ABNORMAL SEGREGATION DURING MEGASPORO-GENESIS IN MAIZE

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THE principle of random segregation of contrasting alleles during mega-sporogenesis and microsporogenesis is commonly accepted. Knobs on the chromosomes of maize may be considered as alleles which are visible under the microscope. Any deviation from a random orientation and distribution of bivalent chromosomes during meioses that lead to aberrant genetic ratios and nonrandom segregation of knobs is considered abnormal.

Observations made during the study of chromosome knobs of maize suggested that the segregation of paired chromosomes, one with and the other without a knob, was not strictly random. Recently RHOADES (1942) discovered a preferential segregation at megasporogenesis of plants heterozygous for the abnormal and normal types of chromosome 10 in which approximately 70 per cent of the basal cells of the linear tetrad received the abnormal type of this chromosome. His studies suggested that a more critical study be made of the accumulating data on knob segregation and the segregation of some contrasting alleles known to be near the knob locus of different chromosomes.

Acetocarmine smear preparations of pollen mother cells were used to determine the number and position of knobs in the parent strains, in random samples of all F_1 progenies, and in a limited number of progeny plants obtained from the backcrosses. The number and position of the knobs of parent strains were checked each season as sib-pollinated and self-pollinated seed replaced the original stocks. Determinations of the knobs present in F_1 plants served only as a check on the knob conditions of the two parents that had been combined.

Genetic studies of preferential segregation of contrasting genes were possible through the use of several seed and seedling characters obtained from the MAIZE GENETICS COOPERATION, DEPARTMENT OF PLANT BREEDING, CORNELL UNIVERSITY, Ithaca, New York. These were crossed with the contrasting dominant alleles carried in chromosomes possessing the contrasting knobbed or knobless condition. Two of these studies on the segregation of genes on chromosome 10, three on chromosome 9, and one on chromosome 6 are included in this report.

Since it was convenient in preparation of the tables to have some symbol for the knobbed and knobless condition of a chromosome, the symbols K for knobbed, k for knobless, and $K(S)$ for a small knob have been used. The values of x^2 have been computed for each population and are reported in the tables. Since each distribution has only one degree of freedom, a x^2 value of 3.8 indi-

cates odds of 19:1 and a value of 6.6 indicates odds of 99:1 against the deviations being due to chance alone.

EXPERIMENTAL RESULTS
Cytological studies

Each of the ten maize chromosomes may exhibit one or more knobs at the prophase of the first reduction division. Many strains, however, have few or even no knobs on their chromosomes. Consequently, selected strains may be crossed to produce F_1 plants with many of the homologous pairs of chromosomes heterozygous for knobs. When such F_1 individuals are backcrossed to a strain without knobs, the number of knobs found on the chromosomes of the resulting plants will be the number present in the gametes of the heterozygous parent. Any deviation of the mean number of knobs carried by the backcross population from the mean of the two original parents will indicate that there has been a nonrandom segregation in the F_1 plants at megasporogenesis.

Some of the knobbed parent maize strains used in producing F_1 progenies carried the abnormal type of chromosome 10 used by RHOADES (1942) in his studies of preferential segregation. Data on its segregation are included with

TABLE 1

Knob segregation at megasporogenesis of maize.

CHROMOSOME NO.	CHROMOSOME ARM	TOTAL NUMBER OF CHROMOSOMES	KNOBBED CHROMOSOMES		χ^2
			NUMBER	PERCENTAGE	
1	Short	136	79	58.1	3.56
	Long	108	68	63.0	7.26
2	Short	59	35	59.3	2.05
	Long	93	55	59.1	3.11
3	Short	113	72	63.7	8.50
	Long	169	116	68.6	·23.49
4	Long	106	87	82.1	43.62
5	Long	77	56	72.7	15.91
6	Long	212	125	59.0	6.81
	Long	212	138	65.1	19.32
8	Long	90	57	63.3	6.40
9	Long	207	148	71.5	38.27
Total		1,582	1,036	65.5	Highly sig.
10	Long	142	106	74.6	34.51

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TABLE 2

*Summary of knob segregation in megasporogenesis and
microsporogenesis of maize.*

CHARACTER OF SEGREGATION	TOTAL CHROMOSOMES	KNOBBED CHROMOSOMES		χ^2
	NUMBER	NUMBER	PERCENTAGE	
Plants segregating for Abnormal 10				
Megaspores with Abnormal 10	918	616	67.10	107.4
Megaspores with Normal 10	664	420	63.25	46.65
Microspores (both types of 10)	115	62	53.91	.70
Plants with Normal 10 only				
Megaspores	195	122	62.56	12.31

the cytological data on the segregation of the knobs on the other nine chromosomes.

Data on knob frequency from counts made on plants of the first backcross generation are shown in tables 1 and 2. These data are not all from the same cross and so all knobs are not equally represented. The data on the segregation of individual knobs at megasporogenesis are given in table 1. Some data were obtained on the segregation of 12 different knobs. Each knob was present in well above the expected 50 per cent of the plants of the first backcross generation, thus giving definite evidence of preferential segregation of the knobbed over the knobless homologues at megasporogenesis of the F_1 plants. All these F_1 plants were also segregating for the abnormal and the normal types of chromosome 10. The preferential segregation of 74.6 per cent for the abnormal type substantiates RHOADES' (1942) data and approximates the figures he gives.

The data in table 1 are from two kinds of plants, those from eggs with and those from eggs without the abnormal chromosome 10. A summary of the prevalence of knobs in these two kinds is given in lines 1 and 2 of table 2. The data show that the megaspores of F_1 plants that receive the abnormal chromosome 10 receive 67.1 per cent of the other knobs segregating, whereas the megaspores receiving the normal chromosome 10 receive 63.25 per cent of the knobs segregating. These figures indicate that preferential segregation of knobs at megasporogenesis is the rule and is slightly more biased when the abnormal type goes to the basal cell of the linear tetrad. The data on the same 12 knobs in the last line of table 2 substantiate those in line 2 and indicate that when knobbed and knobless chromosomes segregate, the former are included in the megaspore more than the expected 50 per cent even when the abnormal chromosome 10 is not present.

The meager data in line 3, table 2, show only a slight departure from the expected 50:50 distribution of knobs in the functioning pollen of F_1 plants in which there was an opportunity for the segregation of paired knobbed and knobless chromosomes and of the segregation of the two types of chromosome

10. These data from heterozygous F_1 plants do not distinguish between the possibility of abnormal segregation at microsporogenesis, which might give two of the cells of the tetrad many knobs and the other two but few, and the possibility of a differential viability between pollen with few and pollen with many knobs. However, the number of knobs present in the plants of the first backcross generation indicates that the presence of knobs does not handicap pollen in effecting fertilization.

Genetic studies

When this study was extended to include the segregation of contrasting genes at loci close to knob loci, it was apparent that morphological studies of the chromosomes could not be made of all plants. A knowledge of the knobs present in the parent strains is essential. A check, however, on the homozygosity of the parent strains was kept by determining the number and position of knobs in a random sample of all F_1 progenies. Determining the effect of preferential segregation of the knobbed over the knobless type of a chromosome on the segregation of closely linked genes required no additional cytological determinations. If the paired homologues carrying the contrasting segregating alleles were at a locus so close to the knob locus that little or no crossing-over was taking place, the ratio of recovery of the two contrasting alleles should measure as accurately as cytological determinations the amount of preferential segregation.

The ratio of contrasting genes recovered in backcrossed and selfed progenies expected from random segregation at megasporogenesis and microsporogenesis is 50:50 in progenies from backcrossed plants and 75:25 in progenies from selfed F_1 plants. A deviation from these ratios was expected in the segregation of contrasting alleles whenever the preferential segregation shown by the cytological data was affecting the same chromosomes. The amount of departure of a ratio from that for random segregation also should be a measure of the distance between the knob locus and the locus of the segregating genes if there is no differential viability.

Segregation of the R r and G g genes

It has been shown that more than 70 per cent of the megaspores of plants in which the two types of chromosome 10 are present receive the abnormal type. Tables 3 and 4 show that this preferential segregation affects the segregation of the contrasting alleles R and r and G and g, the former at a locus close to and the latter at a locus an appreciable distance from the end of the long arm of chromosome 10. The data on the segregation of these two pairs of contrasting alleles at megasporogenesis approximate those given by RHOADES (1942) for their preferential segregation and serve merely to substantiate his studies.

The data in line 3, table 3, are from the reciprocal cross of those shown in line 1 and shows no appreciable deviation from the 50 per cent expected from random segregation at microsporogenesis and equal viability of the two types of pollen. Similar conclusions are drawn from the data in lines 2 and 4 of table 4 which show the segregation of the contrasting $G g$ alleles. The 81.93 per cent of

TABLE 3

Segregation of the dominant and recessive R r alleles.

PARENTS		TOTAL SEEDS NUMBER	COLORLESS SEEDS		χ^2
♀	♂		NUMBER	PERCENTAGE	
$\dfrac{r \ Ab. \ 10}{R \ Nor. \ 10}$	r Nor. 10	35,110	24,229	69.01	Highly sig.
$\dfrac{r \ Nor. \ 10}{R \ Nor. \ 10}$	r Nor. 10	5,923	2,892	48.83	3.26
r Nor. 10	$\dfrac{r \ Ab. \ 10}{R \ Nor. \ 10}$	226	110	48.67	.16

green plants recovered (line 2) from selfed progenies fits closely the calculated expected 81.52 per cent when the 63.04:36.96 ratio (table 4, line 1) of the two types of eggs is combined with an assumed 50:50 ratio of the two types of pollen, and the 73.96 per cent of green plants recovered (line 4) is close to the 75 per cent expected from random segregation of the contrasting alleles.

Segregation of the paired C c genes

The data from several tests of segregation of the C c pair of genes for aleurone color are given in table 5. There is approximately 23 per cent recombination between C and the end of the short arm. Data on the segregation at megasporogenesis of chromosome 9 in plants heterozygous for the two types of chromosome 10 are shown in the first line. The 63.87 per cent of colored seeds recovered is a definite departure from the expected 50 per cent and shows a preferential segregation at megasporogenesis of the chromosome 9 bearing a knob and the dominant allele C. The next two lines of table 5 serve as checks to the data in line 1 and show approximately random segregation of the dominant C allele at megasporogenesis both when it is on a knobbed and when it is on a

TABLE 4

Segregation of the dominant and recessive G g alleles.

PARENTS		TOTAL SEEDS NUMBER	GREEN SEEDLINGS		χ^2
♀	♂		NUMBER	PERCENTAGE	
$\dfrac{G \ Ab. \ 10}{g \ Nor. \ 10}$	g Nor. 10	1,196	754	63.04	8.14
$\dfrac{G \ Ab. \ 10}{g \ Nor. \ 10}$	Self	20,008	16,393	81.93	Highly sig.
$\dfrac{G \ Nor. \ 10}{g \ Nor. \ 10}$	g Nor. 10	1,042	550	52.78	3.23
$\dfrac{G \ Nor. \ 10}{g \ Nor. \ 10}$	$\dfrac{G \ Ab. \ 10}{g \ Nor. \ 10}$	2,857	2,113	73.96	1.65

knobless type of chromosome 9 and paired with the recessive c allele on a knobless type of 9. Since the abnormal type of chromosome 10 is absent in these two tests, it may be concluded that the presence of the abnormal type of chromosome 10 is associated with the preferential segregation of the knobbed type of chromosome 9. This preferential segregation of chromosome 9 is confirmed by the data in line 5 of table 5 in which 81.28 per cent colored seeds were obtained. This is a very good fit to the expected 82.27 per cent calculated by combining 63.87 per cent C bearing eggs with a 50.92 per cent (line 4, table 5)

TABLE 5

Segregation of the dominant and recessive C c alleles.

PARENTS				TOTAL SEEDS NUMBER	COLORED SEEDS NUMBER	PERCENTAGES OF COLORED SEEDS		χ^2
♀		♂				OBSERVED	EXPECTED WITH RANDOM SEGR.	
$\dfrac{C\,K}{c\,k}$ $\dfrac{\text{Ab. 10}}{\text{Nor. 10}}$		$c\,k$ Nor. 10		43,523	27,799	63.87	50	Highly sig.
$\dfrac{C\,K}{c\,k}$ Nor. 10		$c\,k$ Nor. 10		29,995	14,878	49.60	50	1.90
$\dfrac{C\,k}{c\,k}$ Nor. 10		$c\,k$ Nor. 10		12,415	6,106	49.15	50	3.32
$c\,k$ Nor. 10		$\dfrac{C\,K}{c\,k}$ $\dfrac{\text{Ab. 10}}{\text{Nor. 10}}$		2,219	1,130	50.92	50	.76
$\dfrac{C\,K}{c\,k}$ $\dfrac{\text{Ab. 10}}{\text{Nor. 10}}$		$\dfrac{C\,K}{c\,k}$ Nor. 10		1,448	1,177	81.28	75	30.50
$\dfrac{C\,k}{c\,k}$ Nor. 10		Self		6,445	4,771	74.03	75	3.26

of pollen carrying the dominant C allele, or to the expected 81.94 per cent calculated when the types of pollen are assumed to be functioning at random.

The data in line 4, table 5, were obtained from the reciprocal of the cross of that which furnished the data of line 1. The percentage of colored seed approximates closely the 50 per cent expected and definitely indicates that the presence of the knob on chromosome 9 does not exert any appreciable influence on the type of pollen that effects fertilization.

A final check on the normal segregation of the dominant C allele when paired with the recessive c allele, and both alleles are on the knobless type of chromosome 9 is given in line 6, table 5. The observed 74.03 per cent colored seeds is close to the expected 75 per cent.

The foregoing data have demonstrated an abnormal segregation at megasporogenesis of the dominant allele C when on the knobbed type of chromosome 9 and paired with the recessive allele borne on the knobless type, but only when the two types of chromosome 10 also are segregating. They also have demonstrated that all classes of pollen from plants heterozygous for the $C\,c$ al-

leles, the knobbed and knobless type of 9, and the two types of 10 effect fertilization in approximately equal numbers.

The data in table 6 combine the preferential segregation at megasporogenesis of the recessive *r* allele borne on the abnormal type of chromosome 10 and the associated preferential segregation of the dominant *C* allele on chromosome 9, caused by the presence of a knob terminating the short arm. It must be remembered that these two preferential segregations work against each other in the production of colored seed. However, the data in tables 3 and 5 show that the tendency to reduce is greater than that to increase the number of colored seeds, consequently there should be a deficiency of colored seeds in selfed progenies in which both preferential segregations occur. The effect of the more pronounced preferential segregation of the abnormal type of chromosome 10 is

TABLE 6

Segregation of the dominant and recessive C c and R r alleles.

PARENTS			TOTAL SEEDS NO.	COLORED SEEDS NO.	PERCENTAGES OF COLORED SEEDS				
					OBSERVED	EXPECTED		χ^2	
♀		♂				PREFERENTIAL SEGREGATION	RANDOM SEGREGATION	PREFERENTIAL	RANDOM
$\frac{C\,K}{c\,k}$ $\frac{r\,\text{Ab. 10}}{R\,\text{Nor. 10}}$		Self	48,735	25,758	52.85	53.66	56.25	12.76	Highly sig.
$\frac{C\,k}{c\,k}$ $\frac{r\,\text{Nor. 10}}{R\,\text{Nor. 10}}$		Self	13,655	7,609	55.72	—	56.25	—	1.53
$\frac{C\,K}{c\,k}$ $\frac{r\,\text{Ab. 10}}{R\,\text{Nor. 10}}$	$c\,k$	$\frac{r\,\text{Ab. 10}}{R\,\text{Nor. 10}}$	17,121	7,233	42.25	41.83	37.5	1.22	Highly sig.
$c\,k$ $\frac{r\,\text{Ab. 10}}{R\,\text{Nor. 10}}$	$\frac{C\,K}{c\,k}$	$\frac{r\,\text{Ab. 10}}{R\,\text{Nor. 10}}$	11,399	3,736	32.77	32.75	37.5	.003	Highly sig.

illustrated by the data in line 1. The observed 52.85 per cent colored seeds is appreciably below the 56.25 per cent expected from random segregation, but it approaches the 53.66 per cent calculated when preferential segregations at megasporogenesis of 63.87 per cent and 69.01 per cent for the dominant allele *C* and the recessive allele *r*, respectively, are combined with pollen in which all classes are functioning at random.

Line 2 of table 6 is check material in which the observed 55.72 per cent colored seeds is close to the 56.25 per cent expected from a random segregation of these two factors contributing to seed color.

The data in lines 3 and 4 of table 6 are less valuable for measuring the preferential segregation of these two pairs of contrasting alleles. The abnormal type of chromosome 10 and the associated recessive *r* allele are present in the male and female parents in both sets of data, but the absence of a dominant *C* allele in the female parent of one set and the male parent of the other should give 37.5 per cent colored seed if the segregations all were random. The combined effect of preferential segregation of the dominant allele *C* and the recessive allele *r* gave 42.25 per cent colored seeds, a percentage considerably above 37.5

and somewhat higher than the 41.83 per cent calculated from the known preferential segregation. The data in line 4 are a measure of the preferential segregation of the recessive r allele only. The observed 32.77 per cent colored seeds is appreciably below that expected from random segregation and is close to the 32.75 per cent expected from a preferential segregation at megasporogenesis of 69.01 per cent. These data show some of the aberrant ratios that are produced when two preferential segregations are taking place simultaneously.

Segregation of the paired *Sh sh* genes

Shrunken, a seed character, is controlled by a gene on chromosome 9. There is about 26 per cent recombination between sh and the end of the short arm. Segregation of the contrasting *Sh sh* alleles was determined in heterozygous plants where the sh allele was on a knobless chromosome 9.

TABLE 7

Segregation of the dominant and recessive Sh sh alleles.

PARENTS		TOTAL SEEDS NUMBER	*Sh* SEEDS		x^2
♀	♂		NUMBER	PERCENTAGE	
$\frac{Sh\ K}{sh\ k}$	Ab. 10 Nor. 10	*sh k* Nor. 10	2,272	1,493	65.71	Highly sig.
$\frac{Sh\ K}{sh\ k}$	Ab. 10 Nor. 10	Self	34,443	28,350	82.31	Highly sig.
$\frac{Sh\ K}{sh\ k}$	Nor. 10	*sh k* Nor. 10	1,210	606	50.08	.003
$\frac{Sh\ K}{sh\ k}$	Nor. 10	Self	24,634	18,756	76.14	17.04

The data in table 7 show the recovery of the dominant *Sh* allele in progenies in which abnormal 10 was segregating and in check progenies in which only the normal 10 was present. Again the preferential segregation of *Sh* is distinctly associated with the presence of the abnormal 10 in a heterozygous condition.

That the degree of preferential segregation should be slightly higher than that found for the dominant *C* allele was unexpected, since the shrunken locus is a little farther removed from the knob than the *C* locus. The checks, however, may explain this higher percentage, since they, too, exceeded slightly the 50 and 75 per cents expected from random segregation. Shrunken seeds occasionally are not sharply differentiated in strains having a tendency to have a dent type of kernels and so the higher than expected number of nonshrunken seeds in all tests may be due partly to faulty seed classification.

The data on the segregation of the contrasting *Sh sh* alleles, however, are in agreement with the data on the segregation of the contrasting *C c* alleles and show that preferential segregation occurs when contrasting knob types of chromosome 9 and the two types of chromosome 10 are segregating.

Segregation of the paired Wx wx genes

A third seed character controlled by genes on chromosome 9 used to test preferential segregation is the wx gene, which has about 44 per cent recombination with the end of the short arm. At this distance from a knob it was uncertain if preferential segregation would affect the ratio of waxy to nonwaxy seeds.

Considerable data were accumulated on the segregation of the contrasting Wx wx alleles. These data are presented in tables 8 and 9, and in all the progenies tested the recessive wx allele was on the knobless or almost knobless type of chromosome 9.

TABLE 8

Segregation of the dominant and recessive Wx wx alleles.

PARENTS		TOTAL SEEDS NUMBER	Wx SEEDS		x^2
♀	♂		NUMBER	PERCENTAGE	
$\frac{Wx\ K}{wx\ k}$ Ab. 10 / Nor. 10	$wx\ k$ Nor. 10	24,961	13,336	53.43	Highly sig.
$\frac{Wx\ K}{wx\ k}$ Ab. 10 / Nor. 10	Self	117,450	90,684	77.21	Highly sig.
$\frac{Wx\ k}{wx\ k}$ Ab. 10 / Nor. 10	$wx\ k$ Nor. 10	1,079	521	48.29	1.27
$\frac{Wx\ k}{wx\ k}$ Ab. 10 / Nor. 10	Self	13,949	70,454	75.09	.07
$\frac{Wx\ K}{wx\ k}$ Nor. 10	$\frac{Wx\ K}{wx\ k}$ Nor. 10	21,677	10,927	50.41	1.45
$\frac{Wx\ K}{wx\ k}$ Nor. 10	Self	23,272	17,358	74.59	2.11
$\frac{Wx\ k}{wx\ k}$ Nor. 10	$wx\ k$ Nor. 10	15,792	8,055	51.01	6.40
$\frac{Wx\ k}{wx\ k}$ Nor. 10	Self	35,136	26,399	75.13	.34

Data on four different combinations of the dominant Wx allele, both backcrossed and selfed progenies, are reported in table 8. Two of these have the Wx allele on a knobbed type and two on a knobless type of chromosome 9. In one of each of these two combinations the Wx allele was in plants segregating for abnormal 10 and in the other it was in plants with only the normal type of 10. Only one of these four combinations would be expected, on the basis of the preceding data, to show preferential segregation. In lines 1 and 2 are given the data on the backcross and selfed progenies of this combination, and they both depart from the 50 and 75 per cent expected from random segregation. The data in lines 3 and 4 are the first presented which suggest that the preferential segregation of the abnormal type of chromosome 10 does not influence the segregation of contrasting alleles if these are on paired knobless chromosomes.

The data in table 8 show little to support but nothing to contradict the presence of a preferential segregation at megasporogenesis of a chromosome bearing a knob over the knobless type when abnormal 10 also is segregating.

The data in table 9 are from two tests of pollen behavior when the dominant Wx allele is on a chromosome bearing a knob and the recessive wx allele is on a knobless chromosome. The percentages of nonwaxy seeds in both tests are about equal, although in one test the two types of chromosome 10 are segregating. Both tests show an appreciable departure from the 50 per cent expected from random segregation; however, such departures are not unusual in segregations of waxy and nonwaxy pollen, and consequently the departure observed

TABLE 9

Segregation of the dominant and recessive Wx wx alleles.

PARENTS				TOTAL SEEDS NUMBER	Wx SEEDS		χ^2
♀		♂			NUMBER	PER-CENTAGE	
$wx\ k$ No. 10	$\dfrac{Wx\ K}{wx\ k}$		Ab. 10 Nor. 10	2,835	1,549	54.64	24.4
$wx\ k$ Nor. 10	$\dfrac{Wx\ K}{wx\ k}$		Nor. 10	2,515	1,361	54.21	17.04

when abnormal 10 was present loses its significance as far as preferential segregation and selective viability is concerned.

Segregation of the paired $Py\ py$ genes.

Chromosome 6 is known to have as many as three knobs in some strains of maize. The seedling character known as pigmy controlled by genes on chromosome 6 has lent itself to this study of aberrant segregation. Data from this study of the segregation of the contrasting Py and py alleles gave the first clue to the effect of the abnormal type of chromosome 10 on the segregation of other chromosomes heterozygous for knobs. Preferential segregation of the abnormal type of chromosome 10 caused preferential segregation of contrasting alleles on chromosome 6 when one of the segregating pair was almost knobless and the other a much knobbed type. This same knobbed and knobless pair of chromosome 6 failed to show preferential segregation when chromosome 10 was normal. These and other observations are shown by the data of tables 10 and 11.

The preferential segregation at megasporogenesis shown in line 1, table 10, is almost as great as that shown in table 3 for the recessive r allele. This preferential segregation of the dominant Py allele is due to the presence of the abnormal 10, as is apparent when these data are compared with those in line 2, in which the same types of chromosome 6 were present, but abnormal 10 was absent. The data in lines 3 and 4 serve only to further substantiate the fact that only when abnormal 10 is present is there preferential segregation of other homologous chromosomes heterozygous for knobs.

TABLE 10

Segregation of the dominant and recessive Py py alleles.

PARENTS			TOTAL SEEDLINGS NUMBER	Py SEEDLINGS		χ^2
♀	♂			NUMBER	PER-CENTAGE	
$Py\,K\,K(S)\,K$ ___ $py\,k\,K(S)\,K(S)$	Ab. 10 ___ Nor. 10	$py\,k\,K(S)\,K$ (S) Nor. 10	7,278	4,891	67.20	Highly sig.
$Py\,K\,K(S)\,K$ ___ $py\,k\,K(S)\,K(S)$	Nor. 10	$py\,k\,K(S)\,K(S)$ Nor. 10	2,647	1,301	49.15	.77
$Py\,k\,k\,k$ ___ $py\,k\,K(S)\,K(S)$	Nor. 10	$py\,k\,K(S)\,K(S)$ Nor. 10	4,027	1,967	48.85	2.15
$Py\,k\,k\,k$ ___ $py\,k\,K(S)\,K(S)$	Nor. 10	$py\,k\,K(S)\,K(S)$ Nor. 10	704	348	49.43	.09
$py\,k\,K(S)\,K(S)$	Nor. 10	$\dfrac{Py\,k\,K\,k}{py\,k\,K(S)\,K(S)}$ Nor. 10	132	66	50	.00
$py\,k\,K(S)\,K(S)$	Nor. 10	$\dfrac{Py\,k\,k\,k}{py\,k\,K(S)\,K(S)}$ Nor. 10	610	303	49.67	.03

The last two lines of table 10 give some meager data on the character of the pollen that effects fertilization when the contrasting alleles *Py* and *py*, associated with slight differences in the number and character of the knobs of the two segregating chromosomes, are present at microsporogenesis. Both sets of data show that approximately equal numbers of the different types of pollen effect fertilization of the eggs of the homozygous recessive parent.

TABLE 11

Segregation of the dominant and recessive Py py alleles.

PARENTS			TOTAL SEEDLINGS NUMBER	Py SEEDLINGS		χ^2
♀	♂			NUMBER	PER-CENTAGE	
$Py\,K\,K(S)\,K$ ___ $py\,k\,K(S)\,K(S)$	Ab. 10 ___ Nor. 10	Self	9,366	7,717	82.39	Highly sig.
$Py\,K\,K(S)\,K$ ___ $py\,k\,K(S)\,K(S)$	Nor. 10	Self	4,574	3,323	72.65	13.48
$Py\,k\,K\,k$ ___ $py\,k\,K(S)\,K(S)$	Nor. 10	Self	11,466	8,438	73.59	12.13
$Py\,k\,k\,k$ ___ $py\,k\,K(S)\,K(S)$	Nor. 10	Self	5,577	4,277	76.97	11.46
$Py\,k\,K(S)\,K(S)$ ___ $py\,k\,K(S)\,K(S)$	Nor. 10	$\dfrac{Py\,K\,K(S)\,K}{py\,k\,K(S)\,K(S)}$ $\dfrac{\text{Ab. 10}}{\text{Nor. 10}}$	579	448	77.37	1.74
$Py\,k\,K(S)\,K(S)$ ___ $py\,k\,K(S)\,K(S)$	Nor. 10	Self	861	656	76.19	.65

Other tests of the segregation of the contrasting Py py alleles are reported in table 11. The data in the first four lines are from selfed plants of the same progeny that were used in producing the first backcross plants, the data from which are reported in the first four lines of table 10. They serve principally to confirm the observations from backcross progenies. The data in line 1, however, do give an indirect test of the pollen from plants heterozygous for the two types of chromosome 6. This pollen is functioning at random for the Py and py types, since the 82.39 per cent of Py seedlings is close to the 83.60 per cent expected when a 67.20 per cent preferential segregation at megasporogenesis shown in line 1 of table 10 is combined with an assumed 50:50 ratio of Py and py types of pollen effecting fertilization.

In spite of the rather extensive data on the segregation of the contrasting Py and py alleles, they are not sufficient to determine which of the three knobs is most effective in bringing about preferential segregation of those alleles. The central knob may exert little or no influence according to the data of the first line of tables 10 and 11, since preferential segregation occurs when the F_1 plants were homozygous for this particular knob. Only when either the outer or inner knob of chromosome 6 is heterozygous and the other homozygous in a plant segregating for the two types of chromosome 10 will the segregation of the Py py alleles show which of these two knobs is nearest the pigmy locus.

False linkage between nonhomologous chromosomes

The data showing that preferential segregation of the two types of chromosome 10 causes a preferential segregation of the knobbed type of chromosomes 9 and 6 over the knobless or almost knobless type also might be interpreted as showing that the recessive r allele of the abnormal type of chromosome 10 appears to be linked with the C, Sh, and Wx alleles of chromosome 9 and Py allele of chromosome 6. Such apparent linkage is designated as "false linkage," as the term "linkage" usually is restricted to the association of genes in inheritance which results from their being located on the same chromosome. Data showing the false linkage between the Py and C and the contrasting py and c alleles that results from preferential segregation are shown in table 12. This false linkage with 41.51 per cent of recombination closely approximates that expected when the preferential segregation for Py, C, and r is 67.2 per cent, 63.87 per cent, and 69.01 per cent, respectively. In contrast, the data from a similar progeny in

TABLE 12

False linkage between the dominant allele Py and the dominant allele C.

F_1 GENOTYPE		LINK-AGE PHASE	NUMBERS OF INDIVIDUALS					RECOMBINATIONS			χ^2
								NUM-BER	PERCENTAGE		
			$Py\,C$	$Py\,c$	$py\,C$	$py\,c$	TOTAL		OB-SERVED	EX-PECTED	
$Py\,K\,K(S)\,K$ $C\,K$ Ab. 10		C B	1,119	461	488	218	2,286	949	41.51	42.36	.66
$py\,k\,K(S)\,K(S)$ $c\,k$ Nor. 10											
$Py\,K\,K(S)\,K$ $C\,K$ Nor. 10		C B	731	775	773	749	3,036	1,548	50.99	50	1.19
$py\,k\,K(S)\,K(S)$ $c\,k$ Nor. 10											

which there is no preferential segregation of chromosome 10 shows no evidence of association between *Py* and *C* alleles.

<div align="center">DISCUSSION</div>

Preferential segregation at megasporogenesis has been established for maize chromosomes other than chromosome 10, which are heterozygous for a knob or knobs in plants in which the normal and abnormal types of chromosome 10 also are segregating. This preferential segregation was established by both cytological observations and by its effect on the segregation of contrasting alleles at loci not too far removed from the knob locus.

RHOADES (1942) pointed out that the preferential segregation of the abnormal type of chromosome 10 is unique. The effect of its segregation upon the segregation of other chromosomes is even more unusual. The reason for the preferential segregation of abnormal 10 is at present unexplained, but the preferential segregation of other chromosomes is associated with this unexplainable segregation. Preferential segregation depends upon the presence of knobs, since it is absent when both homologues are knobless.

Cytological data suggest that knob segregations at megasporogenesis may be preferential even when chromosome 10 is normal. Such a preferential segregation was not confirmed by genetic data, but may become apparent when more critical tests are available.

The relationship between the preferential segregation of knobs and the presence of the abnormal type of chromosome 10 must have led, in the past, to the accumulation of knobs in certain maize strains. A glance at LONGLEY's (1938) data on the chromosome morphology of strains of Indian corn shows that abnormal 10 was found in four out of 33 strains and that these four are among the six strains with the largest numbers of knobs. This seeming relationship between a large number of knobs and the presence of abnormal 10 is further substantiated by unpublished data on maize strains from Guatemala. The abnormal type of chromosome 10 is quite prevalent in these strains, and all plants with the abnormal type had more than ten knobs on the remaining nine chromosomes.

This study has been confined largely to the effect of preferential segregation on contrasting alleles at loci near a knob locus. It has shown conclusively that preferential segregation of abnormal 10 causes other chromosomes to segregate abnormally at megasporogenesis if the two homologues consist of one knobbed and one knobless chromosome. The resulting aberrant ratios show the expected approach to ratios of random segregation as the distance from the knob locus to the locus of the segregating alleles increases. This was illustrated in RHOADES' (1942) study of the preferential segregation affecting the contrasting *R r* and *G g* alleles and is further substantiated by the data presented for both chromosomes 10 and 9.

The amount of preferential segregation depends upon the proximity of the gene in question to the knob which is segregating preferentially. The deviation from the expected preferential segregation may be used to determine the dis-

tance between the knob locus and the loci of other alleles on the same chromosome.

False linkage between genes in different linkage groups may lead to some confusion. This effect is not pronounced, however, and under the most extreme preferential segregation it will not indicate linkage with less than 40 per cent of recombination.

SUMMARY

Cytogenetic data have confirmed the studies of RHOADES (1942) on the preferential segregation at megasporogenesis of the abnormal type of chromosome 10. In addition it has been shown that when this preferential segregation occurs in megasporogenesis there will be a preferential segregation of the knobbed over the knobless type of other chromosomes heterozygous for knobs.

The effect of preferential segregation is apparent as aberrant genetic ratios obtained when loci of segregating alleles are near the locus of the segregating knob. Furthermore, the amount of aberrrance may be used as a measure of the distance between a knob locus and the locus of segregating alleles.

Preferential segregation may result in the associated inheritance of genes located on different chromosomes. This association is termed "false linkage."

Since preferential segregation of the abnormal type of chromosome 10 tends to concentrate knob-bearing chromosomes in the megaspore, it may be predicted that abnormal chromosome 10 generally will be found in maize strains with a large number of knobs.

LITERATURE CITED

LONGLEY, A. E., 1938   Chromosomes of maize from North American Indians. J. Agric. Res. **56:** 177–195.

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