Desynapsis in the Bothriochloa Hybrids

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A number of meiotic abnormalities which are genetically controlled have been described (Darlington, 1937). One of these, desynapsis (Li *et al.*, 1945), affects normal meiosis and results in the arrival of most of the chromosomes at the metaphase plate as univalents rather than bivalents. The chromosomes pair normally at pachytene but begin to unpair at diplotene and are completely unpaired at diakinesis and metaphase I.

Celarier (1955) slightly modified the classification originally established for asynapsis by Prakken (1943), and mentioned two readily distinguishable types of desynapsis. In the "medium-strong" type some of the chromosomes remain paired until metaphase I, but in the "complete" type none of the chromosomes remain paired.

Desynapsis in Bothriochloininae was first reported by Celarier and Mehra (1959). A desynaptic plant of *Dichanthium annulatum* was discussed and the desynapsis was of the "medium-strong" type. *Bothriochloa intermedia* is a highly polymorphic species extending from southern Africa to Australia and the Pacific Islands. Comparative morphological data suggest that this species hybridizes in nature with *Bothriochloa ischaemum, B. pertusa, B. ewartiana, Dichanthium annulatum, Capillipedium parviflorum* and *C. spicigerum*. In the greenhouse hybrids between *Bothriochloa intermedia* and several species of *Bothriochloa, Dichanthium* and *Capillipedium* can be obtained with relative ease. Cytological studies of these hybrids have shown preferential pairing and/or autosyndesis within genomes of the same species, and formation of a large number of bivalents at metaphase I (de Wet *et al.*, in press) in these hybrids. The present study reports the study of meiosis in some hybrid populations where different degrees of desynapsis were observed.

The plants were grown in an experimental plot at the Oklahoma Agricultural Experiment Station under fairly uniform conditions (Celarier and Harlan 1956). Bud material for cytological studies was fixed in Carnoy's fluid and stored in a refrigerator. Microsporocytes were smeared and stained with acetocarmine.

Experimental Results

Hybrids were produced by using *B. intermedia* (X-750), a highly sexual and self sterile tetraploid plant, as the female parent; and *B. intermedia* 5450, *B. caucasica* 4066 and *Dichanthium annulatum* (X-98) as the male parents. The chromosome configurations at metaphase I in these plants are presented in Table 1. Except for *B. intermedia* (X-750), all other parent plants are fairly regular in their meiotic behaviour. On an average 18 to 19 bivalents were observed at diakinesis and metaphase I. Trivalents and quadrivalents were rare or absent. At anaphase and telophase I some cells are characterized by the presence of 2 to 4 dividing or nondividing laggards. These lagging chromosomes were usually incorporated in the daughter nuclei and at dyad spore stage rarely 1 to 2 micronuclei were observed. The second divisions were regular and at the tetrad spore stage, usually no micronuclei were formed.

The maternal parent plant *B. intermedia* (X-750) has a comparatively irregular meiotic behaviour. On an average 7.32 univalents per cell were

TABLE 1. CHROMOSOME CONFIGURATIONS OF HYBRIDS AND THEIR PARENTS AT METAPHASE I

No.	Plant	2n	Av. per cell and range I	II	III	IV
	Parents					
	(i) Bothriochloa					
			7.3	16.3	0.03	0
1	B. intermedia (X-750)	40	0-16	12-20	0-1	0
			1.9	18.9	0	0.06
2	B. intermedia 5450	40	0-0	18-20	0	0-1
			3.50	18.00	0	0.12
3	B. caucasica 4066	40	2-6	16-19	0	0-1
	(ii) Dichanthium					
			1.2	17.10	0.1	1.1
4	D. annulatum (X-98)	40	0-6	15-20	0-1	0-3
			4.2	17.9	0.1	0.1
5	(X-750) X5450---1	40	1-10	15-20	0-1	0-1
			7.14	16.3	0	0.1
6	-2	40	0-14	13-20	0	0-1
			22.8	8.6	0	0
7	-3	40	0-40	1-20	0	0
			27.1	6.4	0.04	0
8	(X-750) X4066---1	40	20-38	1-10	0-1	0
			26.8	6.6	0.04	0
9	-2	40	20-34	3-9	0-1	0
			37.5	1.3	0	0
10	(X-750) X (X-98)-1	40	36-40	0-3	0	0
			17.4	10.0	0.8	0.1
11	-2	40	12-22	8-12	0-2	0-1
			3.1	18.0	0.2	0.1
12	-3	40	1-6	16-10	0-1	0-1
			36.0	1.5	0	0
13	(X-750) O. P.*	39	29-39	0-5	0	0

*Progeny from open pollinated seed of B. intermedia (X-750) where the male parent was an unknown B. intermedia.

observed at diakinesis and metaphase I with a range of 0 to 16. The average number of bivalents was 16.3, trivalents were rare and quadrivalents were never observed. At anaphase and telophase I a large number of dividing and nondividing laggards (average 6.4 per cell) were present. Some cells with unequal chromosome distribution at anaphase I, such as, 18-22, 19-21 were recorded. The laggards frequently formed 1 to 4 micronuclei. No bridges or fragments were recorded. In the second division, at anaphase, nondividing laggards were observed which gave rise to micronuclei formation in some cases at the tetrad spore stage.

Even though hybrids with "complete" desynapsis were not observed, a number of hybrids showing different degrees of "medium-strong" desynapsis were recorded (Fig. 1-6). Chromosome configurations at metaphase I of such "medium strong" desynaptic hybrids along with some synaptic hybrids are presented in Table 1. They demonstrate the occurrence of desynapsis in hybrids between, and within, different species, and between different genera in the Bothriochloininae.

The meiotic behaviour of the synaptic hybrids (X-750) X (5450) - 1 and (X-750) X (X-98) - 3 was fairly regular and similar to the male parent. The hybrid (X-750) X (5450) - 2 had an irregular meiosis similar to the maternal plant (X-750).

In the other hybrids, which can be classified as desynaptic, the range of desynapsis varies from an average of 17 univalents per cell at metaphase I in (X-750) X (X-98) - 2, to an average of 37.5 univalents per cell in (X-750) X (X-98) - 1. The material is not suitable for a detailed study of chromosome pairings at early prophase I. Observations at pachytene and diplotene, of the desynaptic plants (X-750) O.P. and (X-750) X (X-98) - 1, revealed, on an average a larger number of bivalents than at diakinesis and metaphase I. Detailed studies at diakinesis showed on an average 1 to 2 more bivalents per cell than at metaphase I in all the desynaptic hybrids. Although at diakinesis and metaphase I most of the chromosomes appeared as univalents, in most cases these univalents were arranged in pairs on the slide. Rarely a trivalent was seen and no quadrivalents were recorded. At anaphase and telophase I lagging chromosomes were invariably seen in all cells of the desynaptic plants. These laggards were, in general, observed to be dividing univalents and in (X-750) X (4066) hybrids the number was often so large that it became impossible to get an accurate count. At least more than 20 dividing laggards were observed, however, in these hybrids. In other desynaptic plants the number of dividing laggards was not so large and varied between an average of 5 and 10 per cell. Not more than three and often only one or two micronuclei were formed at the dyad spore stage, as most of the dividing univalents appeared to reach the poles and to be incorporated in the daughter nuclei. Unequal distribution of chromosomes at anaphase I was common.

In the second division, at anaphase and telophase, nondividing laggards were commonly observed and at tetrad spore stage up to 4 micronuclei were seen.

Cytology of the hybrid (X-750) X (5450) - 3 was of particular interest. Cells with 0 to 40 univalents at metaphase I were observed. The average number of univalents per cell was 22.8 and the extremes were found only in a few cells.

Discussion and Conclusions

Desynapsis in the hybrids reported here is of the "medium-strong" type as defined by Prakken (1943) and modified by Celarier (1955). However, the range of variation is great and approaches complete desynapsis in some hybrids. In all cases a large number of cells with a varying number of bivalents are always present. There is a decrease in the average number of bivalents as meiosis proceeds from prophase to metaphase I, (with a relatively small decrease after diakinesis). Chromosome behaviour in the desynaptic hybrids is similar to the previously reported solitary case of desynapsis in *Dichanthium annulatum* (Celarier and Mehra 1959). Dividing laggards are invariably present at anaphase I. These dividing univalents in the "medium-strong" type of desynapsis are considered to be associated with the formation of metaphase plate by Johnsson (1944). As a result of the dividing univalents in the first anaphase the second division is also very irregular and a number of nondividing laggards which, finally, may constitute several micronuclei, are seen at anaphase II and telophase II.

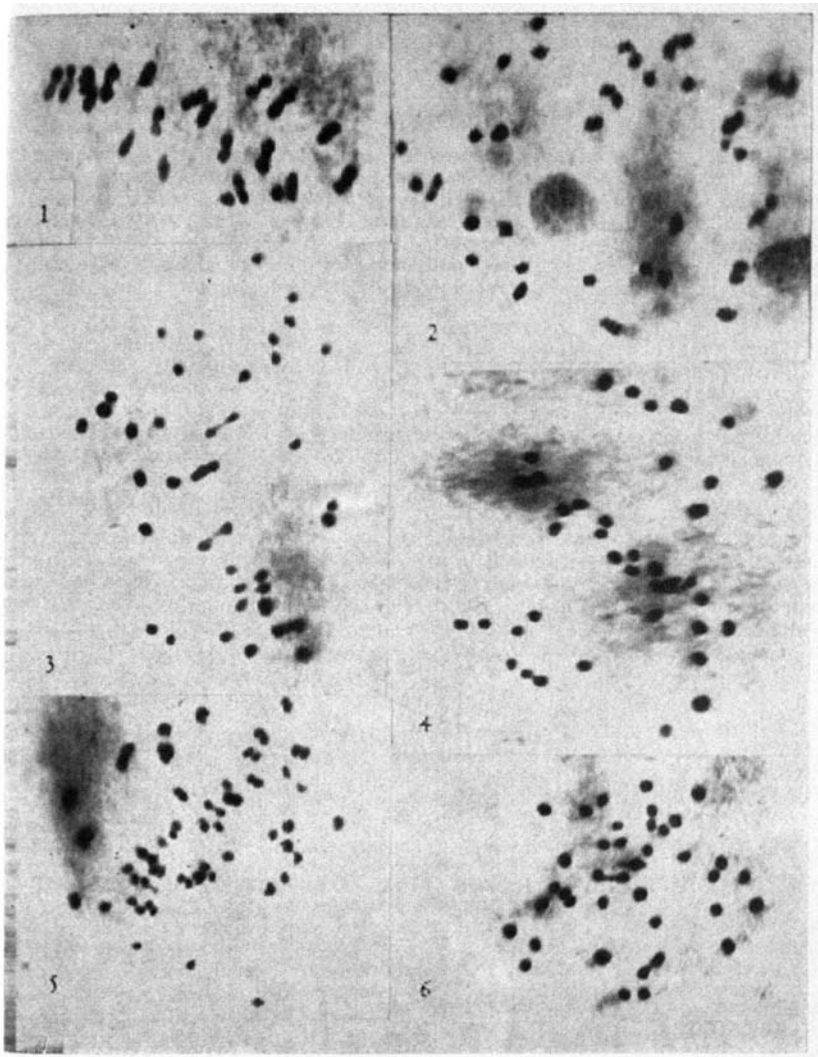

Figure 1. Metaphase I in (X-750) X (5450) - 3, showing 19 bivalents and 2 univalents.

Figure 2. Diakinesis in (X-750) X (X-98) - 1, showing some univalents lying in pairs.

Figure 3. Metaphase I in (X-750) X (4066) - 2, showing 6 bivalents and 28 univalents.

Figure 4. Anaphase I in (X-750) X (5450) - 1, showing 21 nondividing laggards.

Figure 5. Anaphase I in (X-750) X (4066) - 2, showing large number of dividing univalents.

Figure 6. Metaphase I in (X-750) X (5450) - 3, showing 2 bivalents and 36 univalents.

Several studies on the genetics of desynapsis have been reported. These point to the fact that the desynaptic behaviour of chromosomes is due to the presence of one, or at the most a few pairs of recessive genes (Beadle, 1930; Richardson, 1935; Prakken, 1943; Li *et al.,* 1945; Celarier, 1955; Krishnaswamy and Meenakshi, 1957). The results of this study indicate that the gene or genes controlling desynapsis are recessive and present in some species and genera of the Bothriochloininae in the heterozygous condition.

Even though desynapsis is the result of a particular genetic constitution, it appears to be partly affected by different environmental conditions. The fact that varying number of bivalents are present in different cells of the same plant and in particular the extreme situations where a hybrid was found to have from 0 to 40 univalents suggest that desynapsis is also influenced by extra-genetic factors. Li, *et al.,* (1945) have shown temperature as an influencing factor in bivalent formation. Ehrenberg (1949) also suggests environment as an influencing factor in bivalent formation.

De Wet, *et al.,* (in press) have suggested that chromosome pairing in the hybrids within Bothriochloininae seems to be by autosyndesis rather than allosyndesis, and demonstrated preferential pairing of genomes. If their hypothesis is correct it could be assumed that desynapsis in the Bothriochloininae actually represents a breakdown of preferential pairing among genomes and that this mode of pairing is genetically controlled.

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