NOTES AND COMMENTS

THE INTER-RELATIONSHIP BETWEEN CHIASMA FREQUENCY AND INTERLOCKING *

MILKA SHOPOVA

Department of Botany, Faculty of Natural and Mathematical Sciences,
Skopje, Yugoslavia

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It is now sixty years since bivalent interlocking was first found in *Salamandra maculosa* (Schreiner and Schreiner, see Belar, 1929) and numerous instances of it have been described subsequently (see Smith and Boothroyd, 1942; Matsuura, 1944). Most of these cases have been studied with a view to elucidating the mechanism of chiasma formation and their value is now only historical. Few have been connected with the relationship between interlocking and chiasma frequency and even these have produced conflicting results (see Smith and Boothroyd, *loc. cit.*). During a study of chromosome behaviour in *Allium flavum* and *Capsicum annum*, frequent interlocking was observed and the chiasma frequency relationship in interlocked and non-interlocked cells was studied.

1. MATERIAL AND METHODS

Meiotic material of *Allium flavum* was obtained from the John Innes collection and from natural populations collected in Macedonia and North Bulgaria. The material of *C. annum* is from the collection of Professor Hawkes (see Shopova, 1966b).

Flower buds were fixed in acetic-alcohol 1 : 3 and subsequently squashed in acetic orcein.

2. OBSERVATIONS

1. *Allium flavum*. This species is a member of the Paniculatum group (section Macrospatha) and is characterised by large chromosomes with, however, a relatively low chiasma frequency (Levan, 1935). In all three collections interlocking occurred commonly, though it varied in extent between individuals and from locality to locality. It was highest in John Innes material and lowest in that from Bulgaria.

As has been commonly observed by other authors, interlocked bivalents in *Allium* are of two principal types according to whether the interlocking is true or false in character. False interlocking in fact occurs more commonly than true interlocking, but attention was confined to the latter. All the observed cases of true interlocking were of the proximal type involving two ring bivalents each of which possessed one terminal and one sub-terminal chiasma.

Under normal circumstances, bivalents in *Allium flavum* form either one

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or two chiasmata which tend to be distally located (see table 1). In all three collections it was observed that :

- (i) Individuals with the most extensive interlocking had lower mean chiasma frequencies than equivalent individuals in which interlocking was either absent or else only occasional (see table 1).
- (ii) Cells with interlocked bivalents have a higher mean chiasma frequency than those cells from the same individual without interlocking. This increase is, in fact, due to a general rise in chiasma frequency and is not confined to those chromosomes which are either involved or not involved in interlocking.
- (iii) The increased chiasma frequency in cells with interlocking was, however, due, in part at least, to an increase in interstitial chiasmata in those chromosomes not involved in the interlock, thus producing three-chiasmate bivalents (see table 1).
- (iv) Where a reduced chiasma frequency was present, pairing was always complete.

When material from different localities is compared some further differences become apparent :

- (i) Significant differences exist between localities for chiasma frequencies in cells both with and without interlocking (see table 2).
- (ii) A negative correlation exists between chiasma frequency and the extent of interlocking.

Interlocking is most common in the John Innes material and less common in the Bulgarian. Chiasma frequency, on the other hand, is lowest in the John Innes material and highest in the Bulgarian (see table 1).

2. *Capsicum annum*. Interlocking was observed in only one individual. But two interlocked bivalents were observed often enough to permit a comparison of chiasma characteristics (table 3). There is a significant difference between the mean chiasma frequency of cells with and without interlocking (table 4). This difference depends upon an increase in chiasma frequency in the cells showing interlocking. The chiasma frequency in cells where no interlocking occurs is in fact identical to that of cells taken from other individuals of the same variety which show little or no interlocking (table 3). As far as they go, the results from *Capsicum* support those from *Allium*.

3. DISCUSSION

Interlocking occurs where there is an increase in the chiasma potential of the cells within an individual. Since all cells within an anther must share a common genotype this must imply that the elevation in chiasma frequency depends upon internal differentiation of the environment within that anther. The nature of this variation in intra-anther environment is not known but Rees and Naylor (1960) have described and analysed an equivalent situation in rye. Here, too, different regions of the same anther include cells with different chiasma frequencies.

Normally in both *Allium flavum* and *Capsicum annum* the chiasma frequency is low. Interlocking is impossible where the chiasma potential of a pair of bivalents is also low, for a minimum of two chiasma in each of two bivalents is required to produce an interlock. It would seem reasonable to conclude

TABLE 1

Chiasma frequencies at diakinesis in Allium flavum (2n=16) without and with interlocking (in all three cases both + and — cells are taken from the same plant)

Material	Interlocking	No. cells analysed	No. Xta per biv.			Frequency of bivs. with			Mean Xta/cell	Mean Biv. Xta per plant	Percentage of interlocking per plant
			1	2	3	Inter. Xa	Term. Xa	Total Xa			
John Innes	—	50	150	250	—	20	630	650	13		
	+	25	40	150	10	80	290	370	15	1.7	26
Macedonia	—	50	100	300	—	28	672	700	14		
	+	20	10	142	8	60	258	318	16	1.8	12
Bulgaria	—	50	50	350	—	50	700	750	15		
	+	10	—	70	20	40	140	180	18	2.1	8

TABLE 2

A comparison of the chiasma properties of cells with and without interlocking in three individuals of Allium flavum from different localities (see table 1)

Cell type	Mean cell Xa frequency			Com- parison of	df	<i>t</i>	<i>p</i>
	John Innes (1)	Mace- donia (2)	Bul- garia (3)				
With interlocking	15.0	16.0	18.0	(1) <i>v.</i> (2)	43	2.61	0.02-0.01
				(1) <i>v.</i> (3)	33	10.41	0.001
				(2) <i>v.</i> (3)	28	4.54	0.001
Without interlocking	13.0	14.0	16.0	(1) <i>v.</i> (2)	98	1.87	0.1-0.05
				(1) <i>v.</i> (3)	98	6.38	0.001
				(2) <i>v.</i> (3)	98	3.82	0.001
Locality	Mean cell Xa frequency			df	<i>t</i>	<i>p</i>	
	With interlocking		Without interlocking				
John Innes Macedonia Bulgaria	15.0		13.0	73	5.5	0.001	
	16.0		14.0	68	3.66	0.01-0.001	
	18.0		16.0	58	4.82	0.001	

TABLE 3

A comparison of Xa frequency in cells with and without interlocking in three individuals of var. S₆ of C. annum (2n=24)

Variety-S ₆ , plant type		No. cells	No. Xta per biv.		Frequency of bivs. with		Total Xa	Mean	
			1	2	Inter Xa	Term Xa		Xta/ cell	Xta/ biv.
Individual with 20 per cent. inter- locking	Cells with interlocking	10	25	95	4	211	215	21.5	1.79
	Cells with- out inter- locking	10	60	60	—	180	180	18.0	1.50
Individuals with only occasional interlocking	Individual no. 1	10	67	53	—	173	173	17.3	1.44
	Individual no. 2	10	64	56	—	176	176	17.6	1.46

TABLE 4

A comparison of the chiasma frequency of cells with and without interlocking in the same individual of C. annuum (see table 3)

Mean cell Xa frequency		df	t	P
With interlocking	21.5	18	6.97	0.001
Without interlocking	18.0			

therefore that, in both species, the occurrence of interlocking depends on an initial increase in chiasma frequency in a proportion of the cells within a common anther.

What is difficult to accommodate on this basis is the surprising fact that individuals of *Allium flavum* from different localities show a negative correlation between interlock frequency and chiasma frequency (table 1).

Equally surprising, at first sight, is the fact that related species may show quite different behaviour with regard to their capacity for interlocking. Thus *Allium pulchellum* and *A. paniculatum*, both of which are very similar to *A. flavum*, rarely undergo interlocking. Yet both species have a higher chiasma frequency than that normally found in *A. flavum*. The same principle applies in the genus *Capsicum* where *C. frutescens* with a chiasma frequency greater than in *C. annuum* interlocks but rarely. However, the behaviour of autopolyploid cells in different species illustrates admirably the difficulties of extrapolating from the behaviour within the species to that found between different species (John and Henderson, 1962). It is not adequate to simply compare chiasma conditions in different species when discussing variations in the frequency of interlocking. Thus any factor capable of producing an association of non-homologous chromosomes either prior to or during pairing might be expected to influence the capacity for subsequent interlocking provided, of course, that the chiasma frequency is adequate for interlocking. One such factor is the extent and distribution of heterochromatic material, which is known to have a marked propensity for non-homologous association.

It is clear then that the conditions which determine interlocking are likely to vary from species to species. As yet it is impossible to formulate general rules governing its occurrence. In part this stems from the fact that to date it has been possible to observe only the end product of the process of interlocking. Thus, the actual process, like chiasma formation itself, is inferred from its observable consequences.

4. SUMMARY

1. Interlocking of bivalents has been observed in 8 to 26 per cent. of the *p.m.c.*'s in diploid individuals of *Allium flavum* and *Capsicum annuum*.

2. A comparison of the chiasma properties of cells with and without interlocked bivalents shows that there is an increase in the chiasma frequency of both the chromosomes involved in the interlock and in those not so involved.

3. Chiasma frequency is only one of the conditions governing the occurrence of interlocking. Thus in species related to *A. flavum* and *C. annuum*, where the chiasma frequency is sufficient to allow it, interlocking has been observed only in occasional cells and there is a negative correlation between chiasma frequency and interlock frequency in individuals of *A. flavum* from different localities.

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