effects were noted in anthers of RNA-treated plants, but not in the control ones. These were: 1) fusion of meiocytes forming plasmodial masses of varying sizes; 2) polyploid metaphase plates; 3) single cells with both hypoploid and hyperploid metaphase plates; 4) elongation of spindle; 5) precocious anaphase separation of some chromosomes, etc. These effects are similar to those found by Morgan (J. of Hered, 1956) in a monosomic plant (a member of two monozygotic twins). In both cases there might be a common basis in disturbed nucleic acid balance.

Further studies on the effect of variously induced nucleic acid imbalance on meiosis are in progress with a view to testing the hypothesis of a critical nucleic acid balance in the interconversion of meiosis and mitosis.

-- S. K. Sinha

5. Preferential pairing in trisomes, triploids, and tetraploids which are heterozygous for inversion 3a.

In the Maize News Letters (1958 and 1959) preliminary data were presented which indicated that preferential pairing was active in chromosome 3 trisomes and in tetraploids which were heterozygous for inversion 3a (3L.4 -.95). Rhoades (MNL 1957) has presented data which showed the presence of preferential pairing in triploids which were heterozygous for In 3a and In 3b. These data concerned the effect of preferential pairing on gene segregation (Rhoades 1957, Doyle 1958 and 1959) and on chromatid bridge frequency (1959). More extensive data have been collected and will be reported here. In addition, another method of detecting preferential pairing based on the trivalent frequency in control and inversion heterozygote trisomes will be discussed and data obtained by use of this method will be analyzed.

A. Gene segregation in inversion heterozygotes and corresponding controls.

CROSS	PROGENY					
TRISOME	CONTROL			INVERSION HETEROZYGOTE		
	ASh	aSh	ash	ASh	aSh	ash
ASh*/aSh/ash X ash/ash	1868 47.1%	1322 33.3%	777 19.6%	2473 44.2%	1654 29.6%	1462 26.2%
ash/ash X ASh*/aSh/ash	116 33.6%	119 34.5%	110 31.9%	847 21.7%	1530 39.4%	1518 38.9%
	A	a	A : a	A	a	A : a
a/a X A*/a/a	1843 33.6%	3644 66.4%	1 : 1.98	1481 22.1%	5234 77.9%	1 : 3.53
a/a X A*/A*/a	7473 66.8%	3722 33.2%	2.01 : 1	3092 78.6%	840 21.4%	3.68 : 1
A*/A*/a X a/a	2592 79.5%	667 20.5%	3.84 : 1	1355 90.7%	139 9.3%	9.75 : 1
A/A/a* X a/a				150 92.0%	13 8.0%	

CROSS	PROGENY					
	CONTROL			INVERSION HETEROZYGOTE		
TRIPLOID	A	a	A : a	A	a	A : a
A/A/a* X a/a	944 79.3%	246 20.7%	3.84 : 1	5647 84.1%	1068 15.9%	5.29 : 1
TETRAPLOID						
A*/a/a/a X 4n a	446 45.4%	537 54.6%	1 : 1.20	434 47.1%	488 52.9%	1 : 1.12
4n a X A*/a/a/a	1385 48.2%	1488 51.8%	1 : 1.07	763 48.8%	802 51.2%	1 : 1.05
4n a X A*/A*/A*/a	2227 97.5%	57 2.5%	39.1 : 1	440 98.7%	6 1.3%	73.3 : 1
A*/A*/a/a X 4n a	3498 79.3%	915 20.7%	3.82 : 1	2468 88.9%	309 11.1%	7.99 : 1
A/A/a*/a* X 4n a				5124 87.6%	727 12.4%	7.05 : 1
4n a X A*/A*/a/a	6674 80.2%	1647 19.8%	4.05 : 1	3802 86.7%	581 13.3%	6.54 : 1
4n a X A/A/a*/a*				8177 86.2%	1308 13.8%	6.26 : 1

* indicates that the gene so marked is included in the inverted chromosome in the inversion heterozygote.

The differences between the gametic ratios of the various types of inversion heterozygotes and their corresponding controls are all highly significant, except in the cases of the simplex and triplex tetraploids. When three chromosomes are of one type and one is of another type there is no chance for preferential pairing to be expressed, since the odd chromosome must pair with an unlike chromosome. When the simplex tetraploid is used as the female parent the chi-square is .55 ($p > .40$); when it is used as the male parent the chi-square is .11 ($p > .70$). The chi-square for the triplexes is 2.2 ($p > .10$). However, it is believed that with sufficient data it could be shown that the ratios in the progeny of these plants are significantly different. The frequency of double reduction should be less in polyploid inversion heterozygotes because of the presence of the inversion which decreases crossing over.

A detailed discussion of the theoretical effect of preferential pairing on gene segregation would be too lengthy to include in this report. However, the general principles may be stated briefly.

In a trisome or a triploid when a bivalent and a univalent are formed, the pairing may be homosynaptic or heterosynaptic. The random frequencies of homosynapsis and heterosynapsis are 1/3 and 2/3, respectively. When preferential pairing is active, these frequencies become 1/3 + p and 2/3 - *p*. The factor "p" may be defined as the frequency with which homosynapsis occurs over the random amount.

It may be seen that the frequency of a gametes in the progeny of a duplex (AAa) trisomes and duplex triploids used as the female parent would be 1/4(2/3 - p) if only bivalents and univalents were formed. When a trisome is used as the pollen parent the frequency of a gametes would be about 1/2(2/3 - p) since disomic pollen rarely functions.

Since In 3a includes only about 37% of the length of the chromosome three, the other parts of the chromosome may pair at random. Preferential pairing probably only takes place in the region of the inversion. Thus it is possible to have homosynaptic or heterosynaptic trivalents, depending on the way the inverted region is paired. The expected gametic ratios depend on the way these trivalents disjoin and on the frequency with which the chromosomes acquire the equational constitution (AA-Aa-Aa). Assuming that the disjunction of the trivalent is at random, it may be theorized that an excess in the frequency of homosynaptic trivalents should increase the A : a ratio. Random segregation from the reductional mode gives a 5A : 1a ratio, while random segregation from the equational mode (AA-Aa-Aa) gives a ratio of 3.8A : 1a. Homosynaptic trivalents may be expected to contribute less to the equational mode than the heterosynaptic trivalents do. For a homosynaptic trivalent to form equational chromosomes an exchange of pairing partners and crossing over must take place in the region between the centromere and the proximal break point of the inversion. This is probably a rare event.

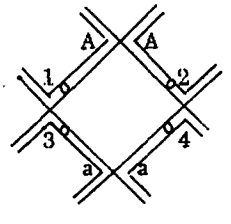
An additional factor to be considered is the loss of one of the chromosomes during meiosis, which will give a proportion of monosomic to disomic gametes of greater than one. A further complication is the effect of the formation of dup-def. and def. chromosomes (arising from breakage of chromatid bridges) on the gametic ratios.

It should be noted that triploid and trisomic inversion heterozygotes do not give the same ratio. This may be the result of a higher trivalent frequency in the triploid than in the trisome.

On the tetraploid level the situation is analogous. The frequency of homosynaptic bivalents and heterosynaptic bivalents is (1/3 + p) and (2/3 - p) respectively. If only bivalents were formed the expected frequency of aa gametes should be 1/4(2/3 - p). The p value for the tetraploid inversion heterozygotes would not be expected to be the same as the p value for the trisomes and triploids.

When a quadrivalent is formed, it may be either homosynaptic or heterosynaptic. An excess over random of homosynaptic quadrivalents should increase the A : a ratio, since double reduction may be expected to detract less from the Aa class of gametes than in the control. A further decrease in double reduction would be caused by a decrease in the quadrivalent frequency in the duplex inversion heterozygote.

If the chromosomes of a quadrivalent do not disjoin at random, preferential pairing will modify the gametic ratios. The random frequency with which two chromosomes of a quadrivalent go to the same pole is 1/3. If two chromosomes which had their marker genes paired go to the same pole, this is called genetic non-disjunction and its frequency is designated by Mather as "a". Thus the frequency of aa gametes arising from a homosynaptic quadrivalent is 1/2 a. See diagram below.



		AA	Aa	aa
(a) genetic non-disjunction	1,2/3,4	1/2	0	1/2
(1-a) genetic disjunction	1,3/2,4 1,4/2,3	0	1	0

There is some suggestive evidence that the value of "a" is less than 1/3. If only ring quadrivalents were formed the frequency of genetic non-disjunction would be half the frequency of adjacent disjunction assuming that the two types of adjacent disjunction (1,2/3,4)and (1,3/2,4) are of equal frequency. In translocation heterozygotes where a somewhat analogous situation is present adjacent disjunction is around 50%. There is only a small reduction (12%) in the chromatid bridge frequency of the simplex inversion heterozygote from that of the diploid inversion heterozygote. Since genetic non-disjunction would prevent the resolution of a chromatid bridge at the first division in a heterosynaptic quadrivalent, the reduction in the frequency of first division bridges in the simplex is related to the frequency of genetic non-disjunction. The frequency of crossing over is assumed to be about the same on the tetraploid and diploid levels. Half of the unresolved first division bridges should be resolved at the second division. It may be seen that the frequency of second division bridges is not much greater in a simplex than that found in the diploid inversion heterozygote where 2nd division chromatid bridges are derived solely from certain types of double exchanges (3 strand doubles, one in the loop and one in the proximal segment.) The frequency of regular second division bridges in the simplex tetraploid and the diploid is probably not the same, because of the possible exchange of pairing partners in tetraploids in the region proximal to the inversion which prevents 3 strand doubles of the type which give 2nd division bridges.

B. Chromatid bridge frequency in inversion heterozygotes.

CHROMATID BRIDGE FREQUENCY

INVERSION HETEROZYGOTE	FIRST DIVISION				SECOND DIVISION	
	No Bridge	Single Bridge	Double Bridge		No Bridge	Bridge
DIPLOID	667	394	18		1940	126
(In/N)	61.8%	36.5%	1.7%		93.9%	6.1%
TRISOME	935	156	4		1365	37
(In/N/N)	85.4%	14.2%	0.4%		97.4%	2.6%
TETRAPLOID						
SIMPLEX	656	324	9	Two	885	63
(In/N/N/N)	66.3%	32.7%	0.9%	Bridges	93.4%	6.6%
DUPLEX	754	103	6	13	460	24
(In/In/N/N)	86.1%	11.8%	0.7%	1.5%	95.0%	5.0%

Since a chromatid bridge is formed after crossing over in a paired inverted and standard segment, it follows that the frequency of chromatid bridges is a function of the frequency of heterosynapsis. If there were no preferential pairing, the chromatid bridge frequency of the trisomes should be about 2/3 of that of the diploid heterozygote. Two difficulties arise; crossing over may not take place with the same frequency in a diploid and a trisome and secondly, some of the bridges formed will not be resolved at the first division because two chromosomes of a trivalent with a potential bridge may go to the same pole. Half of the unresolved first division bridges should be resolved at the second division. Unfortunately, these bridges cannot be distinguished from the ordinary second division bridges which arise following a 3 strand double exchange with one crossover in the loop and one in the proximal segment. The frequency of this event would probably be lower in the trisomic inversion heterozygote, because of the exchange of pairing partners in the segment proximal to the inversion loop. However,

the low chromatid bridge frequency of the trisomics (14.6%) provides qualitative evidence for presence of preferential pairing since the expected frequency of chromatid bridges, 2/3 the chromatid bridge frequency of the diploid heterozygote, is 25.5%.

However, by comparing the chromatid bridge frequency of simplex (In/N/N/N) and duplex (In/In/N/N) tetraploid inversion heterozygotes, an estimate of the magnitude of preferential pairing can be made. The simplex tetraploid provides a fairly good control for the expected frequency of bridge formation following crossing over in a paired inverted and standard segment as the frequency of crossing over in a simplex and duplex tetraploid should be the same. Also the frequency of unresolved bridges, resulting when two chromosomes of a quadrivalent with a potential bridge pass to the same pole, should be about the same.

If there were no preferential pairing, then the chromatid bridge frequency of the duplex should be twice that of the simplex times 2/3 -- since by chance alone the two inverted segments should pair together 1/3 of the time. Since (2 X .336 X 2/3) $\neq$ .154, the frequency of heterosynapsis is not the random value 2/3 but is reduced by the preferential pairing factor "p". Thus by inserting the term 2/3 -p, the equation may be balanced and the factor "p" may be solved for.

$$2 \times .336 \times (2/3 - p) = .154$$
$$p = .438$$

This means that the frequency of homosynapsis is 77% (1/3 + p) in the duplex tetraploid.

C. Trivalent frequency in control and inversion heterozygote trisomes.

Another cytological manifestation of preferential pairing is the frequency of trivalent formation in trisomic plants. When there are three chromosomes capable of pairing together, two of which have greater pairing affinity for each other than toward a third chromosome, there will be a tendency for them to form a bivalent leaving the unlike chromosome represented as a univalent. This, of course, is true for the triploid as well as the trisome and there should be an analogous effect at the tetraploid level on the quadrivalent vs. two bivalent ratio for chromosome three. However, since chromosome three is not distinguishable from the other chromosomes at diakinesis, it is impossible to obtain a good estimate of the disturbance in the type of pairing configuration in the triploid and tetraploid. Such data can be obtained in trisomic plants, however, and the frequencies of chromosome 3 trivalents as opposed to univalent plus bivalent configurations are given below.

	No. of Plants		TYPES OF $1^{I}1^{II}$	1^{III}				1^{III}		
TRISOMIC CONTROLS	4	No.	184	407	125	208	74	0
		%	31.1	68.9	30.7	51.1	18.2	0
TRISOMIC INVERSION HETEROZYGOTES	7	No.	185	242	62	97	57	26
		%	43.3	56.7	25.6	40.1	23.6	10.7

The trivalent frequency is significantly lower in the trisomic inversion heterozygotes than in the controls. The X^2 is 29.5, which has a "p" value of $< .005$. It should be noted that one type of trivalent was observed in the inversion heterozygotes and not in the control, the type shown diagrammati-

cally on the far right of the table. This type of trivalent arises probably when pairing takes place between an inverted chromosome and the normal chromosome when they are oriented in opposite directions, in which case the homology of the two chromosomes for the inverted region is the same.

-- G. G. Doyle

6. Further evidence on the relationship between maize and teosinte.

The relative phylogenies of maize and teosinte have long been a matter of disagreement. Diploid hybrids between maize and teosinte made by Emerson and Beadle (Zeit. f. Ind. Abstmmgs. u. Vererbungslehre 62:305-315, 1932) and Arnason (Genetics 21:40-60, 1936) showed essentially normal rates of crossing over in marked regions. Cytological observation has shown chromosome pairing in 2N hybrids to be normal, and only small differences in length have been found. Cases of observed major failures in pairing and modification of crossing over in 2N hybrids can be traced to the presence of relatively inverted segments in some strains of teosinte. It must be concluded that study of 2N hybrids has failed to show significant differences between the genomes of maize and teosinte.

The next logical step in determining degree of relationship is the tetraploid hybrid test. Since there are two teosinte and two maize chromosomes present for each member of the set of 10 chromosomes, an opportunity for preference in pairing at meiosis is allowed. Therefore the tetraploid test should be a more sensitive test in determining degrees of chromosome homology. If pairing were strictly preferential, only bivalents would be formed, and recessive alleles introduced by the maize parent would not be expressed in the backcross progeny. Such a plant would be a stable amphidiploid. If pairing were random in the 4N hybrid, the frequency of recovery of recessives would be the same as in similarly marked autotetraploid maize controls. Therefore, preferential gene segregation from 4N "intergeneric" hybrid plants gives a measure of preference in chromosome pairing, and a measure of the degree of chromosome homology between maize and teosinte.

Seven sets of hybrids were made, using the tetraploid perennial form of teosinte and different tetraploid maize genetic stocks. F_1 hybrid plants used in backcrosses were determined from root tips to have 40 chromosomes, and from meiotic study to be balanced euploids. The backcross results are given in table 1.

TABLE 1. Percent of Recessives in Backcross Progenies of the 4N Hybrid of Maize and Perennial Teosinte, and of Corresponding Autotetraploid Maize Controls.

	4N Intergeneric Hybrid		Autotetraploid Maize	
Gene Marker	No.	Percent Recessive	No.	Percent Recessive
B	1952	6.4	2134	18.7
lg_1	1952	7.8	2134	21.6
lg_2	1640	9.9		
a_1	1640	11.6	4413[1]	20.7[1]
su_1	4213	4.9	2268	16.5
gl_3	4213	7.8	2268	21.9
Y	2021	2.8	2555	17.2
Pl	2021	4.4	2555	19.3
wx	9140	4.4	9008	16.5
sh_1	3019	4.6	4199	17.2
C	2317	3.3	4809	17.7
yg_2	2610	3.0	2391	22.9

1. Unpublished data kindly supplied by G. G. Doyle.