Inheritance of Flower Color in Chickpea

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Flower color is a useful morphological marker in chickpea (*Cicer arietinum* L.). Inheritance of this trait was studied using two white-flowered chickpea genotypes, P 9623 and RS 11, and one blue-flowered genotype, T 39-1. The genetic constitutions of the white flower colors of P 9623 and RS 11 were different, for in an earlier study their F_1 produced pink flowers. The two F_1s of the crosses P 9623 × T 39-1 and RS 11 × T 39-1 also produced pink flowers. Each of the two F_2 populations segregated in 9 pink:3 blue:4 white-flowered plants. These results can be explained by a three-gene model. These three independently segregating genes are probably the same as *C, B,* and *P* reported in the literature earlier. Allelic tests could not be undertaken, as the genetic stocks used in the earlier studies are not available. The genetic constitutions of the three parents and their F_1s are proposed. These accessions should be useful for conducting allelic tests for determining flower color loci in chickpea and for comparative studies with field pea. The seeds of these genetic stocks are maintained at the Genetic Resources and Enhancement Program at ICRISAT and are available for research purposes on request.

Chickpea or garbanzo (*Cicer arietinum* L.) is the third most important food legume worldwide and the most important in South Asia, the Middle East, and Eastern Africa. It is the premier pulse crop of India, accounting for 28% of the total pulse crop area and 38% of its production (FAO 1998). In chickpea, three major and distinct flower colors are identified, namely pink, blue, and white. About two-thirds of the world germplasm accessions at ICRISAT are pink flowered and nearly one-third have white flowers. Those with blue flowers are rare (Pundir et al. 1988).

Kumar (1997) reported complementary gene action for pink flower color in a cross of two white-flowered germplasm accessions, P 9623 (ICC 4854) and RS 11 (ICC 4992). Khan and Akhtar (1934) and Ayyar and Balasubramanian (1936) also reported such complementation. However, the genetic stocks available with the same names as those used by Khan and Akhtar do not correspond with the names in the world chickpea germplasm collection maintained at ICRISAT. In their study, stocks T 9, T 11, and T 39, all with white flower color, have accession numbers ICC 5870, ICC 5874, and ICC 5861, respectively, whereas the listed flower colors of these stocks are pink, blue, and pink, respectively. Thus these do not correspond with the original testers used by Khan and Akhtar (1934) and Ayyar and Balasubramanian (1936). It is highly improbable that those stocks can be traced. Therefore allelic tests are not possible with the original genetic stocks.

Kumar (1997) suggested the need for flower color and genetic studies with P 9623 and RS 11 as two different white flower color testers. Therefore our study was conducted to establish new genetic stocks for flower color in chickpea.

Materials and Methods

An experiment was conducted with three chickpea genotypes: P 9623 (ICC 4854), RS 11 (ICC 4992), and T 39-1 (ICC 5912). Stock T 39-1 is blue flowered and was used as the common male parent in both crosses. Stocks P 9623 and RS 11 are both white flowered and were used as female parents. The crosses P 9623 × T 39-1 and RS 11 × T 39-1 were made in the *Rabi* season 1995 to provide the F_1 generations. The hybrid seeds were grown during the *Rabi* season 1996 to obtain the F_2 seeds. Reciprocal crosses produced in 1996 showed similar results for flower color as those in 1995. Therefore only the first set of crosses made in 1995 was studied further.

The parental, F_1, and F_2 generation seeds of the two crosses were sown on 14 October 1997 on 60 cm ridges on a deep Vertisol under conserved soil moisture conditions at the ICRISAT center. The plot sizes were 10 rows, 4 m long, 60 cm apart for each F_2, and one row each for parents and F_1s. The seeds were planted at a 20 cm spacing within the row. Normal crop management practices were followed. Plants were classified into pink-, blue-, and white-flowered types based on the color of the corolla. Observations on corolla color of freshly opened flowers were recorded on 160 random competitive plants in the F_2 generation of the cross P 9623 × T 39-1 and on 150 plants in the cross RS 11 × T 39-1. For each of the parental and F_1 generations, all 20 plants were observed. The chi-square test was applied to the observed segregation in the two F_2 generations.

Results and Discussion

In both crosses between the white-flowered female parents P 9623 and RS 11 and the blue-flowered male parent T 39-1, the F_1s were pink, suggesting interaction of blue and white flower colors. The data for the three flower colors fit well to the ratio of 9 pink:3 blue:4 white in the F_2 generations of both the crosses, P 9623 × T 39-1 and RS 11 × T 39-1 (Table 1). Results for both crosses showed a supplementary type of gene action for flower color based on segregation for two independent loci.

The same segregation ratio in the F_2 generation of both crosses in this study suggested similar genetic constitutions for the two white-flowered parents P 9623 and RS 11. However, Kumar (1997) reported a pink-flowered F_1 between the two white-flowered parents. This suggested that these parents had different genetic constitutions for their white flower colors. Therefore the trigenic model of inheritance is found appropriate to explain this flower color segregation. Such segregation has been implied or reported earlier (Ayyar and Balasubramanian 1936; D'Cruz

Table 1. Segregation for flower color in the F_2 generation of two crosses of chickpea, *Rabi* season 1997–1998

Cross	Parent/ generation	Flower color	Expected ratio (F_2)	No. of plants		χ^2	*P*
				Observed	Expected		
P 9623 × T 39-1	P 9623	White					
	T 39-1	Blue					
	F_1	Pink					
	F_2	Pink	9	77	90.00	4.44^{NS}	.10–.25
		Blue	3	34	30.00		
		White	4	49	40.00		
RS 11 × T 39-1	RS 11	White					
	T 39-1	Blue					
	F_1	Pink					
	F_2	Pink	9	88	84.38	1.18^{NS}	.50–.75
		Blue	3	30	28.12		
		White	4	32	37.50		

NS = not significant.

and Tendulkar 1970; Phadnis 1976). It would be ideal if allelic tests could be done using the earlier genetic stocks. As pointed out above, those genetic stocks are unlikely to be traced after such a long time. Therefore we suggest that P 9623, RS 11, and T 39-1 be used as new genetic stocks for chickpea flower color studies in the future.

Ayyar and Balasubramanian (1936) used the gene symbols *P, C,* and *B* to indicate flower colors. The symbols Pco_a, Pco_{b1}, and Pco_{b2} used by D'Cruz and Tendulkar (1970) and *A, B,* and *C* used by Phadnis (1976) could be the same as *P, B,* and *C,* respectively. These workers used different gene symbols for flower color without conducting allelic tests with the genetic stocks used in earlier studies. Since the original genetic stocks used in earlier studies are unavailable, a fresh look at the flower color genes and their symbols is necessary.

Assuming the model of Ayyar and Balasubramanian (1936), the flower color in the present study was controlled by three genes: *C, B,* and *P.* All three genes in the dominant condition produced pink color. The pink color of the F_1 would have the genetic constitution of *C-B-P-.* The gene *B* imparted blue color to the petals in association with *C.* Therefore the genetic constitution of the blue-flowered parent, T 39-1, could be *CCBBpp.* The white-flowered parents, P 9623 and RS 11, could have any of six possible genotypes for white flower color; namely *CCbbPP, CCbbpp, ccBBPP, ccBBpp, ccbbPP,* and *ccbbpp.* However, as the two parents produce a pink F_1, between them they must have all three dominant alleles. This suggests only three possible genotypes, namely, *CCbbPP, ccBBPP,* and *ccbbPP.* The absence of trihybrid ratio in the F_2 ruled out the possibility of *ccbbPP.* Kumar (1997) suggested the genetic constitution for P 9623 to be *CCbbPP.* This is based on the observation that this genotype produces white flower color when crossed with most other white flower color lines (Kumar J, unpublished data). Therefore the genetic constitution for RS 11 could be *ccBBPP.* The genetic constitutions of the two pink flower-colored F_1s of these parents with T 39-1 would be *CCBbPp* or *CcBBPp,* as segregation was observed only for two genes in their F_2 generations. Therefore the proposed genetic constitutions and resulting phenotypes of the three parents and F_1s are P 9623, *CCbbPP* (white); RS 11, *ccBBPP* (white); T 39-1, *CCBBpp* (blue); F_1(P 9623 × T 39-1), *CCBbPp* (pink); F_1(RS 11 × T 39-1), *CcBBPp* (pink).

Thus genes *B* and *C* complement each other in the absence of *P* resulting in the appearance of blue color but individually impart white color to the petals. The gene *P* showed supplementary action converting blue to pink color, but without any effect by itself, thus imparting white color to the petals when present singly or in combination with either *C* or *B.* The recessive alleles of all three genes together also produce white petal color.

These results were further confirmed by observing crosses between white-flowered F_2 segregants obtained from P 9623 × T 39-1 and those from RS 11 × T 39-1 (Kumar J, unpublished data). As expected, only pink and blue flowers were obtained from these crosses. This further confirms the genetic constitutions postulated for these genetic stocks in this article.

In our study, flower color was controlled by three independent genes. The study confirmed that white-flowered phenotypes could have different genetic constitutions (Ayyar and Balasubramanian 1936; Davis 1991).

Twenty-two genes are known to govern flower color in the related genus *Pisum.* In another related genus, *Lens,* only two genes have been identified thus far. Muehlbauer et al. (1995) believe that more genes for flower color may exist in *Lens* also. Therefore more than three loci may govern flower color in chickpea (Kumar 1997). Further studies are warranted to investigate this character and determine the evolutionary relationships between chickpea and related genera. Flower color, as a phenotypic marker, will also be useful in molecular marker studies in this crop.

The genetic stocks used and the results obtained in this investigation should be useful in conducting further studies on flower color in chickpea. The seeds of these genetic stocks are maintained at the Genetic Resources and Enhancement Program at ICRISAT and are available for research purposes on request.

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Ph^l Gene Derived from *Aegilops speltoides* Induces Homoeologous Chromosome Pairing in Wide Crosses of *Triticum aestivum*

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The present study was conducted to investigate the effectiveness of the *Ph*^{l} gene transferred from *Aegilops speltoides* into bread wheat cultivar Chinese Spring (CS) in inducing homoeologous chromosome pairing in interspecific crosses using the Chinese Spring line, CS(*Ph*^{l}), carrying the gene. Chinese Spring, as well as CS(*Ph*^{l}), were crossed as female parents with three accessions of *Ae. kotschyi* (UUSS), one accession of *Secale cereale* (RR), two amphiploids of *Triticum durum–Ae. caudata* (AABBCC), and one amphiploid of *Triticum durum–Ae. umbellulata* (AABBUU). Meiotic metaphase I chromosome pairing was studied in all the interspecific crosses with CS as well as CS(*Ph*^{l}). There was significant increase in chiasma frequency in all the crosses with CS(*Ph*^{l}) over those with CS. The extent of induced homoeologous chromosome pairing by *Ph*^{l} in crosses of

CS(*Ph*^{I}) with *S. cereale* was higher than with those of *Ae. kotschyi,* as indicated by higher chiasma frequency per pollen mother cell. Significant reduction in frequency of univalents and increase in bivalents (>14), multivalents, and chiasma frequency in crosses of amphiploids with CS(*Ph*^{I}) as compared to those of CS indicated induced homoeologous pairing between C and D, D and U, and C, D, and U genomes with AB genomes in the presence of *Ph*^{I}. The results of the present study unequivocally demonstrate the effectiveness of *Ph*^{I} gene transferred from *Ae. speltoides* in hexaploid wheat in inducing homoeologous chromosome pairing and suggest that the line CS(*Ph*^{I}) can be effectively used for precise transfer of useful alien genetic variations with least linkage drag.

Related wild and progenitor species of wheat represent a large reservoir of useful variability that can be exploited for wheat improvement. Wide hybridization has contributed significantly to germplasm enhancement of bread wheat. Many agronomically important traits, including resistance to diseases, pests, and abiotic stresses, have been transferred from related species and genera into wheat (Friebe et al. 1996; Gale and Miller 1987; Jiang et al. 1994; Knott and Dvorak 1976; Sharma and Gill 1983).

Although a large number of genes for various traits have been transferred, very few have been successfully incorporated into wheat cultivars and commercially exploited. Most of the alien segments in the translocations either do not compensate well for the loss of wheat chromatin or contain undesirable genes (Jiang et al. 1994). Induction of homoeologous chromosome pairing and molecular tagging of the desirable alien genes are helpful in reducing the linkage drag by retaining the desirable derivatives with markers closely linked to the gene of interest (Dundas and Shepherd 1996).

In wheat, diploid-like behavior and lack of homoeologous chromosome pairing is mainly controlled by gene *Ph1* (Pairing homologous) present on the long arm of chromosome 5B (Okamoto 1957; Riley and Chapman 1958; Sears and Okamoto 1958). Homoeologous chromosome pairing can be achieved either by eliminating chromosome 5B (Sears 1972) or using the *ph1b* mutant (Koebner and Shepherd 1985; Sears 1981). Although induced homoeologous pairing between wheat chromosomes and alien chromosomes has been demonstrated, using different techniques such as the *ph1* mutant, nullisomic 5B stocks, and some accessions of *Aegilops speltoides,* but they require elaborate crossing schemes to achieve the desired gene transfer (Riley et al. 1968; Sears 1973). Therefore a genetic system epistatic to the dominant *Ph* system would be more desirable.

Some genotypes of *Ae. speltoides* harbor genes that are epistatic to *Ph1* as a result of which homoeologous pairing is observed in F_1 plants of *Ae. speltoides* with wheat (Dover and Riley 1972; Feldman and Mello-Sampayo 1967; Riley et al. 1968). Recently the *Ph*^{I} gene (*Ph* inhibitor) of *Ae. speltoides* has been transferred to bread wheat cultivar Chinese Spring (Chen et al. 1994). The *Ph*^{I} gene suppresses the effect of *Ph1* gene and permits homoeologous chromosome pairing. Using the *Ph*^{I} gene stock, Chen et al. (1994) demonstrated homoeologous pairing between the wheat and *Haynaldia villosa* (syn. *Dasypyrum villosum*) chromosomes. The *Ph*^{I} gene stock may, therefore, be a versatile tool for affecting rapid and efficient alien genetic transfers to wheat (Gill 1993).

The results of cytological analysis of interspecific hybrids of Chinese Spring carrying *Ph*^{I} with distantly related species and synthetic amphiploids, demonstrating the effectiveness of the *Ph*^{I} gene(s) in induced homoeologous pairing, are reported in this article.

Table 1. Species and amphiploids used in various crosses

Series no.	Species/amphiploid	2*n*	Genomic formula
1	*Triticum aestivum* cv. Chinese Spring (CS)	42	AABBDD
2	*Triticum aestivum* cv. Chinese Spring carrying *Ph*^{I} gene [CS(*Ph*^{I})]	42	AABBDD
3	*Secale cereale*	14	RR
4	*Ae. kotschyi* accession no. 3502	28	UUSS
5	*Ae. kotschyi* accession no. 3573	28	UUSS
6	*Ae. kotschyi* accession no. 3790	28	UUSS
7	(*T. durum* cv. WH868–*Ae. caudata* accession no. 3556) amphiploid	42	AABBCC
8	(*T. durum* cv. A206–*Ae. caudata* accession no. 3556) amphiploid	42	AABBCC
9	(*T. durum* cv. WH890–*Ae. umbellulata* accession no. 3732) amphiploid	42	AABBUU

Material and Methods

Three accessions of *Ae. kotschyi* (UUSS), one accession of *Secale cereale* (RR), two amphiploids of *Triticum durum–Ae. caudata* (AABBCC), and one amphiploid of *T. durum–Ae. umbellulata* (AABBUU) (Table 1) were crossed as male parents with *T. aestivum* (AABBDD) cv. Chinese Spring (CS) and *T. aestivum* cv. Chinese Spring possessing *Ph*^{I} gene(s), CS(*Ph*^{I}). The seeds of CS(*Ph*^{I}) were obtained from the Wheat Genetics Resource Center, Kansas State University, Manhattan, Kansas, from Dr. Bikram S. Gill.

The spikes of hybrid plants were fixed in 6:3:1 Carnoy's solution for meiotic analysis. The spikes were transferred to 70% ethanol and the anthers squashed in 2% acetocarmine. Pollen mother cells (PMCs) (153–655) at meiotic metaphase I were scored for chromosome pairing in different crosses. Photographs were taken with a Nikon type 104 photomicroscope using Nova 125 ASA film.

Differences within each category of chromosome association in crosses of CS and CS(*Ph*^{I}) with different accessions of wild species and amphiploids were examined statistically using *t*-test statistics. However, significance of differences in overall comparisons between CS and CS(*Ph*^{I}) in each of the crosses was tested by using the chi-square test, considering chromosome pairing (I, II, III + IV) in crosses with CS as the expected values.

Results

Meiotic chromosome pairing at metaphase I and chiasma frequency in PMCs in crosses of *S. cereale, Ae. kotschyi,* and *T. durum–Ae. umbellulata* as well as *T. durum–Ae. caudata* amphiploids with CS and CS(*Ph*^{I}) are given in Table 2, and some photographs of the representative PMCs are also given in Figure 1.

Analysis of chromosome pairing in CS × *S. cereale* revealed very low average chromosome associations, with an average of 0.49 II + 0.05 III + 0.01 IV, and chiasma frequency of 0.61 per PMC. Whereas the cross CS(*Ph*^{I}) × *S. cereale* showed significantly increased (almost 10-fold) chromosome pairing (5.18 II + 0.53 III + 0.16 IV, and 7.47 chiasma frequency per PMC). Furthermore, univalent frequency in CS(*Ph*^{I}) × *S. cereale* was 15.62, which was significantly lower than the 26.84 ob-

Table 2. Mean, standard error and range of meiotic metaphase I chromosome pairing and chiasma frequency in F_1 intergeneric crosses of CS and CS(*Ph^I^*) with *S. cereale*, *Ae. kotschyi*, and amphiploids

Series no.	Cross	2*n*	PMC	Chromosome pairing I	II rod	II ring	II total	III	IV	Chiasma frequency	χ^2
1	CS × *S. cereale*	28	490	**26.84** ±0.094 (18–28)[a]	**0.47** ±0.039 (0–5)	**0.02** ±0.008 (0–2)	**0.49**	**0.05** ±0.011 (0–2)	**0.01** ±0.04 (0–1)	**0.61**	
2	CS(*Ph^I^*) × *S. cereale*	28	280	**15.62** ±0.193 (4–22)	**4.37** ±0.107 (0–0)	**0.81** ±0.069 (0–5)	**5.18**	**0.53** ±0.048 (0–4)	**0.16** ±0.026 (0–3)	**7.47**	69.07**
	|X̄1–X̄2|			11.22**	3.90**	0.79*	—	0.48*	0.15	—	
3	CS × *Ae. kotschyi* accession no. 3502	35	309	**34.30** ±0.085 (28–35)	**0.32** ±0.052 (0–3)	— —	**0.32**	**0.004** ±0.003 (0–1)	— —	**0.33**	
4	CS(*Ph^I^*) × *Ae. kotschyi* accession no. 3502	35	217	**29.67** ±0.227 (21–35)	**2.53** ±0.110 (0–7)	**0.05** ±0.009 (0–1)	**2.58**	**0.04** ±0.014 (0–1)	— —	**2.71**	16.91**
	|X̄3–X̄4|			4.63**	2.21*	0.05	—	0.036	—	—	
5	CS × *Ae. kotschyi* accession no. 3573	35	374	**33.72** ±0.10 (23–35)	**0.62** ±0.054 (0–5)	**0.01** ±0.005 (0–1)	**0.63**	**0.004** ±0.004 (0–1)	**0.002** ±0.005 (0–1)	**0.66**	
6	CS(*Ph^I^*) × *Ae. kotschyi* accession no. 3573	35	153	**28.43** ±0.364 (11–35)	**3.01** ±0.173 (0–2)	**0.01** ±0.006 (0–1)	**3.02**	**0.18** ±0.038 (0–2)	— —	**3.39**	14.94**
	|X̄5–X̄6			5.29**	0.39**	0.00	—	0.18*	0.002	—	
7	CS × *Ae. kotschyi* accession no. 3790	35	213	**34.08** ±0.115 (25–35)	**0.49** ±0.061 (0–5)	— —	**0.49**	— —	— —	**0.49**	
8	CS(*Ph^I^*) × *Ae. kotschyi* accession no. 3790	35	209	**25.21** ±0.297 (17–35)	**4.45** ±0.148 (0–9)	**0.07** ±0.018 (0–1)	**4.52**	**0.22** ±0.033 (0–2)	**0.01** ±0.006 (0–1)	**5.07**	28.21**
	|X̄7–X̄8|			8.89**	3.96**	0.07	—	0.22	0.01	—	
9	CS × Amph. [*T. durum*WH868–*Ae. caudata*]	42	346	**14.69** ±0.168 (9–28)[+]	**8.00** ±0.167 (0–15)	**5.11** ±0.139 (0–12)	**13.11**	**0.34** ±0.032 (0–3)	— —	**18.90**	
10	CS(*Ph^I^*) × Amph. [*T. durum*WH868–*Ae. caudata*]	42	638	**7.87** ±0.074 (3–14)	**9.52** ±0.109 (4–15)	**5.71** ±0.103 (0–12)	**15.23**	**1.13** ±0.40 (0–5)	**0.01** ±0.004 (0–1)	**23.23**	5.39*
	|X̄9–X̄10|			6.82**	1.52[+]	0.60	—	0.79**	0.01	—	
11	CS × Amph. [*T. durum*A206–*Ae. caudata*]	42	283	**19.11** ±0.297 (10–32)	**5.34** ±0.103 (0–16)	**5.42** ±0.141 (0–1)	**10.76**	**0.48** ±0.042 (0–4)	— —	**17.14**	
12	CS(*Ph^I^*) × Amph. [*T. durum*A206–*Ae. caudata*]	42	655	**8.41** ±0.074 (4–13)	**10.01** ±0.105 (2–17)	**5.60** ±0.90 (0–13)	**15.61**	**0.77** ±0.035 (0–5)	**0.01** ±0.05 (0–2)	**22.78**	8.36**
	|X̄11–X̄12|			10.70**	4.67**	0.18	—	0.47[+]	0.01	—	
13	CS × Amph [*T. durum*WH890–*Ae. umbellulata*]	42	324	**14.41** ±0.087 (12–20)	**9.01** ±0.131 (4–15)	**4.65** ±0.12 (0–11)	**13.66**	**0.04** ±0.110 (0–1)	— —	**18.39**	
14	CS(*Ph^I^*) × Amph [*T. durum*WH890–*Ae. umbellulata*]	42	571	**8.16** ±0.086 (4–14)	**9.67** ±0.105 (3–15)	**5.64** ±0.90 (0–11)	**15.31**	**0.97** ±0.039 (0–4)	**0.01** ±0.003 (0–1)	**22.92**	25.00**
	|X̄13–X̄14|			6.25**	0.66	0.99*	—	0.93**	0.01	—	

[a] Figures in parentheses indicate the range; +, *,** significant at 0.1, 0.05, and 0.01 levels of probability, respectively.

served in CS × *S. cereale* (Table 2 and Figure 1a,b).

Comparison of univalent frequency and chromosome pairing in crosses of three accessions of *Ae. kotschyi* with CS and CS(*Ph^I^*) (Table 2 and Figure 1c,d) also indicated significant reduction of univalent frequency and a high level of induced homoeologous pairing in the presence of *Ph^I^*. A cross of *Ae. kotschyi* accession 3790 with CS(*Ph^I^*) showed a large reduction in univalent frequency and increased chromosome associations (25.21 I + 4.52 II + 0.22 III + 0.01 IV, and 5.07 chiasma frequency per PMC) compared to crosses of this accession with CS (Table 2 and Figure 1d).

Chromosome pairing in crosses of synthetic amphiploids involving *T. durum* and *Ae. caudata* or *Ae. umbellulata* as one of the parents with CS(*Ph^I^*) as the other was significantly different from those with CS as indicated by chi-square test. The univalent frequency per PMC was almost half, which was significantly lower than those in crosses with CS. In each class of chromosome associations, an increased level of chromosome pairing was observed in crosses with CS(*Ph^I^*) as compared to crosses with CS, although the differences were not statistically significant in some cases. However, when chromosome associations (II + III + IV) were pooled, significant differences (*t* values ranging from 5.71 to 14.23, significant at 0.01 level of probability) between crosses of CS(*Ph^I^*) and CS were observed, indicating the effectiveness of *Ph^I^* for induced homoeologous pairing (Table 2 and Figure 1e–h).

Discussion

The present study showed that the *Ph^I^* gene(s), transferred from *Ae. speltoides* into *T. aestivum* cv. Chinese Spring could be used efficiently to induce homoeologous chromosome pairing in crosses of related wild species with wheat. There was significant reduction in univalent frequency and a considerable increase in frequency of chromosome associations in crosses of *S. cereale, Ae. kotschyi,* and synthetic

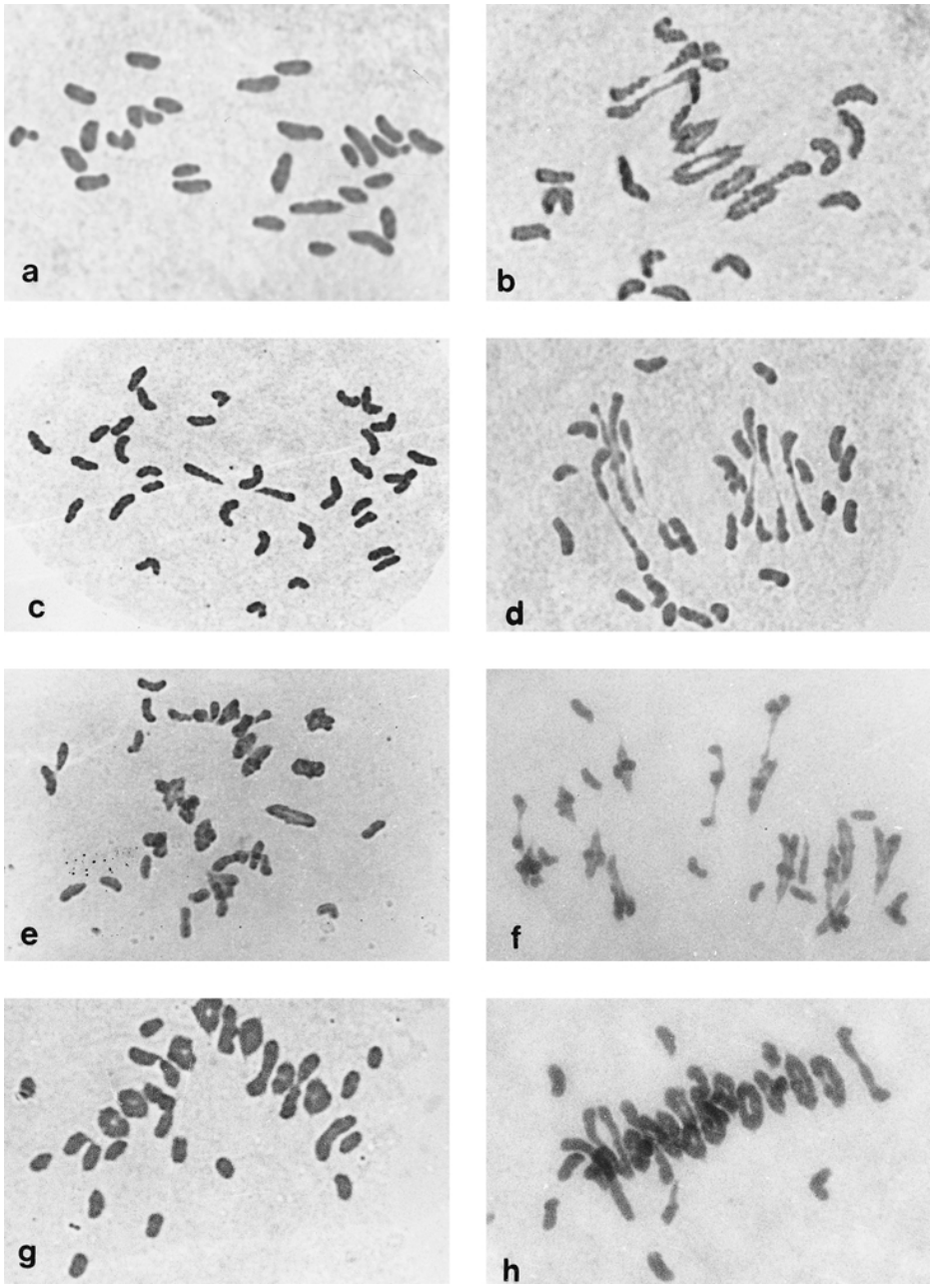

Figure 1. Meiotic chromosome pairing of (a) *Triticum aestivum* cv. Chinese Spring (CS) × *S. cereale* (28 I); (b) *Triticum aestivum* cv. Chinese Spring carrying *Ph*^{I} gene [CS(*Ph*^{I})] × *S. cereale* (12 I + 5 II + 2 III); (c) CS × *Ae. kotschyi* accession no. 3790 (33 I + 1 II); (d) CS(*Ph*^{I}) × *Ae. kotschyi* accession no. 3790 (19 I + 5 II + 2 III); (e) CS × (*T. durum* cv. WH868–*Ae. caudata* accession no. 3556) amphiploid (14 I + 14 II); (f) CS(*Ph*^{I}) × (*T. durum* cv. WH868–*Ae. caudata* accession no. 3556) amphiploid (9 I + 9 II + 5 III); (g) CS × (*T. durum* cv. WH890–*Ae. umbellulata* accession no. 3732) amphiploid (14 I + 14 II); (h) CS(*Ph*^{I}) × (*T. durum* cv. WH890–*Ae. umbellulata* accession no. 3732) amphiploid (7 I + 16 II + 1 III).

amphiploids of *T. durum–Ae. caudata*/*Ae. umbellulata* with CS(*Ph*^{I}) compared to those with CS.

Chromosome pairing in crosses of *S. cereale* with CS was very low and comparable with that reported by Miller and Riley (1972), Schlegel and Weryezco (1979), and Romero and Lacadena (1982) (Table 3). The *Ph*^{I} gene was effective in inducing a high level of homoeologous chromosome pairing in the F_1 hybrid of CS(*Ph*^{I}) × *S. cereale.* The extent of induced chromosome paring in this cross with rye was also comparable with those in crosses of *T. aestivum* nullisomic 5B × *S. cereale* and *T. aestivum ph1* mutant × *S. cereale* (Table 3) reported by Dhaliwal et al. (1977), Riley (1960), and Shneider and Prilinn (1984). In crosses of CS(*Ph*^{I}) × *Ae. kotschyi,* a high level of induced homoeologous pairing was observed which was comparable with that reported by Sears (1977) in crosses of *T. aestivum* nullisomic 5B stock with *Ae. kotschyi* (Table 3).

The extent of induced homoeologous pairing by *Ph*^{I} in crosses of CS(*Ph*^{I}) with *S. cereale* was slightly higher than that of *Ae. kotschyi,* as indicated by a higher chiasma frequency per PMC. This may be attributed to differences in residual homology among genomes participating in homoeologous pairing in the two sets of crosses. *Ae. kotschyi,* being an allopolyploid, might possess a diploidization mechanism capable of interaction with *Ph* and *Ph*^{I}.

In crosses of synthetic amphiploids with genomic constitution of AABBDU and AABBDC containing *Ph*^{I}, a significant reduction in univalent frequency and an increased frequency of bivalents, multivalents, and chiasma frequencies indicated the induced chromosome association of C and D, D and U, and D, C, and U with A and B genomes. The precise identification of the associating genomes in the presence of *Ph*^{I} can, however, be unequivocally established through the genomic *in situ* hybridization (GISH) or fluorescent *in situ* hybridization (FISH) techniques (Le et al. 1989; Mukai 1996; Mukai and Gill 1991).

The results of this investigation clearly demonstrated that the *Ph*^{I} gene(s) derived from *Ae. speltoides* is capable of inducing homoeologous chromosome pairing by suppression of the activity of the *Ph1* gene of wheat. Although induced homoeologous pairing and transfer of desirable genes from related species of wheat into hexaploid wheat using the *ph1b* mutant, nullisomic 5B, and some accessions of *Ae. speltoides* have been demonstrated, the systems require development of special cytogenetic stocks and elaborate crossing schemes to achieve the desired gene transfer (Riley et al. 1968; Sears 1973). Riley et al. (1968) were able to transfer a segment carrying the stripe rust resistance gene (*Yr8*) from *Ae. comosa* to wheat by first crossing a wheat monosomic addition line carrying the alien chromosome with *Ae. speltoides* and then selecting for recombinants among the backcross progeny. With the use of *Ph*^{I} transferred from *Ae. speltoides,* transfer of any other undesirable chromatin from *Ae. speltoides* can be avoided. The wheat stock carrying *Ph*^{I} has the advantage over the *ph1*^{b} mutant because it eliminates the need for aneuploid stock such as nullisomic 5B. This stock can, therefore, be successfully used for precise transfer of useful variability from related species into wheat through interspecific hybridization with least linkage drag.

Table 3. Meiotic chromosome pairing in F_1 hybrids of *Triticeae* with manipulation of genetic systems that control meiotic pairing

Series no.	Chromosome pairing Cross	2*n*	I	II	III	IV–V	Reference
1	*T. aestivum* × *Ae. kotschyi*	35	3 2.8	1.03	0.05	—	Sears (1977)
2	*T. aestivum* (nullisomic 5B) × *Ae. kotschyi*	35	12.0	7.80	1.96	0.12	Sears (1977)
3	*T. aestivum* × *S. cereale*	28	27.8	0.10	—	—	Miller and Riley (1972)
			27.1	0.40	—	—	Romero and Lacadena (1982)
			26.9	0.52	—	—	Schlegel and Weryezco (1979)
4	*T. aestivum* (nullisomic 5B) × *S. cereale*	27	17.3	3.36	0.88	0.08	Riley (1960)
5	*T. aestivum* (*ph1*) × *S. cereale*	28	12.4	4.90	1.80	0.08	Dhaliwal et al. (1977)
6	*T. aestivum* (*ph1*) × *S. cereale*	28	13.2	5.70	0.58	0.37	Shneider and Prilinn (1984)

The use of synthetic amphiploids of *T. durum* with nonprogenitor species like *Ae. caudata* and *Ae. umbellulata* in crosses with hexaploid wheat stock carrying *Ph*^{I}, will facilitate controlled and compensated introgression of alien genes into the D genome of wheat, as it is generally believed that the manipulation of the D genome chromosomes causes fewer genetic imbalances among the derivatives of wide crosses. Moreover, the recovery of fertile derivatives with introgression of desired variability is relatively easy and faster in crosses of synthetic amphiploids with wheat stocks like CS(*Ph*^{I}) as compared to direct crosses of nonprogenitor species with these stocks.

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