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WHY HAVEN'T WE FOUND THE B-GENOME DONOR FOR WHEAT?

Various species of the Sitopsis Section Zhuk. of the genus Aegilops have been considered as possible donors of the B-genome of the polyploid wheats, Triticum aestivum (AABBDD) and T. turgidum (AABB)(1). However, mainly due to the lack of support from cytological evidence, the origin of the B genome in polyploid wheats remains controversial. The species of the Sitopsis Section were assigned the genome symbol S rather than B (2).

Reading a series of papers by Charpentier et al. (3), I have detected the interaction of Ph1 gene and the hemizygous ineffective bivalentization genes (Table 1). In the absence of the Ph1 gene, the bivalentization system in hemizygous condition allowed both homologous and homoeologous pairing to occur so that homology and homoeology were fully expressed by the 18.87 to 20.84 chiasmata expected for the ABDEE genome constitution in hybrids of T. aestivum (AABBDD) and naturally-occurring tetraploid Agropyron elongatum (=Thinopyrum scirpeum; EEEE= $J^eJ^eJ^eJ^e$). In the presence of one or two doses of the Ph1 gene, homoeologous pairing was inhibited and the bivalentization genes reduced the chiasmata number between the two E genomes by greatly decreasing the number of ring bivalents. The ABDEE hybrids involving the accession Ae31 had the genotype which reduced the chiasma frequency to the extent that the two homologous E genomes might be regarded as homoeologous. These data demonstrated that the interaction(s) of various genetic systems controlling chromosome pairing might lead us to erroneous conclusions.

With this insight, I reviewed the meiotic pairing data between T. turgidum

(AABB) and diploid species having the A or S genome that were kindly provided by Dr. G. Kimber of University of Missouri, Columbia, Missouri, who maintained a rich database of meiotic data. An interesting pattern emerged as shown in Table 2. Among the triploid hybrids between I. turgidum and a putative A-genome donor species, 15 showed 4.3 to 6.1 bivalents with low trivalent frequency and only one case of high homoeologous pairing revealed by high trivalent frequency. In contrast, when triploid hybrids involved an S-genome diploid species there were three classes of pairing pattern. In addition to the two observed in AAB hybrids, 14 cases of ABS hybrids had low bivalent frequency. Most hybrids showing this class of pairing pattern involved the diploid A. longissimum (S^lS^l) as one of the parents. Most of the hybrids involving A. speltoides (SS) showed high number of trivalents. However, all three classes of pairing pattern were observed among the hybrids involving either of these diploid species. Therefore, it can be concluded that only the gene frequencies differ in these species so that one pairing pattern may become more prevalent than the others.

It was well known that A. speltoides accessions used in studies possess genes which can overcome the effect of the Ph1 gene so that homoeologous pairing occurs. The first class of pairing pattern is attributable to these pairing promoter genes. The third class of pairing pattern would have to be attributed to the gene(s) found in the low pairing A. longissimum shown by Avivi (4). This low pairing genotype of A. longissimum resulted in reduced multivalent frequency in the induced tetraploid and reduced pairing in the hybrid with I. aestivum. Thus the genes responsible for the third pairing pattern are similar to the ones in natural tetraploid Agropyron elongatum studied by Charpentier et al. (3). Since the same gene system tends to reduce the pairing even between distant

homologues in the presence of the Ph1 gene (Table 1), the third class of pairing pattern observed in ABS hybrids (Table 2) should be regarded as abnormal. The second class, although occurring 5 out of 33 cases of ABS hybrids, represents the genotypic condition allowing the expression of true homology. This class of pairing had similar c values (5) for both AAB and ABS triploid hybrids. If we could conclude that T. monococcum is the A-genome donor, we should also conclude that one(or more) of the species in the Sitopsis Section is(are) the B-genome donor(s). Accordingly, the basic genome symbol for these species should be changed from S to B, as done by some people already (6), but superscripts should be used to indicate the modifications that made them slightly different from the B genomes in the tetraploid and hexaploid wheats.

I hope that my observations presented here can stimulate the reassessment of scientific evidence for and/or against the identity of the B-genome donor.

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Table 1. Interactions between the Ph1 gene of *Triticum aestivum* and the bivalentization gene system of natural tetraploid *Agropyron elongatum* (= *Thinopyrum scirpeum*) in their pentaploid hybrids having the genome constitution ABDEE*.

Dosage of Ph1	Accession of Agropyron	I	rod II	ring II	total II	xta
0	Ae05	6.52	4.89	6.21	11.10	20.84
0	Ae31	7.44	5.40	4.21	9.61	18.87
1	Ae05	19.85	5.20	2.28	7.48	9.96
1	Ae31	25.24	3.26	1.30	4.56	6.28
2	Ae05	22.49	4.46	1.55	6.01	7.90
2	Ae31	24.38	3.50	1.44	4.94	6.89

*Excerpt from Charpentier et al. (1988).

Table 2. Classes of meiotic pairing pattern in triploid hybrids between tetraploid wheat Triticum turgidum and diploid species having either A or S genome.

Genome	Class	II	III	c*	No. cases
AAB	1	2.16	1.67	0.47	1
	2	4.30-6.10	0-0.32	0.31-0.76	15
ABS	1	3.65-5.96	1.00-2.50	0.51-0.75	14
	2	3.55-6.17	0.04-0.80	0.32-0.61	5
	3	0.40-2.50	0-0.28	0.03-0.20	14

*c value as defined in Alonso and Kimber (5)