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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 F_2 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

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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/CD/AD/CB/CB zygote would be represented als 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, 1021, 0121 or 0112 gametes with adjacent 2 disjunction. Because all the subtypes occur with equal

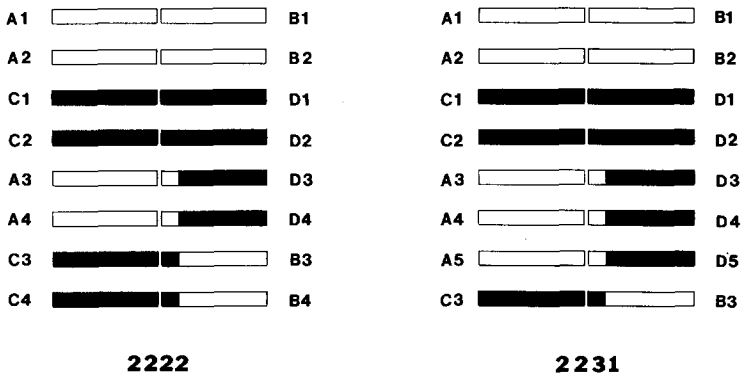

Fig. 1. Diagrams of two eight-chromosome zygotic genotypes with reciprocal translocations

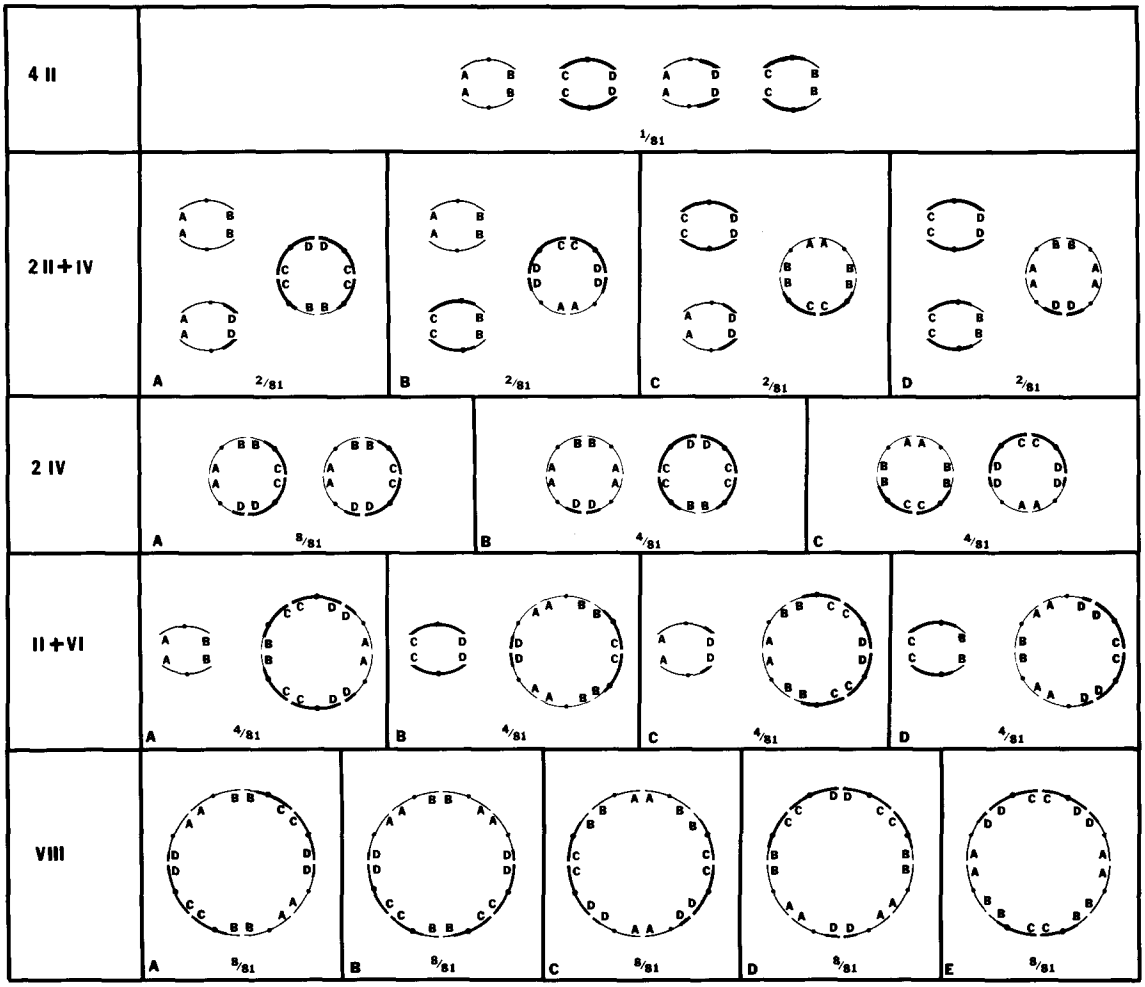

Fig. 2. Diagrams of the five possible pairing configurations and their sub-types in a 2222 eight-chromosome zygotic genotype showing the chromosome arrangements and their expected frequencies

frequency, each of the eight gametes occur with equal frequency and for the sake of brevity they will be treated together and called the 2110 set. A set can be constructed by the restricted permutation of the four numbers such that the pair of numbers in the leftmost two positions in any member of the set may not be separated. They may be reversed or placed (or reversed) in the rightmost two positions but must always be adjacent. A similar condition exists for the rightmost pair of numbers. Thus the gamete 2011 (AB/AB/AD/CB) does not belong to the 2110 set but to another (2011, 0211, 1120, and 1102). Similar combinatorial reasoning may be exploited for the construction of zygotic sets also.

Results and discussion

Tables 1 and 2 list the results expected in the model from a range of eight chromosome genotypes. Interestingly it is immediately obvious that all members of a zygotic set have identical pairing configurations, for example 2123 = 3212. This allows a considerable simplification of the tables in that all members of a zygotic set may be listed by one example. The arrays of pairing configurations were also determined for all seven- and nine-chromosome zygotic sets but will not be presented here for the sake of brevity. Similarly, the pairing configurations were determined for many of the five-, six- and ten-chromosome zygotic sets.

Among the eight-chromosome zygotic sets, two pairs; (5210 and 4310, and 5111 and 3131) have identical frequencies of pairing configurations. Also, if we ignore whether the figures are chains or rings then the 4220 (with all rings) belongs to the 5210 and 4310 groups. Two groups of sets have very similar pairing configuration frequencies (4211, 3320 and 3122) and (3230 and 3221). The eight-chromosome zygotic sets fall into two classes. The genotypes of the sets shown in Ta-

Table 1. The expected percentages of pairing configurations and the expected numbers of meiotic figures per cell in twelve eight-chromosome sets where odd-numbered multivalents are not expected

Configurations	Zygotic sets											
	4400	3311	2222	5111	3131	5210	4310	4220	4121	4022	3220	3221
[II] ⁄ 3 (II)	–	–	–	–	–	2.2	2.2	–	0.4	–	1.3	0.7
4 (II)	11.1	–	1.2	–	–	–	–	2.2	–	1.3	–	–
2 (II) + [IV]	–	–	–	–	–	13.3	13.3	–	2.7	–	8.0	4.4
[II] + (II) + (IV)	–	–	–	–	–	4.4	4.4	–	6.2	–	5.3	5.9
2 (II) + (IV)	44.4	11.1	9.9	6.7	6.7	–	–	17.8	–	13.3	–	–
[IV] + (IV)	–	–	–	–	–	8.9	8.9	–	12.4	–	10.7	11.8
2 (IV)	44.4	44.4	19.8	13.3	13.3	–	–	8.9	–	10.7	–	–
[II] + (VI)	–	–	–	–	–	–	–	–	10.7	–	5.3	8.9
(II) + [VI]	–	–	–	–	–	35.6	35.6	–	17.8	–	26.7	20.7
(II) + (VI)	–	–	19.8	26.7	26.7	–	–	35.6	–	32.0	–	–
[VIII]	–	–	–	–	–	35.6	35.6	–	49.8	–	42.7	47.4
(VIII)	–	44.4	49.4	53.3	53.3	–	–	35.6	–	42.7	–	–
Figures												
[II]	–	–	–	–	–	0.07	0.07	–	0.17	–	0.12	0.16
(II)	1.33	0.66	0.44	0.40	0.40	0.73	0.73	0.80	0.31	0.64	0.52	0.38
[IV]	–	–	–	–	–	0.22	0.22	–	0.15	–	0.19	0.16
(IV)	1.33	0.11	0.49	0.33	0.33	0.13	0.13	0.36	0.19	0.35	0.16	0.18
[VI]	–	–	–	–	–	0.36	0.36	–	0.18	–	0.27	0.21
(VI)	–	0.44	0.20	0.27	0.27	–	–	0.36	0.11	0.32	0.05	0.09
[VIII]	–	–	–	–	–	0.36	0.36	–	0.50	–	0.43	0.47
(VIII)	–	0.44	0.39	0.53	0.53	–	–	0.36	–	0.43	–	–

[a] □ indicates open (chain) figures and ○ closed (ring) figures respectively

ble 1 have no odd-numbered multivalents or univalents. The sets in Table 2 have odd-numbered multivalents.

All the seven-chromosome zygotic genotypes are unique and recognizable while among the nine-chromosome zygotic genotypes there are two different groups of sets, the members of which all have very similar pairing configurations to each other ((6111, 4131, 4122, 3231 and 3222) and (4221, 4032 and 3321)).

Definite pairing patterns are recognizable in the arrays of Tables 1 and 2 and also in the arrays for seven- and nine-chromosome zygotic sets. First, univalents and odd-numbered multivalents will be formed if there are an odd number of homologous arms on both sides of the centromeres. Of course, seven- and nine-chromosome zygotic sets will always have odd-numbered multivalents or univalents present. Second, in seven- and nine-chromosome zygotic sets even-numbered chain meiotic figures should not be observed. This is a consequence of the assumption of total synapsis and an odd number of chromosomes. If there is an even numbered chain and the ends are homologous then they would pair and it would become a closed figure. If the ends are not homologous then one of the remaining, unpaired chromosome arms will be homologous to one end or other of the chain and synapsis will produce an odd numbered chain. Even numbered multivalents are expected in some eight-chromosome zygotic sets. Third,

Table 2. The expected percentages of pairing configurations and the expected number of meiotic figures per cell in four eight-chromosome sets where odd-numbered multivalents are expected

Configurations	Zygotic sets			
	5300	4211	3320	3122
2 II + 2 II	–	0.9	0.9	0.6
II + II + IV	–	7.1	7.1	4.7
2 II + IV	–	0.6	–	2.4
2 IV	–	7.1	7.1	4.7
II + VI	–	9.5	7.1	14.2
2I + 3 II	2.2	0.1	0.4	0.1
2I + II + IV	4.4	1.5	1.8	1.2
2I + VI	–	2.4	1.8	1.8
I + 2 II + III	13.3	2.7	4.4	2.1
I + III + IV	8.9	4.1	3.6	7.1
I + II + V	17.8	13.0	14.2	9.5
I + VII	–	23.7	17.8	24.9
II + 2III	17.8	5.9	8.9	4.1
III + V	35.6	21.3	24.9	22.5
Figures				
I	0.53	0.52	0.48	0.50
II	–	0.20	0.16	0.25
II	0.73	0.35	0.44	0.25
III	0.93	0.40	0.51	0.40
IV	–	0.21	0.21	0.14
IV	0.13	0.06	0.05	0.11
V	0.53	0.34	0.39	0.32
VI	–	0.09	0.07	0.14
VI	–	0.02	0.02	0.02
VII	–	0.24	0.18	0.25

chain figures will be formed in eight-chromosome zygotic sets only when there are odd numbers of homologous arms on one side of the centromere.

To determine the expected gametic output of an autotetraploid with translocated chromosomes the types of pairing patterns of the various disjunctional patterns must be considered separately. This has been done for the 2222 zygotic genotype. The results are given in Table 3 where the disjunction of the chromosomes is 4–4.

The gametes from the cells with four bivalents are always 1111. As previously discussed the gametes from cells with 2II + IV are 1111 if the disjunction is alternate (a) or adjacent 1 (b); whereas adjacent 2 (c) disjunction gives 2110 type gametes. When two quadrivalents (2IV) are present it is assumed that they disjoin independently from each other and the results are derived from $(a+b+c)^2$ events. When dealing with sexivalents and octavalents the terms adjacent 1 and adjacent 2 become meaningless because of anomalous disjunction patterns (part alternate and part adjacent). If the disjunction is not all alternate then, in order to simplify the calculations, the pattern was considered random (r). The value r was determinded by tabulating all the possible 3:3 disjunctions of the sexivalents and 4:4 disjunctions of the octavalents.

Numerical non-disjunction (for example, 5–3 separations resulting from non-cooriented multivalents) can complicate the pattern of gametic output. The rate of numerical non-disjunction of translocation heterozygotes in diploids varies from species to species and for different translocations in the same species. In the progeny of a translocation heterozygote in *Pisum sativum* Sutton (1939) found 18% trisomes. In barley an average of about 1% trisomes are found in the progeny of a translocation heterozygote (Ramage 1960). These studies would indicate a range of maximum values for numerical non-disjunction of 2 to 36%. Rings in *Oenothera* are quite irregular in their disjunction (Emerson 1935). Table 4 shows the expected gametes in a 2222 zygotic genotype if all numerical non-disjunction takes place. The values

Table 3. Expected gamete production of 2222 plants without numerical non-disjunction

Gametic set	No. of types	Pairing configurations						
		4II	2II + IV	2IV – A[a]	2IV – B 2IV – C	II + VI	VIII – A	VIII B – E
1111	1	1	a + b	$1/2\,(a^2+b^2+c^2)$	a^2+b^2+2ab	a + 1/3r	8/34r	a + 7/34r
2110	8	–	c	2ab + 2bc	2ac + 2bc	4/9r	16/34r	16/34r
2011	4	–	–	2bc	–	2/9r	8/34r	8/34r
2200	2	–	–	$1/2a^2$	$1/2c^2$	–	a	1/34r
2020	4	–	–	$1/2\,(b^2+c^2)$	$1/2c^2$	–	2/34r	2/34r

[a] A–E refer to the sub-types of pairing shown in Fig. 2, a–c and r indicate the frequency of disjunctional patterns: a = alternate, b = adjacent 1, c = adjacent 2 and r = random

Table 4. Expected gamete production of 2222 with all numerical non-disjunction

Gametic set	No. of types	Pairing configurations				
		4II	2II+IV	2IV	II+VI	VIII
2210	4	–	–	3/32	1/30	1/14
2120	8	–	–	3/32	1/15	1/7
2111	4	–	1/2	5/16	2/5	2/7
1110	4	–	1/2	5/16	2/5	2/7
2100	4	–	–	3/32	1/30	1/14
2010	8	–	–	3/32	1/15	1/7

in Table 4 were determined by tabulating all the possible 3:1 disjunctions from a quadrivalent, 4:2 disjunctions from a sexivalent and 5:3 disjunctions from an octavalent.

From the values in Tables 3 and 4 and the pairing configuration frequencies shown in Fig. 2, formulae may be derived to predict the frequencies of all the gametes. However, these formulae are too lengthy to be presented here. If values of 0.50 for alternate disjunction, 0.25 for adjacent 1, 0.25 for adjacent 2, 0.05 for numerical non-disjunction and 0.50 for random are assumed then the expected frequencies of the gametic sets may be derived. The values chosen for this example are those that would be expected in maize and other species without strong directed alternate segregation. Two of the sets (2010 and 2020) would be expected to have lethal gametes, because of multiple deficiencies, with frequencies of 0.0051 and 0.0226 respectively. To restore the sum of the viable gametes to unity their initial frequencies were divided by 0.9723 (1−(0.0051+0.0226)). From this calculation the corrected frequencies of the gametic sets (number of types is given in parentheses) are: 1111 (1)=0.5302, 2110 (8)=0.2650, 2011 (4)=0.0903, 2200 (2)=0.0690, 2210 (4)=0.0031, 2120 (8)=0.0053, 2111 (4)=0.0170, 2100 (4)=0.0031 and 1110 (4)=0.0170. The total number of types is 39.

Assuming that balanced (1111, 2200 and 0022) gametes and the remaining unbalanced gametes function with equal frequency in fertilization and that all zygotes have equal viability it is possible to construct a 39×39 table from which zygotic F_2 genotypes may be derived. The summation of such a table is given in Table 5.

There are seven six-chromosome zygotic sets with a total of 28 genotypes but their cumulative frequency is 0.0004 and they may be neglected. Similarly there are 68 ten-chromosome genotypes but their cumulative frequency is also very low (0.0006) and they too may be neglected. Of the seven- and nine-chromosome zygotic sets only a few (2221, 3231 and 3222) can be expected with a frequency of 1% or more. Only 0.3809 of the progeny are eight-chromosome and balanced (2222+3311 (2)+4400 (2)). Two of the eight-chromosome zygotic sets are very common: 3221 (8)=0.3236 and 3122 (4)=0.1135.

Of course if the values given to the various frequencies of disjunction were changed then the array of genotypes in Table 5 would be different. Some species have a higher frequency of directed alternate disjunction with corresponding reductions in the other classes. In such a case there would be a higher frequency of 1111 gametes and 2222 zygotes.

Table 5. Zygotic genotypes expected in the self fertilized progeny of a 2222 zygotic genotype when the values of a[a], b, c and r are 0.5, 0.25, 0.25 and 0.5 respectively and numerical non-disjunction is 5%

Sets	No. in set	Freq.	Sets	No. in set	Freq.	Sets	No. in set	Freq.
Six chromosome sets			Eight chromosome sets			Nine chromosome sets		
(7)	(28)	0.0004	2222	1	0.2945	4410	4	0.0002
Ten chromosome sets			4400	2	0.0024	4320	8	0.0011
(13)	(68)	0.0006	3311	2	0.0820	4311	4	0.0016
Seven chromosome sets			4310	8	0.0183	4221	8	0.0032
4300	4	0.0002	4220	8	0.0088	4131	8	0.0006
4210	8	0.0004	4211	4	0.0150	4122	4	0.0011
4111	4	0.0001	4121	8	0.0120	4032	8	0.0002
3310	4	0.0016	4022	4	0.0020	3330	4	0.0005
3220	8	0.0025	3320	4	0.0150	3321	4	0.0076
3211	4	0.0069	3230	8	0.0120	3231	8	0.0100
3121	8	0.0042	3221	8	0.3236	3222	4	0.0223
3022	4	0.0008	3131	4	0.0129	Total	68	0.0484
2221	4	0.0217	3122	4	0.1135			
Total	48	0.0384	Total	65	0.9120			

[a] see Table 3

The computer program used gave no indication of the composition of the pairing figures. In the 2222 zygotic genotype there are five different quadrivalents, four sexivalents and five octavalents (Fig. 2). In other genotypes there are many other figures possible. In general there are $4\times2^{n-1}$ odd-numbered multivalents and $4\times2^{n-2}$ even numbered chain multivalents where n is the number of chromosomes in the figure. Thus there are 1024 different nonavalents possible in different genotypes. There is no general formula for ring multivalents because some of the permutations are restricted since there are no end chromosomes.

To determine the gametic output of the vast array of genotypes expressed in Table 5 would require the consideration of every pairing configuration and the construction of tables equivalent to Tables 3 and 4 (which are peculiar to the 2222 genotype) for every genotype. Thus to predict accurately the composition of the F_3 or a randomly mating population derived from the F_2 would be extremely difficult and probably very unrealistic.

Never-the-less, there are certain predictions that can be made. The six-, seven-, nine- and ten-chromosome zygotic sets should increase the amount of aneuploid gametes in the next generation. Also some of the eight-chromosome zygotic sets as given in Table 2 have high frequencies of pairing configurations with univalents and odd-numbered multivalents which should give one half aneuploid gametes. One of these zygotic sets (3122) is expected in a high frequency (0.1132). On the other hand unbalanced and aneuploid gametes are probably selected against and the population undoubtedly would achieve an unstable equilibrium.

Under natural conditions the translocated chromosomes would probably be in the minority (the initial genotype would be 3311) and if there is selection against unbalanced and aneuploid gametes the translocated chromosomes would disappear from a cross-breeding population after several generations. This rate of elimination cannot be predicted easily. Actual data are needed.

Conclusions

Reciprocal translocations in autotetraploids create very complex cytological and genetical situations. This theoretical study was undertaken to determine if an actual investigation was feasible and to devise efficient methods of analysis.

If reciprocal translocations behave in nature as suggested by this model, it would not be advisable to use them in an attempt to allotetraploidize (or diploidize) a species. They would cause a great amount of aneuploidy and genic imbalance, while their ability to cause preferential pairing is questionable. It is perhaps better to rely on inversions, duplications, deletions, heterochromatic differences and on genes affecting the expression of differential affinity.

The use of pairing configurations to determine genotypes is not possible. Not only do the genotypes fall into sets that have identical frequencies of pairing configurations within them, but some sets have very similar, or in two cases (5210 and 4310, and 5111 and 3131) identical pairing configuration frequencies. Also the remaining chromosomes of the genome may be present three or five times as a result of numerical non-disjunction and this would add trivalents or quinquevalents to the pairing configurations arising from the translocations.

Perhaps the best method for determining genotypes is to use mitotic figures from root tips. The translocated chromosomes used must be easily distinguished from each other and the rest of the chromosomes. Chromosome banding techniques may be helpful. Having determined the genotype from root tip counts the pairing configurations of the selected plants could be determined to see if they fit the expected model. Chromosome counts from a very large number of plants would be needed to detect some genotypes (Table 5).

The relative viability and fertility of the various unbalanced genotypes are probably quite different as the segments involved and the degree of imbalance varies. For example the zygotic genotype 3221 is less unbalanced than is 3131. To assume any values for selection gainst unbalanced gametes and zygotes would probably not be illuminating.

Clearly the introduction of some actual data is needed. The identification of specific chromosomes in root tips would help as could the use of the nucleolar organizing chromosome in studies of diakinesis. One or both of the translocated chromosomes could be marked with genes but it would be necessary to monitor the material closely to insure that the markers are not recombined onto normal chromosomes.

While a complete analysis of the population genetics of reciprocal translocations is impossible, never-theless it appears feasible to devise experiments that would determine some of the general parameters of this phenomenon.

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