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ANALYSIS OF MEIOTIC PAIRING IN HYBRIDS OF COMMON WHEAT WITH THREE ALIEN SPECIES

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ABSTRACT

Meiotic analysis based on mathematical models was carried out to investigate genomic relationships in some tetraploid and pentaploid wheat F_1 hybrids. High optimized value of x (relative affinity) and observed value of c (chromosome arm pairing frequency) below 0.5 in the tetraploid hybrids of *Triticum aestivum* (2n=42) with *Aegilops mutica* (2n=14) and *Thinopyrum bessarabicum* (2n=14) indicated that there were no chromosomal homologies between the genomes of *T. aestivum* and *Ae. mutica* and between those of *T. aestivum* and *Th. bessarabicum*. The study also revealed that there are no homologous genomes present between *T. aestivum* and the tetraploid *Aegilops variabilis* (2n=28).

Key words: Relative affinity, meiotic analysis, *Aegilops mutica*, *Ae. variabilis*, *Thinopyrum bessarabicum*.

Chromosome pairing in the hybrids is a reliable method of assessing the genomic relationships. As early as in 1930, Kihara [1] made chromosome pairing as the primary means of understanding the genomic affinities. Various workers since then have used chromosome pairing as a cytological tool to demonstrate homology or homeology between the chromosomes of different species. Kimber et al. [2] on the basis of the work done by previous workers [3, 4] developed methods for measuring genomic relationships in triploid, tetraploid and pentaploid hybrids when the genomes had unequal affinities. A theory has been put forward [3, 5] which predicts chromosome pairing in hybrids and species, both euploid and aneuploid. The theory can be extended to more complicated situations where both homologous and homoeologous pairing occurs in the absence of chromosome 5B of wheat.

Models have been developed [6–8] which simulate expected chromosome pairing in triploid, tetraploid and pentaploid wheat F_1 hybrids. Meiotic analysis of hybrids involving *Aegilops mutica*, *Thinopyrum bessarabicum* and *Ae. variabilis* is scanty. In the study reported, meiotic analysis of F_1 hybrids utilizing these species was done to investigate their

evolutionary relationships and genomic affinities with A, B and D genomes of hexaploid wheat.

MATERIALS AND METHODS

The meiotic analysis was carried out at the Division of Genetics, Indian Agricultural Research Institute, New Delhi. The calculations were done by Dr. Gordon Kimber, Department of Agronomy, University of Missouri, Columbia, USA. The material used in the present study comprised the crosses (i) *Triticum aestivum* (2n=6x=42, genomes AABBDD) cv. Chinese Spring monosomic 5B (CS mono5B) x *Aegilops mutica* Boiss. (*T. tripsacoides* Jaub. and Spach., 2n=2x=14, genome TT), (ii) CS mono5B x *Thinopyrum bessarabicum* (Savul. & Rayss) A. Love. (=*Agropyron junceum* (L.) P.B., 2n=2x=14, genome JJ), (iii) *T. aestivum* 5BL 7BL of Bersee x *Aegilops variabilis* Eig. (*T. perigrinum* Hackel, or *T. kotschyi* Boiss., 2n=4x=28, genome UUSS), (iv) *T. aestivum* cv. Zlatka x *Ae. variabilis*, and (v) dw 5BL 7 BL Maulin x *Ae. variabilis*. Anthers of the F_1 hybrids were stained in leucobasic fuchsin and smeared in a drop of 1% acetocarmine. All observations were made on temporary slides. Chromosome configurations were recorded at meiotic metaphase I in all the F_1 hybrids. Open and closed meiotic figures were recorded separately. The various terms used, such as pairing, meiotic figure, meiotic configuration and meiotic analysis, c (chromosome arm pairing frequency), relative affinity, x and y have been defined earlier [2, 3, 6]. The symbol Xt (chiasmata) stands for the number of pairs of chromosome arms connected by chiasmata. In a tetraploid, it has the maximum value of four times the basic number while in pentaploid, Xt and c are indicated by the expression c = Xt/4xB where B is the basic number of the species.

The four possible types of tetraploid hybrids are designated 4:0, 2:2, 2:1:1 and 3:1 depending on the closeness of the genomes involved in the hybrid. The tetraploid hybrids are designated 4:0 when all the genomes have equal affinity. The number of possible combinations increases at higher ploidy levels. At the pentaploid level, there are six possible situations, i.e. 5:0, 2:2:1, 2:1:1:1, 3:2, 3:1:1 and 4:1. The genomic constitution of the 4:1 model seems to be rare and so far no examples have been observed. Models can be discriminated based on the c value for the expected number of different meiotic configurations. They can also be differentiated with the increase of decrease in x. The best fit model is one which gives the smallest sums of squares of differences between the observed and calculated meiotic figures.

RESULTS AND DISCUSSION

The expected frequencies of different meiotic figures were calculated from the available models [3, 5–7]. The models of chromosome pairing in tetraploid and pentaploid hybrids have been derived from hexaploid x diploid and hexaploid x tetraploid crosses. For tetraploid hybrids, situations such as AAAA, AABB, ABCD, AAAB can be used. The results are presented in Tables 1 and 2.

Table 1. Observed and calculated meiotic analysis in hexaploid x diploid F_1 hybrid of intergeneric crosses of wheat

Hybrid/genome	Obs/ model	Univa- lents	Bivalents rod	Bivalents ring	Triva- lents	Quadrivalents ring	Quadrivalents chain	c	SS	x
T. aestivum Chinese	obs	8.56	5.12	1.48	1.68	0.20	0.10	0.44		
spring monosomic 5B	2.:2	9.01	4.89	1.69	1.09	0.58	0.07		0.79	0.78
x *Aegilops mutica*	2:1:1	9.25	4.06	1.21	0.40	0.84	0.16	2.16	0.72	
ABDT (2n=28)	3:1	9.13	4.05	1.00	1.46	0.91	0.18	2.25	0.50	
T. aestivum Chinese	obs	12.16	5.18	1.18	0.56	0.07	0.02	0.32		
spring monosomic 5B	2:2	13.12	5.34	1.14	0.47	0.13	0.00		0.95	0.90
x *Agropyron junceum*	2:1:1	13.34	4.16	0.54	1.13	0.41	0.05		3.29	0.55
ABDJ (2n=27)	3:1	13.34	4.16	0.54	1.14	0.41	0.05		3.29	0.50

obs—observed; c—mean chromosome arm pairing frequency; SS—sums of squares; and x—relative affinity of the most closely related genomes.

TETRAPLOID HYBRIDS

(i) *CS mono 5B* x *Ae. mutica*. Although Chinese Spring monosomic 5B was crossed to *Ae. mutica* to obtain euploid (2n=28) and aneuploid (nulli5B, 2n=27) hybrids, only 2n=28 F_1 hybrid was obtained. The optimized value of x is 0.78 and 0.72 for 2:2 and 2:1:1 models, respectively. The value of c is 0.44, hence the analysis fits the 2:2 model better than 2:1:1. The value of c would suggest that there are no homologous genomes present. The fit between the observed and expected values for the 2:2 model is quite good, as the sum of squares for 2:2 model is low (0.79) as compared to 2:1:1 (2.19) and 3:1 (2.29) models. Simulating the 2:2

Table 2. Optimized value of relative affinity (x) and sums of squares (SS) of the differences between observed and expected values in different models for pentaploid F_1 hybrids

Hybrid/genome	c	Parameter	Values in different models 2:2:1	3:2	2:1:1:1	3:1:1	4:1
T. aestivum Bersee 5BL7BL	0.09	SS	0.01	0.01	0.01	0.005	0.001
x *Aegilops variabilis*		x	0.50	0.50	0.78	0.81	0.86
ABDUS (2n=35)							
T. aestivum cv. Zla tka	0.08	SS	0.003	0.003	0.003	0.003	0.003
x *Ae. variabilis*		x	0.50	0.50	0.50	0.50	0.50
ABDUS (2n=35)							
T. aestivum Maulin 5BL7BL	0.05	SS	0.015	0.015	0.012	0.003	0.007
x *Ae. variabilis*		x	0.50	0.50	0.95	1.0	1.0
ABDUS (2n=35)							
T. aestivum Bersee 5BL7BL	0.50	SS	12.04	10.09	12.67	12.67	12.67
x *Ae. variabilis*		x	0.81	0.99	0.50	0.50	0.50
ABDUS (2n=34)							

c—mean chromosome arm pairing frequency.

model, Kimber and Alonse [7] analysed data of several hybrids obtained from different sources. In the two examples involving *Ae. speltoides* and *Ae. mutica* from the Sitopsis section, it has been found that an increase in association may lead to a better fit to the 2:2 model. In these hybrids the value of c ranged from 0.12 to 0.63. The same explanation also applies to the present results.

Even under the circumstances when F_1 hybrid mono5B *T. aestivum* x *Ae. speltoides*, was deficient for chromosome 5B, the 2:2 model was the best fit and the sum of squares very small (Alonso, unpublished). Similar observations that gave a value of x equal to 0.70 have been recorded [9]. It has also been observed [7] that the suppression of the Ph1 gene results in two effects. First, an increase in synapsis, and second, the revealing of small but otherwise undetectable differences in affinity. From these results, they concluded that the A, B and D genomes of *T. aestivum* are equally separated from the S genome of *Ae. speltoides*. The accession of *Ae. mutica* in the present study carries the mechanism which suppresses the Ph1 gene of *T. aestivum* and *T. turgidum*. In these cases the presence of trivalents and quadrivalents may not be only due to the presence of translocations but also pairing between homoeologous chromosomes due to suppression of gene Ph1 by the presence of the *Ae. mutica* genome. Thus, the affinity of the *Ae. mutica* genome with any of the wheat genomes is no greater than among the A, B and D genomes in the hybrid. These results support the findings obtained earlier [7, 10, 11] for the species *Ae. speltoides* and *Ae. longissima* of the Sitopsis section.

(ii) *CS mono5B* x *Thinopyrum bessarabicum*. The tetraploid hybrid involving monosomic 5B of *T. aestivum* x *Th. bessarabicum* also fits the 2:2 model best but with a low value of c (0.32), which shows that there is no homology between the genomes of *T. aestivum* and *Th. bessarabicum*. The optimized value of x is quite high (0.90) and the sum of squares low (0.95) as compared to both 2:1:1 and 3:1 models. The fit between the observed and expected for the 2:2 model is quite good, particularly when the hybrid has only 27 chromosomes. The increase in association of chromosomes is due to the absence of Ph1 gene which allows homoeologous chromosome pairing. A similar pattern of chromosomes pairing was observed in the hybrid *T. aestivum* cv. Chinese Spring x *Ae. mutica*.

Trivalents and quadrivalents were observed in both the tetraploid hybrids involving *Ae. mutica* and *Th. bessarabicum* and were predicted by the 2:2 model. Many of the multivalent associations may not be the consequence of translocation heterozygosity arising in the F_1 hybrid but are expected due to homoeologous pairing in the hybrids were gene Ph1 is either missing or suppressed. These results support the findings of Kimber and Alonso [7] for different genomes in the crosses of several *Triticum* and *Aegilops* species.

The use of these models of chromosome pairing helps in determining the genomic relationship and affinities between the species and the information on chromosome pairing reveals the potential for transferring alien genetic variation into breadwheat. Genome analysis based on the study of chromosome pairing continues to be a single most useful

criterion of revealing phyletic relations between the species. Further, these mathematical models allow calculation of similarities between genomes and the calculations of MI associations due to each possible pairwise combination of genomes [12].

PENTAPLOID HYBRIDS

The three 35-chromosome hybrids between wheat varieties and *Ae. variabilis* (syn. *Aegilops kotschyi*) have very low pairing (c = 0.09, 0.08 and 0.05), therefore, no conclusions can be derived regarding genomic affinity. The sums of squares of the differences between the observed and expected meiotic pairing values are also low. Similar results were also obtained by Espinasse and Kimber [8] in *T. aestivum* x *Ae. kotschyi* (2n=35, genome ABDUS[1]) which did not show strong genomic affinity. In this case also, the c value was quite low (0.001).

The value of c for the 34-chromosome hybrid Bersee 5BL7BL x *Ae. variabilis* is typical of that observed in the absence of Ph locus. The optimized value of x is highest (0.99) for the 3:2 model as compared to 2:2:1, 2:1:1:1, 3:1:1, and 4:1 models, even though the optimized values of x (0.81) and sum of squares (12.04) are also high for 2:2:1 models as compared to 3:2 model (sum of squares 10.09). The high value of the sum of squares of differences is partly due to the absence of the chromosome carrying Ph locus. The value of c (0.50) in this hybrid also indicates best fit to the 3:2 model. Of course, it does not mean that there are three and two sets of homologous genomes present. It only means that they are pairing in a group of two. Also, it does not confirm which particular genomes are pairing. It could be speculated that S and B genomes form the group of two, and A, D and U the group of three genomes. However, there is no evidence to support this speculation. The Sitopsis species involved in the evolution of *Ae. kotschyi* are not yet defined [13].

The value of x in the 3:2 model is determined both by the relative affinity of the three and the two more closely related genomes. If one of the three most closely related genomes is slightly different from the other two, then the competition for the pairing partners will result in two genomes pairing more frequently [8]. The competition will be more acute in the 3:2 situation than in the 3:1:1 model because of the presence of the another pair of most closely related genomes.

In the present study, the value of x for 2:2:1 model is 0.81, which is next lower to 3:2 model, and the sums of squares for 2:2:1 model is 12.04, which is higher than 10.09 (for 3:2 model) but lower than for the other three models. The observations tend to fit the 2:2:1 model, but the features of the 3:2 model are such that it allows the recognition of genetic differentiation that otherwise may not be observed.

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