

a — number of florets pollinated ; b — % of seed set F₁

The variation among the cross-combinations of mono-5D Chinese Spring with the related species ranged from 6.6% to 0.6% seed set. Four different groups could be distinguished, but the highest values presented four cross-combinations with *T. durum* Desf., *Ae. speltoides* Taush., *T. karamyshevii* Zhukov., and *T. timopheevii* Zhukov. The second group comprised two cross-combinations with *T. timopheevii* Zhukov and *T. dicoccoides* Korn. The third group contained six cross-combinations with *Ae. ovata* L., *T. boeoticum* Boiss., *Ae. squarrosa* L., *Ae. variabilis* Eig.,

Ae. triuncialis L., and *T. monococcum* L. The last group with the lowest value was represented by one cross-combination with *L. perenne* L., only.

The hybridization of the variety Chinese Spring with the related species revealed very low effectiveness of seed set ranging from 2.6% - 0.3%. The highest effectiveness involved one cross-combination with *T. sphaerococcum* Perc.. The second distinct group consisted of two cross-combinations developed with *T. durum* Desf., and *T. timopheevii* Zhukov. The third group included six cross-combinations with the species *T. karamyshevii* Zhukov., *Ae. ovata* L., *Ae. squarrosa* L., *Ae. triuncialis* L., *T. dicoccoides* Korn., and *Ae. speltoides* Taush. The lowest effectiveness exhibited in four cross-combinations including *T. boeoticum* Boiss., *Ae. variabilis* Eig., *T. monococcum* L., and *L. perenne* L.

The effectiveness of hybridization using the varieties Jara and Favorit in crosses with the related species was the same (0.7%) in all 117 cross - combinations made. The variation ranged between 1.7% and 0.2%. In the cross-combinations of Jara, three different groups were separated. The highest effectiveness group presented two cross-combinations with *T. sphaerococcum* Perc., and *Ae. variabilis* Eig. The second group with lower values contained nine cross-combinations with the following species *Ae. speltoides* Taush., *Ae. ovata* L., *Ae. triuncialis* L., *T. boeoticum* Boiss., *Ae. squarrosa* L., *T. monococcum* L., *T. durum* Desf., *T. karamyshevii* Zhukov., and *L. perenne* L. Two cross-combinations with *T. dicoccoides* Korn., and *T. timopheevii* Zhukov. were in the third group having the lowest values.

The cross-combinations of the variety Favorit with the related species indicated three different groups of the effectiveness. The first group involved one cross-combination only with *T. sphaerococcum* Perc. The second one having lower values contained seven cross-combinations with the species *Ae. variabilis* Eig., *Ae. speltoides* Taush., *Ae. ovata* L., *Ae. triuncialis* L., *T. durum* Desf., *T. karamyshevii* Zhukov., and *Ae. squarrosa* L. The lowest effectiveness group involved five cross-combinations with the components of *T. boeoticum* Boiss., *T. dicoccoides* Korn., *T. timopheevii* Zhukov., *T. monococcum* L., and *L. perenne* L.

DISCUSSION

Wild relatives of wheat are a rich source of new genes which can be used for cultivar improvements. Many authors have reported on introgressions of alien genes into bread wheat but disease resistance has been most frequently exploited character in the introgressive hybridization (Rong *et al.* 2000, Ma *et al.* 2001, Aghaee-Sarbarzeh *et al.* 2002, Dhaliwal *et al.* 2002, Liu *et al.* 2002, Hsam *et al.* 2003, Leonova *et al.* 2004, Cai *et al.* 2005, Mobler *et al.* 2005).

In such introduction of alien variation and in the transfer of desirable traits from wild species to wheat cultivars, the *Ph 1* - homoeologous pairing system of *T. aestivum* L. has been frequently included for obtaining the hybrid F₁ - bridge generation (Simon *et al.* 2001, Aghaee-Sarbarzeh *et al.* 2002, Liu *et al.* 2002, Cai *et al.* 2005, Mohier *et al.* 2005). Although other considerations are involved, the decision as to whether to use mono-5B chromosome or *ph1b* systems in an alien-transfer should primarily depend on which technique will yield more

wheat-alien recombinations, and this in turn will depend on which induces the higher level of seed set in F₁ hybrids.

Presented data showed that the 5B chromosome monosomics of the varieties Chinese Spring, Jara and Favorit exhibited higher percentage of seed set in F₁-bridge hybrids in comparison to the *Ph*-mutant Chinese Spring (*ph1b ph1b*). This indicated that the deficiency of one chromosome 5B exerted the stronger influence than the recessive gene *ph1b*. Particularly that in mono-5B Chinese Spring and the *Ph*-mutant Chinese Spring (*ph1b ph1b*) the composition of the crossability genes *Kr1*, *Kr2* were the same and they presented the recessive genotype *kr1 kr1 kr2 kr2* (Riley and Chapman 1967). Therefore, the genes *Kr1*, *Kr2* could not be a cause in the difference of the percentage of seed set between them. Among the monosomic-5B chromosome varieties, the highest effects were observed in mono-5B Chinese Spring not the mono-5B Jara and mono-5B Favorit. In these instances, the advantage has been attributed probably to the recessive genotype of the alleles *Kr1*, *Kr2*. The variety Chinese Spring represented the homozygous recessive composition (*kr1 kr1 kr2 kr2*) which in the Lein's classification (1943) provided the highest percentage of seed set (over 50%) in the intergeneric hybridization, in the generation F₁. Apart from this, in Chinese Spring the next crossability genes were revealed; *kr3* on the chromosome 5D (Krolow 1970, Fedak and Jui 1982), and *kr4* on the chromosome 1A (Luo *et al.* 1992) which could accumulate activity. On the contrary, the varieties Jara and Favorit exhibited the homozygous dominant genotype of the genes *Kr1*, *Kr2*, which in the Lein's classification belonged to the group with the lowest percentage (0 - 10%) in the seed set F₁ bridge hybrids.

Numerous publications showed a higher effectiveness of the recessive gene *ph1b* over that of the deficiency of chromosome 5B in inducing homoeologous pairing of wheat with *Secale*, *Agropyron*, and *Agroticum* hybrids (Dhaliwal *et al.* 1977, Naranjo *et al.* 1988, Wu *et al.* 1989, Ahmad and Comeau 1991). Additionally, they recommended that the gene *ph1b* should be more useful for inducing the transfer of alien genes from *Secale* and *Agropyron* to wheat.

As pointed out by our results, these conclusions have not transmitted to the seed set in F₁-bridge hybrids with other related species. Also, it was shown in the F₁-hybrids between *T. aestivum* L. and *T. urartu* Tum. (Dvorak 1978). Apparently, Koebner and Shepherd (1986) and Murai *et al.* (1997) recorded the higher level of homoeologous pairing between wheat and rye and barley chromosomes by using 5B nullisomy rather than using the *ph1b* mutation of wheat. Their findings suggested that 5B chromosome deficiency may induce increased pairing between wheat and rye, barley homoeologous chromosomes. The results showed that the mono-5A and mono-5D of the variety Chinese Spring exhibited the higher percentage seed set in F₁-bridge hybrids over that of the cultivars Jara, Favorit and Chinese Spring despite of all possessed the gene *Ph1* in the homozygous status. It should be emphasized that in *T. aestivum* L., apart of the *Ph1*, a number of minor genes that either suppress or promote homoeologous pairing were detected on the chromosomes 3AS (Driscoll 1972), 3DS (Mello-Sampayo 1971), 4D (Sears 1976) and 5A, 5D (Feldman 1966). These minor genes could promote seed set in F₁-bridge hy-

brids involving mono-5A and mono-5D Chinese Spring and that is why their genotypes is advantageous.

The variation in the percentage of the seed set in F₁-bridge hybrids between wheat varieties Chinese Spring, Jara and Favorit might be due to either multiple crossability alleles (Krolow 1970) or polymorphisms of the loci *Kr1*, *Kr2* (Snape *et al.* 1995).

Differentiation in the percentage of seed set F₁ hybrids between the related species could be due to; (1) the presence of some crossability genes in their genotypes and; (2) greater homoeology with the wheat chromosomes. Such crossability genes were identified in many species of the genera *Secale* L., *Hordeum* L., *Aegilops* L. and (4x) *Triticum* L. (Riley and Chapman 1967, Falk and Kasha 1981, Farooq *et al.* 1989). Due to the lack of homoeology of the barley chromosomes with wheat chromosomes, Martin and Laguna (1980) observed slightly increase pairing despite the 5B chromosome deficiency in hybrids *H. chilense* × *T. aestivum* L. With respect to the lack homoeology, barley differs more from wheat than rye (Flavell *et al.* 1977). In hybridization involving the species *Ae. speltoides* Taush. the activity of the dominant gene *Ph I* could be revealed (Riley *et al.* 1961, Riley *et al.* 1968, Chen *et al.* 1994, Aghaee-Sarharzeh *et al.* 2002). This gene suppressed the effect of the *Ph I* locus of *T. aestivum* L. and permitted homoeologous recombination between wheat and alien chromosomes in F₁ hybrids. Dvorak (1972) found that *Ae. speltoides* Taush. was polymorphic for the promotion of homoeologous pairing, and identified high- intermediate- and low-pairing type strains. Chen and Dvorak (1984) and Chen *et al.* (1994) suggested that probably two genes in *Ae. speltoides* Taush were involved in the promotion of homoeologous pairing with one system being composed of two duplicate gene loci segregating independently of each other and the other system being composed of several minor genes modifying the effects of major genes. As a result, there was a gradual increase in homoeologous pairing from low to high depending upon the number of genes. Intermediate pairing was determined by dosages of the two *Ph I* genes that can vary from 1 to 3 which also explained why high-intermediate- and low- pairing types existed. In our results, the graduation in the percentage of seed set F₁ with *Ae. speltoides* Taush was observed ranging from 0.5% to 9.9%. This can be interpreted with the 2-gene hypothesis that high chromosome pairing in *Ae. speltoides* Taush was controlled by two genes that showed different effectiveness depending upon the number of genes.

Similar *Ph*-suppressors of wheat system as in *Ae. speltoides* Taush were identified in other wild species like *A. fragile* (Roth) Candargy and *A. cristatum* L. (Almad and Comeau 1991). In *S. cereale* L. and *S. montanum* L. Lelley (1976) and Dvorak (1977) found at least two dominant genes located on different chromosomes suppressing the *Ph I*-locus activity.

Chen, Tsujimoto and Gill (1994) suggested easier transfer of alien genetic material to wheat with the gene *Ph I* than using recessive the *ph1b* mutation or nulli-5B chromosomes induced introgressions. In our results the effectiveness of the *Ae. speltoides* Taush genotype was much lower than the gene *ph1b* or mono-5B chromosome and have not confirmed their prediction.

CONCLUSIONS

1. The deficiency of one 5B-chromosome proved to be the most effective system than the recessive gene *ph1b* in the induction of the seed set in F₁-bridge hybrids of *T. aestivum* L. with the related species.
2. Out of the mono-5B chromosome system in varieties Chinese Spring, Jara and Favorit, the deficiency 5B chromosome of the variety Chinese Spring exhibited the stronger effectiveness in seed set of F₁-bridge hybrids probably due to the presence of the recessive crossability genes. For this reason, this genotype can be recommended as most effective source for the production of fertile F₁-bridge hybrids in wide hybridization of *T. aestivum* L. with its relatives within the family *Poaceae*.
3. Among the related species used in the study, three genotypes could be identified as highly effective: *T. monococcum* L., *T. dicoccoides* Kom. and *Ae. speltoides* Taush. and complementary to the deficiency of 5B-chromosome and the recessive gene *ph1b*. for obtaining the bridge-hybrids.

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