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Multiple Chromosome Triplication in *Liatris*

Abstract. A plant with four and one with six extra *A* chromosomes were discovered in a hybrid swarm involving *Liatris aspera* and *Liatris spicata*. In each plant, the extra chromosomes formed trivalents with chromosomes of the normal complement. This pairing behavior indicates that of the ten chromosomes in the complement the plants are triplicate for four and six chromosomes, respectively.

Trisomics are known from numerous plant genera. They occur in natural populations and have been produced experimentally. The number of extra and different chromosomes which a diploid genome can tolerate rarely exceeds two (1). I now report the occurrence of four-chromosome and six-chromosome trisomics in *Liatris* (Compositae). To my knowledge, this degree of chromosome imbalance at the diploid level has never been described.

Two hybrids with several extra chromosomes have been discovered in a complex population involving *Liatris aspera* and *L. spicata* located near Zion, Lake County, Illinois. Whereas the two species and their hybrids usually have 20 chromosomes (2, 3), one hybrid possessed 26 chromosomes and the other 24 chromosomes. The extra chromosomes were the same size as those of the normal complement, and they displayed similar chromatic features and coiling cycles. The extra chromosomes were synapsed intimately with the normal complement at pachytene and remained that way through diplotene and usually through diakinesis and metaphase I. They may be regarded as type A chromosomes. Surprisingly, the external morphology of the two hybrids was not rendered distinctive because of the extra chromosomes.

The pairing relationships of chromosomes at diakinesis in the plants with 26 chromosomes are presented in Table 1. The chromosomes of this plant were

arranged in 25 different associations based upon various combinations of univalents (I), bivalents (II), trivalents (III), and quadrivalents (IV). Figure 1 illustrates 6II + 4III + 2I. The most frequent deviation from normal pairing is the trivalent which occurs in 99 percent of the pollen mother cells (PMC's) examined. In fact, trivalents were more frequent than bivalents. The trivalents formed several different figures, but rings of three were notably absent. The number of trivalents varied from one to six with a mean of 4.6 per PMC. The frequent occurrence of 4II + 6III and 3II + 6III + 2I strongly suggests that six different chromosomes were present in triplicate. The rare formation of quadrivalents is informative in this regard. Should two of the extra chromosomes have been of the same type, quadrivalents should be common. This plant does produce quadrivalents, but only at a rate similar to that of chromosomally balanced interspecific hybrids (2, 3). Chromosome-pairing relationships indicate that the plant in question is a sixfold trisomic.

The morphology of the ten chromosomes in the set is similar at diakinesis so that identification of all of the extra chromosomes was not possible. The SAT chromosome (satellite-bearing), which is recognizable because of its association with the nucleolus, was present in triplicate.

The absence of rings of three and chains of five chromosomes suggests that each trisomic element is of the primary type (1). However, in view of the hybridity of the plant and the small reciprocal translocations which differentiate the parental complements (2, 3), it is possible that one or perhaps two of the trisomic elements is tertiary. Figures of five may have dissociated prior to diakinesis because of the small size of the translocated segments.

The chromosome-pairing behavior of the 24-chromosome hybrid is presented in Table 2. The chromosomes were arranged in 14 different associations. As in the other aneuploid, trivalents were the most common deviation from normal pairing. All PMC's contained trivalents which averaged 3.2 per PMC. The frequent formation of 6II + 4III and 5II + 4III + 2I strongly suggested that four different chromosomes were present in triplicate. This interpretation was strengthened by the near absence of quadrivalents. It may be concluded that each of the extra chromosomes is different, and that this plant is a fourfold trisomic. Since rings of three and

associations of five chromosomes were lacking, it is likely that each trisomic element is of the primary type.

The identity of three of the extra chromosomes is unknown. The fourth

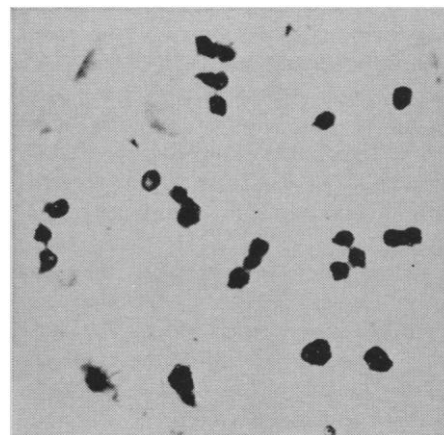


Fig. 1. The chromosomes of the sixfold trisomic; 6II + 4III + 2I ($\times 1350$).

Table 1. Chromosome relationships at diakinesis in the plant with six trisomes.

Chromosome association	PMC (No.)	PMC (%)
10II + 6I	1	.5
9II + 1III + 5I	1	.5
8II + 1III + 1IV + 3I	1	.5
8II + 2III + 4I	2	1.0
7II + 3III + 3I	19	9.9
7II + 2III + 6I	2	1.0
6II + 4III + 2I	27	14.0
6II + 3III + 5I	5	2.6
6II + 3III + 1IV + 1I	2	1.0
6II + 2III + 8I	1	.5
5II + 3III + 7I	1	.5
5II + 5III + 1I	48	25.0
5II + 4III + 1IV	1	.5
5II + 3III + 1IV + 3I	1	.5
5II + 4III + 4I	9	4.7
4II + 6III	34	17.7
4II + 5III + 3I	19	10.0
4II + 4III + 6I	2	1.0
4II + 4III + 1IV + 2I	1	.5
3II + 6III + 2I	10	5.0
3II + 5III + 5I	4	2.1
3II + 4III + 1IV + 4I	1	.5
2II + 6III + 4I	1	.5
2II + 7III + 1I	1	.5
1II + 6III + 6I	1	.5

Table 2. Chromosome relationships in the plant with four trisomes.

Chromosome association	PMC (No.)	PMC (%)
9II + 1III + 3I	12	8.0
8II + 2III + 2I	8	5.3
7II + 3III + 1I	45	29.8
7II + 2III + 4I	1	.7
6II + 4III	48	31.8
6II + 3III + 3I	13	8.6
6II + 2III + 4I	3	2.0
5II + 4III + 2I	16	10.6
5II + 3III + 5I	1	.7
5II + 1IV + 3III + 1I	1	.7
4II + 1IV + 4III	1	.7
4II + 4III + 4I	1	.7
4II + 1IV + 3III + 3I	1	.7
3II + 5III + 3I	1	.7

chromosome synapsed intimately with the SAT chromosomes, thereby indicating that the SAT chromosome was present in triplicate.

Univalents were present in most PMC's of the two hybrids. In some PMC's, a supernumerary nucleolus was associated with a univalent, the latter ostensibly being the triplicated SAT chromosome. Univalents either migrated to the poles or remained near the equator. The laggards were later eliminated in the form of micronuclei in microspores or as miniature microspores.

The imbalance imparted by the extra chromosomes appears to promote precocious bivalent disjunction. Consider the situation in the sixfold trisomic. The mean number of univalents per PMC in this plant averaged 2.1 as compared to .2 in the euploid hybrids (3). The "excess" univalents were due, in part, to precocious dissociation of trivalents into bivalents and univalents or into three univalents. Precocious dissociation, if it is assumed that a bivalent remained intact, would contribute an average of only 1.4 univalents per PMC since an average of 4.6 chromosomes participated in trivalents which remain intact through diakinesis. The origin of univalents in this manner would account for only a portion of the excess univalents. If trivalents are considered to be the only source for the excess univalents, over 10 percent of the trivalents would have to desynapse completely in order to generate an adequate supply of univalents. Since this is most unlikely (1), bivalents must be serving as the "excess" univalent source.

It is evident that the two aneuploids are similar in a number of ways, in spite of their different chromosome numbers. The most striking common feature is the fact that each extra chromosome is different, and thus each represents a distinctive triplication. The SAT chromosome was triplicate in each plant, and, on statistical grounds, there is a likelihood that at least one other chromosome is shared. The degree of trivalent retention through diakinesis was high in both plants. In the six-chromosome trisomic, 75 percent of the trivalents remained intact as did 80 percent in the four-chromosome trisomic.

The origin of the multiple trisomics remains an enigma. The plants could be products of an ascending aneuploid series, but the less imbalanced forms have yet to be found. The plants could be products of a descending aneuploid

series beginning at the triploid level. This alternative is less plausible than the first, for polyploidy is unknown in *L. aspera* and *L. spicata*. On the other hand, it is conceivable that the plants are not steps in a series, but arose directly from euploid parents in which meiotic irregularities yielded grossly imbalanced gametes.

Regardless of the mode of origin, one-half of the gametes involved in the formation of the aneuploids must have carried at least two extra chromosomes in the case of the four-chromosome trisomic, and at least three extra chromosomes in the case of the six-chromosome trisomic. Therefore, gametes can be viable and effectual in

spite of 20 to 30 percent duplication. Equally surprising is the fact that an organism can develop in a normal and robust fashion in spite of 40 to 60 percent triplication of its genome. Perhaps the toleration of chromosomal novelties is related in some manner to the hybridity of the plants in question.

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References and Notes

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Lateralized Suppression of Dichotically Presented Digits after Commissural Section in Man

Abstract. *Right-handed patients with surgical disconnection of the cerebral hemispheres cannot report verbal input to the left ear if different verbal stimuli have been channeled simultaneously to the right ear. With monaural stimulation, they show equal accuracy of report for the two ears. These findings highlight the dominance of the contralateral over the ipsilateral auditory projection system. Suppression of right-ear input is obtained in nonverbal tests. Dissociation between verbal and left-hand stereognostic responses indicate a right-left dichotomy for auditory experience in the disconnected hemispheres.*

It has been shown (1) that when the main commissures joining the two cerebral hemispheres of man are sectioned [as has been done to relieve intractable epilepsy (2)], the surgically disconnected hemispheres continue to function normally to a large extent; but only one, the left in the typical right-hander, appears capable of propositional speech and writing. The minor, right hemisphere does show some rudimentary verbal comprehension but emits few if any words. Hence the commissurotized patient is able to tell us in any detail only about sensory information that has reached his verbally dominant left hemisphere. For example, such a patient cannot name or describe objects flashed in his left visual field, but only those flashed on the right, because each field projects solely to the contralateral hemisphere. Nor can he name objects palpated with the left hand, although he manipulates them appropriately with that hand, and is able to remember and select the same object when it is placed among a collection of other items.

In audition, with which this report deals, the anatomical situation is quite different from that in vision or somes-

thesis. Each ear is represented bilaterally at every stage of the afferent pathway, from the cochlear nucleus to the auditory cortex in the temporal lobe, and therefore sound input cannot be restricted to one cerebral hemisphere; either hemisphere is able to hear through either ear. Yet, by presenting different verbal stimuli to the two ears simultaneously, we have been able to demonstrate, in commissurotized patients, a complete or near-complete suppression by the left or speaking hemisphere of input from the left ear.

We have tested seven patients with presumed complete midline section of the cerebral commissures, including the corpus callosum, the anterior and hippocampal commissures and, in at least two cases, the massa intermedia. These operations had been carried out at the White Memorial Hospital, Los Angeles, by Dr. Philip Vogel and his associates to help control severe convulsive disorders. The patients (five male, two female) were examined from 6 months to 4 years after operation, at which time their ages ranged from 14 to 44 years, with a mean age of 26 years. Below, their results on the auditory task are compared with those of 32