A computer simulation of the behavior of reciprocal translocations in autotetraploids*

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Summary. Reciprocal translocations in autotetraploids create extremely complex cytological and genetic situations. Along with three types of heterozygotes with one, two or three pairs of translocated chromosomes, a large array of aneuploid and unbalanced genotypes can be expected in the F2 and advanced generations. These types arise from gametes formed by adjacent and anomalous disjunctions of multivalents and by numerical non-disjunction of non-cooriented multivalents.

To determine the expected patterns of meiotic chromosome pairing configurations in all of these genotypes without the use of a computer program that constructs all possible pairing configurations, and recognizes and sums both the individual meiotic figures (univalents, rod and ring bivalents etc.) and combinations of meiotic figures, would be a very difficult task. The program has been used to construct all the possible meiotic configurations for a large array of normal and translocated genotypes with five, six, seven, eight, nine or ten chromosomes. Several inferences about the behavior of translocated chromosomes in autotetraploid populations have been drawn.

Key words: Reciprocal translocation – Autotetraploid – Chromosome pairing – Simulation

Introduction

Reciprocal translocations are chromosome aberrations where non-homologous chromosomes have undergone an exchange of segments. The meiotic and genetic consequences of reciprocal translocations have been extensively studied in diploids (see Burnham 1962 for review) but rarely in autotetraploids. Sybenga (1973a) investigated a reciprocal translocation in autotetraploid rye and found no evidence of preferential pairing. Similarly no preferential pairing was found in tetraploid Oenothera lamarckiana by Renner (1933). This absence of preferential pairing could be predicted if pairing initiation tends to be subterminal or terminal and the translocation points are proximal to the pairing initiation sites. Preferential pairing might be expected if the translocation points are subterminal, as indicated by the work of Burnham et al. (1972).

Along with insights into the problems of chromosome pairing a more pragmatic reason for studying reciprocal translocations in autotetraploids may be the provision of a theoretical basis of an understanding of the processes of allotetraploidization or diploidization when an autotetraploid is converted into an allotetraploid. Several workers have described such attempts (Bender and Gaul 1966; Gaul and Friedt 1975; Sybenga 1969, 1973b; Doyle 1979a, b, 1982) but actual progress has been slow. Clearly the behavior of translocations in autotetraploids could provide a mechanism by which cytological diploidization could proceed. Their study is obviously important.

Several authors have discussed the pairing configurations expected in an autotetraploid, among them are Durrant (1960), Morrison and Rajhathy (1960) and Sved (1966). However, they did not consider the effects of reciprocal translocations on the pairing patterns.

Because of the formation of unbalanced gametes from adjacent and anomalous disjunction of multivalents and the formation of aneuploid gametes by numerical non-disjunction, there is a large array of genotypes possible in the F2 and advanced generations of autotetraploid populations that contain reciprocal translocations. Therefore a general theoretical model has been devised to predict the cytological and genetic behavior of many of the possible genotypes and to allow some
estimation of the types and frequencies of the genotypes found in selfed progeny of autotetraploids with a single reciprocal translocation.

Theory

For the sake of brevity and clarity, the genotypes of both gametes and zygotes will be described by a set of four numbers. If the normal, untranslocated chromosomes are represented as AB and CD and the two possible translocated chromosomes by AD and CB then the set of four numbers are the numbers of the AB, CD, AD and CB chromosomes, respectively. Thus an AB/CD/AD/CB gamete would be represented as 1111 while an AB/AB/CD/AD gamete would be represented as 2110. Similarly an AB/AB/CD/CD/AD/CB/CB zygote would be represented as 2312. The behavior of the normal chromosomes in the rest of the genome that are not related to the translocated chromosomes are not included in this model.

Further, it must be immediately recognized that the cytological behavior of reciprocal translocations in an autotetraploid can be very complex. In order to make calculations several simplifying assumptions have been made. First, it is assumed that all arms will pair if there are potential pairing partners. Second, it is assumed that there will be no switching of pairing partners within an arm and third, there is no pairing interference across the centromere.

Figure 1 shows diagrammatically 2222 and 2231 zygotes. In the 2222 genotype the A arms can pair in three equally possible combinations (12-34, 13-24, or 14-23) as can the B, C, or D arms. Thus there are 3^4 or 81 possible pairing configurations. It is not too complex a matter to make drawings of them all and construct a table. However to undertake this task for the 2231 genotype is more complex and tedious. In this case there are five A and three C arms on one side of the centromere and similarly five D and three B arms on the other. Within the restrictions imposed by the simplifying assumptions five arms can pair in 15 possible combinations of two pairs and three arms in three combinations of one pair. Thus the number of possible pairing configurations for the 2231 genotype is 15 \times 3 \times 15 \times 3 or a total of 2025. The number of possible pairing configurations in some genotypes with two additional chromosomes would require the consideration of 50,625 (15 \times 15 \times 15 \times 15) events.

To attempt to determine the theoretical pairing configurations of all genotypes by drawing all the possible arrangements would be particularly tedious and prone to error. Consequently a micro computer program was devised that would construct all the possible pairing combinations, recognize and sum both the individual meiotic figures (univalents, rod and ring bivalents etc.) and combinations of meiotic figures within a cell (meiotic configuration). The program is capable of constructing all meiotic configurations not only for zygotic genotypes involving eight chromosomes but also for most aneuploid genotypes involving five, six, seven, nine and ten chromosomes.

The gametes that are produced from a particular zygotic genotype depend on the relative frequencies of the various pairing configurations and the patterns of disjunction from the different meiotic figures. For example, the 2222 genotype has five general types of pairing configurations as shown in Fig. 2. These types can be divided into subtypes depending on the chromosomes involved in the figures or their arrangement in multivalents. If we consider the 2II+IV subtype A it may be seen that the possible gametes produced depends entirely on the disjunctional pattern of the quadrivalent if we assume that the bivalents always disjoin normally. Thus, if the disjunction of the quadrivalent is alternate or adjacent 1 (CD, CB/CD, CB) then the gametes will always be 1111 with the AB and AD chromosomes coming from the bivalents. If it is adjacent 2 (CD, CD/CB, CB) then the gametes 1210 and 1012 will be formed. The other subtypes of 2II+IV will yield 2110, 2101, 1201, 0121 or 0112 gametes with adjacent 2 disjunction. Because all the subtypes occur with equal

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**Fig. 1.** Diagrams of two eight-chromosome zygotic genotypes with reciprocal translocations