Developments in the meiotic analysis of hybrids. I. Review of theory and optimization in triploids

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The theory, construction and optimization of a model of chromosome pairing in triploid hybrids are re-examined and the model reconstructed. A new approach to optimization is described that removes a bias in the estimation of x , the measure of relative affinity, by weighting the observed and calculated meiotic figure frequencies by the number of chromosomes in each figure type. The amended analysis is compared with its antecedent and with other models.

Keywords: meiotic analysis, pairing models, triploids.

Introduction

The meiotic analysis of polyploid hybrids is an important element in taxonomic and evolutionary studies of plants. It first developed as a somewhat subjective comparison of the meiotic behaviours of various diploid and polyploid interspecific hybrids. To the extent that the hybrids formed bivalents in approximate multiples of the basic chromosome number for those taxa so it was interpreted that their parental species held that many genomes in common.

The earliest known example is the work of Rosenberg (1909) on *Drosera* (sundew) species. He observed 10 bivalents among the 30 chromosomes of a triploid interspecific hybrid and concluded that 10 of the 20 pairs of chromosomes of the tetraploid species were homologous with those of the diploid. Much more extensive, pioneering work was carried out by Kihara and colleagues from 1919 onwards on the genome analysis of the 25 or so species in the genera *Triticum* and *Aegilops* (see review by Lilienfeld, 1951). Subsequent research, much of it non-cytogenetic, has borne out the essential correctness of these conclusions. An understanding of genomic relationships is now a common element in plant taxonomy, e.g. the Triticeae (Dewey, 1984); *Brassica* (U, 1935); *Gossypium* (Phillips, 1966); *Oryza* (Chang, 1976).

In the past decade more objective, quantitative approaches to the analysis of meiosis in polyploid hybrids have been developed by Driscoll *et al.* (1980) for one type of hexaploid hybrid, and by Alonso & Kimber (1981), Kimber & Alonso (1981), and

Espinasse & Kimber (1981) for triploid, tetraploid and pentaploid hybrids in general. These assess the relative affinities of the more and less closely related genomes in a hybrid by proposing models of chromosome pairing and then searching for the values of affinity which give the best fit between the data and the model. Since models of this kind approximate the pattern of preferential pairing amongst the genomes present, they are applicable only to triploid or higher ploidy hybrids where each chromosome has a 'choice' of pairing partners.

Other approaches to the meiotic analysis of triploid hybrids have been described by Sybenga (1988). These allow a range of parameters to describe the meiotic behaviour to be estimated, depending on the assumptions incorporated in the particular model. More complex models for triploids and tetraploids have also been developed by Crane & Sleper (1988 and 1989). These are described as 'overparametrized', proposing more variables than there are degrees of freedom in the data from which they can be estimated. As a result they return possible ranges for the various parameters rather than single solutions.

The use of meiotic analysis to examine genome relationships has a number of theoretical and practical advantages over other methods which compare, directly or indirectly, the DNA from different species. As emphasized by Kimber *et al.* (1981) and Kimber & Yen (1990), it assesses more DNA, which is better dispersed among and within chromosomes, than any other technique. It is less demanding of expensive chemicals and equipment than molecular genetics. The

results are of relevance to population genetics, genetic resources and breeding work in that the demonstration that two genomes are sufficiently similar to pair at meiosis is direct evidence that genes may be moved between them by recombination. This approach does require, however, that the hybrid can be produced and brought to flowering. Moreover, in representing a comparison across whole genomes, detailed similarities and differences may be obscured.

The models of Alonso & Kimber (1981), Kimber & Alonso (1981) and Espinasse & Kimber (1981) are in the process of being modified and extended. In this, the first of a series of papers, the theory behind the models is examined afresh, the process of model building amended and a revised approach to optimization outlined, all in the context of triploid hybrids. These principles will subsequently be applied to higher ploidy levels.

Theory

A number of definitions, simplifications and assumptions are necessary to describe and construct the various models of pairing in polyploid hybrids. Whilst many have been described elsewhere (see Driscoll *et al.*, 1979; Kimber *et al.* 1981; Alonso & Kimber, 1981), a few are new and others changed. For completeness they are summarized below.

Pairing is defined as the consequence of both synapsis and chiasma formation between two chromosome arms, or among two or more chromosomes, the result of which is seen as bound arms at metaphase I of meiosis. Thus 'pairing' among three chromosomes may lead to the formation of a trivalent.

Meiotic figure refers to any chromosome (univalent) or group of chromosomes connected by chiasmata (bivalents, trivalents, etc.).

Meiotic configuration is the set of meiotic figures generated from a single homoeologous group of chromosomes within a cell. Similarly *arm configuration* is the consequence of pairing among a single homoeologous group of chromosome arms.

The mean of all meiotic figures, whether observed or calculated, on a per cell basis, will be referred to as a *dataset*. *Optimization* is the reduction of an observed dataset to a model, and the estimation of values for the variables within it. The term *meiotic analysis* is defined more broadly than by Kimber *et al.* (1981), and includes both the collection of data on meiotic figure frequencies and their interpretation.

The value c is the measure of the mean arm-pairing frequency and is the proportion of paired arms observed compared to the maximum possible for that level of ploidy. Cases of two arms bound by two or more chias-

mata are treated as equivalent to those bound by only one as the consequences for meiotic figure formation are the same.

The development of all the models is based on a number of simplifications and assumptions about the nature of meiosis. The first is that each chromosome arm represents an independent pairing element, in particular uninfluenced by the pairing activity of the other arm of that chromosome. Much of the justification for this assumption lies in the proposition developed by Sved (1966) that synapsis is initiated near the telomeres of a chromosome and then extends towards the centromere. Subsequent reviews of meiosis (Sybenga, 1975; Fussell, 1987; Jones, 1987) endorse this as a general principle. Although this is a simplistic view of the pairing process (Maguire, 1984), it does form a pragmatic basis for model building.

Direct evidence of interference across the centromere is to be found largely in the meiotic behaviour of autotetraploids, where it is assumed that the four homologous chromosomes are essentially identical. The results are mixed. The studies of Morrison & Rajhathy (1960) and Callow *et al.* (1984), for example, show independence between chromosome arms, whilst others, e.g. Timmis & Rees (1971), Kuspira *et al.* (1984), Yen & Kimber (1990), show an excess of bivalents. It is unclear, however, whether these latter observations have relevance to pairing in interspecific hybrids for two reasons. First, it is unknown if the cause of excess bivalents is interference across the centromere or preferential pairing due to cryptic differences among homologues. Secondly, in most hybrids the more closely related genomes will not be truly homologous and the interference (if such it is) observed in autotetraploids may not occur where there are greater differences among homoeologous chromosomes.

A second assumption is that the pairing of one arm with another precludes any involvement of a third. This derives from the observation that in many hybrids simple multivalents, i.e. chains and rings, predominate. More complex figures, e.g. 'frying-pan' trivalents, indicating that one arm has exchanged pairing partners somewhere along its length, tend to be rare. It is also assumed that the role of any translocations present in generating multivalents is negligible. Should a dataset include a high frequency of complex figures, or figures whose number of chromosomes exceeds the ploidy level of the hybrid, it is generally unanalysable by these methods.

The last assumption is that the tendency to pair between homoeologous arms of two genomes is the same regardless of the homoeologous group or arm they represent. The equality of pairing in either arm of

Fig. 1 Relationship between observed and calculated rod bivalents in triploid hybrids.

a homoeologous group can be justified retrospectively because when the 24 triploid hybrids, listed by Kimber & Alonso (1981), were analysed by the methods described below, they revealed close to a 1:1 ratio between observed and calculated rod bivalent numbers (see Fig. 1); whereas any inequality should be manifest as an excess of observed rod bivalents.

The identity of pairing patterns amongst homoeologous groups cannot be generally demonstrated as most reported datasets do not differentiate between groups. In fact there is good reason to suspect that they may be heterogeneous where a genome has been restructured in the evolution of a new polyploid species (see, for example, Feldman, 1966). Nevertheless, Kimber *et al.* (1981) demonstrated that the assumption of equality of pairing among homoeologous groups in the calculation of a 'C similarity' between genomes of wheat species gave values very close to a much more exhaustive 'T similarity', which incorporated individual estimates of pairing for each homoeologous group. In practice, therefore, this assumption appears tenable but it should be understood that the best-fit model and estimates of relative affinity represent an integration across all the homoeologous groups.

The triploid model, the particular subject of this paper, can be built up by considering first the pairing among a single group of homoeologous arms of the genomes 1, 2 and 3. As with the model of Alonso & Kimber (1981) and the restricted model of Sybenga (1988), a symmetrical relationship among the genomes is assumed. Genomes 1 and 2 are designated the more closely related pair (not necessarily homologous) with a

relative affinity of x . Both are equally and more distantly related to genome 3 with a relative affinity of y , so that $x > y$. The relative affinity is expressed in the proportions of the three different arm pairings that may be formed; i.e. the ratio among the (1-2), (1-3) and (2-3) arm pairs is $x:y:y$. Finally, to further relate the two variables, by definition $x + y = 1$ and x lies in the range 0.5–1.0.

In triploids any homoeologous group may form up to two arm pairs. From this it follows that the mean arm-pairing frequency, c , may be calculated from an observed dataset as $(\text{rod bivalents} + 2 \times (\text{ring bivalents} + \text{trivalents})) / (2 \times \text{basic number})$. With the relative affinity reflected in the ratio of pairing, the frequency of genomes 1 and 2 pairing will be $cx/(x + 2y)$, and of genomes 1 and 3, or 2 and 3, $cy/(x + 2y)$. The proportion of homoeologous arm groups with no pairing will be $(1 - c)$. From these considerations the frequencies of the four possible arm configurations can be found (Table 1).

The result for a homoeologous group of three chromosomes in terms of meiotic configurations may be determined by establishing a 4×4 array and siting the arm configurations and their frequencies along the margins. The resulting configuration for each cell is established by considering the behaviour of the two set of arms (nominally long and short) and its frequency as the product of the marginal frequencies (Table 2). Summing over the whole array gives the frequencies of each meiotic configuration and figure (Table 2).

For any given observed dataset, the best estimate of x is that which minimizes the differences between it and the calculated dataset. The merit function chosen here is a Weighted Sums of Squares of Differences (WSSD) defined as

$$\Sigma(O - E)^2$$

where, on a per cell basis, O is the observed meiotic figure number $\times$ number of chromosomes in that figure, and E is the calculated (expected) meiotic figure number $\times$ number of chromosomes in that figure. To carry out this optimization a computer program has been written in Turbo Pascal for the Apple Macintosh,

Table 1 Calculation of arm configuration frequencies

Genome pairs	Relative affinity	Pairing frequency	Arm configurations	Frequency
1-2	x	$cx/(x + 2y)$	(1-2,3)	$cx/(x + 2y)$
1-3	y	$cy/(x + 2y)$	(1-3,2)	$cy/(x + 2y)$
2-3	y	$cy/(x + 2y)$	(2-3,1)	$cy/(x + 2y)$
			(1,2,3)	$(1 - c)$

Table 2 Meiotic configurations, figures and their frequencies

Arm configurations and frequencies	Long arm			
	(1-2, 3) $cx/(x+2y)$	(1-3, 2) $cy/(x+2y)$	(2-3, 1) $cy/(x+2y)$	(1, 2, 3) $(1-c)$
Short arm				
(1-2, 3) $cx/(x+2y)$	Ⓐ*+I $c^2x^2/(x+2y)^2$	III $c^2xy/(x+2y)^2$	III $c^2xy/(x+2y)^2$	Ⓒ+I $c(1-c)x/(x+2y)$
(1-3, 2) $cy/(x+2y)$	III $c^2xy/(x+2y)^2$	Ⓐ+I $c^2y^2/(x+2y)^2$	III $c^2y^2/(x+2y)^2$	Ⓒ+I $c(1-c)y/(x+2y)$
(2-3, 1) $cx/(x+2y)$	III $c^2xy/(x+2y)^2$	III $c^2y^2/(x+2y)^2$	Ⓐ+I $c^2y^2/(x+2y)^2$	Ⓒ+I $c(1-c)y/(x+2y)$
(1, 2, 3) $(1-c)$	Ⓒ+I $c(1-c)x/(x+2y)$	Ⓒ+I $c(1-c)y/(x+2y)$	Ⓒ+I $c(1-c)y/(x+2y)$	3I $(1-c)^2$
Meiotic figures	Frequency			
I	$c^2(x^2+2y^2)/(x+2y)^2+2c(1-c)+3(1-c)^2=c^2(x^2+2y^2)/(x+2y)^2+c^2-4c+3$			
Ⓒ	$2c(1-c)(x+2y)/(x+2y)=2c(1-c)$			
Ⓐ	$c^2(x^2+2y^2)/(x+2y)^2$			
III	$c^2(4xy+2y^2)/(x+2y)^2$			

*I = univalent; Ⓒ = rod bivalent; Ⓐ = ring bivalent; III = trivalent.

which searches the permissible values of x for that which returns the smallest WSSD.

For the analysis of Alonso & Kimber (1981), C. F. Crane provided an analytical solution. For the present analysis one is also possible from the formulae:

$$w = \frac{8c^2 + 4c - 3 - 9t + 4g + u}{14c^2}$$

and

$$x = \frac{2 - 2w \pm \sqrt{6w - 2}}{3 - w}$$

where t is the number of trivalents per cell/ b ; g is the number of ring bivalents per cell/ b ; u is the number of univalents per cell/ b ; b is the basic number; and c is the mean arm-pairing frequency. As a square root is involved, two solutions for x are theoretically possible but in practice only the positive root results in x in the feasible range of 0.5–1.0.

Observations and discussion

The amended analysis developed here differs in two respects from that of Alonso & Kimber (1981). The first is that here the relative affinities within each set of homoeologous arms are considered first, then the

pattern of pairing for those arms that results for a given value of c , and finally the consequences for meiotic configuration formation when both the long and the short arms of the homoeologous group are considered. In contrast, Kimber & Alonso (1981) commenced by distributing pairing amongst homoeologous groups according to the expansion of the binomial $[1 + (1-c)]^2$, then the resultant configurations are derived in the light of the relative affinities amongst the chromosome arms. In practice, at the triploid level, this leads to the same formulae for configuration and figure frequencies as those developed here. At higher ploidy levels, however, it results in discrepancies between the resulting equations and independent theoretical expectations of chromosome behaviour. These are discussed in later papers.

The second distinction is that Kimber & Alonso (1981) optimized x by seeking to minimize the sums of squares of difference between meiotic figure numbers in observed and calculated datasets. This appears unsatisfactory because it gives equal consideration to a univalent as, for example, to a trivalent, even though the former represents the disposition of one chromosome rather than three. This would bias x towards estimates favoured by the frequencies of smaller figures.

The present analysis was applied to the datasets reported in Alonso & Kimber, (1981) and representative results are shown in Table 3. Overall there is good

Table 3 Comparison between the present approach to meiotic analysis and that of Alonso & Kimber (1981). [For sources of data see Alonso & Kimber, (1981)]

Hybrid and genomes	<i>c</i>	O/A/C*	I	III	II	III	<i>x</i>
1. (<i>Triticum umbellulatum</i> × <i>T. dichasians</i>) × <i>T. umbellulatum</i> CUU	0.714	<i>O</i>	7.20	2.90	2.70	0.85	
		<i>A</i>	7.25	2.86	2.68	0.88	0.925
		<i>C</i>	7.29	2.86	2.72	0.86	0.929
2. <i>T. timopheevii</i> × <i>T. boeoticum</i> AAG	0.743	<i>O</i>	7.31	2.18	3.18	0.93	
		<i>A</i>	7.18	2.67	3.12	0.74	0.945
		<i>C</i>	7.09	2.67	3.03	0.84	0.937
3. <i>T. turgidum</i> × <i>T. sharonensis</i> ABS ¹	0.321	<i>O</i>	12.85	3.30	0.25	0.35	
		<i>A</i>	12.97	3.05	0.25	0.47	0.595
		<i>C</i>	13.04	3.05	0.32	0.40	0.753
4. <i>T. timopheevii</i> × <i>T. sharonensis</i> AGS ¹	0.351	<i>O</i>	12.05	3.62	0.25	0.40	
		<i>A</i>	12.31	3.19	0.29	0.58	0.500
		<i>C</i>	12.40	3.19	0.37	0.49	0.740
5. <i>Collinsia austromontana</i> × <i>C. solitaria</i> PPQ	0.905	<i>O</i>	6.67	1.33	5.34	0.33	
		<i>A</i>	6.74	1.21	5.34	0.39	0.982
		<i>C</i>	6.77	1.20	5.38	0.36	0.984
6. <i>Gossypium hirsutum</i> × <i>G. longicalyx</i> × ADF	0.377	<i>O</i>	22.25	5.63	1.15	0.93	
		<i>A</i>	22.28	6.10	1.02	0.82	0.834
		<i>C</i>	22.25	6.10	0.99	0.86	0.824

**O* = observed frequencies of figures; *A* = calculated frequencies through analysis of Kimber & Alonso (1981); *C* = calculated frequencies through analysis described here.

agreement between the two approaches. As might be expected, when observed and calculated frequencies of figures are compared, the present analysis tends to produce a better fit for numbers of trivalents at the expense of a poorer one for the ring bivalents, due to the weighting applied. Two exceptions to the general consensus of the two approaches are the crosses of *Triticum turgidum* and *T. timopheevii* with *T. sharonensis*, which now appears to show some preferential pairing. Given that genomes from *Sitopsis* species bear the best, although not a good, resemblance to the second genomes of tetraploid wheats (Kimber, 1983), then a somewhat stronger affinity between the B and S¹ and G and S¹ genomes, respectively, as compared to the A genome, may be suspected. However the value of *x* is still low and there are no grounds to dispute the earlier conclusion that none of the genomes in these hybrids show homology.

A direct comparison may also be made with the restricted preferential pairing model of Sybenga (1988). Again, his formulae for figure frequencies and those developed here are equivalent but *x* is estimated by

considering only the ratio of trivalents to ring bivalents, a simplification justified in this special case by the frequency of meiotic configurations of three univalents, or one univalent and one rod, depending solely on the value of *c* and not of *x*. A comparison is made in Table 4. The present approach gives very similar estimates of *x*, and has the advantage of general applicability to any optimization in any meiotic analysis, regardless of the model or ploidy level.

A less direct comparison may be made with the more complex triploid model of Crane & Sleper (1989). This seeks permissible ranges for seven variables defining meiotic chromosome behaviour, and is overparametrized because only 3 d.f. (number of figure classes minus one) are available. With fewer assumptions and a greater number of variables this model achieves very good fits between observed and calculated figure frequencies.

The computational burden is immense, however, a single analysis apparently taking from 13.6 min to 3.3 h on a mini-computer, whereas the present model takes less than 1 s on a micro-computer. Table 5 makes a

Table 4 Comparison between the present approach to meiotic analysis and that of Sybenga (1988). [For sources of data see Sybenga (1988)]

Hybrid	x estimated by Sybenga	x estimated by present method
<i>Trifolium repens</i> $\times$ <i>T. nigrescens</i>	0.912	0.929
<i>Hordeum jubatum</i> $\times$ <i>H. californicum</i>	0.936	0.937
Hybrid involving <i>Avena barbata</i>	0.890	0.888
Hybrid involving <i>Avena barbata</i>	0.821	0.797
<i>H. vulgare</i> $\times$ <i>H. bulbosum</i>	0.932	0.932

Table 5 Comparison between the present approach to meiotic analysis and that of Crane and Sleper (1989). [For sources of data see Crane & Sleper (1989)]

Hybrid and genomes	Estimates by Crane & Sleper			Estimates by present method		
	s_1	s_2	s_3	s_1	s_2	s_3
<i>Triticum kotschy</i> $\times$ <i>T. umbellulatum</i> UUS ¹	0.962	0.036	0.002	0.953	0.023	0.023
<i>T. kotschy</i> $\times$ <i>T. dichasians</i> CUS ¹	0.333	0.333	0.333	0.499	0.250	0.250
<i>T. columnare</i> $\times$ <i>T. umbellulatum</i> UUM	0.911	0.089	0.000	0.910	0.045	0.045
<i>Critetion californicum</i> $\times$ <i>Elymus canadensis</i> SHH ^v	0.543	0.229	0.228	0.537	0.231	0.231
<i>T. turgidum</i> $\times$ <i>T. sharonensis</i> ABS ¹	0.569	0.216	0.215	0.604	0.198	0.198
<i>Medicago falacata</i> $\times$ <i>M. sativa</i>	0.334	0.334	0.333	0.442	0.279	0.279

comparison between some of Crane & Sleper's (1989) estimates of s_1 , s_2 and s_3 , the ratio of association among the three possible pairs of genomes, where $s_1 > s_2 > s_3$, and corresponding estimates from the present model where $s_1 = x/(x + 2y)$, and $s_2 = s_3 = y/(x + 2y)$. In none of these six examples, nor in a further 10, unlisted here, did the present model lead to markedly different conclusions concerning genomic relationships. We believe that the complexity of their approach is unjustified when set against the simplifying assumptions it still contains (that the chromosomes in each homoeologous group are similarly differentiated and the absence of translocations) and the inherent quality of meiotic data, subject as it is to sampling and observational error.

The amended approach to optimization in triploids, described here, removes a bias in estimating x compared to that described by Alonso & Kimber (1981) and is applicable to any other model. In general it does not require any revision of earlier conclusions drawn from the analysis of triploid hybrids. Although it is possible to generate more sophisticated analyses, their real value is questionable.

A note on programs

All the programs for the analysis of meiosis in species hybrids described in this series have been written in Turbo Pascal to run on the Apple Macintosh. Copies of

the source code and the compiled programs are available from the authors upon receipt of an 800 K or 1.4 MB initialized disk. Use of the source code requires Turbo Pascal.

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