preferential pairing. Progress toward allotetraploidy will be monitored by observing the quadrivalent frequency and modifications of gene segregation. The exact details of the breeding system remain to be worked out.

G. G. Doyle

4. X-ray induced duplications from translocations between homologous chromosomes.

Translocations between the same arms of homologous chromosomes lead to the formation of a chromosome with an interstitial deletion and a chromosome with a tandem duplication, if the breakpoints are not identical. If it is assumed that the chromosomes in the interphase nucleus in somatic tissue are arranged at random, then the expected frequency of this event would be very low. Translocations between opposite arms of homologous chromosomes form pseudo-isochromosomes. The frequency of pseudo-isochromosomes has been found by Koo to be 1/4 (n-1) times the frequency of translocations between non-homologues, where n equals the haploid chromosome number. However, if there is a tendency for homologous chromosomes to be in a semi-paired state in the interphase nucleus as numerous investigators now believe, then we would expect the frequency of tandem duplication production to be higher than that of pseudo-isochromosomes. The probability of two broken ends uniting to form a new structural rearrangement is a function of the distance between them. A chromosome arm may be just as far away from the opposite arm of its homologue as it is from the arms of non-homologues, but may be much nearer the homologous arm of its homologue, than to any other arm.

The method used to detect tandem duplications has been presented in previous reports. In brief, they are detected by aberrant ratios from plants in the X_2 generation which come about by crossing over in one of the duplicated segments. Kernels which were heterozygous for 10 different markers were given 10,000 r in two different trials. The constitution of these kernels was Kys (with all dominant genes) over Mangelsdorf's tester (*bm*$_2$, *lg*$_1$, *a*$_1$, *su*, *pr*, *y*, *gl*$_1$, *j*, *wx*, and *g*). Only the *lg*, *su*, *y*, *gl*, *wx*, and *g* loci were followed. The plants grown from the irradiated seed were crossed to Kys to form the X_2 generation. There were 1169 X_2 plants which were crossed to Mangelsdorf's tester or to a

hybrid of Mangelsdorf's tester and Kys. The results are given in Table 5 and are summarized in Table 6.

Table 5

The genotypes of X_2 plants with aberrant ratios found in 27 independent cases

Case #	Treatment #	Locus	No. of ears from X_1	Genotypes AA*	Aa*	Aberr.	Pollen parent	Aberrant ratio A*	a*	%a	Reconstitution test A-a?/A X aa
1	1	y	31	13	17	1	a/a	118	6	4.8	negative
2	2	y	10	4	5	1	A/a	166	26	13.5	---
3	2	y	5	1	3	1	A/a	470	1	0.2	---
4	2	y	9	4	4	1	A/a	180	23	11.3	---
5	1	lg	23	9	13	1	a/a	415	3	0.7	---
6	1	lg	16	9	6	1	a/a	95	1	1.0	positive
7	1	lg	18	9	8	1	a/a	145	3	2.1	positive
8	1	lg	16	7	8	1	a/a	91	1	1.1	---
9	1	lg	12	6	5	1	a/a	88	1	1.1	positive
10	2	lg	5	1	3	1	a/a	225	1	0.4	---
11	1	gl	19	12	6	1	a/a	59	1	1.7	negative
12	1	gl	10	4	4	2	a/a	63	1	1.6	negative
							a/a	220	2	0.9	"
13	1	gl	27	10	15	2	A/a	211	27	11.3	---
							A/a	138	29	17.4	---
14	2	gl	5	1	2	2	A/a	224	2	0.9	---
							A/a	230	1	0.4	---
15	1	g	23	7	11	5	a/a	69	1	1.4	positive
							a/a	447	2	0.4	"
							a/a	307	7	2.2	"
							a/a	103	43	29.5	"
							A/a	93	14	13.1	
16	1	g	20	6	12	2	a/a	34	1	2.9	---
							A/a	191	2	1.0	---
17	1	g	17	9	7	1	a/a	69	12	14.8	positive
18	1	g	11	6	3	2	A/a	148	21	12.4	---
							A/a	99	15	13.2	---
19	1	g	19	7	11	1	A/a	181	22	10.8	---
20	1	g	25	17	7	1	a/a	97	1	1.0	---
21	1	g	22	12	9	1	a/a	65	1	1.5	---
22	1	g	11	3	7	1	A/a	191	3	1.5	---
23	1	g	11	6	4	1	A/a	146	10	6.4	---
24	2	g	9	4	4	1	A/a	264	2	0.8	---
25	2	g	7	4	2	1	A/a	240	5	2.0	---
26	2	g	4	1	2	1	A/a	230	2	0.9	---
27	2	g	5	1	3	1	A/a	292	2	0.7	---

*A and a refer to any of the six genes.

Table 6

Locus	Cross	Genotypes found No. of ears				
		A/A	A/a	a/a	Aberrant	
su	#1 X MT	276	257	0	0	
	#1 X Kys/MT	155	128	0	0	
	#2 X Kys/MT	172	181	0	0	
y	#1 X MT	236	296	0	1	(1)*
	#1 X Kys/MT	137	146	0	0	
	#2 X Kys/MT	180	170	0	3	(3)
wx	#1 X MT	263	270	0	0	
	#1 X Kys/MT	141	141	0	0	
	#2 X Kys/MT	164	188	0	0	
lg	#1 X MT	282	245	1	5	(5)
	#1 X Kys/MT	133	150	0	0	
	#2 X Kys/MT	167	180	0	1	(1)
gl	#1 X MT	242	283	1	3	(2)
	#1 X Kys/MT	134	147	0	2	(1)
	#2 X Kys/MT	168	178	0	2	(1)
g	#1 X MT	265	260	0	8	
	#1 X Kys/MT	141	133	0	9	(9)
	#2 X Kys/MT	173	171	0	4	(4)
					36	27

*Figures in parentheses indicate number of independent cases.

There were 27 independent cases of aberrant ratios possibly indicating the presence of a duplication. In six of these cases there was more than one aberrant ratio found in the progeny of an X_1 ear. The presumptive duplication sectors on the X_1 ears seem to be very small. An aberrant ratio in itself is not proof of the existence of a duplication as there are other possibilities, such as the loss of the chromosome segment with the dominant marker which results in a plant hemizygous for the locus--allowing the recessive to be expressed. Another possibility is induction of a gametic lethal or sub-lethal which is linked to the recessive gene and which lowers the transmission frequency of the recessive. The only sure criterion is to restore the original situation (A-a/A) by crossing the presumptive duplication with the dominant gene

marker and to see if there is a reversion to a when it is backcrossed to the recessive. This has been done with eight of these cases; in five cases the original situation was restored and there were aberrant ratios. In three cases the results were negative. One problem is that the original cross yielded A and A-a gametes in about equal frequencies. These two types cannot be readily distinguished. The duplication shows a lowered transmission rate through the pollen (in most cases around 40%), but this is not adequate to accurately distinguish between them. This difficulty can be surmounted by taking a larger sample so we can be sure the A-a chromosome is represented, or by making the original testcross with the heterozygote (A/a) so that the A-a/a types are formed immediately and there is no chance for the duplication to be lost.

Data on the reconstitution tests will be presented when they are completed.

The expected frequency of tandem duplications for any one gene in this material is 1/36 or 1/4(n-1) times the frequency of translocations between non-homologous chromosomes (observed value 15.4%) times 1/20 (since there are 20 arms in maize) times 1/2 (the maximum probability that a gene will have one break proximal and one break distal to it) times total number of ears. This works out to 0.12 per gene in this experiment. Since 6 genes were followed the total frequency should be 0.72.

This calculation is based on the premise that the chromosomes are arranged at random in the interphase nucleus. Since the observed value of 36 is considerably greater (even if some of the cases are spurious), the data may be taken as evidence that there is predilection for translocations between the same arms of two homologous chromosomes probably as a result of a semi-paired condition in the interphase nucleus.

Another method for detecting translocations between homologous chromosomes is to irradiate diploid material which is marked with two very closely linked genes in the repulsion phase. This is the case with A sh/a Sh. A duplication will have the phenotype of A Sh. Genetic tests can be used to separate these kernels from A Sh kernels arising from crossing over. The results of this experiment are given in Table 7 and Table 8.

Table 7

Treatment	No. of ears	Total gametes	No. of gametes				Percent	
			A sh	a Sh	A Sh	a sh	A Sh	a sh
Control	77	25,059	12,241	12,777	20	21	0.08	0.08
5000 r	79	21,926	10,745	11,105	60	16	0.27	0.07
10000 r	71	17,774	8,656	9,065	37	16	0.21	0.09

Table 8

Treatment	Number of ears with n number of A Sh kernels											Total
	n 0	1	2	3	4	5	6	7	8	9	10	
Control	58	18	1	0	0	0	0	0	0	0	0	77
5000 r	49	21	3	3	1	0	0	0	0	0	2	79
10000 r	50	12	5	2	1	1	0	0	0	0	0	71

The excess of kernels with the A Sh phenotype in the irradiated material is highly significant. It cannot be explained by an enhancement of crossing over by irradiation since the reciprocal class remains the same. The corresponding class (the deficient chromosomes) is presumed to be lethal.

Each kernel corresponds to one X_2 plant in the previous experiment. It is a much more efficient way to duplicate endosperm characters. It should be noted that the first method did not uncover any duplications for su or wx. One explanation for this is that these twc genes are linked very closely to the centromere. Since the reversion to the recessive phenotype depends on a crossover proximal to the locus any duplications involving su or wx would be difficult to detect. The lg, gl, and g loci have more proximal crossovers since the map distance between these loci and the centromere is large. The y locus is fairly close to the centromere and is also difficult.

Where two closely linked gene loci are not available, an artificial set-up can be used with the aid of translocations. For example, a

homozygous 6-9 translocation with the constitution of Y - T - wx/ y - T - Wx can be irradiated and kernels with the phenotype Y Wx can be isolated. The duplication can then be introduced into a normal background by crossing over.

G. G. Doyle

NATIONAL COLONIAL FARM
Accokeek, Maryland

1. Mutations from seed irradiation of B14 maize inbred.

The seed irradiation study, proposed in 1965, has proved to be rather effective in mutation induction. In 1967, seed of B14 was treated with thermal neutrons at the Brookhaven National Laboratory through the courtesy of Robert W. Briggs, whose cooperation is much appreciated. After treatment the seed was planted in an isolated field and allowed to interpollinate. In this way every mutant gamete, even in a small sector of the ear or tassel had the opportunity to participate in fertilization. No self pollinations were made in this field. At harvest time the ears were shelled together. In 1968 a small field was grown and more than 1000 hand pollinations made. After harvest a small sample of seeds was taken from each ear and planted in a seedling bench in the greenhouse.

The results are now complete. Of 1074 seedling rows in the greenhouse, 49 or 4.6% were segregating for some seedling character. These included albinos, luteus, yellow green, virescent and one dwarf. Most, by far, showed segregation for albinos. Of the 49 progenies, 39 were segregating albinos, 6 luteus, 2 virescent, 1 variegated, and the one dwarf previously mentioned. Also many mutations for defective and germless seed were observed. These need further testing to determine how many are true mutations. Also a number of ears presumably heterozygous for translocations were found. Further testing of these is necessary. Limited quantities of seed of stocks heterozygous for the various mutants are available.